

Mechanisms of soil bacterial and fungal community assembly differ among and within islands

Pandeng Wang^{1,2†}, Shao-Peng Li^{3,4†}, Xian Yang², Jizhong Zhou^{5,6}, Wensheng Shu^{7*} and Lin Jiang^{1,2*}

¹State Key Laboratory of Biocontrol, Guangdong Key Laboratory of Plant Resources and Conservation of Guangdong Higher Education Institutes, School of Life Sciences, Sun Yat-sen University, Guangzhou, 510275, People's Republic of China.

²School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA, 30332, USA.

³Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China.

⁴Institute of Eco-Chongming (IEC), Shanghai, 200062, China.

⁵Department of Microbiology and Plant Biology, Institute for Environmental Genomics, and School of Civil Engineering and Environmental Sciences, University of Oklahoma, Norman, OK, 73019, USA.

⁶State Key Joint Laboratory of Environment Simulation and Pollution Control, School of Environment, Tsinghua University, Beijing, 100084, People's Republic of China.

⁷School of Life Sciences, South China Normal University, Guangzhou, 510631, People's Republic of China.

Summary

The study of islands has made substantial contributions to the development of evolutionary and ecological theory. However, we know little about microbial community assembly on islands. Using soil microbial data collected from 29 lake islands and nearby mainland, we examined the assembly mechanisms of soil bacterial and fungal communities among and within

islands. We found that deterministic processes, especially homogeneous selection, tended to be more important in shaping the assembly of soil bacterial communities among islands, while stochastic processes tended to be more important within islands. Moreover, increasing island area increased the importance of homogeneous selection, but reduced the importance of variable selection, for soil bacterial community assembly within islands. By contrast, stochastic processes tended to dominate soil fungal community assembly both among and within islands, with dispersal limitation playing a more important role within than among islands. Our results highlight the scale- and taxon-dependence of insular soil microbial community assembly, suggesting that spatial scale should be explicitly considered when evaluating the influences of habitat fragmentation on soil microbial communities.

Introduction

Islands are geographically discrete landmasses separated by a matrix inhospitable for most island-dwelling organisms, making them a useful model system for addressing various ecological and evolutionary questions (Warren *et al.*, 2015). Indeed, the study of islands has made substantial contributions to the development of evolutionary and ecological theory (Darwin, 1859; MacArthur and Wilson, 1967; Warren *et al.*, 2015). Nevertheless, almost all island studies (Losos and Ricklefs, 2009) have focused on plants and animals; little attention has been paid to microbes whose roles in ecosystems are of paramount importance (Bahram *et al.*, 2018). As a result, we know virtually nothing about patterns and mechanisms of microbial community assembly on islands. Elucidating insular microbial community assembly mechanisms not only fills an important gap in our knowledge, but also helps predict how habitat fragmentation, an important element of anthropogenic environmental changes, influences microbial communities, and, in turn, the functions that they perform.

Mechanisms regulating community assembly fall into two general categories. On the one hand, the niche theory (Chase and Leibold, 2003) emphasizes the role of deterministic ecological selection, which can result in low

Received 1 June, 2019; revised 10 November, 2019; accepted 14 November, 2019. *For correspondence. E-mail lin.jiang@biology.gatech.edu; Tel. 1(404)385-2541; Fax 1(404)894-0519. E-mail shuws@mail.syu.edu.cn; Tel. 86(20)85211850; Fax 86(20)85211850. †These authors contributed equally to this work. **Data Availability Statement:** DNA sequence data are accessible at the NCBI-SRA under the accession number PRJNA517449. All other data that support the findings of this study have been deposited to figshare (<https://doi.org/10.6084/m9.figshare.10728242.v1>).

and high compositional turnover across space through homogeneous selection (i.e., community convergence caused by similar environmental conditions across localities) and variable selection [i.e., community divergence caused by heterogeneous environmental conditions across localities; also known as heterogeneous selection (Zhou and Ning, 2017)], respectively (Vellend, 2010; Dini-Andreote *et al.*, 2015; Stegen *et al.*, 2015). On the other hand, the neutral theory (Bell, 2001; Hubbell, 2001) emphasizes the role of dispersal and ecological drift in shaping community assembly, independent of ecological selection. Under this framework, high dispersal rates (homogenizing dispersal) may allow species to persist in their unfavourable habitats, leading to low species turnover among localities, whereas dispersal limitation may cause species to be absent from their preferred habitats, resulting in high spatial species turnover (Leibold *et al.*, 2004; Vellend, 2010; Stegen *et al.*, 2015). Likewise, ecological drift, driven by stochastic demographic events, can result in dissimilar communities among localities sharing similar environmental conditions (Bell, 2001; Hubbell, 2001; Zhou and Ning, 2017). The general consensus now is that niche (deterministic) and neutral (stochastic) processes could simultaneously contribute to natural community assembly, although their relative importance may depend on the study system and environmental context (Gravel *et al.*, 2006; Leibold and McPeck, 2006; Adler *et al.*, 2007; Chase, 2007; Zhou *et al.*, 2013; Guo *et al.*, 2018). Applying these perspectives to microbial communities has shown that the relative importance of these two processes could be influenced by a variety of factors, such as disturbance (Ferrenberg *et al.*, 2013), soil pH (Tripathi *et al.*, 2018), succession time (Zhou *et al.*, 2014; Dini-Andreote *et al.*, 2015), host development stages (Burns *et al.*, 2016) and anthropogenic environmental changes (Zhang *et al.*, 2016). However, their roles in shaping insular microbial community assembly have not been explored.

Scale-dependence is a widespread phenomenon in ecology (Levin, 1992; Chave, 2013; Ladau and Elloe-Fadrosh, 2019). For instance, the scale of investigations is known to influence the shape of the productivity–diversity relationships (Chase and Leibold, 2002), species–energy relationships (Tariq and Andrew, 2008), biodiversity patterns along spatial gradients (Rahbek, 2005; Nogues-Bravo *et al.*, 2008) and the drivers of beta diversity (Martiny *et al.*, 2006; Martiny *et al.*, 2011; Xing and He, 2018). Meanwhile, spatial scale may also have the potential to influence the importance of niche and neutral processes in shaping ecological communities (Chase, 2014; Garzon-Lopez *et al.*, 2014). On the one hand, larger spatial areas (e.g., larger islands) could contain more environmental heterogeneity (Brose, 2001) and support larger community size, which may result in the

increased role of selection and the decreased role of ecological drift (Stein *et al.*, 2014; Curd *et al.*, 2018). On the other hand, larger areas may be subject to more frequent disturbances by virtue of their larger sizes (Wardle *et al.*, 2003), and therefore experience increased stochasticity. Smaller spatial areas (e.g., smaller islands or within-island localities) tend to support fewer individuals, which would increase the role of demographic stochastic processes (Lande *et al.*, 2003), resulting in stronger ecological drift (Orrock and Watling, 2010; Vellend, 2010; Zhou and Ning, 2017). However, the decreased environmental heterogeneity in small spatial areas may increase the importance of deterministic processes through homogeneous selection. Therefore, how the relative importance of deterministic and stochastic processes varies across spatial scales remains an open question.

The spatial discreteness of islands offers an excellent opportunity to study community assembly across spatial scales. Traditional island biogeographic studies, however, generally treat the whole island as the unit of analysis. In this study, we aimed at elucidating the assembly mechanisms of soil microbial (both bacteria and fungi) communities at two different spatial scales (i.e., among and within islands), using data collected from a group of land-bridge islands in subtropical China (Fig. S1). Under the premise that islands can support larger population size (tending to decrease the role of ecological drift) than within-island localities, we predict that niche (deterministic) processes would be more important in shaping soil microbial community assembly among islands, whereas neutral (stochastic) processes would be more important for shaping soil microbial community assembly within islands. Here, we used a null-model based approach, developed by Stegen *et al.* (2013), to disentangle the relative contribution of niche and neutral processes to community assembly of soil bacteria and fungi (see Experimental procedures for details). Briefly, under the assumption that more closely related species tend to possess more similar niches, variable and homogeneous selection would result in phylogenetic/taxonomic turnover among localities/islands being significantly greater and smaller than null expectation, respectively. On the other hand, neutral processes would result in phylogenetic turnover being no different from null expectation, but dispersal limitation and homogenizing dispersal would result in taxonomic turnover being significantly greater and smaller than null expectation, respectively. The approach of Stegen *et al.* (2013) essentially recognizes that non-random phylogenetic turnover arises from selection, while non-random taxonomic turnover could arise from selection, dispersal limitation or homogenizing dispersal. Thus, if our predictions are correct, most among-island phylogenetic turnovers should be significantly different from null expectation ($\beta\text{NTI} > 2$ or < -2 ; βNTI : a standardized

measure of phylogenetic turnover; see Experimental procedures for details), while most within-island phylogenetic turnovers should not differ from null expectation ($-2 < \beta\text{NTI} < 2$).

Results

A total of 9 022 457 and 4 535 687 high-quality sequences were obtained for soil bacteria and fungi across all 306 samples, respectively, with an average of $29\,485 \pm 10\,109$ (mean $\pm$ SD) sequences for bacteria and $14\,822 \pm 9553$ sequences for fungi per sample. After clustering sequences at the 97% similarity level and removing singletons (unique sequences that were only detected once across all samples), we obtained 20 078 and 10 579 operational taxonomic units (OTUs) for bacteria and fungi, respectively. After rarefying all samples to the same number of sequences (8381 for bacteria and 2720 for fungi), an average of 1434 ± 177 bacterial

OTUs and 337 ± 52 fungal OTUs were detected per sample. On average, 4718 bacterial OTUs and 1287 fungal OTUs were obtained per island, with the range being 1750–7788 and 463–2229, respectively.

Community assembly among islands

Consistent with our prediction, we found that the phylogenetic turnover of soil bacteria among most ($\sim 60\%$) island pairs was significantly different from the null expectation ($\beta\text{NTI} < -2$ in 39.31% cases, $\beta\text{NTI} > 2$ in 19.31% cases; Fig. 1A). In the remaining island pairs, most exhibited smaller taxonomic turnover than expected by chance ($\text{RC}_{\text{bray}} < -0.95$; RC_{bray} : Bray–Curtis based Raup–Crick metric, a standardized measure of taxonomic turnover) (Fig. 1B). These results suggest that selection, particularly homogeneous selection, may have dominated the community assembly of soil bacteria among most islands, while homogenizing dispersal may have played

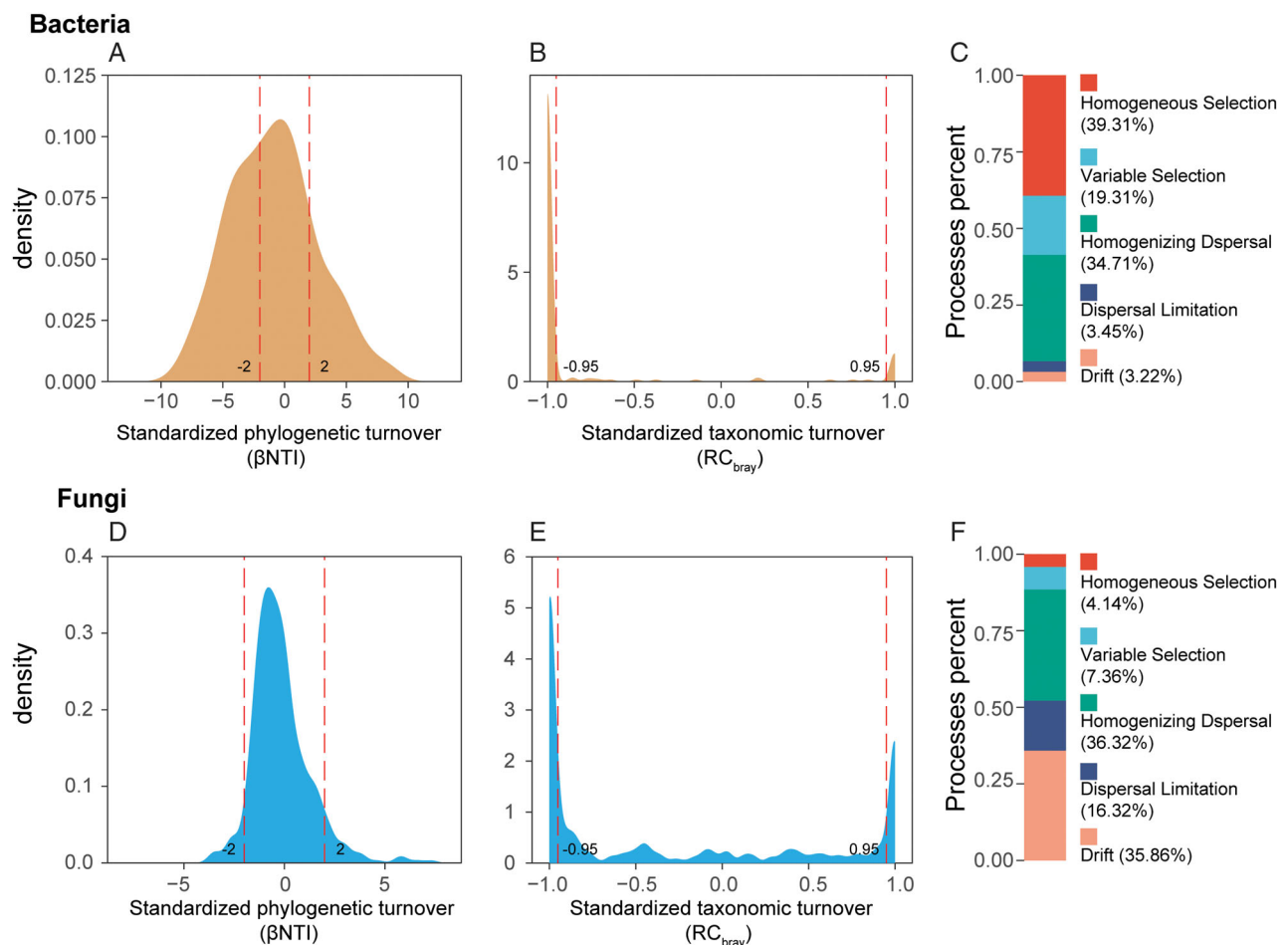


Fig. 1. The distribution of among-island standardized phylogenetic turnover (βNTI ; panel A: bacteria, panel D: fungi) and taxonomic turnover (RC_{bray} ; panel B: bacteria, panel E: fungi), and the percentages of the five structuring processes considered in this study (panel C: bacteria, panel F: fungi). The vertical dashed lines mark the positions of -2 and 2 in panels A and D, and -0.95 and 0.95 in panels B and E. [Color figure can be viewed at wileyonlinelibrary.com]

Table 1. The relative importance of soil properties, spatial distance and island area for explaining β NTI.

		Bacteria		Fungi	
		Island level	Sample level	Island level	Sample level
Soil properties	Available Al		0.008	0.006	
	Available Ca	0.026	0.009	0.019	0.011
	Available Mg	0.077	0.020		0.001
	Available P	0.043	0.008	0.005	0.001
	Moisture		0.003		0.005
	pH		0.005		
	TOC		0.004	0.017	0.002
	Total N		0.002	0.023	0.001
	Total P		0.001	0.014	
Spatial distance		0.008			
Island log area		0.003	0.104	0.012	0.016
Total R^2		0.157	0.164	0.097	0.034

The best multiple regression on distance matrices models was selected based on AIC. The values represent the amount of variation explained by each factor. Island area (m^2) was $\log_{10}$ -transformed.

an important role in causing taxonomic turnover among other islands (Fig. 1C). By contrast, we found that the phylogenetic turnover of soil fungi among most island pairs (~88%) was not significantly different from the null expectation (Fig. 1D). Among these island pairs, most exhibited smaller taxonomic beta diversity (~41%) than or no significant difference (~40%) from null expectation (Fig. 1E). These results suggest that stochastic processes may have played the most important role in causing phylogenetic turnover of soil fungi among most islands, with homogenizing dispersal and drift tending to be the main drivers of the observed taxonomic turnover (Fig. 1F). Consistent with the more important role of selection for soil bacteria than fungi among islands, we found that soil properties explained more variation in among-island β NTI for soil bacteria than fungi (Table 1).

Community assembly within islands

Consistent with our prediction, a large proportion of the phylogenetic turnover (average: ~58%) and taxonomic turnover (average: ~45%) of soil bacteria across samples of the same islands were not different from null expectation (Fig. 2A and B), indicating that the role of stochastic processes, particularly drift, was important for the assembly of soil bacterial communities within islands (Fig. 2C). In addition, the values of within-island β NTI for soil bacteria exhibited a decreasing trend as island area increased (Fig. 2A), indicating the increased role of homogeneous selection on the larger island (Fig. 2D). As for soil fungi, phylogenetic turnover between almost all samples within islands (average: ~89%) did not differ from the null expectation (Fig. 3A). Among these sample pairs, most of their taxonomic turnover (average: ~71%) was significantly greater than expected by chance (Fig. 3B), suggesting dispersal limitation as the main driver for

fungus taxonomic turnover within islands (Fig. 3C and D). Consistent with the important role of stochastic processes for both soil bacteria and fungi within islands, soil properties accounted for relatively little variation in β NTI of soil bacteria and fungi between samples within islands (Table 1).

Discussion

Our study, to our knowledge, represents the first attempt to identify the difference in community assembly mechanisms of insular soil microbes (both bacteria and fungi) across spatial scales. Consistent with our prediction, our analyses suggest that in our island system, niche-based processes, especially homogeneous selection, maybe most important in regulating the community assembly of soil bacteria among islands, while the role of neutral processes, especially ecological drift, maybe most important within most islands. In partial agreement with our prediction, we found that neutral processes might have played a more important role than niche-based processes for soil fungi both among and within islands, such that homogenizing dispersal and drift tend to dominate the assembly of fungal communities among islands, and dispersal limitation tends to dominate the fungal community assembly within islands. Together, these results suggest that different ecological processes may underline the community assembly of soil bacteria and fungi among and within islands.

Microbial community assembly among islands

We found that niche-based processes were likely the main drivers for soil bacterial community assembly among islands (Fig. 1A–C). Among the niche-based processes, homogeneous selection tended to dominate,

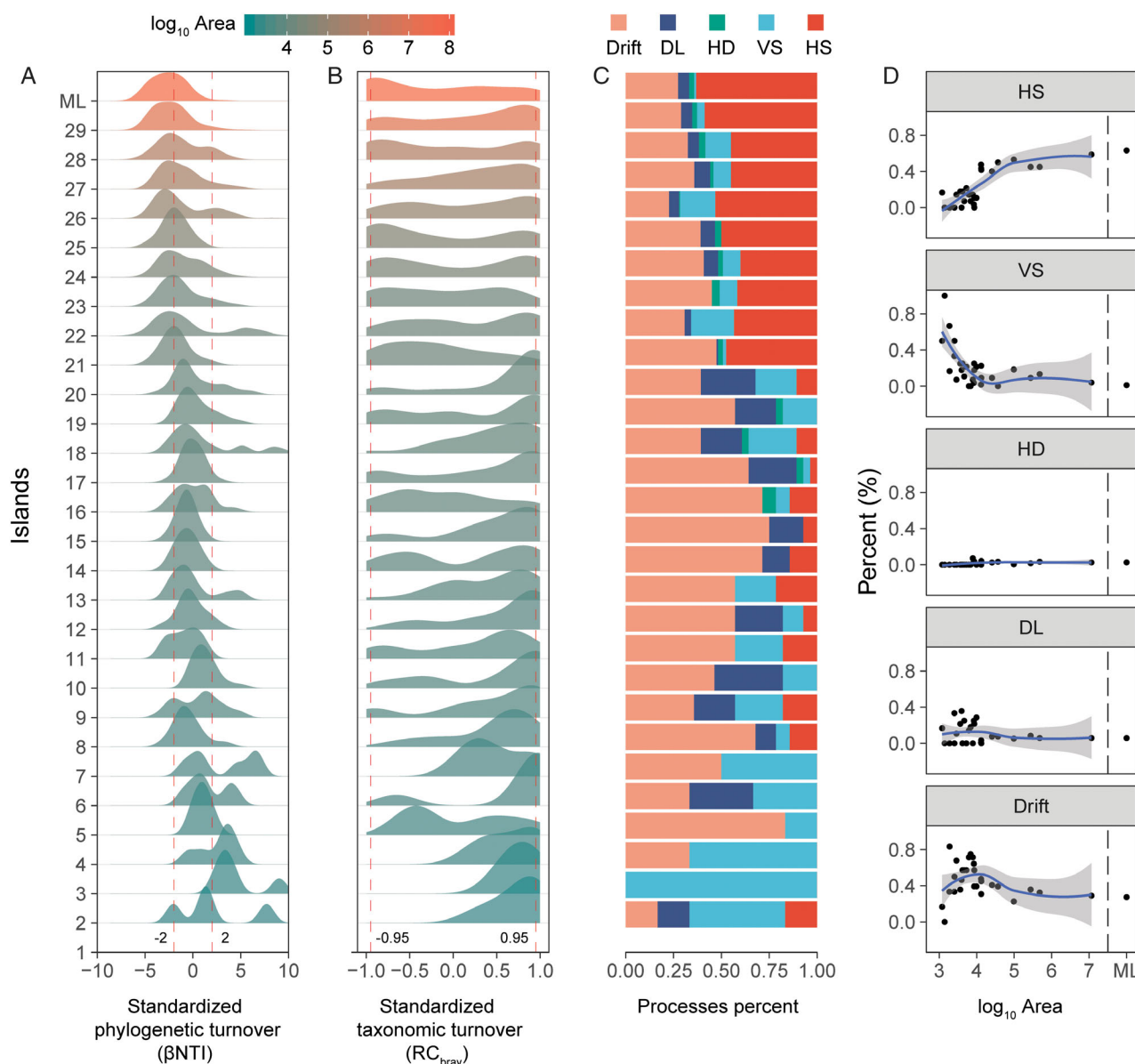


Fig. 2. The distribution of within-island standardized phylogenetic turnover (β NTI: panel A) and taxonomic turnover (RC_{bray} : panel B) of soil bacteria, the percentages of the five structuring processes (panel C), and their variation along the island area (m^2 ; $\log_{10}$ -transformed) gradient (panel D). HS: homogeneous selection; VS: variable selection; HD: homogenizing dispersal; DL: dispersal limitation. Islands are sorted based on their area and labelled from 1 to 29 (from smallest to largest). ML is short for the mainland. No analyses were conducted for the smallest island (island No. 1), which had too few samples (two) to give reliable results. The vertical dashed lines mark the positions of -2 and 2 in panel A, and -0.95 and 0.95 in panel B. Each line in panel D was fitted using local polynomial regression with a 95% confidence interval. [Color figure can be viewed at wileyonlinelibrary.com]

suggesting that similar environmental conditions across islands imposed significant selective force that resulted in greater similarity in the structure of soil bacterial communities than expected by chance. Recent research has identified the importance of a host of environmental factors, such as climate (Maestre *et al.*, 2015; Zhou *et al.*, 2016; Guo *et al.*, 2018; Delgado-Baquerizo *et al.*, 2018a), salinity (Lozupone and Knight, 2007; Thompson *et al.*, 2017), soil pH (Fierer and Jackson, 2006; Thompson

et al., 2017; Delgado-Baquerizo *et al.*, 2018b) and nutrient availability (Ramirez *et al.*, 2010; Ramirez *et al.*, 2012; Leff *et al.*, 2015), in shaping bacterial community structure across large (e.g., continental, global) spatial scales. One possible explanation for the prevalence of homogeneous selection for bacterial communities on our study islands is the similarity in climate and soil environmental conditions across the islands. All the islands share essentially the same climate due to their close

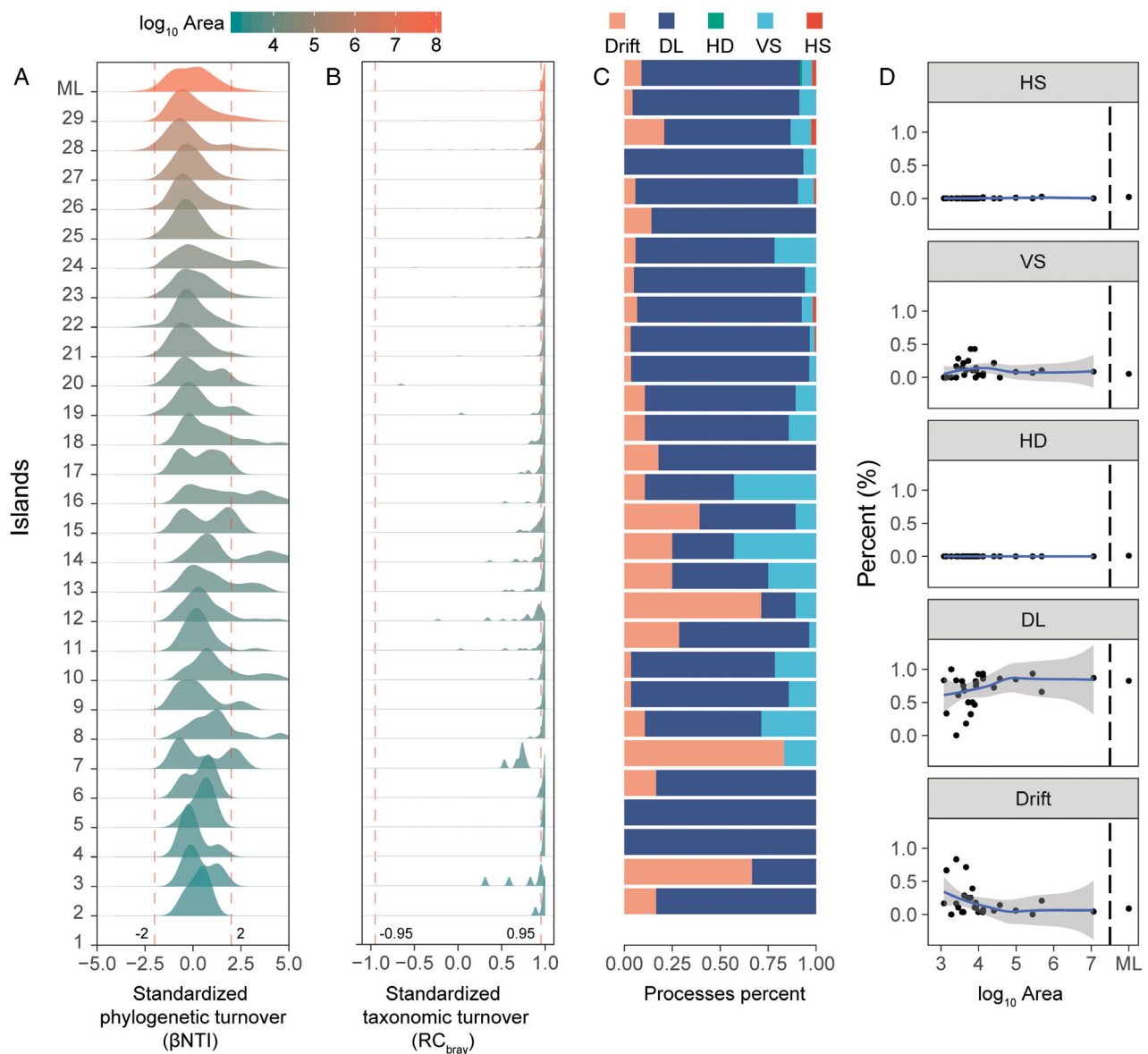


Fig. 3. The distribution of within-island standardized phylogenetic turnover (β NTI; panel A) and taxonomic turnover (RC_{bray}; panel B) of soil fungi, the percentages of the five structuring processes (panel C), and their variation along the island area (m^2 ; $\log_{10}$ -transformed) gradient (panel D). HS: homogeneous selection; VS: variable selection; HD: homogenizing dispersal; DL: dispersal limitation. Islands were sorted based on their area and labelled from 1 to 29 (from smallest to largest). ML is short for the mainland. No analyses were conducted for the smallest island (island No. 1), which had too few samples (two) to give reliable results. The vertical dashed lines mark the positions of -2 and 2 in panel A, and -0.95 and 0.95 in panel B. Each line in panel D was fitted using local polynomial regression with a 95% confidence interval. [Color figure can be viewed at wileyonlinelibrary.com]

proximity (average distance: 6.13 km; longest distance: 12.16 km; Fig. S1), and there are no or weak gradients in measured soil properties across these islands (Fig. S2). As an example, although pH has frequently been recognized as an important abiotic factor structuring bacterial communities (Fierer and Jackson, 2006; Thompson *et al.*, 2017; Tripathi *et al.*, 2018; Delgado-Baquerizo *et al.*, 2018b), it failed to predict bacterial phylogenetic turnover across our study islands, due likely to its relatively small range (4.03 ± 0.09 to 4.48 ± 0.19 ;

mean $\pm$ SD) among the islands. Note that the observed small ranges in pH and other soil variables, while presumably constraining bacterial community structure memberships (i.e., homogenous selection) on these islands, may have also contributed to the relatively low explanatory power of measured soil properties for bacterial community structure (see Table 1).

Compared with the importance of environmental selection for soil bacteria, stochastic processes, especially homogenizing dispersal and ecological drift, may have

contributed primarily to soil fungal community turnover among islands (Fig. 1D–F). The lack of significant selection effects on fungal communities may be explained by the fact that fungal hyphal network facilitates water and nutrient uptake, which may confer them greater resistance against changing environmental conditions than bacteria (Yuste *et al.*, 2011; Barnard *et al.*, 2013). Consistent with this idea, we found that soil properties had a lesser effect on the phylogenetic turnover of soil fungi than bacteria across the 29 studied islands (Table 1). More directly, Powell *et al.* (2015) have shown that bacterial, but not fungal, community turnover was mainly driven by habitat turnover. Additionally, Yuste *et al.* (2011) also found that soil bacterial, but not fungal, diversity responded to seasonal variation as well as to experimentally imposed drought treatments in two Mediterranean ecosystems. The finding of homogenizing dispersal being important for fungi among many island pairs suggests that their dispersal rate was sufficiently high to make fungal communities more homogenous than null expectation. This result contrasts with significant dispersal limitation shaping the assembly of plant communities on the study islands (Hu *et al.*, 2016). The lack of dispersal limitation for soil bacteria and fungi between islands may be because soil microbes and their spores are generally much smaller compared with plant seeds, allowing them to disperse more readily between islands by wind or water currents (Gregory, 1945).

Microbial community assembly within islands

Analyses of community turnover of soil bacteria within islands suggested different assembly mechanisms from those among islands, such that the role of stochastic processes, particularly ecological drift, appeared most important within most islands (19/29). The increased role of ecological drift at the sample scale may be attributed to two non-deterministic processes. First, it likely reflects the increased importance of demographic stochasticity associated with small community sizes (Orrock and Watling, 2010) at the sample scale. Second, priority effects, known to be stronger at smaller spatial scales (Fukami, 2004), may have also contributed to this pattern. More specifically, stronger priority effects, coupled with random species immigration, may have caused communities at the sample scale to diverge from each other in their assembly trajectories, leaving the signature of stochastic community assembly. In addition to stochastic processes, deterministic processes, including homogenizing and variable selection, also played a non-negligible role in the community turnover of soil bacteria within islands. In particular, the role of homogenizing selection for soil bacteria increased with island area (Fig. 2C and D), while the role of variable selection

decreased with island area (Fig. 2C and D). One possible explanation for this result is that although the heterogeneity of some soil properties [i.e., total organic carbon (TOC) and moisture] increased with island area (Fig. S3), which would serve to promote variable selection, average soil quality (i.e., TOC and moisture) also increased with island area (Fig. S2). Better environmental quality on larger islands may result in more individuals per sample, which, combined with the strong dispersal ability of bacteria, may have led to increased mass effects (Leibold *et al.*, 2004; Holyoak *et al.*, 2005). Combined with the selection pressure imposed by consistent small environmental gradients, the increased mass effects may have promoted homogenizing selection, overwhelming variable selection associated with increased soil heterogeneity on larger islands. Additionally, smaller islands tend to experience stronger edge effects (Ewers *et al.*, 2007), which could also contribute to the increased role of variable selection on smaller islands.

Our analyses suggest that dispersal limitation was the only dominant driver for the turnover of fungal communities within islands and that the role of dispersal limitation was greater on larger islands (Fig. 3C and D). These findings are consistent with previous work showing that the dispersal of fungal spores is typically constrained to short distances (Peay *et al.*, 2012; Adams *et al.*, 2013). Considering both bacteria and fungi, our within-island results also suggest that dispersal limitation is more important for shaping fungal than bacterial communities, which has received some previous empirical support, albeit across substantially larger spatial scales (i.e., thousands of kilometres; Barberán *et al.*, 2015; Powell *et al.*, 2015; Jiang *et al.*, 2016; Wang *et al.*, 2017). One reason may be that the sizes of bacterial cells [length typically within 0.5–10 μm (Madigan *et al.*, 2015)] are generally smaller than fungal spores [length typically within 3–21 μm (Bässler *et al.*, 2015)], which makes it easier for bacteria to disperse via air. Surprisingly, we found that dispersal limitation played a more important role in structuring soil fungal communities within than among islands. One explanation for this counterintuitive finding is that the mode of fungal dispersal among and within islands could be different. Fungal spores could disperse between islands via air or water currents without any barriers. In contrast, the presence of forest canopy on islands may significantly reduce wind speed and, in turn, the transmission of fungal spores within islands (Tisserat and Kuntz, 1983). Thus, the colonization of mycelia may have played a more important role in fungal dispersal within islands, leading to stronger dispersal limitation of fungi within than between islands.

One caveat worth noting is the observational nature of our study, which makes it difficult to exclude the possibility that mechanisms other than the ones considered here

may have also contributed to the observed phylogenetic and taxonomic turnover patterns. While this concern was eased somewhat by the consistency between our findings with and without considering soil environmental variables, our findings should be treated as tentative. Future experimental manipulations of soil characteristics and species dispersal on our study islands will allow a more direct evaluation of the mechanisms we identified in this study.

Conclusions

Our study, to our knowledge, is the first to compare assembly mechanisms of soil bacterial and fungal communities on actual islands. We show that the mechanisms underlying microbial community assembly may not only differ between soil bacteria and fungi but also differ across spatial scales. For soil bacteria, deterministic processes tended to dominate at the larger spatial scale (among islands), whereas the role of stochastic processes increased at the smaller spatial scale (within islands). For soil fungi, non-deterministic processes tended to dominate both scales, with dispersal limitation being important within but not among islands. These findings improve our understanding of how habitat fragmentation alters soil microbial communities across different spatial scales, necessitating the need to design effective means to conserve soil microbes and their functions in Earth's increasingly fragmented landscapes. The robustness of these findings, however, awaits future experimental tests.

Experimental procedures

Study sites and sampling

We conducted our study in the Thousand Island Lake (29°22'N–29°50'N and 118°34'E–119°15'E), formed by damming on the Xin'an River in Southern China in the 1950s. Before the formation of the islands, almost all hardwood plants were eliminated from the region for firewood exploitation. After more than 50 years' natural succession, a single pine species (*Pinus massoniana*) now dominates the vegetation on these islands (Si *et al.*, 2017). We selected 29 islands (area range: 815 m²–11.5 million m²; Fig. S1) with minimum levels of human disturbance as our study sites. Within each island, 1–6 (roughly in proportion to the island area on the logarithmic scale) permanent 20 × 20 m² plots were established. We further divided each plot into four quadrats (10 × 10 m²). In addition, one large plot (10 000 m²) on the adjacent mainland was established as the control; a total of 20 quadrats (10 × 10 m²) were evenly distributed within the mainland plot. In each quadrat, four evenly

distributed soil cores (top 10 cm) were collected and placed in a sterile plastic bag to be homogenized as one sample. The samples' locations were recorded by a global positioning system. Together, we obtained 306 soil samples in Mid-May 2015. All samples were placed on ice and transported to the laboratory immediately after the completion of soil sample collection. Each soil sample was separated into three subsamples: one (~2 g) was stored at –80 °C until DNA extraction, one was used for soil moisture measurements and one was air-dried for subsequent soil chemistry analysis.

Soil properties

Nine soil chemistry variables, including soil moisture, pH, TOC, total N and P, and available P, Ca, Al, Mg, were measured. We measured soil moisture by drying fresh soil to constant weight at 105 °C. We used a pH meter (Sartorius PB-10, Göttingen, Germany) to determine soil pH based on the soil suspension (1:2.5 of soil to deionized water) of each sample. TOC was measured following the potassium dichromate oxidation method; the Semimicro-Kjeldahl method was used for total N measurement. We measured soil total P and available P using the colorimetric method with a UV–visible Spectrophotometer (UV-2550, Shimadzu, Japan). We extracted soil available Ca, Al, Mg using the Mehlich III solution and measured them using Inductively Coupled Plasma Optical Emission Spectrometry (Optima 2100DV; Perkin-Elmer, MA, USA).

DNA extraction and sequencing

For each sample, we extracted DNA from 0.5 g fresh soil using the MoBio PowerSoil DNA extraction kit (Carlsbad, CA, USA), following the manufacturer's instructions. We then amplified the V4 regions of 16s rRNA gene using the primer set: 515 (GTGCCAGCMGCCGCGGTAA) and 806 (GGACTACHVGGGTWTCTAAT) for bacteria following the protocol described by Zhou *et al.* (2016) and the ITS2 region of the rRNA operon using the primer set: ITS3 (GCATCGATGAAGAAGCAGC) and ITS4 (TCCTCCGCTTATTGATATGC) for fungi following the protocol described by Tedersoo *et al.* (2014). To permit the multiplexing of samples, we attached a 12-bp barcode unique to each sample to the 5' end of primers 806 and ITS3. We then pooled PCR products from all samples in equimolar concentrations and purified them by using the E.Z.N.A.[®] Gel Extraction Kit (Omega Bio-Tek, Doraville, USA). The purified PCR products were subsequently sequenced on a 2 × 300 bp paired-end Illumina MiSeq platform (Illumina; San Diego, CA, USA).

Bioinformatic analysis

We used software MOTHUR (Schloss, 2009) to process raw reads for quality filtering and assembling. Then, high-quality sequences were assigned to samples according to their unique barcodes. We removed chimeras and clustered high-quality sequences into OTUs at the 97% similarity threshold by using USEARCH (Edgar, 2013). After removing singletons, we classified each OTU by using the Ribosomal Database Project classifier (Wang *et al.*, 2007) against the SILVA [version 123; (Quast *et al.*, 2012)] database for bacteria and the UNITE [version 7.0; (Abarenkov *et al.*, 2010)] database for fungi. We removed OTUs that were not classified into bacteria and fungi before subsequent analyses. To correct for sampling effects, we rarefied each sample to equal sequencing depth (8381 and 2720 for bacteria and fungi, respectively).

To construct the phylogenetic tree for bacteria, we first aligned the bacterial OTUs' representative sequences against the SILVA alignment database (version 123). Then, we used FastTree (Price *et al.*, 2010) to construct a maximum-likelihood tree based on these aligned sequences. As for fungi, we used software PASTA (Mirarab *et al.*, 2015) to align the representative sequences and build a maximum-likelihood phylogenetic tree with the parameters: '-aligner=mafft -tree-estimator=fasttree -merger=opal'. PASTA uses the divide-and-conquer algorithm to estimate the alignment. It first divides sequences into smaller subsets basing on their similarity and aligns each subset separately. Then, these subset alignments are merged into a final alignment. This method is suitable for the alignment of fungal ITS sequences whose lengths are highly variable.

Community assembly analysis

We studied the community assembly of soil bacteria and fungi at two spatial scales: island level (among islands) and sample level (within islands). At the island level, we combined all samples within one island to represent the species composition on that island. We used the null-model-based approaches, which have been widely used in microbial ecology studies (Stegen *et al.*, 2013; Wang *et al.*, 2013; Dini-Andreote *et al.*, 2015; Stegen *et al.*, 2015; Zhou and Ning, 2017), to disentangle the relative contribution of niche and neutral processes to the community assembly of soil bacteria and fungi. These approaches were based on analyses of standardized phylogenetic beta diversity and taxonomic beta diversity, following the analytical framework developed by Stegen *et al.* (2013). An important assumption of this framework is that more phylogenetically closely related species tend to own more similar niches. Previous simulations have

shown that when this assumption is met, robust ecological inferences can be made via this analysis framework (Dini-Andreote *et al.*, 2015). To test whether the assumption holds for soil microbes in our study, we first calculated the relative-abundance-weighted mean value of each soil property for each OTU as its environmental optima, following the method described by Dini-Andreote *et al.* (2015). Then, the Mantel correlogram ('mantel.correlog' function in R package 'vegan') was used to calculate the correlation coefficients between niche differences (pairwise Euclidean distances of OTUs' environmental optima) and phylogenetic distances using different phylogenetic distance thresholds. The significance of these correlations was determined by permutating the distance matrix 999 times with Bonferroni correction. A significantly positive correlation means that more closely related OTUs tend to occupy more similar niches. Consistent with previous studies (Stegen *et al.*, 2013; Wang *et al.*, 2013; Dini-Andreote *et al.*, 2015; Tripathi *et al.*, 2018), we found significant phylogenetic signals at relatively short phylogenetic distances (Fig. S4), supporting the assumption of this analysis framework.

We calculated the pairwise phylogenetic turnover (β MNTD) among and within islands by using the 'comdistnt' function (abundance.weighted = TRUE) in the R 'picante' package (Kembel *et al.*, 2010). Then, we shuffled the taxa labels of the phylogenetic tree 999 times and generated a null distribution of β MNTD among islands or samples within each island. The standardized effect size of β MNTD (alias to beta Nearest Taxon Index (β NTI), a standardized measure of phylogenetic turnover among samples) was calculated as the difference between observed β MNTD and mean of the null distribution of β MNTD normalized by its standard deviation. β NTI values were separated into three regions: >2 , which means that phylogenetic turnover is significantly greater than expected by chance, indicating variable selection; <-2 , which means that phylogenetic turnover is significantly lower than expected by chance, indicating homogeneous selection; $|\beta$ NTI| <2 , which means that phylogenetic turnover is not significantly different from null expectation, indicating the importance of stochastic processes that may be attributed to homogenizing dispersal, dispersal limitation, or ecological drift (Stegen *et al.*, 2013; Stegen *et al.*, 2015). We further differentiated stochastic processes into finer categories by calculating standardized taxonomic beta diversity—the Bray–Curtis based Raup–Crick metric (RC_{bray})—based on the difference between the observed Bray–Curtis dissimilarity and its null distribution. The null distribution of Bray–Curtis dissimilarity was calculated from 999 null sample $\times$ species tables, which were generated by randomly assigning sequences but keeping OTU richness and the number of sequences of each sample unchanged, following the

procedure described by Stegen *et al.* (2015). RC_{bray} approaching 1 means that the observed taxonomic turnover is greater than null expectation, indicating dispersal limitation or variable selection, while RC_{bray} approaching -1 means that the observed taxonomic turnover is less than null expectation, indicating homogenizing dispersal or homogeneous selection. Therefore, combining the value of βNTI and RC_{bray} , we could infer the potential mechanisms of community assembly (Dini-Andreote *et al.*, 2015; Stegen *et al.*, 2015). More specifically, $|\beta\text{NTI}| < 2$ and $RC_{\text{bray}} > 0.95$ indicate dispersal limitation; $|\beta\text{NTI}| < 2$ and $RC_{\text{bray}} < -0.95$ indicate homogenizing dispersal; $|\beta\text{NTI}| < 2$ and $|RC_{\text{bray}}| < 0.95$ indicate that community turnovers are not distinguishable from expected by chance (i.e., drift). Then, we estimated the relative importance of different processes by calculating the fraction of values of βNTI and RC_{bray} that fell into different categories as previously stated, among all pairwise comparisons between islands as well as between samples within each island. In our study, the number of samples differed across islands, which could potentially contribute to changes in the relative importance of different assembly mechanisms across islands. To find out if this is really a problem for our study, we subsampled our data by keeping four samples for each island (except for the one with only two samples) and reran the analyses using the subsampled data. Results based on the subsampled data (Figs S5–6) were qualitatively similar to results based on the full data (Figs 2 and 3), which indicates that our findings (Figs 2 and 3) were not caused by uneven sample numbers.

Statistical analysis

Data on soil properties were standardized to have mean 0 and variance 1 before subsequent analyses. Island area (m^2) was logarithmically (base: 10) transformed. At the island level, we used the mean values of the nine soil properties for each island, island area and spatial distances between islands to explain βNTI by using multiple regression on matrices. At the sample level, the nine soil properties of each sample, island area and spatial distances between samples were used. We first selected the best regression model based on AIC by using the 'step' function in the 'stats' package. Then, the lmg metric (developed by Lindemann, Merenda and Gold (Lindeman *et al.*, 1980) to calculate the relative contribution of each predictor to the R^2) in the 'relaimpo' package (Grömping, 2006) was used to determine their relative influence on βNTI . All the statistical analyses were performed in R [version 3.3.2; (R Core Team, 2013)].

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Authors' Contributions

L.J., W.S.S., S.P.L., and P.W. conceived the study. P.W., S.P.L. and X.Y. performed the experiments. P.W. performed the data analyses. P.W. and L.J. wrote the manuscript with contributions and input from all authors.

Data Availability Statement

DNA sequence data are accessible at the NCBI-SRA under the accession number PRJNA517449. All other data that support the findings of this study have been deposited to figshare (<https://doi.org/10.6084/m9.figshare.10728242.v1>).

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1 The locations of the 29 surveyed islands in the Thousand Island Lake, Zhejiang Province, China and the nearby mainland site (indicated with the red dot). Islands are ordered according to their area (from the smallest to largest).

Fig. S2. The relationship between island area (m^2 ; $\log_{10}$ -transformed) and each soil property (mean $\pm$ SD). Soil properties were standardized to have mean 0 and variance 1. **AP**: available P; **TP**: total P; **TN**: total N; **TOC**: total organic carbon; **AAI**: available Al; **ACa**: available Ca; **AMg**: available Mg. 'ML' is short for mainland.

Fig. S3. The relationship between island area (m^2 ; $\log_{10}$ -transformed) and heterogeneity of each soil property. Heterogeneity was calculated as the mean Euclidean distance of each soil property within islands. **AP**: available P; **TP**: total P; **TN**: total N; **TOC**: total organic carbon; **AAI**: available Al; **ACa**: available Ca; **AMg**: available Mg.

Fig. S4. Mantel correlograms between the pairwise Euclidean distances of OTUs' optimal environmental conditions

(calculated using abundance-weighted means) and phylogenetic distances (panel a: bacteria; panel b: fungi). Closed squares indicate significant phylogenetic signals at the significance level of $\alpha = 0.05$ after Bonferroni correction for multiple testing.

Fig. S5. The distribution of bacterial standardized phylogenetic turnover (βNTI : panel a) and taxonomic turnover (RC_{bray} : panel b), and the percentages of the five structuring processes (panel c), and their variation along the island area (m^2 ; $\log_{10}$ -transformed) gradient (panel d), after subsampling each island to four samples. **HS**: homogeneous selection; **VS**: variable selection; **HD**: homogenizing dispersal; **DL**: dispersal limitation. Islands are sorted based on their area and labelled from 1 to 29 (from smallest to largest). ML is short for mainland. No analyses were conducted for the smallest island (island No. 1), which had too few samples (two) to give reliable results. The vertical dash lines mark the positions of -2 and 2 in panel a, and -0.95 and 0.95 in panel b. Each line in panel d was fitted using local polynomial regression with 95% confidence interval.

Fig. S6. The distribution of fungal standardized phylogenetic turnover (βNTI : panel a) and taxonomic turnover (RC_{bray} : panel b), and the percentages of the five structuring processes (panel c), and their variation along the island area (m^2 ; $\log_{10}$ -transformed) gradient (panel d), after subsampling each island to four samples. **HS**: homogeneous selection; **VS**: variable selection; **HD**: homogenizing dispersal; **DL**: dispersal limitation. Islands are sorted based on their area and labelled from 1 to 29 (from smallest to largest). ML is short for mainland. No analyses were conducted for the smallest island (island No. 1), which had too few samples (two) to give reliable results. The vertical dash lines mark the positions of -2 and 2 in panel a, and -0.95 and 0.95 in panel b. Each line in panel d was fitted using local polynomial regression with 95% confidence interval.