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Polypore Communities and Their Substrate Characteristics in Atlantic Forest Fragments in Southeast Brazil

Atte Komonen[1], Miia Kokkonen[1], Lucimar S. Araujo[2], Panu Halme[1], and Cristiano Lopes-Andrade[3]

Abstract

Anthropogenic environmental changes have resulted in biodiversity crisis. Although tropical rainforests are one of the global biodiversity hotspots, their biodiversity is still poorly known. Especially fungi are poorly represented in national Red Lists and conservation plans, despite their important role in ecosystem functioning. We studied wood-inhabiting fungi (polypores) in four areas within two Atlantic rainforest fragments in Southeast Brazil. Our aim was to investigate fungal substrate characteristics and community composition. Deadwood amount ranged from 27 to 82 m^3/ha among the four study areas and altogether we recorded 53 polypore species. More species were observed in intermediate and late decay stages than in early decay stages, but other deadwood variables did not explain the occurrence of polypores. Similarity in polypore community composition within and among the areas was low. Dissimilarity originated mostly from species turnover from a transect and area to another, and no nestedness in species occurrence pattern was detected. Hence, the observed dissimilarity in community composition was probably a result of heterogeneity in forest composition and structure, instead of environmental gradients or substrate limitations. These results corroborate previous polypore studies from the Atlantic forest in that tropical polypores are specialists toward particular decay stages. To develop ecologically effective conservation program for tropical polypores, more studies are needed on their distribution and abundance globally.

Keywords

biodiversity, community ecology, deadwood, rainforest, tropical forest, wood-decaying fungi, wood-inhabiting fungi

Introduction

Habitat loss, fragmentation, and degradation are threatening species persistence and ecosystem integrity. The Atlantic rainforest in southeastern Brazil, Paraguay, and northeastern Argentina is one of the global biodiversity hotspots with a high degree of endemism (da Silva & Casteleti, 2003; Lindner, 2010; SOS Mata Atlântica, 2015). It is one of the most degraded hotspots in the world: Currently, only about 8% of the original extent are remaining, and the habitat loss is still ongoing due to agri- and silviculture, as well as livestock farming (Eisenlohr, de Oliveira-Filho, & Prado, 2015; Leal & de Gusmão Câmara, 2003; Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). Globally, most conservation activities have focused on charismatic organisms such as plants, mammals, and birds (Brooks, 2010; Walker, 1992). Fungi, on the other hand, have been largely neglected in global red-listing and conservation planning because of taxonomic ambiguities, cryptic lifestyles, and limited ecological knowledge (Heilmann-Clausen & Vesterholt, 2008; Lonsdale, Pautasso, & Holdenrieder, 2008). Conservation of fungi is important, as they may have significant impacts on ecosystem functioning (Heilmann-Clausen et al., 2015). In this article, we

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studied community and substrate characteristics of wood-inhabiting fungi in Brazilian Atlantic rainforest.

Wood-inhabiting polypore fungi, polypores, are mostly saprotrophic, as their hyphae grow in wood that is already dead or dying (Ryvarden & Melo, 2014). Being one of the few taxa that can decay coarse hard wood, polypores play a significant role in decomposition (Deacon, 2013; Gilbert, Gorospe, & Ryvarden, 2008). In tropical rainforests, where the effective nutrient cycle is crucial for ecosystem functioning, the role of polypores is particularly significant (Gibertoni, Nogueira-Melo, de Lira, Baltazar, & Santos, 2015; Gibertoni & Santos, 2007; Laurance et al., 2002). By decomposing cellulose and lignin, polypores circulate carbon, nitrogen, phosphorus, and other nutrients (Ryvarden & Melo, 2014). Over 600 polypore species in Hymenochaetaceae and Polyporaceae have been recorded in South American tropical forests (Maia et al., 2015). Most research on tropical polypores has focused on taxonomy and ecological knowledge is limited (Gibertoni et al., 2015; Lindblad, 2001; Lonsdale et al., 2008). This hinders the conservation of tropical polypores and their use as indicators of broader biological conservation values (Eisenlohr et al., 2015; Gibertoni et al., 2015).

All species tolerate a restricted range of environmental conditions and require certain resources (substrates). The extant evidence about polypore substrate requirements and environmental tolerances comes mostly from boreal and temperate forests (Junninen & Komonen, 2011; Markkanen & Halme, 2012; Norstedt, Bader, & Ericson, 2001; Nordén, Ryberg, Götmark, & Olausson, 2004), although there is an increasing number of studies from the tropics (Gibertoni et al., 2015; Gibertoni & Santos, 2007; Lindblad, 2001). For polypores, the most important substrate characteristics are tree species, tree size and decay stage. Strict host specificity appears to be rare among tropical wood decomposer fungi (Gilbert, Ferrer, & Carranza, 2002; Gibertoni et al., 2015; but see Gilbert et al., 2008; Gilbert & Sousa, 2002). Most species, however, do prefer certain types of deadwood, such as large and intermediately decayed logs (Lodge, 1997; Urcelay & Robledo, 2009; but see Gibertoni et al., 2015). Thus, the number of polypore species and especially the number of endangered polypore species is highest in natural-like forests with a large amount and a long temporal continuity of suitable substrates (Bader, Jansson, & Jonsson, 1995; Junninen & Komonen, 2011; Norstedt et al., 2001; Penttilä, Siitonen, & Kuusinen, 2004). Environmental conditions, such as light and humidity, are also important. They are influenced by structural characteristics such as tree species composition, canopy cover, tree density, and volume (Markkanen & Halme, 2012; Penttilä et al., 2004). It is known, for example, that certain polypore species prefer open-canopy conditions (Lodge & Cantrell, 1995).

Differences in species substrate preferences and environmental tolerances manifest themselves as variation in community composition among forests if forests differ in substrate quality and quantity as well as in environmental conditions. Generally, tropical forests have been acknowledged for high spatial variation in species composition. Such variation can be quantified as species turnover and nestedness (Anderson et al., 2011). Spatial turnover means that species are replaced with more or less random species in different areas. Nestedness in turn means that species are replaced more predictably such that the species poor community is a subset of the richer community. Turnover is increased by environmental filtering, species interactions, dispersal limitations, and historical differences between areas (Baselga, 2010; Oldén & Halme, 2016), whereas nestedness is a result of environmental gradients that create selective extinctions and colonizations (Ulrich, Almeida-Neto, & Gotelli, 2009). Disentangling these two may shed light on processes driving polypore communities and thus are important in practical conservation.

Our aim was to increase understanding of the polypore species composition and substrate characteristics in Brazilian Atlantic rainforest. We asked: (a) what is the community composition, (b) what type of substrates polypores occupy, (c) how similar are the polypore communities within and between areas (d) is there evidence of species turnover or nestedness, and (e) does deadwood diversity affect the diversity of polypore communities within and between areas? We hypothesized that large, intermediately decayed trunks are the most important resource for the polypores in the Atlantic forest. We also hypothesized that the number of polypore species increases with deadwood diversity. Finally, we hypothesized that community composition varies significantly within and between study areas.

Methods

Study Forests

Polypores were studied in two forest fragments: Mata do Paraíso (255 ha) and Mata do Seu Nico (26 ha) (between 20 °46′ and 20 °50′ S, and 42 °51′ and 42 °49′ W; altitude 690–870 m a.s.l.) in the city of Viçosa, state of Minas Gerais, Southeast Brazil (Figures 1 and 2). These fragments are connected to each other by narrow wooded corridors, the distance being less than 500 m. Together these fragments make up the largest forest area in Viçosa and surrounding cities and one of the most pristine Atlantic rainforest fragments in the state of Minas Gerais with about 300 tree species (Gastauer, Sobral, & Meira-Neto, 2015). Topography of the forests is typical for the region with steep hills and dried river valleys in between. Both surveyed fragments were protected

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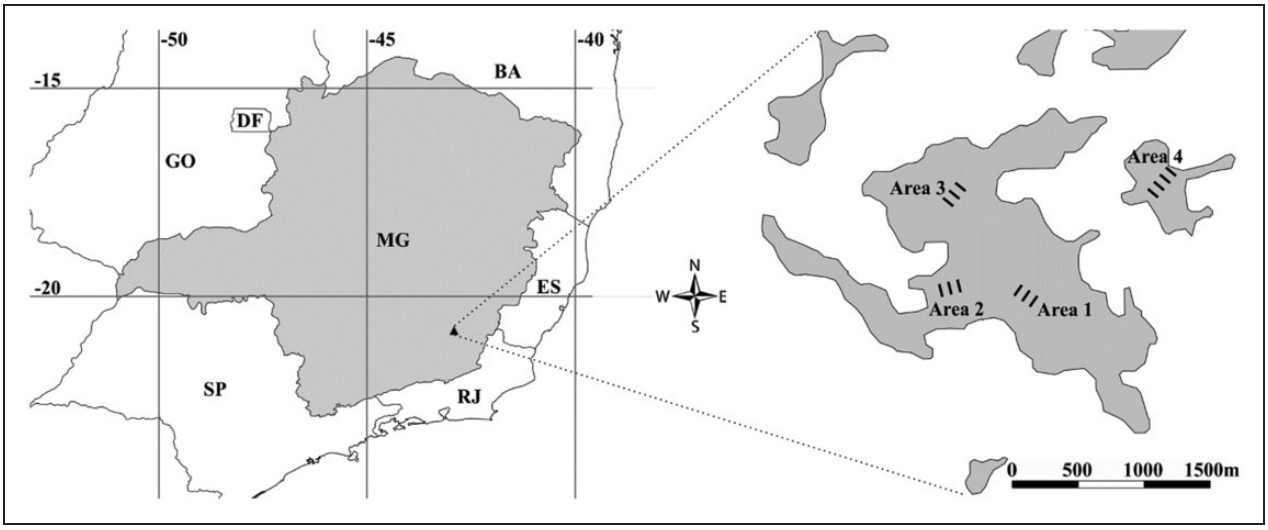


Figure 1. Left: Southeast Brazil; the state of Minas Gerais is indicated in gray and the city of Viçosa by a triangle. Right: outlines of the studied forest fragments and surveyed areas in Mata do Paraíso (Areas 1–3) and Mata do Seu Nico (Area 4). Transects are drawn to scale. The scale bar refers only to the right panel. The shapefile of Atlantic Forest fragments was provided by the SOS Mata Atlântica Foundation. Abbreviations of the states: BA = Bahia; DF = Distrito Federal; ES = Espírito Santo; GO = Goiás; MG = Minas Gerais; RJ = Rio de Janeiro; SP = São Paulo.



Figure 2. Mata do Paraiso is one of the most pristine Atlantic rainforest fragment in the state of Minas Gerais, with some 15% of pristine forest. Photo: Cristiano Lopes-Andrade.

50 years ago. They have restricted access only for educational and scientific purposes.

In the past, parts of Mata do Paraíso were coffee plantation and pasture (beginning of the 20th century) or *Pinus* plantation (50 years ago); thus, today a majority of trees are less than 50 years old, but there are pristine areas (ca. 15%) with large living trees and old fallen logs. In our study, Area 1 was situated in the old *Pinus* plantation area, but no coffee plants were observed. Area 2 was a secondary forest with a few large trees (>40 cm in diameter), whereas Area 3 was more natural with many large trees; neither *Pinus* nor coffee plants were observed in Areas 2 and 3. Mata do Seu Nico (Area 4) has never been cut, but some decades ago cattle grazing affected the understorey near to the reserve borders (Gastauer et al., 2015). There has been some

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wood extraction for household purposes in the past, but we did not see any signs of selective logging.

Survey Methods

We established four study areas, of which three were located in Mata do Paraíso and one in Mata do Seu Nico (Figure 1). The areas were chosen based on accessibility for field work but avoiding forest gaps and borders. In each area, we established three transects (100×20 m), but in Mata do Seu Nico, we established an additional transect because the first one reached a previously grazed young forest. Transects were always orthogonal to the pathways and parallel to each other (distance between transects was 50 m). Overall, the surveyed area was 2.6 ha.

To study substrate characteristics, we measured all deadwood (diameter breast height (DBH) > 10 cm and length > 100 cm) and identified all polypores based on their fruit bodies (Figure 3); only trees whose base lay inside transects were included. Measured trunk variables were wood type (lying on the ground, standing snag or leaning against other trees), DBH (cm), length (cm), decay stage (1–5, *sensu* Renvall, 1995), bark cover (%), and mean distance to the ground (cm). Bark cover was estimated visually with the accuracy of 10 percentage points. Distance to the ground was measured from the middle of the trunk. Data were collected in October 2015. Specimens that could not be identified in the field were taken to laboratory for further microscopic identification. Voucher samples of the collected fungi are deposited in the Natural History Museum of Central Finland.

Data Analysis

The volume (V) of the wood pieces was calculated using the equation of cut cone:

$$V = \frac{\pi h\left(r_1^2 + r_1 r_2 + r_2^2\right)}{3}$$

where h is the length of the piece, r_1 is DBH/2 and r_2 is radius at the height h (practically at the end of the piece). In measuring r_2, we applied the following equation for tropical trees (Chambers, Higuchi, Schimel, Ferreira, & Melack, 2000): $r_2 = d_h/2 = (1.59\ \mathrm{DBH}\ (h^{-0.091}))/2$, where d_h is the diameter at height h. The final equation was:

$$V = \frac{\pi h\left[\left(\frac{DBH}{2}\right)^2 + \left(\frac{DBH}{2} + \left(\frac{1.59DBH(h^{-0.091})}{2}\right)\right) + \left(\frac{1.59DBH(h^{-0.091})}{2}\right)^2\right]}{3}$$

To analyze what type of deadwood polypores occurred on, we used binary logistic regression; the data were pooled across all transects. The response variable was polypore occurrence, that is, the presence of at least one polypore specimen on a deadwood. All explanatory variables were entered in a single-step, categorical



Figure 3. *Phellinus* was the most species-rich genus with 12 species. *Phellinus anchietanus* (shown in figure) was recorded from six large logs. Photo: Cristiano Lopes-Andrade.

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variables as fixed factors (ordinal or nominal) and continuous variables as covariates. Explanatory trunk variables were wood type, decay stage, volume, bark cover, and distance to ground. Wood type and decay stage were marked as categorical variables with simple contrasts, where each category of the predictor variable is compared to the reference category. Significance of the full model and the individual explanatory variables were evaluated with the χ^2 statistic and the model fit with the Nagelkerke's pseudo R^2. Statistical analyses were conducted with SPSS IBM Statistics 24.

We analyzed the diversity of deadwood and polypore community within areas using Shannon's diversity index. It gives equal weight for common and rare species (Magurran, 2004).

$$\text{Shannon Index(H)} = -\sum_{i=1}^{s} p_i \ln p_i$$

where p_i is the proportion of individuals of a particular species (n) divided by the total number of individuals (N), and s is the number of species (or deadwood types). The relationship between the diversity of deadwood types and polypores (response variable) was analyzed using linear regression. Because the data were too scattered to run an ordination analysis, we only list the average substrate preferences for each polypore species.

To analyze variation in community composition in space (turnover and nestedness), we calculated beta diversity among transects within areas, as well as among areas (transects pooled for each area). We used the abundance-based Chao-Jaccard similarity estimator because it gives more reliable estimates in situations with high numbers of rare and undetected species (Chao, 2005). We also calculated the nestedness of the communities among the study areas using SDR simplex software and percentage relativized nestedness function (Podani & Schmera, 2011). Species accumulation curves were estimated (S_{est} statistic with resampling 100 times and without replacement of individuals) for each area separately. The nonoverlap of 95% confidence intervals (CIs) was used to infer statistical difference, which is a conservative criterion (Payton, Greenstone, & Schenker, 2004). The total species richness in the studied fragments was estimated using sample-based first- and second-order Jackknife richness estimators (Jack 1 and Jack 2, respectively). These analyses were done with EstimateS 9.0 (Colwell, 2013).

Results

Summary

Altogether, we measured 465 pieces of deadwood (mean $\pm$ $SD = 49 \pm 23\ m^3ha^{-1}$), of which 96% were deciduous. Seventy-three percent of the deadwood pieces were lying on the ground, 19% were snags, and 9% were leaning against other trees. The mean $\pm$ SD of DBH and decay stage was 17.94 ± 10.60 cm and 3.12 ± 1.43, respectively; in subsequent analyses, Decay Stages 1 and 2, and 4 and 5 were pooled. The amount of deadwood varied between the four areas (Table 1). Altogether, 53 polypore species and 159 species occurrences were recorded (Appendix A); 30 specimens remained unidentified due to poor condition. On average, there were 18 (12–24) species per study area and 1.15 species (0–3) per occupied trunk. *Datronia caperata* and *Phellinus gilvus* were the most frequent species, whereas other species were mostly singletons or doubletons (Appendix A). These two species were most often found on rather small (DBH = 15 cm and 18 cm, respectively) deadwood of intermediate decay stage (ca. 3). Seventy-eight percent of *D. caperata* and 83% of *P. gilvus* occurred on deadwood lying on the ground.

Substrate Characteristics

Polypore occurrence (presence of at least one polypore specimen on a deadwood) was affected by substrate characteristics (logistic regression: $\chi^2 = 15.42$, $df = 7$, $p = .031$, Nagelkerke $R^2 = 0.053$; $n = 388$ due to some missing data). More specifically, fewer deadwood pieces were occupied at Decay Stages 1 and 2 than at other decay stages (pairwise comparison, Wald $\chi^2 = 11.45$, $df = 2$, $p = .003$), the clearest difference being between Stages 1 to 2 and Stage 3 (Figure 4). Other trunk variables (wood type, volume, bark cover, and distance to the ground) did not explain the probability of polypore occurrence ($\chi^2 < 2.10$, $p > .15$, $df = 1$; for wood type $df = 2$). Thirty-eight percent of the dead wood pieces on the ground, 27% of the standing dead trees, and 28% of the trees leaning against other trees were occupied by polypores. Thirty-three percent of the dead wood pieces < 20 cm and 43% of the pieces $\geq$ 20 cm in DBH were occupied by polypores.

Effect of Deadwood Diversity

Shannon diversity index values for deadwood types and polypores ranged 2.1 to 2.6 and 1.8 to 2.8, respectively. Deadwood diversity explained 41% of the polypore species diversity within areas, although the relationship was not significant due to small sample size ($F = 1.39$, $n = 4$, $p = .36$, $R^2 = 0.41$).

Species Richness and Composition

Community turnover was high within the study areas (Chao-Jaccard similarity within areas 0.183–0.540, Figure 5). Turnover was high also between the study areas (Chao-Jaccard similarity 0.31), complemented

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Table 1. Total Number of Polypore Observations (Deadwood Pieces Occupied) and Species, as Well as the Mean Deadwood Volume (m^3ha^{-1}), Mean Number of Deadwood Pieces (ha^{-1}), and Mean Deadwood Diameter (cm) Within Each Study Transect and Area.

Area	Transect	Observations	Species	H species	Deadwood volume	Deadwood pieces	Diameter	H deadwood
1	1	23	14		42	230	17	
	2	14	9		147	165	23	
	3	8	7		58	140	20	
	Total/mean	45	24	2.76	82	178	20	2.57
2	4	11	7		24	170	16	
	5	14	9		58	310	16	
	6	13	10		46	165	19	
	Total/mean	38	19	2.56	43	215	17	2.10
3	7	18	7		30	255	16	
	8	23	5		21	160	15	
	9	10	8		29	205	16	
	Total/mean	51	14	1.81	27	207	15	2.11
4	10	6	3		26	125	20	
	11	6	6		19	110	18	
	12	9	8		87	140	22	
	13	4	3		52	150	20	
	Total/mean	25	15	2.49	46	131	20	2.27
All areas	Total/mean	159	53	2.41	49	179	18	2.26

Note. Shannon Diversity Index Values (H) are given for species and dead wood types.

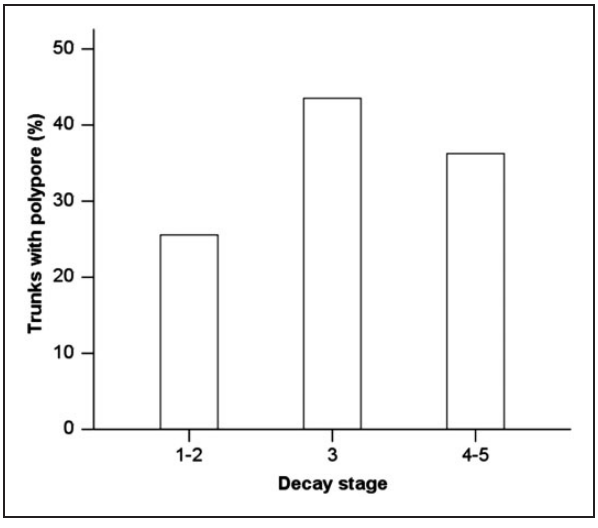


Figure 4. Polypore species' occurrence on trunks at the different decay stages. Decay Stage 1–2 = fresh deadwood, 3 = intermediately decayed, and 4–5 = late decay stages.

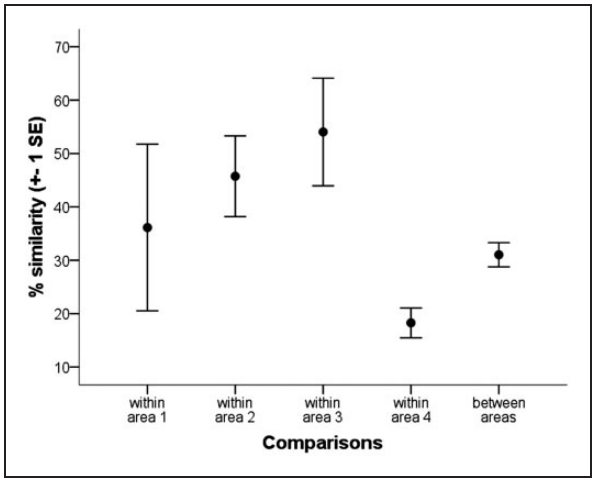


Figure 5. Abundance-based Chao-Jaccard similarities were calculated within each study area (among transects) and between all areas.

with low nestedness (average nestedness between the areas was 0.19). The species accumulation curves show that the asymptote was not reached (Figure 6), and the estimated overall species number varied from 85 (Jack 1) to 106 (Jack 2). Species richness (α diversity) varied between the areas (Figure 6), but these differences were not significant, as judged by the overlap of the 95% CIs. Because the overlap of the CIs in this context is a very conservative criterion for the lack of statistical significance and the overlap for Areas 1 and 4 was only 0.09 species, there was rather strong evidence for difference in species richness among some areas. The steeply increasing accumulation curves indicate a high community turnover (β diversity) within and among the areas.

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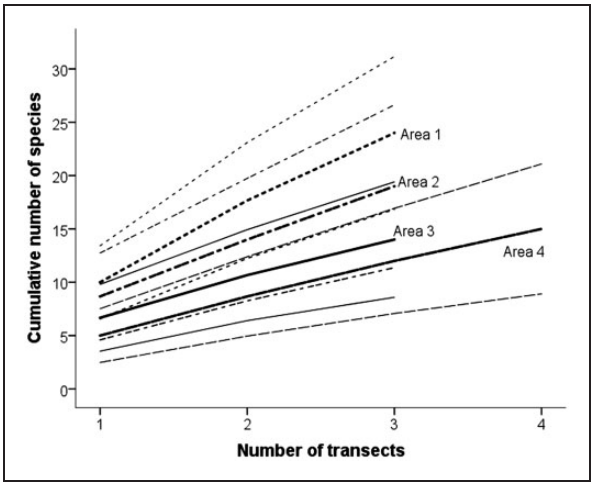


Figure 6. Species mean accumulation curves (thick lines) and their 95% confidence intervals for each study area.

Discussion

Substrate Characteristics

The polypore assemblage was associated with particular decay stage but not with other deadwood characteristics in Mata do Paraíso and Mata do Seu Nico. This corroborates the findings of the few extant studies in Brazilian Atlantic forests (Gibertoni et al., 2015; Gibertoni & Santos, 2007). However, we could not study the effect of tree species, which in boreal and temperate forest is one major factor affecting host affinity (Junninen & Komonen, 2011). The high local diversity of tree species in the studied Atlantic Forest fragments and the fast decay make tree species recognition challenging. Based on the previous research, polypores might be tree-species generalists among the wood-decaying fungi in tropical forests (Gibertoni et al., 2015; Lodge, 1997), but contrasting results exist (Gilbert et al., 2008; Lindblad, 2001; Urcelay & Robledo, 2009). Low specialization might be an adaption to very high host species diversity and consequently low population sizes (Gilbert et al., 2002; Lonsdale et al., 2008). Another possible explanation is the loss of host-specialized polypore species due to severe habitat fragmentation of the Atlantic rainforest in southeastern Brazil.

Polypores occurred more often on logs at intermediate or late decay stages compared to the early decay stage, as we hypothesized. This pattern of occurrence is also known from the boreal and temperate forests (Junninen & Komonen, 2011). Also other wood-inhabiting fungal taxa in Atlantic rainforests seem to occur on intermediately or more decayed substrates (Gibertoni & Santos, 2007). This result suggests, contrary to Gibertoni et al. (2015), that there are only few polypore species that are primary decayers on fresh deadwood. Indeed, it is possible that some other fungal taxa are more important primary decayers than polypores (Huhndorf, Lodge, Wang, & Stokland, 2004). Decay stages cannot easily be compared among studies because the decay stage measure is somewhat subjective and tree species specific; however, the general trend of highest species richness in intermediately decayed logs is clear in most studies in any forest ecosystem. It is also possible that polypores colonize the trees early on and only produce their fruit bodies at later decay stages (but see Berglund, Edman, & Ericson, 2005). The final caveat is that most polypore surveys are based on recording fruit bodies, which may overlook species present as mycelia (Junninen & Komonen, 2011). However, recent molecular-based mycelial surveys show the same trends as the basidiome surveys (Rajala, Peltoniemi, Hantula, Mäkipää, & Pennanen, 2011).

Deadwood size did not explain polypore occurrence, which was surprising given that the diameters of deadwood pieces ranged from 10 to 85 cm; our data, however, included rather few large diameter trunks. Considering the effect of wood size on polypore occurrence or diversity, we are not aware of any studies from lowland tropical areas, but in tropical mountain forests polypores usually occur on large logs (Lindblad, 2001; Urcelay & Robledo, 2009). In boreal and temperate forests, many rare and red-listed species tend to occupy larger logs (Abrego & Salcedo, 2013; Heilmann-Clausen & Christensen, 2005; Junninen & Komonen, 2011). More occurrences on larger logs would be biologically plausible, since there should be more resources, microsites, space, and stable moisture in large diameter deadwood (Bader et al., 1995; Halme, Vartija, Salmela, Penttinen, & Norros, 2013; Lindblad, 2001; Siitonen & Stokland, 2012).

Deadwood Diversity

Deadwood diversity (i.e., diversity of different wood types) did not significantly increase polypore species diversity, unlike we hypothesized (see Junninen & Komonen, 2011). For example, Nordén, Penttilä, Siitonen, Tomppo, and Ovaskainen (2013) found that the variation in polypore species richness in boreal spruce forests was best explained by the diversity of deadwood, especially the diversity of coarse woody debris. Similarly, in tropical rainforests, polypore species richness increases with the forest naturalness (Gibertoni et al., 2007; Gilbert et al., 2002; Huhndorf et al., 2004). The deadwood amount was within the range of documented deadwood volumes in natural tropical forests but smaller than in many natural temperate and boreal forests (Delaney, Brown, Lugo, Torres-Lezama, & Quintero, 1998; Grove, 2001; Harmon et al., 1986; Harmon, Whigham, Sexton, & Olmsted, 1995; Müller

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& Bütler, 2010; Siitonen, 2001). All four areas in this study were located in a relatively natural and similar Atlantic rainforest. Especially, the Area 4 (Mata do Seu Nico) is known to be very close to natural Atlantic forest in its structure and tree species composition (Gastauer et al., 2015). The very high deadwood volume in Transect 2 in Area 1 was mostly due to planted conifers. After excluding conifers, there was little variation in deadwood amounts among areas, which, together with a small sample size, most likely explain why no significant relationship was observed.

Species Richness and Composition

The number of observed polypore species was comparable to other tropical studies considering differences in sampling effort (Gibertoni et al., 2015; Gilbert et al., 2002). Surprisingly, the observed species number was similar or lower in comparison with many boreal and temperate studies, both per deadwood item and per unit of area (Abrego & Salcedo, 2013; Heilmann-Clausen & Christensen, 2005; Hottola & Siitonen, 2008; Komonen, Niemi, & Junninen, 2008; Penttilä et al., 2004; Sippola, Lehesvirta, & Renvall, 2001). The low polypore species richness in tropics seems to be a common as well as a puzzling phenomenon. For example, the total number of recorded polypore species in Brazil is only the double the number in Finland, despite Brazil has 28 times larger land area, over 400 times more tree species (see Hubbell et al., 2008), and a tropical climate. Only a small portion of this difference can be explained by sampling effort or taxonomic progress in the tropics. Furthermore, even though fragmentation of our study site and temporal discontinuity of dead wood might have contributed to low species richness, many boreal and temperate studies have been conducted in similar fragmented landscapes.

Community similarities were low both within and among study areas, as we hypothesized. The low similarities can result from landscape heterogeneity or dispersal limitations, separately or together (Abrego, García-Baquero, Halme, Ovaskainen, & Salcedo, 2014; Kivlin, Winston, Goulden, & Treseder, 2014; Lekberg, Koide, Rohr, Aldrich-Wolfe, & Morton, 2007). We assumed that the complex structure of the Atlantic rainforest and heterogeneous landscape would maintain varying environmental conditions and thus result in high beta diversity. Naturalness increases the number of (micro)habitats and makes the environment more heterogeneous, which should increase beta diversity (Abrego et al., 2014). The observed dissimilarity resulted from community turnover, not from nestedness, which indicates that environmental gradients, if such existed, were not very strong.

There are many possible reasons for the turnover beta diversity, such as environmental filtering, species interactions, dispersal limitations, and differences in the land use history (Baselga, 2010; Oldén & Halme, 2016). High beta diversity among the Atlantic rainforest fragments can be a distance effect (Gibertoni et al., 2015; Gibertoni & Santos, 2007). It is not clear, however, whether high beta diversity is due to the poor spore dispersal or to the differences in habitat quality. The latter would mean that the limiting factors are colonization and establishment, not dispersal *per se* (see Komonen & Müller, 2018). In this study, it was not possible to ascertain the factors that affected the beta diversity patterns within or among the areas. It is also possible that incomplete detection of the polypore community at the forest scale is one explanation for the observed high turnover (see Abrego, Halme, Purhonen, & Ovaskainen, 2016). Furthermore, at the time of the data collection, the dry season had been exceptionally long, which likely decreased the number of fruit bodies produced. Thus, the high dissimilarity may partly be a false impression.

Implications for Conservation

Decay stage of deadwood was the most important factor that affected polypore occurrences. To enhance polypore conservation, a long temporal continuity of deadwood is needed to maintain different decay stages in protected areas. To achieve deadwood continuity, we must allow natural disturbance dynamics or restore deadwood habitat. Although deadwood diversity did not explain polypore species richness among study areas, it is definitely one of the most essential features of forest naturalness, together with dead wood continuity, and thus deserves further scrutiny. Since the Atlantic rainforests are a highly deteriorated and heavily fragmented ecosystem, the protection of the remaining forest fragments is urgent.

Appendix A

Table A1. Recorded Polypore Species, the Total Number of Deadwood Pieces Occupied (*n*), and Average Substrate Preferences.

Species	*n*	DW type	Decay stage	DW ø (cm)	Bark cover (%)	Distance to ground (cm)
Antrodiella angulatoporia	2	Lying	4.5	51	15	0

(continued)

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Table A1. Continued

Species	*n*	DW type	Decay stage	DW ø (cm)	Bark cover (%)	Distance to ground (cm)
Antrodiella versicutis	1	Lying	3.0	23	50	0
Ceriporia viridans	1	Lying	5.0	16	40	0
Coriolopsis byrsina	1	Lying	3.0	10	80	0
Coriolopsis rigida	1	Lying	1.0	10	90	0
Cyclomyces tabacinus	2	Lying+snag	2.5	14	88	0
Daedalea aethalodes	3	Lying	4.0	17	57	47
Datronia caperata	35	All	3.6	15	64	34
Diplomitoporus navisporus	1	Leaning	2.0	25	40	400
Favolus tenuiculus	2	Lying	4.0	16	40	5
Flabellophora obovata	1	Lying	4.0	11	70	0
Fomes fasciatus	1	Lying	4.0	16	60	0
Gloeoporus dichrous	2	Lying	2.5	14	90	30
Gloeoporus thelephoroides	1	Lying	3.0	18	80	0
Grammothele lineata	2	Lying+leaning	3.0	22	35	45
Hydnopolyporus fimbriatus	1	Leaning	2.0	18	98	340
Hyphodontia cf. septocystidiata	3	Lying+snag	3.0	22	73	3
Hyphodontia cf. erikssonii	1	Lying	1.0	10	100	15
Hyphodontia cf. hallenbergii	1	Lying	5.0	16	80	0
Hyphodontia latitans	1	Lying	3.0	24	60	150
Junghuhnia carneola	1	Lying	3.0	24	30	40
Junghuhnia cf. semisupiniformis	1	Lying	2.0	12	95	0
Junghuhnia undigera	3	Lying+snag	3.7	39	63	60
Lentinus bertieri	4	Lying	3.8	24	28	0
Navisporus sulcatus	2	Lying	3.0	11	85	85
Nigroporus vinosus	1	Lying	5.0	22	0	0
Perenniporia tephropora	1	Lying	3.0	10	30	0
Phellinus anchietanus	6	Lying+snag	3.5	31	43	8
Phellinus cf. longisetulosus	1	Lying	3.0	18	15	50
Phellinus chryseus	1	Lying	5.0	12	20	0
Phellinus detonsus	1	Lying	4.0	11	70	20
Phellinus fastuosus	2	Lying	1.5	18	30	95
Phellinus gilvus	43	All	3.2	18	54	51
Phellinus grenadensis	5	All	2.2	19	82	76
Phellinus maxonii	1	Snag	1.0	10	20	130
Phellinus merrillii	1	Lying	5.0	22	10	0
Phellinus noxius	1	Lying	3.0	11	70	0
Phellinus shaferi	1	Snag	5.0	39	0	0
Phellinus umbrinellus	1	Lying	4.0	21	60	20
Polyporus SSTR sp. 1	1	Lying	1.0	12	100	0
Protomerulius caryae	1	Lying	3.0	25	90	30
Pycnoporus sanguineus	1	Lying	2.0	47	95	0
Rigidoporus undatus	1	Lying	3.0	70	90	0
Rigidoporus vinctus	1	Lying	5.0	85	10	0
Schizophyllum commune	2	Lying+snag	1.0	18	88	115
Schizopora flavipora	2	Lying	3.0	14	80	50
Schizopora paradoxa	2	Lying+snag	2.5	28	9	60

(continued)

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Table A1. Continued

Species	*n*	DW type	Decay stage	DW ø (cm)	Bark cover (%)	Distance to ground (cm)
Schizopora radula	2	Lying	3.0	18	40	20
Sidera lenis	2	Lying+snag	3.0	29	48	75
Trametes villosa	1	Lying	2.0	21	95	0
Trechispora regularis	1	Lying	4.0	13	0	0
Trechispora sp.1	1	Snag	2.0	70	95	150
Wrightoporia neotropica	1	Lying	5.0	23	20	0

Deadwood (DW) type: lying on the ground, standing snag, leaning against other trees or all of these. "sp." indicates species identified only to genus, "cf." indicates identification to the species group, that is, the samples resembled the species mentioned but were still somehow different.

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