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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.

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 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

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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, northeastern 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 Yarí (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.