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ORIGINAL PAPER

Biogeographic responses and niche occupancy of microbial communities following long-term land-use change

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Abstract Understanding the effects of forest-to-agriculture conversion on microbial diversity has been a major goal in soil ecological studies. However, linking community assembly to the ruling ecological processes at local and regional scales remains challenging. Here, we evaluated bacterial community assembly patterns and the ecological processes governing niche specialization in a gradient of geography, seasonality, and land-use change, totaling 324 soil samples, 43 habitat characteristics (abiotic factors), and 16 metabolic and co-occurrence patterns (biotic factors), in the Brazilian Atlantic Rainforest, a subtropical biome recognized as one the world's largest and most threatened hotspots of biodiversity. Pairwise beta diversities were lower in pastures than in forest and no-till soils. Pasture communities showed a predominantly neutral model, regarding stochastic processes, with moderate dispersion, leading to biotic homogenization. Most no-till and forest microbial communities followed a niche-based model, with low rates of dispersal and weak homogenizing selection, indicating niche specialization or variable selection. Historical and evolutionary contingencies, as represented by soil type, season, and dispersal limitation were the main drivers of microbial assembly and processes at the local scale, markedly correlated with the occurrence of endemic microbes. Our results indicate that the patterns of assembly and their governing processes are dependent on the niche occupancy of the taxa evaluated (generalists or specialists). They are also more correlated with historical and evolutionary

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contingencies and the interactions among taxa (i.e., co-occurrence patterns) than the land-use change itself.

Keywords Biodiversity hotspots · Historical contingency · Land-use change · Microbial niche specialization · Soil bacterial co-occurrence · Spatial distance

Introduction

The Brazilian Atlantic Forest is the fourth world's richest hotspot of biodiversity, harboring 2.7% and 2.1% of the global endemic species of plants and vertebrates, respectively (Myers et al. 2000). However, in recent decades this biome has suffered from extensive fragmentation and destruction of forest canopies, with only 11.7% of the original vegetation remaining (Ribeiro et al. 2009). The conversion of forests to both croplands and pasturelands represents 20 and 42% of the total human net primary production (HNPP) appropriation in this biome (Weinzettel et al. 2018). By 2100, land-use change is expected to reduce natural vegetative cover by 26–58% in all 34 global hotspots of biodiversity, compared to 2005 (Jantz et al. 2015). The same study predicted that, by the end of the century, forest conversion to croplands and pasturelands could contribute up to 1/3 of the habitat loss and up to 16% loss of plant and animal species in those hotspots due to land-use change only.

As with plants and animals, soil microorganisms are very responsive to land-use change (Lauber et al. 2013; Kaiser et al. 2016; Li et al. 2019; Ceola et al. 2021). Investigations of local microbial communities in the Amazon Forest Biome (Northwestern Brazil) have shown that the conversion of forest in pasturelands and croplands often leads to bacterial diversity loss (Jesus et al. 2009; Rodrigues et al. 2013; Mendes et al. 2015b; Goss-Souza et al. 2020) and affects ecosystem services related to the microbial activity (Paula et al. 2014; Meyer et al. 2017; Goss-Souza et al. 2019; Pedrinho et al. 2019). Most of the works listed above have described taxa trade-offs, diversity turnover, and shifts in microbial functions, resulting from land-use change, as dependent on local abiotic environmental filters (e.g., soil pH, soil organic matter, soil fertility), which is indicative of homogeneous selection process (Stegen et al. 2013). When looking to the Atlantic Forest, just a few works evaluated the diversity of soil bacterial communities in the subtropical region of this biome (Southern Brazil) (Faoro et al. 2010) and the consequences of forest-to-agriculture conversion for both bacterial diversity and ecological processes shaping bacterial distribution (Goss-Souza et al. 2017).

The continuum hypothesis states that stochastic processes along with deterministic selection contribute to the assembly of ecological communities (Stegen et al. 2013; Dini-Andreote et al. 2015; Powell et al. 2015; Tripathi et al. 2018). Spatial distance have been linked with success with the ecological dispersal process (Martiny et al. 2011), which refers to the tendency to migrate by individuals from a local population or community, leading to homogenous dispersal, when rates of migration are high or, dispersal limitation, when the dispersal rates are low (Sengupta et al. 2019). The variation in microbial diversity related to random birth and death or spatial distance between sites, not related to environmental selection, indicates a drift process. Drift could act as the dominant process in microbial communities when overall population abundance and community diversities are low (Nemergut et al. 2013), leading to an increased risk of extinction (Cordovez et al. 2019). Moreover, dispersal and drift can act together as stochastic forces, leading to microbial neutral assembly (Cottenie 2005; Székely and Langenheder 2014; Goss-Souza et al. 2017, 2020).

The homogeneous selection is assumed to be a pivotal driver of local assembly dynamics of bacterial communities (e.g., in the same toposequence) (Jesus et al. 2009; Dini-Andreote et al. 2014; Mendes et al. 2015a). However, several studies have shown weak correlations between assembly and homogeneous environmental filtering in regional or continental scales (Feng et al. 2019; Gao et al. 2019). The explanation could reside in a complementary selection force, the variable selection process, which occurs when heterogeneous selective environments lead microbial communities to be overdispersed (e.g., increase in SOM quantity and/or quality, microbial cooperation and co-occurrence, microbial activity) (Dini-Andreote et al. 2015), with microbial communities modulated by intra- and interspecific biotic relationships among species, in detriment of environmental abiotic filters (Gao et al. 2019). To account for this, species association has been extensively used in

microbial ecology to infer biotic interactions resulting from the variable selection process (Ferrenberg et al. 2013; Nemergut et al. 2013; Wang et al. 2020). Otherwise, just a few studies have used microbial networks for examining species association and variable selection in biogeographical studies (Ma et al. 2016; Gao et al. 2019). The outcome of network topological properties results in co-occurrence and co-exclusion patterns, which can offer valuable insights about biotic interactions within sets of microbial communities (Dini-Andreote et al. 2014; Jones and Hallin 2019), although some studies have argued that spatial associations between species are not a good proxy for ecological interactions (Blanchet et al. 2020). Microbial ecologists are now focusing on the hypothesis that, besides homogeneous selection, other ecological processes, such as variable selection, dispersal limitation, and drift are important drivers of the variability in assembly patterns along with geographic gradients (Hanson et al. 2012; Ranjard et al. 2013). However, a few studies have tested and quantified those complementary processes in biogeography studies (Fan et al. 2017; Feng et al. 2019; Gao et al. 2019).

Recent studies have raised the hypothesis that geographical patterns and the ecological processes governing assembly in bacterial communities could vary between habitat generalists and specialists (Gao et al. 2019; Luo et al. 2019). While generalists follow the Baas Becking theory of "everything is everywhere" (De Wit and Bouvier 2006), habitat specialists are the microorganisms that have restricted occupancy, as represented by their low occurrence across environmental and geographical gradients (Meyer et al. 2018; Gao et al. 2019; Ceola et al. 2021). The competitive/cooperative interactions among microbial populations in a local community (Li et al. 2018) and sets of metapopulations in metacommunity (Hovatter et al. 2011; Rocha et al. 2021) are very intricate (Leibold et al. 2004) and land-use change would alter the role of these interactions in microbial community assembly (Creamer et al. 2016; Brinkmann et al. 2019; Goss-Souza et al. 2020). Some authors have found land-use change and management intensification in tropical soils, as selective abiotic filters, by increasing the competition among species for habitat and limiting resources, according to niche (Mendes et al. 2014; Goss-Souza et al. 2019). Linking the occurrence of those endemic and ubiquitous taxa with the environmental and geographical gradients could enable microbial ecologists to survey the consequences of human intervention on microbial diversity and habitat specialization.

Here, we investigated the patterns of soil bacterial beta diversities and the consequent ecological processes governing microbial assembly along with multiple spatial scales. Moreover, we linked those patterns and processes to habitat transformation, resulting from the long-term conversion of the Atlantic Forest into no-till cropping and pasture areas. Our central hypothesis affirmed that (i) the microbial assembly would vary along land uses, and geographic distance between microbial communities with a decrease in microbial diversity in the converted agriculture soils of local communities. We also hypothesized that (ii) the balance between neutral and niche-based assembly models would differ along land uses and spatial scales, being neutral in the forest soils, and local communities and niche-based in the agriculture soils and regional communities. A third hypothesis stated that (iii) the processes governing microbial assembly would vary from stochastic to deterministic between habitat generalists and specialists, respectively. By combining 16S rRNA T-RFLP fingerprint and a large set of abiotic (43 soil and landscape parameters) and biotic factors (16 metabolic and co-occurrence patterns) in a broad spatial scale (0–378 km), we aimed (i) to verify the changes in bacterial assembly patterns, (ii) to identify the features that impose assembly, and (iii) to underlie the ecological processes governing assembly across spatial scales for overall bacterial communities, generalists, and specialists.

Material and methods

Study areas, soil sampling, and environmental analyses

The sampling sites were located within the subtropical Atlantic Forest Biome, at Santa Catarina State, Brazil (Supplementary Fig. S1a), and represented (1) remnants of the original forest cover, and the long-term conversion of forest into (2) no-till cropping and (3) pasturelands. The forest sites comprised a natural transition between mixed ombrophilous forest and semi-deciduous forest, with a predominance of *Araucaria angustifolia* (fam. Araucariaceae) in the western mesoregion and *Mimosa scabrella* (Fabaceae)

in the plateau mesoregion. Other frequent species in forest sites were *Apuleia leiocarpa*, *Balfourodendron riedelianum*, *Cabralea glaberrima*, *Cedrela fissilis*, *Cordia trichotoma*, *Diatenopterix sorbifolia*, *Enterolobium contortisiliquum*, *Lonchocarpus leucanthus*, *Parapiptadenia rigida*, *Patagonula americana,* and *Peltophorum dubium*. Forest areas were deforested via timber slash-and-burn and converted in two distinct land uses, in the late 1980s: i) No-till cropping systems, characterized by successive rotational cultivation of wheat, and eventually, oat and ryegrass in the winter, followed by soybean and maize in the summer, and; ii) Pasturelands, characterized by a mix of perennial grasses with a predominance of *Axonopus affinis* (Poaceae) in western mesoregion and *Andropogon lateralis* (Poaceae) in plateau mesoregion. The selection of sampling sites was based on land-use history and management, obtained from previous exploratory campaigns, interviewing farmers and experts. The main criterion of selection was the conversion of forest to no-till or pasture at least 10 years before sampling. Grassland and no-till represent the most common land uses employed by farmers at the Santa Catarina State, Brazil. Samples were collected in July and January, comprising winter and summer seasons of the southern hemisphere, respectively, in a gradient of latitude, longitude, and altitude. Sampling counties were São Miguel do Oeste (26°44'S; 53°32'W; 652 m above sea level—masl), Chapecó (27°3'S; 52°40'W; 642 masl) and Xanxerê (26°50'S; 52°28'W; 728 masl) in the western mesoregion and, Campo Belo do Sul (27°52'S; 50°39'W; 978 masl), Lages (27°47'S; 50°35'W; 877 masl) and Otacílio Costa (27°33'S; 49°52'W; 902 masl), in the Plateau mesoregion, Santa Catarina State, Brazil (Supplementary Fig. S1a). The climate in both mesoregions is humid temperate mesothermal (Cfb) (Köppen classification), with no marked dry season and rainfalls equally distributed throughout the year. The historic mean annual temperature varies from 18–22 °C in the western to 14–18 °C in the Plateau.

To evaluate microbial assembly patterns (response variables), non-deformed soil samples from the 0–10 cm profile were collected with sterile PVC tubes (5 cm diameter × 10 cm depth), yielding ~ 500 g of soil each. Each sample was collected in a 3 × 3 Cartesian square-geogrid scheme, equidistantly by 30 m from each other, with 20 m of the border, totalizing an area of one hectare per sampling site (Supplementary Fig. S1b). A total of 324 individual soil samples were collected (9 samples per geogrid × 3 land uses × 6 counties × 2 sampling seasons). Samples were kept on dry ice and transported to the Cell and Molecular Biology Laboratory, Center for Nuclear Energy in Agriculture (Piracicaba, Brazil), within 24 h, to further molecular procedures. For soil physical, chemical, and microbiological parameters, used as explanatory variables, samples were collected at the same points (also totalizing 324 independent samples). Soil samples were maintained at 4 °C and transported to the Soil Analysis Laboratory, Santa Catarina State University (Lages, Brazil). The soil physical analyses performed were soil density, porosity (total-, macro-, micro- and bioporosity), texture, particle density, aggregate diameter, and penetration resistance. The chemical characteristics analyzed were soil pH, total C, H, N, and S, C:N ratio, soil organic matter, soil organic C, P, K, Al, Ca, and Mg. All the physical and chemical analyses were performed following routine methodology (Keeney and Nelson 1982; Gee and Bauder 1986; Dexter 1988; Cambardella and Elliott 1992; Tedesco et al. 1995; Claessen et al. 1997; Dexter et al. 2007; Dhaliwal et al. 2011; Teixeira et al. 2017). Microbiological metabolic analyses included soil microbial C, soil basal respiration, metabolic quotient, and microbial quotient, also performed through a routine methodology (Sparling and West 1988; Sparling 1992; Anderson and Domsch 1993; Alef and Nannipieri 1995). Soil types were classified using the World Reference Base for Soil Resources (Anjos et al. 2015). Details about site management history, sampling, and environmental analyses are available as supporting information and at the Supplementary Table ST1. See also (Bartz et al. 2014; Goss-Souza et al. 2017).

Soil total DNA extraction and 16S rRNA T-RFLP

To investigate bacterial diversity patterns and processes structuring bacterial communities across land uses, seasons, and geographical distances, we used the T-RFLP method. T-RFLP quantifies the variability in DNA sequences of genes or intergenic space regions (e.g., bacterial small subunit 16S rRNA, fungal ITS), generating a DNA 'fingerprint' of unique fragments, with the size and abundance of each fragment in a soil sample. Although sequencing provides more detailed phylogenetic information, T-RFLP as an automated fingerprinting method is a simpler and

less expensive system that allows the comparison of a high amount of soil samples (van Dorst et al. 2014), with sufficient replication to address soil microbial patterns of diversity and structure (Fierer and Jackson 2006; Dumbrell et al. 2010; Székely and Langenheder 2014; Lange et al. 2015; Kari et al. 2019). Also, T-RFLP generates results consistent with that found in high throughput sequencing (Vega-Avila et al. 2014; Powell et al. 2015; Durrer et al. 2017; Karczewski et al. 2017; De Vrieze et al. 2018). To accomplish that, total DNA extraction (250 mg) was performed for the 324 soil samples (See Supplementary Fig. S1), using PowerLyzer PowerSoil™ DNA Isolation Kit (Mo Bio Laboratories, Carlsbad, USA). DNA quality was verified in gel electrophoresis with Tris-buffered saline with sodium boric acid and 1% agarose (Brody and Kern 2004). DNA concentration was measured with the Qubit™ fluorometer (Thermo Fischer Scientific, Waltham, USA). T-RFLP fragments amplification was performed in a thermal cycler GeneAmp PCR System 9700™ (Thermo Fischer Scientific, Waltham, USA), using the 16S rRNA universal set of primers 27F (5' AGA GTT TGA TCC TGG CTC AG 3') labeled with 6-FAM (Edwards et al. 1989) and 1492R (5' GGT TAC CTT GTT ACG ACT T 3') (Turner et al. 1999). The PCR mix contained 10X Platinum Taq PCR buffer, 3.0 mM $MgCl_2$, 0.2 mM of each dNTP, 0.5 mM of each primer and 0.05 U μL^{-1} of Platinum™ Taq DNA polymerase (Thermo Fischer Scientific, Waltham, USA). DNA templates (10–50 ng μL^{-1}) were ten-fold diluted to optimize the reaction. Reaction consisted in a predenaturation step at 94 °C for 3 min, followed by 35 cycles of 94 °C for 30 s, 59 °C for 45 s, and 72 °C for 60 s, with a final extension of 72 °C for 15 min. Reaction products were then purified using GFX™ PCR DNA and Gel Band Purification Kit (GE Health Care, Chicago, USA), according to the manufacturer's instructions. Ten to 60 nanograms of the amplified and purified DNA were used in 10 µl of restriction reaction using *Hha*I endonuclease (Thermo Fischer Scientific, Waltham, USA), at 37 °C for 3 h. Digested DNA was then purified using 60 µl of absolute ethanol with 2 µl of sodium acetate/EDTA (100:1; 0.1%) and centrifuged at 4000 × *g* for 45 min, followed by another step, adding 150 µl of absolute ethanol/water (7:3) and centrifuging at 4000 × *g* for 45 min. The purified DNA pellet was eluted in 9.8 µl of deionized formamide with 0.2 µl of GeneScan-500 ROX™ internal size standard (Thermo Fischer Scientific, Waltham, USA). The product was denatured at 94 °C for 5 min in a thermal cycler GeneAmp PCR System 9700™ (Thermo Fischer Scientific, Waltham, USA). Fragments were analyzed in an ABI Prism 3100™ automated sequencer (Thermo Fischer Scientific, Waltham, USA) following the manufacturer's instructions. The size and the intensity of each terminal restriction fragment were estimated using GeneMapper version 3.0 (Thermo Fischer Scientific, Waltham, USA) and are hereafter described in terms of operational taxonomic units (OTUs) (Schütte et al. 2008; Rodríguez-Valdecantos et al. 2017). Only fragments ranging from 50 to 500 bp were analyzed.

Microbial profiling and assembly patterns

We first calculated the overall Chao-1 estimated richness and Shannon's alpha diversity for each land use and season. Means were compared through ANOVA with Tukey's Honest Significant Difference test (Tukey's HSD) with the function 'tukeyHSD' on R software, version 4.0.2 (R Core Team, 2020). To evaluate the overall distribution of beta diversities, we performed a multivariate Principal Coordinates Analysis (PCoA), with Monte-Carlo permutations on Canoco software, version 5.2 (Lepš and Šmilauer 2005). From the resulting Bray–Curtis distance matrix, we measured the clustering of beta diversities resulting from PCoA ordination, through non-parametric Permutational Analysis of Variance (PERMANOVA), as implemented by 'adonis' function in 'vegan' package, version 2.5–6 (Anderson 2001; Oksanen et al. 2019), on R software. Adonis-PERMANOVA allowed us to test whether beta diversities were separated by land use, season, and geographic location. Then, we calculated the distributions of observed beta Sørensen pairwise dissimilarities, using the function 'beta.pair' in 'betapart' R package, version 1.5.1 (Baselga et al. 2018). We partitioned the values Sørensen pairwise beta diversities (B_{SOR}) into the turnover (B_{SIM}) and the nestedness (B_{SNE}) components of diversity. We found that the turnover component dominated the partitioning for all land-uses and seasons (Supplementary Fig. S2). Moreover, using Sørensen's presence/absence matrices and analyzing samples from a large geographic scale (0–378 km) in the same dataset, pairwise comparisons almost reached the limit of the signal of the Sørensen index ($B_{SOR} = 1$) for all

land uses and seasons. Thus, we decided to depict the variation in diversification through pairwise Bray–Curtis abundance-based dissimilarities, across land uses and seasons, using the function 'beta.multi.abund' (Baselga 2017), in the 'betapart' R package. We performed the Shapiro–Wilk W test for normal probability, using the function 'shapiro.test' on R. Data presented non-parametric distribution, hence we used the Kruskal–Wallis (chi-square) non-parametric test, with corrected P-values to compare the means of beta diversities across land uses and seasons, using the function 'kruskal.test' on R.

Microbial co-occurrence patterns

To obtain a signal of microbial ecological interactions modulating assembly complexity patterns, we performed non-random co-occurrence network analysis, using the Python 'SparCC' tool, which estimates correlation values from compositional data (Friedman and Alm 2012). First, we calculated SparCC co-occurrence metrics for overall communities, according to land use and season (54 samples × 3 land uses × 2 seasons = 324 samples). Complementary, pairwise microbial communities were compiled in local and regional communities, within and over the mesoregion threshold, respectively, according to spatial distance. Local and regional communities were defined by complementary analyses of Moran's I test for spatial autocorrelation. After defining the limit distance for autocorrelation, we calculated SparCC co-occurrence metrics for local communities, which is the set of pairwise communities within Moran's threshold for autocorrelation and regional communities, regarded as the pairs of microbial communities over the limit for autocorrelation. For each network (overall, local, or regional), P-values were obtained by 100 random permutations for each set of samples. Only OTUs with SparCC significant ($P < 0.01$) and correlations with a magnitude of SparCC > 0.6 or < -0.6 were included into the network analyses. The nodes in the reconstructed networks represented the OTUs, while the edges represented significant positive or negative correlations between nodes. Co-occurrence patterns were calculated in the interactive platform Gephi, version 0.9.2 (Bastian et al. 2009), and network graphs were built with the 'Fruchterman Reingold' design. The metrics evaluated were: average clustering coefficient, which indicates how nodes are embedded in their neighborhood and the degree to which they tend to cluster together; average path length, regarding the average network distance between all pairs of nodes or the average length of all edges in the network; average degree distribution, which is the average number of connections per node in the network, that is, the node connectivity; network diameter modularity, or the capability of the nodes to form highly connected communities, that is, a structure with a high density of between-node connections; number of edges, represented by the number of connections/correlations obtained by SparCC analysis; number of nodes, or microbial OTUs with at least one significant ($P < 0.01$) and strong (SparCC > 0.6 or < −0.6) correlation, and; number of communities, as defined by groups of nodes densely connected internally. The resulting values of those metrics were used as biotic factors, representing the variable selection process, in further multivariate partitioning analyses. From the resulting networks, we were also able to extract the major hub taxa, represented by the set of OTUs with the highest betweenness centrality, which measures the extent to which a node lies on paths between other nodes.

To test the turnover of microbial abundances across land uses and seasons, we performed the Multinomial Species Classification Method (CLAM test) (Chazdon et al. 2011), classifying all the possible phylotypes according to their habitat specialization, as generalists and specialists, using the 'clamtest' function, in 'vegan' R package, according to the estimated species relative abundance. The test was applied using the supermajority rule (K = 2/3, $P < 0.005$). After that, we were able to investigate whether the hub OTUs in each network were generalists or specialists.

Assembly models, selection, and dispersal

To investigate the species association patterns across land uses and seasons, we calculated species rank abundance distributions (RADs) for each of the 324 samples and fitted them to four different theoretical assembly models: the zero-sum multinomial (ZSM) and the broken stick (null model), which regard to neutral assembly, and the pre-emption and the log-normal, related to a niche-based assembly. Broken stick, pre-emption, and log-normal models were calculated using the 'radfit' function from the 'vegan' R

package. The ZSM model was calculated on TeTame software, version 2.16 (Jabot et al. 2008). The models were compared based on the AIC. The lowest AIC value indicates the best-fitted model for each sample (Bozdogan 1987). The dispersal rates, related to the tendency to migrate from members of a certain community, were calculated for each sample, through Etienne's formula (Etienne and Alonso 2005), on TeTame.

From the Bray–Curtis dissimilarity matrices, we calculated beta-diversity distributions for local and regional communities with the function 'vegdist' on the 'vegan' R package (Oksanen et al. 2019). Then, we performed permutations resemblance of those Bray–Curtis dissimilarity distance distributions under the null model with the function 'swap_count' from the 'vegan' R package. Afterward, we generated the Z-scores for the set of microbial communities with the function 'oecsimu' (Ulrich and Gotelli 2010), from the 'vegan' R Package. The Z-score refers to the deviation of expected Bray–Curtis pairwise distributions under permutations to the observed value, indicating the distance of a certain set of pairwise beta diversities from the null expectation (Keil 2019). Pairwise diversities with Z-score < -2 reflected aggregation, which means that OTUs co-occurred more than expected by the null model, while pairwise diversities with Z-score $> +2$ reflected segregation, meaning that OTUs co-occurred less than expected by the null model (Dini-Andreote et al. 2015; Gao et al. 2019). We considered the co-occurrence patterns of microbial communities as non-random, resulting from deterministic homogeneous (Z-score < -2) or variable selection (Z-score $> +2$) processes, while Z-scores within those values ($-2 <$ Z-score $< +2$), indicated that communities co-occurred randomly, governed by drift and/or dispersal stochastic processes.

Variation partitioning of factors modulating assembly of microbial communities

To investigate the importance of geographic coordinates as primary predictors of Bray–Curtis dissimilarities across spatial scales, we first performed a Principal Coordinates Analysis of Neighbor Matrices (PCNM), with forward-selection, setting latitude, longitude, and altitude as primary predictors and the resulting coordinates (PCNM axes) as spatial predictors. Latitude and longitude were used as constraining variables in the model. From the resulting PCNM non-collinear and significant variables (Bonferroni correction), we depicted the proportion of the variation in the microbial assembly of overall bacterial communities, generalists and, specialists explained by (1) geography, (2) abiotic factors, and (3) biotic factors, via Mantel and partial Mantel tests, with Pearson correlations and log transformation (Martiny et al. 2011), according to geographic distance, with the functions 'mantel' and 'partial. mantel' (Legendre and Fortin 1989), in the 'vegan' R Package.

Results

Profiling of microbial communities

Chao-1 Richness and Shannon's α-diversity (*H'*) among land uses and seasons were compared through Tukey's HSD test (Supplementary Fig. S3). We found differences in richness only for summer between no-till and pasture ($P = 0.027$). When comparing seasons within the same land use, we found no-till summer richer than winter ($P = 0.018$). The same patterns were observed for α-diversity, which varied across land uses only in the summer ($P < 0.001$). Depicting the variability in summer, no-till presented higher α-diversity than forest ($P = 0.004$) and pasture ($P < 0.001$), with forest α-diversity higher than pasture ($P < 0.001$). Comparing seasons within the same land use, we found only differences for no-till, with summer more diverse than winter ($P = 0.003$).

Beta diversity structures and distributions

We investigated the beta diversity structure among land uses, through PCoA (Fig. 1). The plot based on Bray–Curtis distances showed differences in structures of no-till microbial communities with both forest and pasture communities. Otherwise, forest and pasture communities presented a high degree of overlapping. Variation in Bray–Curtis distances explained in the first two axes of PCoA was 34.78%. Depicting the clustering of beta diversities resulting from principal coordinates ordination we found differences among land uses, seasons, and sampling sites. To explore the first two significant correlations from

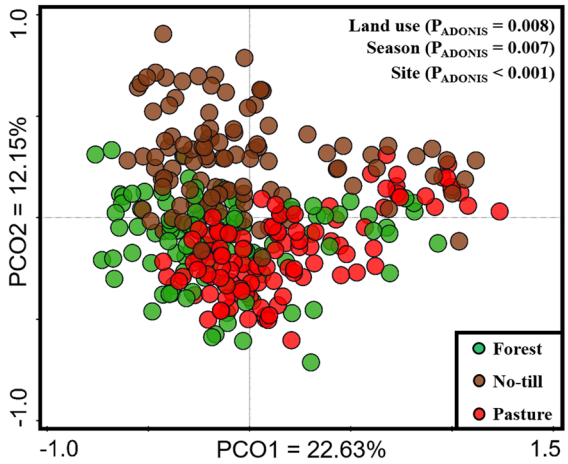

Fig. 1 Principal Coordinates Analysis (PCoA) of soil microbial communities across land uses, in the subtropical Atlantic Forest Biome, Southern Brazil. Plots were generated using Bray–Curtis distance matrices with 1000 Monte-Carlo permutations. Samples are colored as follow: forest, green circles; no-till, brown circles; pasture, red circles; Differences in microbial beta diversities clustering among land uses were evaluated through Adonis-PERMANOVA (n = 324 samples; 999 permutations; $P_{ADONIS} < 0.05$)

PERMANOVA, we depicted the variation in beta pairwise diversities distributions, according to land use ($P = 0.008$) and season ($P = 0.007$) (Supplementary Fig. S4). For summer, mean pairwise beta diversities decreased after long-term forest conversion to both no-till and pasture, with diversities in pasture higher than in no-till. Diversity also decreased from winter to summer in no-till ($P < 0.001$) and pasture ($P < 0.001$).

Microbial co-occurrence patterns

Overall, network complexity increased after forest conversion to both no-till and pasture and decreased from winter to summer, for both land uses (Fig. 2). Pasture communities presented the highest number of microbial OTUs with at least one significant ($P < 0.01$) and strong correlation (SparCC > 0.6 or < −0.6) (Supplementary Table ST2). Pasture also showed the highest number of both positive and negative correlations among pairs of OTUs, the highest modularity, the larger network diameter, the larger average path length, and the larger average degree, in both seasons. The number of nodes, the number of edges, the number of positive and negative connections, network diameter, and average path length decreased from winter to summer in all land uses. The number of microbial communities increased in no-till and decreased in pasture, from winter to summer. The average degree decreased from winter to summer for forest and no-till.

Complementary, we investigated the turnover of microbial abundances across land uses and seasons, according to their habitat specialization, as generalists and specialists (Fig. 3). From a total of 275 OTUs, we found 165 as generalists (60%) and 51 specialists in the plateau mesoregion (18.5%), and 59 specialists in the western mesoregion (21.5%). Investigating the seasonal OTUs turnover, in forest (Supplementary Fig. S5a), we found 160 generalists (62%), 48 specialists in winter (19%), and 48 specialists in summer (19%), of which 27 exclusives for forest winter and 11 exclusives for summer. In no-till (Supplementary Fig. S5c), we found 152 generalists (56%), 59 specialists in winter (22%), and 60 specialists in summer (22%), being 25 exclusives for no-till winter and 21 exclusives for summer. In pasture (Supplementary Fig. S5e), we found 139 generalists (54%), 79 specialists in winter (31%), and 40 specialists in summer (15%), of which 36 exclusives for pasture winter and 9 exclusives for summer. We also compared abundance turnover due to land-use change. In long-term forest-to-no-till conversion (Supplementary Fig. S5b), we found 139 generalists (52%), 63 specialists in forest (23%), and 68 specialists in no-till (25%), with 20 exclusives for forest and 14 exclusives for no-till. Yet in long-term forest-to-pasture conversion (Supplementary Fig. S5d), we found 159 generalists (59%), 69 specialists in forest (26%), and 40 specialists in pasture (15%), of which 10 were exclusives for forest and 12 exclusives for pasture. When comparing the differences in assemblages resulting from long-term land-use change (no-till vs. pasture; Supplementary Fig. S5f), we found 149 generalists (55%), 69 specialists in no-till (26%), and 52 specialists in pasture (19%), with 12 exclusives for no-till and 20 exclusives for pasture.

We also sought potential keystone taxa, the OTUs that hold the networks, as represented by elevated levels of betweenness centrality—the number of times a node plays a role as a connector between two other nodes (Supplementary Table ST3). We found three keystone taxa in forest winter and none in summer. No-till presented three keystone taxa in winter and

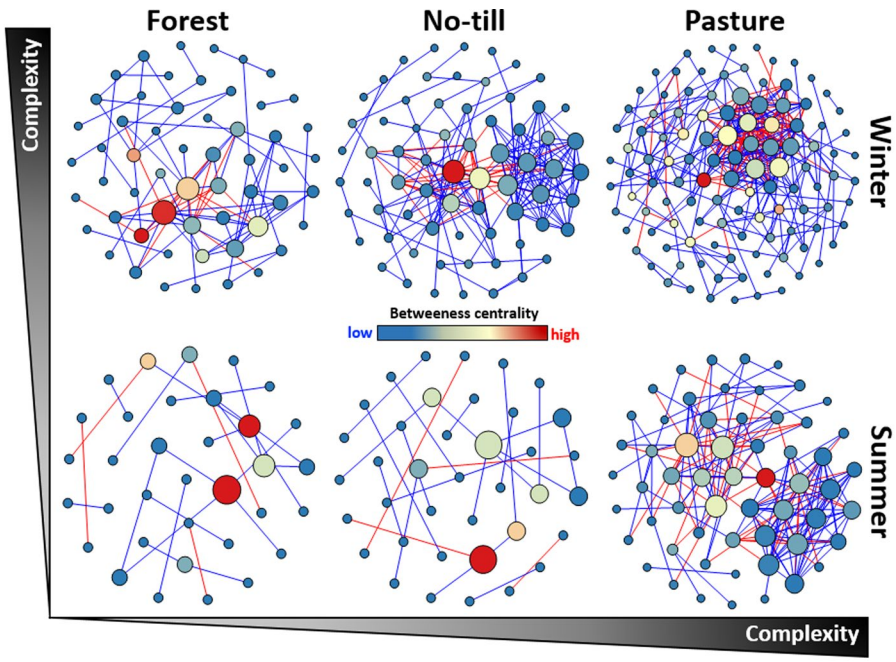

Fig. 2 Overall SparCC network plots of co-occurrence and co-exclusion between OTUs, following long-term land-use change and seasons. Only OTUs with SparCC significant (two-sided pseudo-$P < 0.01$, 100 bootstrapping random permutations) and correlations with a magnitude of SparCC > 0.6 (positive correlation–blue edges) or SparCC < −0.6 (negative correlation–red edges) were included into the network plots. Each node represents an OTU, based on *Hha*I enzyme T-RFLP fingerprint. The size of each node is proportional to the number of connections (that is, degree), while the color of each node is represented by a gradient of betweenness centrality. Network graphs were built with 'Fruchterman Reingold' design, on Gephi software

none in summer. Yet for pasture, several keystone taxa were found for both winter and summer. When classifying the 20 most important keystone taxa holding each network (Supplementary Table ST3), in terms of habitat specialization, we found: (1) Forest winter: nine seasonal specialists and six specialists in forest; (2) Forest summer: five seasonal specialists and three specialists in forest; (3) No-till winter: seven seasonal specialists and eight specialists in no-till; (4) No-till summer: four seasonal specialists and five specialists in no-till; (5) Pasture winter: eight seasonal specialists and six specialists in pasture, and; (6) Pasture summer: three seasonal specialists and four specialists in pasture.

Microbial assembly models across land use and spatial scales

We fitted all the 324 individual samples to theoretical ecological models, according to AIC. From the four tested models, microbial communities fitted most to ZSM neutral model or lognormal niche-based model, with exception of one sample in pasture summer that fitted the preemption niche-based model (Fig. 4a). Most of the samples in forest (61.1%) and no-till (63.9%) fitted the niche-based lognormal distribution, which indicates the prevalence of deterministic processes governing microbial assembly. Otherwise, most of the samples in pasture fitted the ZSM neutral distribution (63.0%), which regards stochastic processes governing assembly. When depicting the seasonal variation in assembly, we found an increase in the number of microbial communities fitting the neutral ZSM assembly from winter to summer, in both forest (35.2 to 42.6%) and pasture (53.7 to 72.2%). We observed a decrease in the number of microbial communities fitting the ZSM model from winter (44.5%) to summer (27.8%) in no-till. When comparing the dispersal rates across land use and seasons (Fig. 4b), through the Kruskal–Wallis test, we observed an increase in the rates of dispersal resulting from the long-term conversion of forest to pasture in

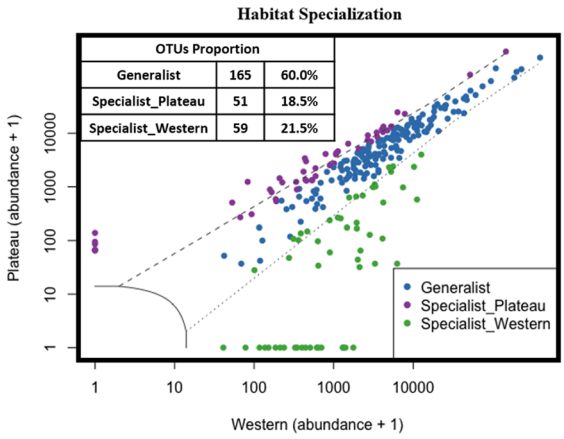

Fig. 3 Habitat microbial specialization across mesoregions. The x and y axes represent the OTUs abundance turnover between regions. The number and the percentage of generalists and specialists for each habitat comparison are shown. The classification of generalists and specialists was performed through the CLAM test function in vegan R package, according to the estimated species relative abundance. The test was applied with arguments of K = 2/3 and $P < 0.005$, according to the supermajority rule. All the counts were added by 1 to let the marginal OTUs evenly arranged in the plot space

both winter ($P < 0.001$) and summer ($P < 0.001$), with no differences observed for the forest to no-till conversion, in both seasons, meaning more predisposition to migration from members of pasture local communities, compared with those from forest and no-till. We observed no seasonal effect on dispersal rates for any of the land uses.

When evaluating the influence of geographic distance in assembly patterns, we observed that beta pairwise diversities were lower in local scale—defined as the set of samples within the autocorrelation limit (< 97.196 km; Supplementary Fig. S6)—compared to the regional scale (> 97.196 km) (Fig. 5). Diversities decreased in summer on a local scale from forest to both no-till and pasture (Fig. 5a), with only no-till presenting a decrease in beta diversities from winter to summer, at the regional scale (Fig. 5b). Comparing diversities within each land use, diversities decreased in summer in both local and geographic scales for no-till. For pasture samples, diversities decreased from winter to summer at the local scale. Thus, we investigated co-occurrence patterns of bacterial OTUs, through Z-scores (Keil, 2019), comparing the observed beta diversities across scales (Fig. 5a and b, dark bars) with the simulated beta diversities (Fig. 5a and b, light bars). The resulting Z-score distributions after simulations are presented (Fig. 5c and d). At the local scale (Fig. 5c), Z-scores of most forest microbial communities, in winter and summer, fitted the null expectation, the same as for pasture communities, evidencing a neutral assembly, which is expected to occur when selection is weak, and assembly is governed by drift and dispersal processes. Yet for no-till, in both seasons, most of the local communities fitted above the null expectation. Thus, local microbial communities in this environment are more segregated than expected by the null model, which is likely to occur when the variable selection process is acting. At the regional scale (Fig. 5d), Z-scores of forest microbial communities in winter and summer fitted above the null expectation, indicating segregation of communities across geographic distances. A similar trend was found for no-till, where the mean Z-scores were above the null expectation, regarding segregation, but with several communities fitting the null model, neutral. Geographic Z-scores of pasture communities presented the same trends as found for local communities, with most of the communities fitting the null model, in both seasons.

Underlying the drivers of microbial community assembly across spatial scales and niche occupancies

To evaluate the role of each set of variables (geography + abiotic + biotic) in structuring generalists and specialists decay profiles, we performed Mantel and Partial Mantel tests (Table 1). Mantel tests have shown that the variation in overall bacterial community dissimilarities, considering all land uses together (overall data) was correlated with the biotic factors, even after controlling for the effect of geographic distance and abiotic factors ($P < 0.001$). Significant correlations were also observed with geographic distance and to a lesser extent with abiotic factors. For generalists, the variation was also correlated strongly correlated with the biotic factors, even after controlling for geographic distance and abiotic factors ($P < 0.001$). Significant correlations were also observed with geographic distance, with a minor effect of both geographic distance, and abiotic factors. When looking for the specialists' correlations, the biotic factors were again the major constraints of dissimilarities distributions, even after controlling for the effect of geographic distance and abiotic factors ($P < 0.001$).

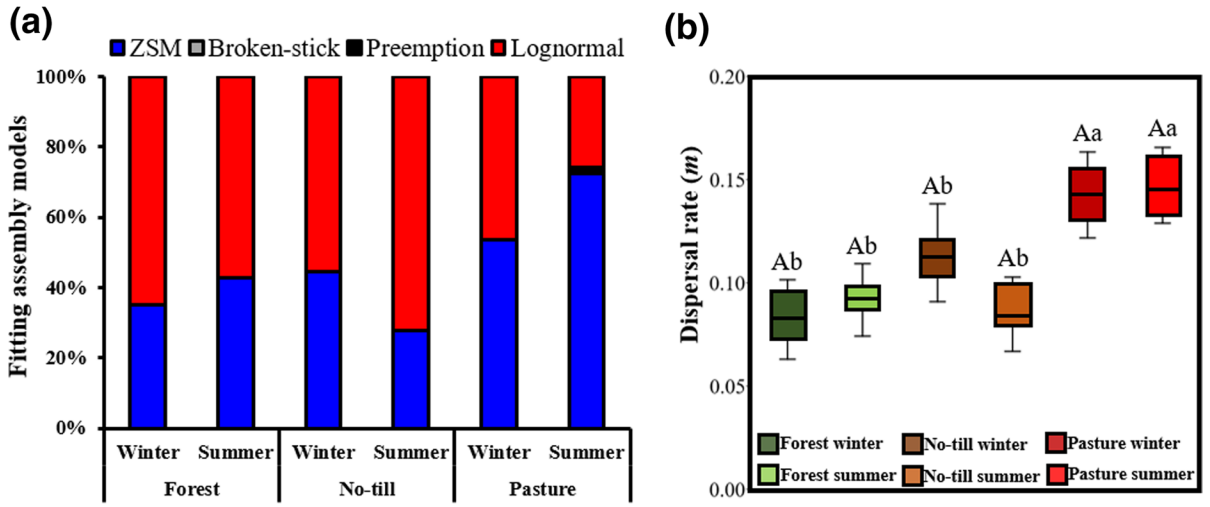

Fig. 4 Samples fitting to theoretical ecological models, based on Akaike information criterion (AIC) for rank abundance distributions of microbial OTUs, across land use and seasons, in the subtropical Atlantic Forest Biome, Southern Brazil. **a** Rank abundance models based on corrected AIC value from Poisson distributions using maximum likelihood estimation. The lowest AIC value for each sample represented the best-fitted model for general community's assembly. Best-fitted models were calculated by the general equation AIC = −2log-likelihood + 2 × npar. ZSM (Zero Sum Multinomial) and Broken-stick are null models regarding theoretical neutral assembly while Preemption and Lognormal are niche-based models regarding deterministic assembly. **b** Boxplots of distributions of calculated dispersal rates across land use and seasons showing the median (thick black line), the first quartile (lower box bound), the third quartile (upper box bound) and the range of data values that deviate from the box (vertical black lines). Dispersal rates were compared through Kruskal–Wallis (chi-square) non-parametric test with Bonferroni correction. Uppercase letters represent differences between seasons for the same land use while lowercase letters represent differences among land uses for the same season ($P_{corrected} < 0.05$). Dispersal rates were calculated by Etienne's formula. Values of dispersal are between 0 and 1, where the higher the value the greater the tendency to migrate of members of a local microbial community, as represented by each of the 324 soil samples

Significant correlations were also observed with abiotic, with a minor effect of geographic distance.

As we found differences in pairwise beta diversities for local and regional scales, we sought for the evidence of differential patterns of correlations within and over the Moran's I autocorrelation threshold (See Supplementary Fig. S6). To achieve that, we divided bacterial, generalists, and specialists in local (from 0 to 97.196 km) and regional communities (> 97.196 to 378.160 km). On the local scale, the variation in overall bacterial community dissimilarities was strongly correlated with the biotic factors (Table 1), even after controlling for the effect of geographic distance and abiotic factors ($P < 0.001$). Strong and significant correlations were also observed with geographic distance, even controlling for abiotic and biotic factors ($P < 0.001$) and to a lesser extent with abiotic factors, even controlling for geographic distance, and biotic factors ($P < 0.001$). For generalists, the local variation was also strongly correlated with the biotic factors, even after controlling for geographic distance and abiotic factors ($P < 0.001$). Strong and significant correlations were also observed with geographic distance, even after controlling for biotic distance and abiotic factors distance ($P < 0.001$), with a minor effect of abiotic factors. Yet for the specialists, we found strong and significant correlations with the three sets of explanatory variables. The biotic factors were the stronger drivers of dissimilarities distributions, even after controlling for the effect of geographic distance and abiotic factors ($P < 0.001$). Strong and significant correlations were also observed with abiotic, even controlling for geographic distance and biotic factors ($P < 0.001$), and to a lesser extent to geographic distance, even controlling for abiotic and biotic factors ($P < 0.001$). Evaluating the mesoregional scale, we observed strong and significant correlations only with biotic factors ($P < 0.001$), for both overall bacterial communities, generalists, and specialists, with a

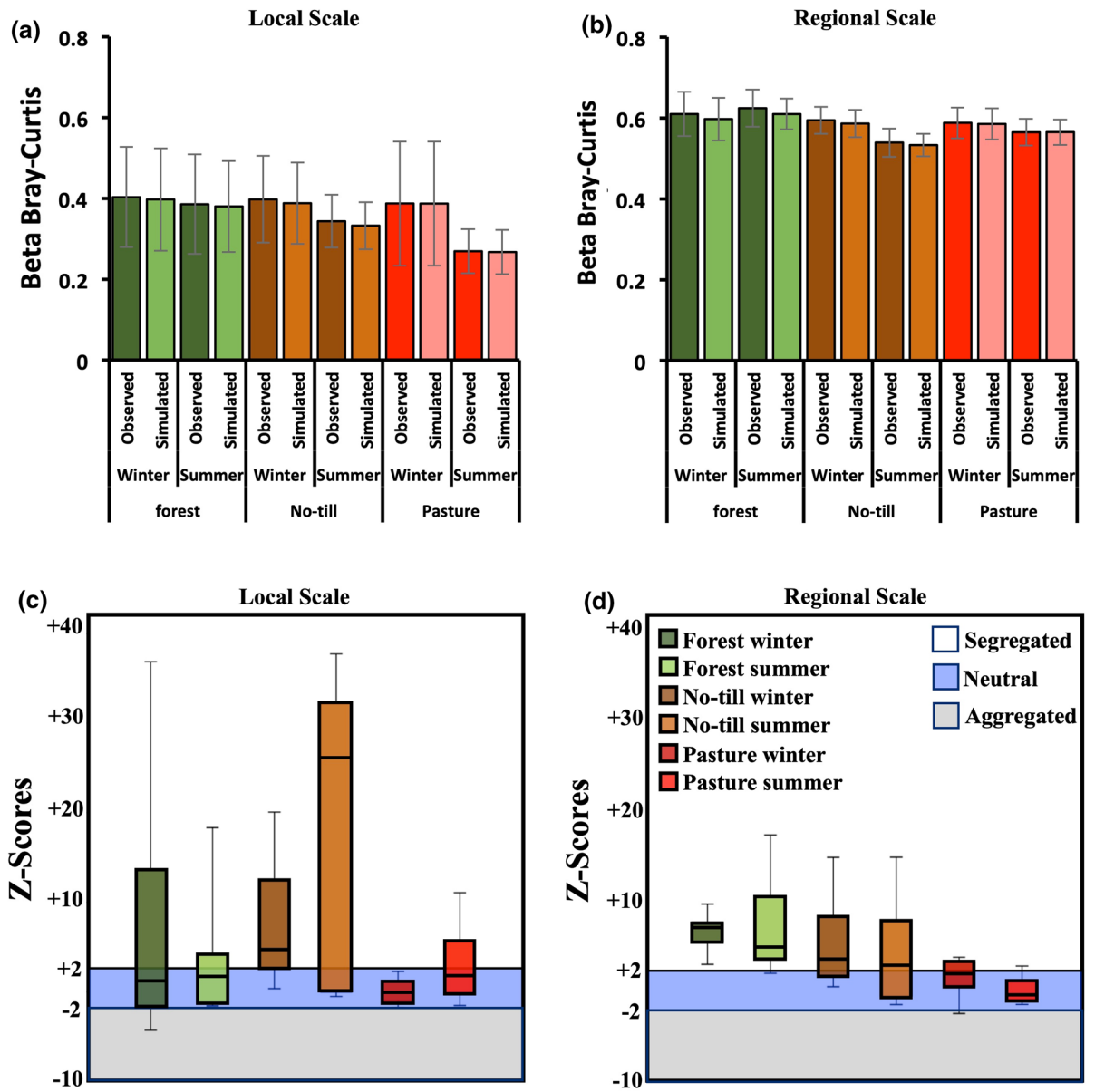

Fig. 5 Pairwise beta diversities distribution and simulated deviation from null expectation. Beta pairwise diversities at **a** local and **b** regional scales. Barplots of Bray–Curtis dissimilarities across land use and seasons showing the mean and the standard deviation (vertical black lines) of observed (dark colors) and simulated (light colors) beta pairwise diversities (10,000 simulations). Z-scores at **c** local and **d** regional scales. Boxplots of distributions across land use and seasons showing the median (thick black line), the first quartile (lower box bound), the third quartile (upper box bound), and the range of data values that deviate from the box (vertical black lines). Horizontal lines separate lower and upper significance thresholds of Z-scores distributions (Z = 2 and + 2, respectively; $P < 0.05$). Z-scores were generated under the null model method 'swap_count' with 10,000 simulations. H_1: observed beta diversity is less or greater than simulated values of beta diversity

Table 1 Relative contribution of geographic distance, abiotic factors, and biotic factors influencing bacterial communities with different niche occupancies at overall, local, and regional scales. We calculated Pearson product-moment correlations from the simple (Mantel test; 1000 permutations; $P < 0.05$) and the controlled effects (partial Mantel test; 1000 permutations; $P < 0.05$). From a set of 64 measured parameters, only non-collinear and significant variables were forward-selected and used in the model. Local and regional microbial communities were selected by the geographic limit for autocorrelation (Moran's I = 97.196 km; $P < 0.05$)

Overall communities	Overall scale		Local scale		Regional scale	
	ρ	*P*	ρ	*P*	ρ	*P*
Geographic distance	0.172	0.001	0.308	0.001	–	–
Abiotic selection	0.135	0.001	0.247	0.001	–	–
Biotic selection	0.292	0.001	0.340	0.001	0.231	0.001
Geographic [Abiotic]	0.131	0.001	0.297	0.001	–	–
Geographic [Biotic]	0.147	0.001	0.260	0.001	–	–
Abiotic [Geographic]	0.073	0.001	0.233	0.001	–	–
Abiotic [Biotic]	0.095	0.001	0.198	0.001	–	–
Biotic [Geographic]	0.278	0.001	0.299	0.001	0.231	0.001
Biotic [Abiotic]	0.277	0.001	0.309	0.001	0.236	0.001
Generalists	Overall scale		Local scale		Regional scale	
	ρ	*P*	ρ	*P*	ρ	*P*
Geographic distance	0.157	0.001	0.285	0.001	–	–
Abiotic selection	0.096	0.001	0.163	0.001	–	–
Biotic selection	0.253	0.001	0.299	0.001	0.206	0.001
Geographic [Abiotic]	0.131	0.001	0.276	0.001	–	–
Geographic [Biotic]	0.134	0.001	0.241	0.001	–	–
Abiotic [Geographic]	0.037	0.003	0.145	0.001	–	–
Abiotic [Biotic]	0.060	0.001	0.114	0.001	–	–
Biotic [Geographic]	0.240	0.001	0.258	0.001	0.206	0.001
Biotic [Abiotic]	0.242	0.001	0.277	0.001	0.210	0.001
Specialists	Overall scale		Local scale		Regional scale	
	ρ	*P*	ρ	*P*	ρ	*P*
Geographic distance	0.160	0.001	0.243	0.001	–	–
Abiotic selection	0.191	0.001	0.325	0.001	–	–
Biotic selection	0.291	0.001	0.356	0.001	0.242	0.001
Geographic [Abiotic]	0.094	0.001	0.229	0.001	–	–
Geographic [Biotic]	0.134	0.001	0.188	0.001	–	–
Abiotic [Geographic]	0.141	0.001	0.315	0.001	–	–
Abiotic [Biotic]	0.155	0.001	0.281	0.001	–	–
Biotic [Geographic]	0.269	0.001	0.324	0.001	0.242	0.001
Biotic [Abiotic]	0.269	0.001	0.318	0.001	0.243	0.001

lower influence of controlling geographic and abiotic effects.

Later, we forward-selected the factors within the sets of significant parameters that could be driving bacterial, generalists, and specialists diversity distributions across spatial scales, through Partial Mantel tests (Supplementary Table ST4). On an overall scale, after controlling all the possible individual factors with their respective matrices (e.g., pH controlling for abiotic), the number of nodes was the key factor for overall bacterial communities ($P=0.002$), whereas no strong factor was found for generalists. Yet for specialists, the number of nodes, and the number of negative edges, and to a lesser extent spatial distance, were the main factors ($P<0.001$). When depicting the variability across spatial scales, we noticed different patterns within and over the mesoregional threshold. At the local scale, spatial distance, elevation, and biopores were the main drivers of overall bacterial communities ($P<0.001$). The number of strong and significant correlations was greater for specialists (11 factors) than for generalists (6 factors). Specialists were correlated with spatial distance, elevation, season, number of nodes, soil type, and average weighted degree ($P<0.001$). In comparison, generalists were most correlated with elevation, spatial distance, and biopores ($P<0.001$). At the regional scale, land use, the number of negative edges, and the number of nodes were the main factors correlated with bacterial communities ($P<0.001$). Land use and negative edges were also the major factors for generalists ($P<0.001$). Yet for specialists, the main constraining factors were number of nodes and negative edges, and to a lesser extent land use ($P<0.001$).

Discussion

Drivers of bacterial assembly patterns and processes across spatial scales

Linking microbial diversity patterns to the ecological processes governing assembly has been often implemented for local (Ferrenberg et al. 2013; Dini-Andreote et al. 2014; Jia et al. 2018; Tripathi et al. 2018) or regional and continental scales communities (Stegen et al. 2013; Ma et al. 2016, 2017; Luo et al. 2019), often not considering the effect of spatial distance between microbial communities. Moreover, just a few studies have quantified the jointing contribution of spatial distance, abiotic and biotic factors on microbial diversity distribution, and ecological processes (Martiny et al. 2011; Gao et al. 2019; Zhao et al. 2019; Ceola et al. 2021). To our knowledge, this is the first study underlying those patterns and processes for bacterial communities across spatial scales in Brazilian subtropical soils.

Our first hypothesis claimed that the patterns of microbial assembly would vary along with land use, and geographic distance between microbial communities, leading to microbial diversity loss due to forest-to-agriculture conversion. Although we did not find differences in alpha diversity and richness, both long-term forest to no-till and forest to pasture conversions led to changes in bacterial beta-diversity distances and consequent loss in pairwise beta diversities, which is indicative of biotic homogenization (Rodrigues et al. 2013; Maaß et al. 2014; Rocha et al. 2021). These results corroborate our previous study, in which we have evaluated, through metagenomics, the patterns of microbial alpha and beta diversities in two out of the six counties evaluated here (Goss-Souza et al. 2017). Other authors also have found the same soil microbial patterns for both subtropical (Ceola et al. 2021) and tropical soils (Rodrigues et al. 2013; Mendes et al. 2015b). When comparing seasons, we have found a loss in pairwise beta diversities from winter to summer in no-till and pasture, the same as found in our previous study (Goss-Souza et al. 2017). Moreover, our microbial co-occurrence networks have raised the hypothesis that land-use change has not only altered microbial composition and diversity but has also increased the complexity of the biotic interactions among taxa, just as found for other tropical and subtropical environments (Mendes et al. 2014; Goss-Souza et al. 2017; Felipe-Lucia et al. 2020). Together, our results emphasize that the long-term forest to agriculture conversion has led to a loss in microbial diversity, just as observed in previous studies in tropical (Rodrigues et al. 2013; Mendes et al. 2014, 2015b; Goss-Souza et al. 2019, 2020) and subtropical agroecosystems (Goss-Souza et al. 2017; Ceola et al. 2021).

We also found a spatial scale dependence on microbial beta diversity distributions, which was inflated at the local scale (< 97 km) and disappeared at the regional scale, suggesting that, according to Baas Becking proposal, bacterial communities are widespread across the regional limit, and filtered by

environmental factors at the local scale (De Wit and Bouvier 2006). Several microbial studies have highlighted the land-use change and soil physical and chemical characteristics (e.g., pH, soil fertility) as the main drivers of local diversity patterns (Brookes et al. 2010; Rodrigues et al. 2013; Lauber et al. 2013; Mueller et al. 2014). Although we observed a loss in bacterial diversity due to land-use change, markedly in summer and a scale dependence for all land uses and seasons, Mantel tests revealed that land use was only significant at the regional scale, as a secondary effect, explaining 16.6% of the variability. The main drivers at this spatial scale were the biotic factors, as represented the number of nodes and negative edges, within other weaker but significant biotic factors, corroborating Gao et al. (2019). At the local scale, we also found a loss of beta diversities after forest conversion for both no-till and pasture and local scales. As observed for overall bacterial communities, land use was not a significant factor modulating local microbial diversity, which goes against other findings for local bacterial communities (van der Gast et al. 2011; Hazard et al. 2013; Karimi et al. 2020; Mirza et al. 2020). The main drivers of local bacterial communities were spatial distance and elevation. A recent study evaluating the geographical distribution of arbuscular mycorrhizal fungal communities in a broad gradient of land-use intensification and spatial distance, have found significant distance-decays for all land uses evaluated (Ceola et al. 2021), but not directly correlated with the land-use change itself, as the main drivers of decays were soil type, total organic carbon, and clay contents, both considered as evolutionary historical contingencies (Fukami and Nakajima 2011). Although we cannot deny that this correlation seems to occur widely, we argue that the arbitrary assignment of soil samples to a determined land use could lead to confounding results. While considering land use as a factor, not a treatment (as we did here), we can observe how this single factor behaves when confronted with other measured or calculated environment characteristics that result from forest to agroecosystem conversion. Thus, we argue that land uses would not be arbitrarily set as treatments, as soil habitats have multiple facets, due to their geographic location, management intensity, soil type and origin, climate conditions, among others (Fierer and Jackson 2006; Delgado-Baquerizo et al. 2018). Together, those soil ecosystem characteristics culminate with different historical (Fukami and Nakajima 2011) and contemporary contingencies (Durrer et al. 2017; Wang et al. 2017; Karimi et al. 2020), leading to different microbial diversity outcomes (Ceola et al. 2021).

In our study, somehow surprisingly, the main filtering factor of bacterial diversities at the overall scale was the number of nodes, a biotic factor, as revealed by microbial networks and Mantel tests. The main local filters were spatial distance and elevation, the same as found in previous biogeographic studies (Fierer and Jackson 2006; Pellissier et al. 2014; Wang et al. 2017; Farrer et al. 2019), with a secondary effect of the season (Goss-Souza et al. 2017; Ma et al. 2017), biopores, an abiotic soil physical factors. The average weighted degree was the major biotic filter of bacterial communities at the local scale, corroborating the findings of a biogeographic study of bacterial communities in paddy soils at a continental scale (Gao et al. 2019). The authors also found coupled effect of geographic distance, abiotic and biotic factors, such as observed in our study.

Another explanation for the spatial correlations is dispersal limitation, as observed by the low immigration rates found in our study, particularly for forest and no-till microbial communities, corroborating our previous study (Goss-Souza et al. 2017). Evidence against the Baas Becking hypothesis comes from studies showing that dispersal of microbes is limited, meaning that "everything is not everywhere" at least at a contemporary pace (Nemergut et al. 2013). By comparing the spatial correlations of bacterial communities with the patterns found for Eukaryotes, including Fungi (Zhao et al. 2019; Ceola et al. 2021), they tend to be lower for Bacteria, but they are often significant, meaning that the higher the distance between pairs of microbial communities, the more contrasting they are (Horner-Devine et al. 2004; Martiny et al. 2006, 2011; Gao et al. 2019). Those results together have led us to partially reject our first hypothesis, since the land-use change, despite being significant, was not found as a ruling driver of microbial assembly patterns.

Our second hypothesis stated that the balance between neutral and niche-based assembly models would differ along land use, and spatial scales. Our T-RFLP data corroborated our previous metagenomics study (Goss-Souza et al. 2017), suggesting

that forest and no-till microbial communities have a niche-based assembly, related to deterministic processes, and are more likely to be governed by environmental filtering, through the ecological selection process (Stegen et al. 2013; Dini-Andreote et al. 2015). Conversely, pasture communities have presented a predominantly neutral assembly, regarding stochastic processes modulating microbial assembly patterns, indicating a pivotal role of the dispersal ecological process (Albright et al. 2019; Li et al. 2020). We have also found a positive correlation between dispersal rates and microbial communities fitting neutral assembly, with pasture samples presenting both higher values of dispersal rates and more samples fitting to the stochastic ZSM rank abundance model. These results have confirmed previous theoretical and experimental models suggesting that dispersal has a key role in microbial community assembly (Hubbell 2005; Martiny et al. 2011; Ferrenberg et al. 2013; Nemergut et al. 2013; Goss-Souza et al. 2020).

Therefore, we depicted the balance between neutral- and niche-based assembly models, according to spatial distance, through Z-scores. At the local scale, forest microbial communities presented assembly based on stochastic processes, but with a large interplay between neutral and niche-based assembly, markedly in the winter; no-till microbial communities were more segregated than expected by chance, regarding deterministic variable selection (Dini-Andreote et al. 2015; Gao et al. 2019; Xue et al. 2021); while pasture fitted stochastic processes (Goss-Souza et al. 2017). Regarding regional scale, only forest communities presented a reverse pattern, following a deterministic variable selection, corroborating (Goss-Souza et al. 2017).

Ecologically, the assembly of microbial communities is dependent on the trade-offs between local and regional microbial communities, which is dependent on the microbial survival at the local species pool and the colonization potential of microbial species in the regional pool (Pärtel et al. 2017; Bittleston et al. 2020). While spatial distance and dispersal acted on the composition of microbial communities, variable selection and drift altered the relative abundances. Our findings have demonstrated an interplay among stochastic and deterministic processes modulating assembly, at temporal and spatial scales, the same as found for other soil and synthetic microbial communities (Ferrenberg et al. 2013; Nemergut et al. 2013; Stegen et al. 2013; Dini-Andreote et al. 2015; Evans et al. 2017; Goss-Souza et al. 2017, 2020; König et al. 2019).

Biogeographic patterns and assembly processes differ between generalists and specialists

Ecologists have long-established the conceptual basis of niche occupancy and habitat specialization for several species of plants and animals (Reznick et al. 2002; Bohn et al. 2014). Several authors have raised the idea of examining microbial life-history strategies to comprehend the patterns and processes that modulate species distribution and trophic relationships in soils (van der Heyde et al. 2017; Powell and Rillig 2018). Here, we separated species as generalists and specialists, based on the frequency of occurrence and habitat specialization of each taxon into our 324 samples representing bacterial communities. Our third hypothesis affirmed that the processes governing microbial assembly would vary between habitat generalists and specialists. Our results have shown that forest microbial communities presented the highest proportion of specialists but the lowest values of betweenness centrality, while pasture communities have presented the opposite pattern. The betweenness centrality is defined as the number of times a node (i.e., taxa) acts as a bridge along the shortest path between two other nodes, which indicates the most important nodes that are interpreted as key taxa with a significant role in the community (Poudel et al. 2016; Mendes et al. 2018; Shi et al. 2020). These results have indicated that forest communities presented a higher number of keystones species that are responsible for regulating the structure and dynamics of the community network (van der Heijden and Hartmann 2016; Banerjee et al. 2019). On the other hand, pasturelands have presented few keystone taxa but with a higher betweenness centrality. Key taxa are associated with many others, and the removal of these nodes may have a significant impact on community structure (Steele et al. 2011). Thus, the lower number of specialists and keystone species in pasture suggest a less resilient and stress-tolerant community.

We depicted the bacterial community patterns across spatial scales, according to microbial life strategies (Barberán et al. 2012; Leff et al. 2015; Gao et al. 2019; Luo et al. 2019). The most prevalent taxa in our study were found to be habitat specialists. Our

CLAM tests coupled with Mantel tests have strongly supported a perspective of microbial distribution in which communities are dominated by endemic species and share very few common taxa between sites and along geographical gradients (Robeson et al. 2011). This local endemism is here supported by the major influence of dispersal limitation in microbial assembly patterns. Moreover, the endemic distribution is emphasized by the high significance of spatial distance at the local scale for overall communities, coupled with the interaction with biotic factors at the local scale for endemic taxa, just as found in another biogeographic study (Gao et al. 2019). Our mantel tests for endemic taxa have shown higher pairwise diversities at larger distances (Luo et al. 2019), directly contradicting the idea of "everything is everywhere". Linking these microbial endemic patterns with the prominent levels of endemism of animals and, especially plants in the Atlantic Forest biome and other global hotspots of biodiversity (Myers et al. 2000; Jantz et al. 2015) is paramount. It also raises the hypothesis that land use, as a contemporary paced human intervention, is not a pivotal shaper of microbial niche occupancy and habitat specialization (Ceola et al. 2021). Our results have shown that other historical contingencies (Fukami and Nakajima 2011; Ceola et al. 2021), as represented by soil type, and seasonal effect, intimately linked to soil formation, and evolutionary contingencies (Hanson et al. 2012; Wang et al. 2013), linked to dispersal limitation and taxa evolution, may be driving microbial niche breadth (Luo et al. 2019) and habitat specialization (Székely and Langenheder 2014), markedly on a local scale. Also, those historical and evolutionary contingencies could be shaping microbial co-occurrence patterns and interacting with biotic deterministic selection (i.e., variable selection) (Barberán et al. 2012; Dini-Andreote et al. 2015; Gao et al. 2019).

Soil type is defined by geological and climatic historical contingencies, which together with the activity of microorganisms, water, and time regulate rock weathering and soil formation (Huggett 1998; Egli et al. 2018). According to the World Reference Base for Soil Resources (Anjos et al. 2015), the soils from all sampling sites in the western mesoregion are classified as Red Ferralsols, which are evolved soils with the dominance of kaolinite and Fe oxides. Otherwise, soils from plateau mesoregion are more diverse. Soils from the counties of Lages and Campo Belo do Sul, were classified as Humic Yellow Nitisols, which are strongly structured soils, characterized by low-activity clay, P fixation, the prevalence of Fe oxides, and accumulation of organic matter in the surface. Meanwhile, soils from Otacílio Costa County were found to be Humic Cambisols, with little profile differentiation, moderately developed, with the accumulation of organic matter on the surface. We argue that soil type, a historical contingency (together with dispersal, an evolutionary contingency), could be locally filtering taxa distributions more strongly than the influence of land-use change, which is historically recent, as all the sites were converted from the forest into agroecosystems in the last decades (Bartz et al. 2014; Goss-Souza et al. 2017; Ceola et al. 2021).

Conclusions

This study represented a step forward to depict the biogeographic patterns of bacterial communities due to land-use change in a broader geographic scale, in the subtropical Atlantic Forest biome. We have shown that soil bacterial diversity and niche occupancy are shaped by spatial distance and long-term historical contingencies related to the soil origin (soil type and climate), which culminates with important coupled patterns of dispersal limitation and spatial correlations. We also demonstrated that—differently from the "everything is everywhere" niche postulation—stochastic processes, represented by the dispersal limitation act to outweigh the effect of the deterministic selection process caused by soil historical contingencies and the formation of small geographic islands, shaped by soil type and climate. Those patterns are inflated when evaluating microbial niche specialists, markedly at a local scale, with consequences for biotic interactions among members from local microbial communities.

Author contributions DG-S, SMT, OK-F, JPS, and DB, designed the project. DG-S, OK-F, and DB collected the soil samples. DG-S and LWM performed molecular biology analyses. DG-S, LWM, and JLMR analyzed the data. All authors wrote, commented, and accepted the definitive version of the manuscript.

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Data availability All data generated or analyzed in this study are included in the article and its supplementary information files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants and/or animals performed by any authors.

Consent to participate Not applicable.

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