



## Linking fungi, trees, and hole-using birds in a Neotropical tree-cavity network: Pathways of cavity production and implications for conservation

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### ABSTRACT

In tropical forests and savannahs worldwide, hundreds of species of cavity-nesting vertebrates depend, for nesting and roosting, on the limited resource of tree cavities. These cavities are produced by avian excavators and decay processes in trees infected with heart-rot fungi. Conservation of cavity-nesting communities requires a solid understanding of how cavities are produced and used; however, no studies have examined the interactions among cavity producers and consumers in tropical forest. Moreover, the role of heart-rot fungi in producing cavities for nesting vertebrates has not been studied at the community level anywhere in the world. We studied a “nest web”, or interspecific hierarchical network of cavity producers and users, in the Atlantic forest, a tropical biodiversity hotspot of high conservation concern, in South America. We searched for active nests in tree cavities from 2006 to 2010, and determined the species of trees, heart-rot fungi, and avian excavators that produced the cavities and the species of non-excavating birds (secondary cavity-nesters) that used them. We identified two main pathways that produced the cavities used by non-excavators. Thirty-three percent of passerine nests and 9% of non-passerine nests were in cavities produced by avian excavators; the majority of nests (83% overall) were in cavities produced directly by decay processes including mechanical damage, invertebrate damage, and fungal decay (non-excavated cavities). Trees bearing cavities produced by excavators were 2/3 the diameter of those bearing non-excavated cavities, had eight times the odds of being dead, and 37 times the odds of being colonized with heart-rot fungi in the family Polyporaceae s.l. (vs. Hymenochaetaceae that were dominant in trees bearing non-excavated cavities). In contrast to nest webs in North America, the Atlantic Forest nest web was characterized by high diversity and evenness of interactions, whereby non-excavating bird species did not depend on any one species of tree, fungus or avian excavator for cavity production. The community should thus be relatively robust to extinctions of cavity producing species. However, on-going destruction of large living trees with non-excavated cavities is likely to disrupt the major pathway of cavity production, and may result in a shift toward greater dependence on excavated cavities in smaller, dead trees, infected with Polyporaceae and occupied primarily by passerine birds. To conserve cavity-using communities in tropical forests, governments and certification agencies should implement policies that result in the retention of several large living trees per hectare.

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### 1. Introduction

Worldwide, over 1000 species of birds and mammals require tree cavities for reproduction and roosting. The majority of these species are non-excavators that depend on other organisms for the production of cavities, a critical resource that can limit their

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populations (Newton, 1998). By far the greatest diversity of these vertebrates is found in tropical rainforests, of which many areas are subject to ongoing habitat loss, degradation, and species impoverishment. Conservation of these communities may depend critically on understanding species interactions and highlighting key relationships between producers and users of the cavity resource (Cockle et al., 2011a; Cornelius et al., 2008).

Formation of tree cavities usually begins with parasitic heart-rot fungi, especially polypores (Basidiomycota). The activities of these fungi modify the chemical and physical properties of wood cells, softening the heartwood at the core of the tree (Robledo

and Urcelay, 2009). After fungal attack, a cavity may be produced relatively quickly when avian excavators penetrate the outer sapwood of the tree and remove the softened heartwood (excavated cavities; Conner and Locke, 1982; Jackson and Jackson, 2004), or more slowly when physical or insect damage to the sapwood exposes the softened heartwood to colonization by saprobe fungi and removal by insects, fire, wind, water, or vertebrates (non-excavated cavities; Gibbons and Lindenmayer, 2002).

The few bird species that excavate tree cavities can control cavity supply and thus directly affect the abundance and diversity of non-excavators, such that in some cases conservation of an entire cavity-nesting community can depend strongly on management for just one or two species of excavators (Daily et al., 1993; Martin and Eadie, 1999; Martin et al., 2004). The strongest avian excavators are woodpeckers (Picidae), which have morphological adaptations in their bills, skulls, tails, neck musculature, ribs and legs that allow them to chisel out cavities in hard tree substrates (Burt, 1930; Kirby, 1980; Spring, 1965). In well-studied communities in North America, one or two woodpecker species may produce up to 90% of cavities used by non-excavators, sometimes in just one or two species of trees, such that these woodpecker and tree species exercise disproportionate bottom-up effects on the rest of the community (Blanc and Walters, 2008; Martin et al., 2004). For example, a recent increase in production of cavities by downy woodpeckers (*Picoides pubescens*) was associated with increased abundance of red-breasted nuthatches (*Sitta canadensis*) at sites in British Columbia, Canada (Norris and Martin, 2010). Forest policies can effectively conserve these communities by insuring that logging operations maintain, in the landscape, the trees and excavators that produce cavities (Drever and Martin, 2010).

In the tropical and subtropical Americas, current forestry practices appear insufficient to maintain an adequate supply of tree cavities for non-excavators. Preliminary data suggest that non-excavators in South American forests rely primarily on non-excavated cavities produced directly by decay, rather than excavated cavities produced by woodpeckers, not because they avoid woodpecker cavities but because non-excavated cavities are more abundant (Cockle et al., 2011a,b; Cornelius et al., 2008). A greater reliance on non-excavated cavities may explain why two recent studies failed to demonstrate correlations in the abundance or richness of woodpeckers and non-excavators in the tropical Americas (Sandoval and Barrantes, 2009; Siqueira Pereira et al., 2009). Non-excavated cavities take longer to form, and conserving them in logged forests may be more challenging than conserving woodpeckers and their cavities. At two sites in northern Argentina, logged forest supported 2–9 times fewer tree cavities and 17 times fewer nests than primary or mature forest, suggesting that current management may be inadequate to maintain populations and communities of cavity-nesting birds (Cockle et al., 2010; Politi et al., 2010).

To improve management decisions for cavity-nesting birds in the tropical and subtropical Americas, there is a need to identify the species and processes responsible for cavity formation. Toward this objective, Brightsmith (2005) highlighted emergent *Dipteryx micrantha* trees as key providers of cavities for macaws in the Peruvian Amazon and Politi et al. (2009) showed that three tree species (*Calycophyllum multiflorum*, *Blepharocalyx gigantea*, and *Podocarpus parlatorei*) were important for cavity-nesting communities in montane forests in the Andes. Little else is known regarding the species and processes responsible for producing tree cavities in the tropical and subtropical Americas. Here, we identify key pathways of cavity production in the Atlantic forest of South America, one of the most diverse and threatened forests globally. We do so by constructing a nest web, an interspecific network that hierarchically links cavity producers (species of trees, heart-rot fungi, and avian excavators) and users (species of non-excavators). We discuss implications of

our results for the resilience of tropical forest communities to forest loss and degradation.

## 2. Methods

We studied cavity-nesting birds, nest trees and heart-rot fungi in the Atlantic forest of the Sierra Central, Misiones province, north-eastern Argentina. Although parts of the Atlantic forest, are located south of the Tropic of Capricorn, including all of Misiones, floristics and physiognomy unite these southern forests with the northern Atlantic forests and we therefore include them under the broader category of tropical moist forests (Negrelle, 2002; Oliveira-Filho and Fontes, 2000). The Atlantic forest is among the top five biodiversity hotspots in the world, characterized by high levels of endemism, habitat loss, and local extirpations of bird species, with very high numbers of globally threatened and near-threatened species (Myers et al., 2000; Ribeiro et al., 2009; Ribon et al., 2003; BirdLife International, 2011). Our study area was a mosaic landscape of primary and logged forest, parks, and small farms from San Pedro (26°38'S, 54°07'W) to Parque Provincial (PP) Cruce Caballero (26°31'S, 53°59'W) and Tobuna (26°27'S, 53°54'W), San Pedro department, and PP Caá Yari (26°52'S, 54°14'W), Guaraní department. The vegetation is classified as semi-deciduous Atlantic mixed forest with laurels (*Nectandra* and *Ocotea* spp.), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera, 1976). Elevation is 520–700 m asl and annual rainfall 1200–2400 mm distributed evenly throughout the year.

We monitored all cavity-nests found over five breeding seasons (August 2006–January 2007; August 2007–January 2008; September–December 2008; October–December 2009; October–December 2010). Each year, we searched for nests mostly from pre-existing trails, covering a total of approximately 60 ha. We stopped frequently to observe the behavior of adult birds and look for evidence of recent wear around cavity entrances, and occasionally asked farmers to show us nesting trees on their properties. If we saw an adult bird repeatedly visit the same tree, fly out of a tree suddenly, disappear from view for long periods, cling to a cavity entrance, perch near a cavity, enter a cavity or exit a cavity, we inspected the cavity using 1.5–5 cm diameter video cameras mounted on a 15 m telescoping pole or carried up the tree using single-rope climbing. When nests could not be accessed with a camera (i.e., 15 cavities that were above 15 m in trees lacking a sturdy fork), we observed the activities of adult birds from the ground. Cavities were considered active nests if they contained eggs and/or chicks, or if the behavior of adult birds indicated nesting (e.g., adult carrying food into cavity; female parrot leaving cavity to be fed by male and returning immediately to cavity). Roosting was inferred when a diurnal bird entered an empty cavity at dusk and did not emerge before dark, or an owl was found in an otherwise empty cavity during the day. Cavity formation process (by avian excavation or decay) was determined by observing excavating activity by birds or by the shape of the cavity entrance and interior. Cavities with round or oval entrances and regular interiors were considered excavated cavities, and those with irregular entrances and interiors were considered formed by decay (Cockle et al., 2011b).

We used a diameter tape to measure the diameter at breast height (DBH in cm) of all nest trees. Nest trees were identified to species with the assistance of López et al. (1987) and local experts. We collected samples of fruiting bodies of polypore fungi from inside the cavities, the same branch as the cavity, or the main stem (tree trunk) below the cavity in October 2009, April 2010, and September–December 2010 (Fig. 1). All samples of fruiting bodies were identified to species by GR and deposited in the Herbarium (CORD), Museo Botánico, Universidad Nacional de Córdoba, Argentina.



**Fig. 1.** (A) Green-barred Woodpecker (*Colaptes melanochloros*) excavates a nesting cavity above a fruiting body of *Fomes fasciatus* (Polyporaceae s.l.) and (B) Cockle studies a fruiting body of *Pyrofomes perlevis* (Polyporaceae s.l.) below a nest of Ferruginous Pygmy-Owl (*Glaucidium brasilianum*). Arrows indicate cavity entrances and dotted line indicates cavity location inside the tree. Photo credits: G. Robledo.

We constructed hierarchical nest webs (*sensu* Martin and Eadie, 1999) to characterize the partitioning of total interaction frequency among different species of plants (trees and palms), facilitators or cavity formation agents (fungi and avian excavators) and non-excavators. A nest web is a quantitative interspecific network in which species that create cavities are linked to species that use the cavities. Links in the network are lines connecting the species that interact with one another around the resource of nesting cavities. For any two species A and B, where A is a cavity producer and B is a cavity user, an interaction occurs when an individual of Species B uses a cavity produced by an individual of Species A. Interaction frequency is the number of times Species B was found using a cavity produced by Species A. Because birds were unmarked, we could not know whether re-use of a given cavity by a given species of non-excavator involved the same individual or a different individual. To avoid double-counting interactions among the same individuals (and thus inflating interaction frequency among their species) we elected to count only the first nesting attempt if the same bird species used the same cavity more than once. We calculated network dominance and evenness to characterize the diversity of interactions between plant species and bird species. Dominance was calculated as the total number of interactions between the two species that interacted most often, divided by the total number of interactions counted for all species (Berger and Parker, 1970; Sabatino et al., 2010). We calculated Hurlbert's PIE (Probability of Interspecific Encounter) as an index of evenness among different links:

$$\text{PIE} = \sum_{i=1}^S \left( \frac{N_i}{N} \right) \left( \frac{N - N_i}{N - 1} \right)$$

where  $S$  is the total number of links in the network,  $N$  is the total number of interactions in the network, and  $N_i$  is the interaction frequency for link  $i$ . Values of PIE near 0 indicate a single dominant link (nearly all interactions occur between one pair of species), and a value of 1 indicates equal partitioning of interaction frequencies

in the network (each pair of species interacts the same number of times as each other pair of species; Hurlbert, 1971; Sabatino et al., 2010).

All statistical analyses were performed using R version 2.12.1 (R Development Core Team, 2010). To determine the extent to which the nest web was divided by taxonomy of non-excavators, we used cavity origin (excavated vs. non-excavated) to predict whether the cavity would be used secondarily by a passerine (order Passeriformes) or a non-passerine (all other orders). To do so, we constructed a generalized linear mixed model with each non-excavator nest as a replicate, bird order (passerine vs. non-passerine) as the binary response variable, cavity origin as a categorical fixed effect, and cavity identity as a random effect (logistic regression). In logistic regression, the coefficients,  $b$ , are the natural logs of the odds ratios (Tabachnick and Fidell, 2001). Using cavity identity as a random effect allowed us to include several nests within the same cavity while avoiding pseudoreplication.

To determine the extent to which tree characteristics influenced cavity origin, we used an information theoretic approach (Burnham and Anderson, 2002) to compare logistic regression models that predicted cavity origin (excavated vs. non-excavated) as a function of tree health (live vs. dead), DBH, and/or substrate health (cavity in live vs. dead part of tree). We evaluated model performance using the ROCR package (Sing et al., 2005) to calculate the area under the curve of the receiver operating characteristic (AUC). AUC is a measure of binary classifier performance independent of cutoff values, whereby a value of 1 indicates perfect classifier performance, >0.8 good performance, and 0.5 performance similar to random. Models within a set were compared based on  $\Delta\text{AICc}$  (difference between the AICc of a given model and the lowest AICc model in the set) and Akaike weight (a measure of the support for a given model relative to the other models in the set; Burnham and Anderson, 2002). We used a  $z$ -test for each parameter estimate in the top model to determine whether its 95% confidence interval (CI) included zero (Tabachnick and Fidell, 2001).



3. Results

We found 132 nests and 5 roosts of 35 species of cavity-nesting birds in 100 tree cavities (Appendix A). Seventeen percent of the 98 nests and roosts of non-excavators were in cavities produced by woodpeckers, and 83% were in non-excavated cavities (Fig. 2). Non-excavators did not use any of the seven cavities produced by trogons (Trogonidae). Nesting cavities occurred in at least 27 species of trees and one palm, from 25 genera in 15 families (Appendix A). The most common cavity-bearing tree was grapia (*Apuleia leiocarpa*, Fabaceae) with 17 cavities (20% of trees that could be identified), followed by yellow laurel (*Nectandra lanceolata*, Lauraceae) with 9 cavities (10%). Of 108 interactions between nesting or roosting birds and trees of known species, the most common interactions were between grapia trees and Maroon-bellied Parakeets (*Pyrrhura frontalis*; 3 interactions), and between grapia trees and Black-tailed Tityras (*Tityra cayana*; 3 interactions). Network dominance was low (0.028) and evenness (Hurlbert's PIE) was high (0.997).

Both passerines and non-passerines relied primarily on non-excavated cavities (67% of passerine nests, 91% of non-passerine nests; Fig. 2). Passerine nests had six times the odds of non-passerine nests of occurring in excavated cavities (Generalized Linear Mixed Model:  $b_{\text{origin(excavated)}} = 1.80$ , SE = 0.59,  $z = 3.07$ ,  $p = 0.0021$ ,  $n = 98$  nests, odds ratio = 6.05).

Mode of cavity production (excavated or non-excavated), was best predicted by a model including cavity substrate (live or dead branch/stem) and tree health (live or dead tree; Table 1). Excavated cavities had 53 times the odds of non-excavated cavities of occurring in dead branches, and 8 times the odds of occurring in dead trees ( $b_{\text{substrate(dead)}} = 3.94$ , SE = 1.10,  $z = 3.59$ ,  $p = 0.0003$ , odds

Table 1

Seven Generalized Linear Models (logistic regression) predicting mode of cavity production (excavated vs. non-excavated) as a function of cavity substrate (dead vs. living branch/stem), tree health (dead vs. living tree), and DBH (diameter at breast height). Models are arranged according to fit, from highest to lowest weighted, with the top model in bold. LL, log-likelihood;  $k$ , number of parameters;  $n$ , number of nesting cavities; AICc, Akaike's Information Criterion corrected for small sample size;  $\Delta\text{AICc}$ , difference in AICc between this model and the minimum AICc model;  $w$ , Akaike weight; AUC, area under the curve of the receiver operating characteristic.

Predictor variables	LL	$k$	$n$	AICc	$\Delta\text{AICc}$	$w$	AUC
<b>Substrate, tree health</b>	<b>-28.98</b>	<b>3</b>	<b>99</b>	<b>66.21</b>	<b>0.00</b>	<b>0.67</b>	<b>0.93</b>
Substrate, tree health, DBH	-29.76	4	99	67.95	1.73	0.28	0.91
Substrate, DBH	-33.20	3	99	72.65	6.43	0.03	0.91
Substrate	-34.85	2	99	73.82	7.61	0.02	0.87
Tree health	-42.80	2	99	89.73	23.51	0.00	0.82
Tree health, DBH	-42.57	3	99	91.39	25.18	0.00	0.84
DBH	-62.39	2	99	128.92	62.70	0.00	0.69

ratio = 52.63;  $b_{\text{tree(dead)}} = 2.12$ , SE = 0.74,  $z = 2.86$ ,  $p = 0.004$ , odds ratio = 8.33). Although tree DBH was not included in the top model, excavated cavities were in smaller trees than non-excavated cavities (mean  $\pm$  SE DBH<sub>Excavated</sub> = 55.1  $\pm$  3.8 cm, DBH<sub>Non-excavated</sub> = 73.4  $\pm$  3.6 cm; Wilcoxon Rank Sum Test  $W = 738$ ,  $P = 0.0006$ ,  $n = 100$ ).

Thirty-four cavities had fruiting bodies of wood-decaying polypores that could be identified to genus, all producers of white rot. These included at least six species in two genera in the Hymenochaetaceae family and six species in five genera in the Polyporaceae s.l. (Fig. 3, Appendix A). Stems with fruiting bodies of Polyporaceae s.l. had 37 times the odds of those with

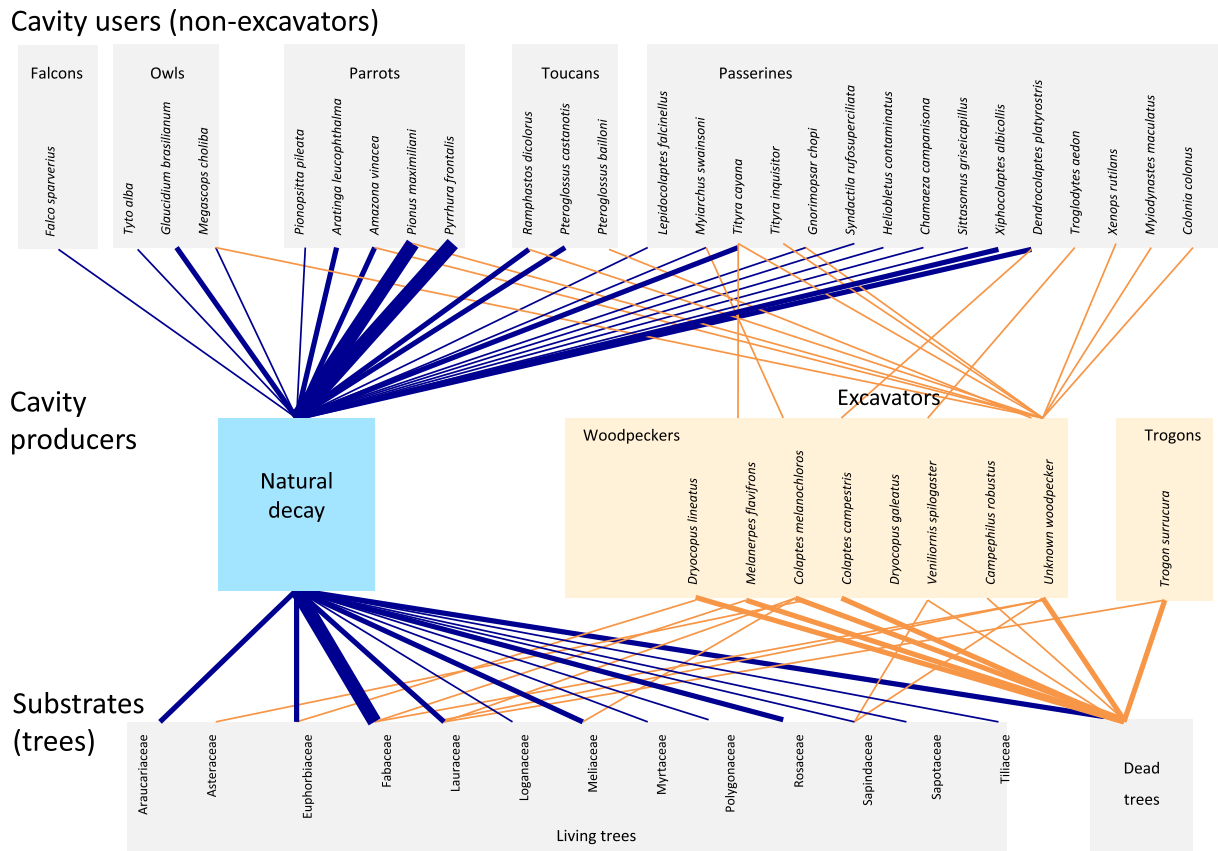


Fig. 2. Nest web showing links between trees, cavity producers (excavators, orange; or decay, blue) and cavity users (non-excavators) in the Atlantic forest of Argentina. Line thickness indicates interaction frequency (the number of times a particular interaction occurred: thin lines, 1–2; medium, 3–9; thick, 10–19). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Hymenochaetaceae of supporting an excavated cavity (as opposed to a non-excavated cavity;  $\chi^2$  test with Yates' continuity correction:  $\chi^2 = 12.17$ ,  $p = 0.0005$ ,  $n = 34$  cavities; odds ratio = 37.4; Fig. 3).

#### 4. Discussion

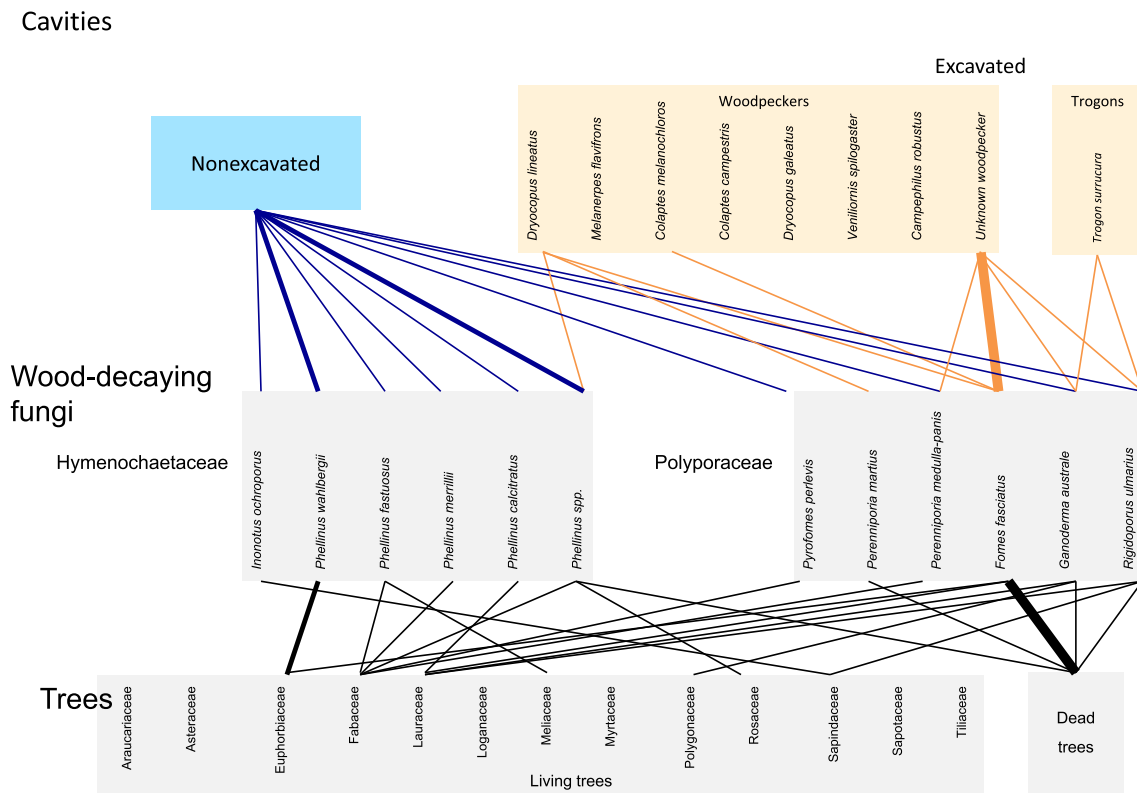
The nest web for birds, trees and polypore fungi in the Atlantic forest is characterized by high diversity and evenness of interactions. Many species of trees, fungi and woodpeckers each provide a small portion of the cavities used by the diverse assemblage of non-excavating birds. Thus, the nest web consists of many weak links between cavity producers and users. Excavators produce only a small proportion of cavities, used mostly by passerines, perhaps because most excavated cavities in the Atlantic forest would be too small for the larger non-passerines. Our results suggest a high level of functional equivalence among cavity substrates (tree species) and facilitators (species of avian excavators and fungi) in the Atlantic forest, in strong contrast to communities in North America where one or two key interactions between tree species and excavator species generate dominance indices an order of magnitude higher (Atlantic forest: 0.028; British Columbia temperate mixed forest: 0.24 calculated from Martin et al. (2004); Florida pine-hardwood forest: 0.43 calculated from Blanc and Walters (2008)).

Our study appears to be the first to examine the wood-decaying fungi associated with formation of tree cavities in tropical forests. Wood-decaying fungi could be divided clearly between excavated and non-excavated cavities along taxonomic lines, with the Hymenochaetaceae facilitating non-excavated cavities and the Polyporaceae s.l. excavated cavities. It is important to note that cavity-bearing trees without fruiting bodies almost certainly also had heart-rot fungi; these fungi may persist for many years without fruiting. Moreover, the presence and abundance of fruiting

bodies of any fungal species do not necessarily directly correlate to the biomass and activity of the vegetative mycelia. Nevertheless, presence of fruiting bodies is considered a reliable indicator of polypore species abundance in natural communities, and the fungi collected are known producers of heartrot (Niemelä et al., 1995; Urceley and Robledo, 2004). In North America, woodpeckers commonly excavate nests in trees infected with *Phellinus* species (Conner et al., 1976; Conner and Locke, 1982; Hart and Hart, 2001; Kilham, 1971; Losin et al., 2006; Parsons et al., 2003; Runde and Capen, 1987). In South America, *Phellinus* species are important parasites on living trees (Gilbert et al., 2002; Robledo et al., 2006); however, in contrast to North America, we found their fruiting bodies were nearly always associated with non-excavated cavities, not woodpecker cavities. In addition to heart-rot fungi, wood-boring insects such as termites and beetles may play an important role in cavity production, a role not yet studied in South America.

Interaction webs can be used to predict the effects of disturbance on communities, and our Atlantic forest nest web can help us understand and predict changes in community function with increased loss and degradation of tropical forests. Whereas cavity-nesting communities in North America may respond rapidly to changes in excavator and competitor abundance and behavior (Aitken and Martin, 2008; Martin et al., 2004; Norris and Martin, 2010), the weak links in the Atlantic forest web suggest that perturbations affecting populations of a single excavator are unlikely to generate strong repercussions for non-excavators. In contrast, a reduction in the abundance of large trees, often the oldest trees most likely to have advanced heart rot and non-excavated cavities, dramatically reduces nesting density of non-excavators (Cockle et al., 2010, 2011b).

In the Atlantic forest and other tropical forests in South America, the harvest of large old living trees continues at unsustainable



**Fig. 3.** Nest web showing links between trees, wood-decaying fungi, and cavity production by excavators (orange) or decay (blue). Line thickness indicates interaction frequency (the number of times a particular interaction occurred: thin lines, 1–2; medium, 3–4; thick, 5–6). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rates, but forest policies do not recognize the importance of these living trees for cavity-nesting vertebrates. In a recent resource-addition experiment, we showed evidence that the supply of tree cavities limits the nesting density of cavity-nesting birds in the Atlantic forest (in both primary and logged forest), suggesting that conservation of tree cavities should be a key management objective (Cockle et al., 2010). Some policies are starting to include guidelines to leave dead trees for woodpeckers to excavate, but woodpecker cavities in the Atlantic forest collapse or fall 12 times sooner than non-excavated cavities, lasting only 2 years on average and thus providing only an ephemeral resource for non-excavators (Cockle et al., 2011a). A key question is whether woodpeckers, with their ability to produce suitable but short-lived cavities in smaller and younger trees, can compensate for the loss of large old living trees and supply non-excavators with sufficient cavities for most species to persist. Under such circumstances, we suspect passerines might fare better than non-passerines, because non-passerines rarely used excavated cavities. To conserve cavity-using communities in tropical forests, governments and certification agencies should implement policies that result in the retention of several large living trees per hectare.

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## Appendix A

List of tree cavities studied in the Atlantic forest, Argentina, showing mode of cavity production (excavated or non-excavated), tree species, species of heart-rot fungus found on the tree, and species of excavator and non-excavator birds that used the cavity for nesting.

	Mode of cavity production	Tree health	Tree species	Tree family	Species of fungus	Excavator species	Secondary users (non-excavators and re-use by excavators)
1	Excavated	Dead	<i>Araucaria angustifolia</i>	Araucariaceae		<i>Campephilus robustus</i>	
2	Excavated	Dead	<i>Araucaria angustifolia</i>	Araucariaceae	<i>Ganoderma australe</i>		<i>Tityra cayana</i>
3	Excavated	Dead	<i>Araucaria angustifolia</i>	Araucariaceae	<i>Ganoderma australe</i>	<i>Trogon surrucura</i>	
4	Excavated	Dead	<i>Enterolobium contortisiliquum</i>	Fabaceae		<i>Colaptes melanochloros</i>	
5	Excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae		<i>Melanerpes flavifrons</i>	<i>Tityra cayana</i>
6	Excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae		<i>Colaptes melanochloros</i>	
7	Excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Fomes fasciatus</i>	<i>Melanerpes flavifrons</i>	
8	Excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Fomes fasciatus</i>	<i>Melanerpes flavifrons</i>	
9	Excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Fomes fasciatus</i>	<i>Colaptes melanochloros</i>	
10	Excavated	Dead	<i>Casearia silvestris</i>	Flacourtiaceae			<i>Xenops rutilans</i>
11	Excavated	Dead	<i>Nectandra lanceolata</i>	Lauraceae			<i>Amazona vinacea</i> , <i>Tityra inquisitor</i> , <i>Tityra cayana</i>
12	Excavated	Dead		Lauraceae	<i>Fomes fasciatus</i>	<i>Colaptes melanochloros</i>	
13	Excavated	Dead	<i>Nectandra lanceolata</i>	Lauraceae	<i>Rigidoporus ulmarius</i>		<i>Megascops choliba</i>
14	Excavated	Dead	<i>Nectandra lanceolata</i>	Lauraceae		<i>Trogon surrucura</i>	
15	Excavated	Dead		Lauraceae	<i>Rigidoporus ulmarius</i>	<i>Trogon surrucura</i>	
16	Excavated	Dead	<i>Cedrela fissilis</i>	Meliaceae		<i>Dryocopus lineatus</i>	

(continued on next page)

## Appendix A (continued)

	Mode of cavity production	Tree health	Tree species	Tree family	Species of fungus	Excavator species	Secondary users (non-excavators and re-use by excavators)
17	Excavated	Dead	<i>Melia azedarach</i>	Meliaceae			<i>Tityra inquisitor</i>
18	Excavated	Dead	<i>Syagrus romanzoffiana</i>	Palmae			<i>Pionus maximiliani</i> , <i>Pteroglossus bailloni</i>
19	Excavated	Dead	<i>Syagrus romanzoffiana</i>	Palmae		<i>Dryocopus lineatus</i>	
20	Excavated	Dead	<i>Syagrus romanzoffiana</i>	Palmae		<i>Colaptes melanochloros</i>	
21	Excavated	Dead				<i>Veniliornis spilogaster</i>	<i>Troglodytes aedon</i>
22	Excavated	Dead				<i>Colaptes campestris</i>	<i>Dendrocolaptes platyrostris</i>
23	Excavated	Dead				<i>Campephilus robustus</i>	
24	Excavated	Dead				<i>Colaptes campestris</i>	
25	Excavated	Dead				<i>Colaptes campestris</i>	
26	Excavated	Dead				<i>Colaptes melanochloros</i>	
27	Excavated	Dead			<i>Phellinus</i> sp.	<i>Dryocopus lineatus</i>	<i>Colaptes melanochloros</i>
28	Excavated	Dead			<i>Fomes fasciatus</i>	<i>Colaptes melanochloros</i>	
29	Excavated	Dead			<i>Fomes fasciatus</i>	<i>Trogon surrucura</i>	
30	Excavated	Dead			<i>Ganoderma australe</i>	<i>Trogon surrucura</i>	
31	Excavated	Dead			<i>Perenniporia martius</i>	<i>Dryocopus lineatus</i>	
32	Excavated	Living	<i>Gotchnactia polymorpha</i>	Asteraceae		<i>Colaptes melanochloros</i>	
33	Excavated	Living	<i>Alchornea triplinervia</i>	Euphorbiaceae	<i>Fomes fasciatus</i>	<i>Dryocopus lineatus</i>	
34	Excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Perenniporia medullapanis</i>		<i>Gnorimopsar chopi</i>
35	Excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae		<i>Melanerpes flavifrons</i>	
36	Excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae	<i>Fomes fasciatus</i>	<i>Colaptes melanochloros</i>	<i>Colaptes melanochloros</i>
37	Excavated	Living	<i>Ocotea puberula</i>	Lauraceae		<i>Trogon surrucura</i>	
38	Excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae			<i>Colonia colonus</i>
39	Excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae	<i>Rigidoporus ulmarius</i>	<i>Trogon surrucura</i>	
40	Excavated	Living	<i>Melia azedarach</i>	Meliaceae		<i>Colaptes melanochloros</i>	<i>Myiarchus swainsonii</i>
41	Excavated	Living	<i>Cedrela fissilis</i>	Meliaceae		<i>Colaptes melanochloros</i>	
42	Excavated	Living	<i>Matayba eleagnoides</i>	Sapindaceae	<i>Rigidoporus ulmarius</i>		<i>Myiodynastes maculatus</i>
43	Excavated	Living	<i>Diatenopteryx sorbifolia</i>	Sapindaceae		<i>Veniliornis spilogaster</i>	
44	Excavated	Living	<i>Chrysophyllum marginatum</i>	Sapotaceae			<i>Ramphastos dicolorus</i>
45	Non-excavated	Dead	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Tityra cayana</i>

## Appendix A (continued)

	Mode of cavity production	Tree health	Tree species	Tree family	Species of fungus	Excavator species	Secondary users (non-excavators and re-use by excavators)
46	Non-excavated	Dead					<i>Pyrrhura frontalis</i> , <i>Ramphastos dicolorus</i> , <i>Pionus maximiliani</i> , <i>Gnorimopsar chopi</i>
47	Non-excavated	Dead					<i>Falco sparverius</i>
48	Non-excavated	Living	<i>Araucaria angustifolia</i>	Araucariaceae			<i>Pyrrhura frontalis</i>
49	Non-excavated	Living	<i>Araucaria angustifolia</i>	Araucariaceae			<i>Amazona vinacea</i>
50	Non-excavated	Living	<i>Araucaria angustifolia</i>	Araucariaceae			<i>Aratinga leucophthalma</i>
51	Non-excavated	Living	<i>Alchornea triplinervia</i>	Euphorbiaceae			<i>Pyrrhura frontalis</i>
52	Non-excavated	Living	<i>Alchornea triplinervia</i>	Euphorbiaceae	<i>Phellinus wahlbergii</i>		<i>Pyrrhura frontalis</i> , <i>Xiphocolaptes albicollis</i>
53	Non-excavated	Living	<i>Alchornea triplinervia</i>	Euphorbiaceae	<i>Phellinus wahlbergii</i>		<i>Chamaeza campanisona</i>
54	Non-excavated	Living	<i>Alchornea triplinervia</i>	Euphorbiaceae	<i>Phellinus wahlbergii</i>		<i>Pionus maximiliani</i>
55	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Pteroglossus castanotis</i> , <i>Pyrrhura frontalis</i> , <i>Xiphocolaptes albicollis</i>
56	Non-excavated	Living	<i>Peltophorum dubium</i>	Fabaceae	<i>Phellinus</i> sp.		<i>Pionus maximiliani</i>
57	Non-excavated	Living	<i>Myrocarpus frondosus</i>	Fabaceae	<i>Pyrofomes perlevis</i>		<i>Pyrrhura frontalis</i> , <i>Xiphocolaptes albicollis</i> , <i>Glaucidium brasilianum</i>
58	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Phellinus merrilli</i>		<i>Pyrrhura frontalis</i>
59	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Pyrrhura frontalis</i> , <i>Pteroglossus castanotis</i>
60	Non-excavated	Living	<i>Ateleia glazioveana</i>	Fabaceae			<i>Pionopsitta pileata</i>
61	Non-excavated	Living	<i>Ateleia glazioveana</i>	Fabaceae			<i>Pyrrhura frontalis</i> , <i>Pionopsitta pileata</i> , <i>Pteroglossus castanotis</i>
62	Non-excavated	Living	<i>Parapiptadenia rigida</i>	Fabaceae			<i>Syndactyla rufosuperciliata</i>
63	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Amazona vinacea</i> , <i>Tityra cayana</i>
64	Non-excavated	Living	<i>Parapiptadenia rigida</i>	Fabaceae			<i>Amazona vinacea</i> , <i>Ramphastos dicolorus</i>
65	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae	<i>Perenniporia medulla-panis</i>		<i>Pionus maximiliani</i>
66	Non-excavated	Living	<i>Parapiptadenia rigida</i>	Fabaceae			<i>Pionus maximiliani</i> , <i>Dryocopus lineatus</i>
67	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Ramphastos dicolorus</i>
68	Non-excavated	Living	<i>Parapiptadenia rigida</i>	Fabaceae	<i>Phellinus fastuosus</i>		<i>Tityra cayana</i>
69	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Aratinga leucophthalma</i>
70	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Aratinga leucophthalma</i> , <i>Dryocopus galeatus</i> , <i>Xiphocolaptes albicollis</i>
71	Non-excavated	Living	<i>Apuleia leiocarpa</i>	Fabaceae			<i>Tityra cayana</i>
72	Non-excavated	Living	<i>Ateleia glazioveana</i>	Fabaceae			<i>Xiphocolaptes albicollis</i>
73	Non-excavated	Living	<i>Ocotea pulchella</i>	Lauraceae			<i>Pionus maximiliani</i>

(continued on next page)



## Appendix A (continued)

	Mode of cavity production	Tree health	Tree species	Tree family	Species of fungus	Excavator species	Secondary users (non-excavators and re-use by excavators)
74	Non-excavated	Living	<i>Ocotea pulchella</i>	Lauraceae			<i>Amazona vinacea</i> , <i>Ramphastos dicolorus</i>
75	Non-excavated	Living	<i>Ocotea diosperifolia</i>	Lauraceae			<i>Megascops choliba</i>
76	Non-excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae	<i>Ganoderma australe</i>		<i>Amazona vinacea</i>
77	Non-excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae	<i>Rigidoporus ulmarius</i>		<i>Sittasomus griseicapillus</i>
78	Non-excavated	Living	<i>Ocotea lancifolia</i>	Lauraceae	<i>Phellinus calcitratus</i>		<i>Pionus maximiliani</i> , <i>Ramphastos dicolorus</i>
79	Non-excavated	Living	<i>Nectandra lanceolata</i>	Lauraceae			<i>Syndactyla rufosuperciliata</i>
80	Non-excavated	Living	<i>Strichnos brasiliensis</i>	Loganeaceae			<i>Myiarchus swainsonii</i>
81	Non-excavated	Living	<i>Cedrela fissilis</i>	Meliaceae			<i>Pionus maximiliani</i> , <i>Aratinga leucophthalma</i> , <i>Ramphastos dicolorus</i>
82	Non-excavated	Living	<i>Cabrlea canjerana</i>	Meliaceae			<i>Pyrrhura frontalis</i>
83	Non-excavated	Living	<i>Cabrlea canjerana</i>	Meliaceae			<i>Aratinga leucophthalma</i> , <i>Glaucidium brasilianum</i>
84	Non-excavated	Living	<i>Melia azedarach</i>	Meliaceae			<i>Myiarchus swainsonii</i>
85	Non-excavated	Living	<i>Cedrela fissilis</i>	Meliaceae	<i>Phellinus fastuosus</i>		<i>Pionus maximiliani</i> , <i>Ramphastos dicolorus</i>
86	Non-excavated	Living	<i>Cabrlea canjerana</i>	Meliaceae			<i>Pyrrhura frontalis</i>
87	Non-excavated	Living	<i>Cedrela fissilis</i>	Meliaceae			<i>Lepidocolaptes falcinellus</i>
88	Non-excavated	Living	<i>Cabrlea canjerana</i>	Meliaceae			<i>Amazona vinacea</i>
89	Non-excavated	Living	<i>Myrciaria rivularis</i>	Myrtaceae			<i>Pyrrhura frontalis</i> , <i>Dendrocolaptes platyrostris</i> , <i>Xiphocolaptes albicollis</i>
90	Non-excavated	Living	<i>Ruprechtia laxiflora</i>	Polygonaceae	<i>Ganoderma australe</i>		<i>Tyto alba</i>
91	Non-excavated	Living	<i>Ruprechtia laxiflora</i>	Polygonaceae			<i>Amazona vinacea</i>
92	Non-excavated	Living	<i>Prunus myrtiflorus</i>	Rosaceae	<i>Phellinus</i> spp.		<i>Glaucidium brasilianum</i> , <i>Dendrocolaptes platyrostris</i>
93	Non-excavated	Living	<i>Prunus myrtiflorus</i>	Rosaceae			<i>Amazona vinacea</i>
94	Non-excavated	Living	<i>Prunus myrtiflorus</i>	Rosaceae			<i>Megascops choliba</i>
95	Non-excavated	Living	<i>Prunus myrtiflorus</i>	Rosaceae	<i>Phellinus</i> sp.		<i>Pyrrhura frontalis</i>
96	Non-excavated	Living	<i>Cupania vernalis</i>	Sapindaceae			<i>Pyrrhura frontalis</i> , <i>Dendrocolaptes platyrostris</i>
97	Non-excavated	Living	<i>Diatenopteryx sorbifolia</i>	Sapindaceae	<i>Inonotus ochroporus</i>		<i>Dendrocolaptes platyrostris</i>
98	Non-excavated	Living	<i>Chrysophyllum marginatum</i>	Sapotaceae			<i>Aratinga leucophthalma</i> , <i>Ramphastos dicolorus</i>
99	Non-excavated	Living	<i>Chrysophyllum marginatum</i>	Sapotaceae			<i>Pionus maximiliani</i>
100	Non-excavated	Living	<i>Luehea divaricata</i>	Tiliaceae			<i>Heliobletus contaminatus</i>

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