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Exploring nest webs in more detail to improve forest management

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ABSTRACT

The interactions between birds that use tree cavities for breeding, roosting and sheltering have been named 'nest webs'. We applied for the first time in nest-web studies some tools developed in network theory, in order to develop conservation and management recommendations of forest biodiversity. We recorded 109 interactions between 15 bird and 11 cavity-bearing tree species, in a subtropical piedmont forest (PF) of northwestern Argentina. Bird species in this nest-web included four woodpecker species, whose cavities were scarcely (9%) used by non-excavator birds, such as parrots, owls, and woodcreepers. Based on the Importance and Strength indices the most important tree species were *Calycophyllum multiflorum* (Rubiaceae) and *Anadenanthera colubrina* (Fabaceae). The nest web contained three main interaction modules: one composed by woodpeckers interacting with both living and standing dead trees; another by non-excavator birds using decay-formed cavities in living trees; and a third small module that had a few birds using woodpecker-excavated cavities in living trees. Important tree species were different for woodpecker and non-excavator modules. Extinction simulation of the most important tree species tripled the negative impact on cavity-using bird assemblage compared with the random extinction of tree species. In logging operations special consideration should be taken to ensure the maintenance of key tree species for the conservation of all the nest-web components in PF.

1. Introduction

Worldwide the loss of native forests due to agriculture, livestock, and timber plantations is one of the major threats for biodiversity (Hunter and Schmiegelow, 2011). However, with proper management remnant forests can represent a complement for biodiversity conservation (Lindenmayer and Franklin, 2002). To implement sustainable forest management, information about functional traits of forest ecosystem is required (Gardner, 2010). A conservation coarse grain multispecies approach (e.g., interaction network theory) can result more efficient than a fine grain individual species strategy (Hunter and Schmiegelow, 2011; Memmott et al., 2006; Soulé et al., 2003). Interaction network theory is an approach that reveals direct and indirect effects between species (Blanc and Walters, 2008a; Vander Zanden et al., 2006), determines their role in a community, and how it can vary over time (Cockle and Martin, 2015), and makes possible the exploration of management scenarios (e.g., simulated disturbances and species extinctions) (Lewinsohn et al., 2006).

Nest webs (*sensu* Martin and Eadie, 1999) study interactions among vertebrate cavity-users (mainly birds) and tree species bearing cavities. In these nest webs, woodpeckers excavate (i.e. excavators) and fungi decompose (i.e. decomposers) wood to create tree-cavities that remain available for one to two decades as breeding, roosting, sheltering, thermoregulation and foraging sites for many other species (i.e. secondary, non-excavator users) (Aitken and Martin, 2007; Cornelius et al., 2008). Many of the species involved in nest webs are of conservation concern, such as parrots and woodpeckers (IUCN, 2015; Jackson, 2006; Rivera et al., 2009). Others, such as toucans, are seed dispersers, whose ecosystem services are essential for many fleshy-fruited plants (Galetti et al., 2013; Howe and Miriti, 2004). Finally, insectivorous birds and owls that use cavities exert a strong control on insect and rodent populations that can be considered agricultural pests and associated to human diseases (Muñoz and Murúa, 1990; Perfecto et al., 2004; Tscharntke et al., 2008). Thus, conservation of tree species that harbor cavities may allow the continual delivery of ecosystem services provided by birds in nest webs. Despite this, bird-cavity-tree species relationships have been poorly studied with a network perspective compared with other plant–animal interactions, such as mutualism, predation, or herbivory.

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The few studies dealing with nest-webs have shown opposite patterns in the structure of the interaction networks. On the one hand, the bulk of interactions in communities from North American temperate forests were performed by only a few woodpecker and tree species (Blanc and Walters, 2008a; Martin et al., 2004). These "keystone species" (Hunter and Schmiegelow, 2011) were considered to be critical for the persistence of many secondary, non-excavator cavity-users, and so, for the stability of the whole network. On the other hand, interactions in a subtropical–tropical Atlantic Forest from Argentina were more evenly distributed between species (especially between cavity-users); secondary, non-excavator cavity-users, which comprised a much more diverse assemblage than excavators (27 vs. 9 species, respectively), largely depended on decay-formed cavities (Cockle et al., 2012). Thus, key species in this system seem to be mostly in the tree species side, especially involving a few species in which decay-formed cavities are often developed. Further comparisons are not possible given that application of network theory tools and determination of keystone species have been limited to graphical description of interspecific links. In other words, there is a great potential to apply analyses from the interaction network theory (Blanc and Walters, 2007; Blüthgen et al., 2008) into nest webs studies, which will provide a more detailed knowledge of the dynamic and structure of these interactions, thereby allowing for sustainable management of forests.

In this study we explore nest-web analysis in more detail in a bird assemblage that excavates and/or uses tree-cavities in Piedmont forests from northwestern Argentina (PF). Approximately 90% of the PF original area has been transformed to sugar-cane and soybean crops (Brown et al., 2006). PF remnants remain under different human uses and the most widespread human use is logging (Brown et al., 2009). Most logging operations in the PF are carried out illegally or with little information to attain sustainability (Politi et al., 2010). In the few cases when some sustainability criteria were set, they refer to ensuring the commercial wood stock (Grulke et al., 2013), which does not necessarily guarantee ecosystem integrity (Bunnell and Dunsworth, 2010). Indeed, logging has negatively affected several tree and bird species populations that are important for nest webs in PF (Politi, 2007; Politi et al., 2009, 2012, 2014; Rivera et al., 2012). Thus, it is urgent to delineate sustainable forest management guidelines for the PF.

The goal of this article is to show how analyses commonly used in network theory can provide information to improve forest management. To achieve this we: (1) describe the nest web structure that involves cavity-using bird species and tree species that harbor cavities in PF, and identify keystone tree species; (2) assess the existence of modules in the network, i.e., groups of species that interact between them more often than they do with species in other groups; and (3) explore alternative scenarios of random and deterministic tree species extinctions in the nest web. Since the structural complexity and diversity of tree species in PF are more alike to Atlantic forests than to North American temperate forests (mixed and deciduous coniferous forests), we expect that: (I) woodpecker species will not play a key role in providing cavities, given that most non-excavators will use decay-formed cavities; (II) PF avian species in the nest-web will be distinctly separated into modules of bird species that use decay-formed cavities and those that excavate cavities (i.e., woodpeckers); (III) simulation of key tree species extinction will lead to a greater disappearance of avian cavity-user assemblage, compared with random processes.

2. Methods

2.1. Study area

This study was carried out in the PF that constitute a distinctive phytogeographic unit of the Tropical Seasonal Forests of South America (Prado, 2000). The PF is located between the subtropical montane forests known as Southern Yungas to the west, and the dry Chaco forests to the east (Brown et al., 2001). The PF has an elevation gradient ranging from 400 to 900 m a.s.l., and has a highly seasonal climate with rains concentrated in the austral summer. Mean annual precipitation is 800–1000 mm, depending on the latitude (Brown et al., 2009), and the mean annual temperature is 21.1 °C (Arias and Bianchi, 1996).

PF have been severely disturbed in Argentina; around 90% of its original forest range has been transformed into agricultural, livestock pasture land, industrial, and urban areas (Brown et al., 2001, 2006). Major, well-conserved PF remnants in Argentina are located in Northern Jujuy and Salta provinces (Brown et al., 2009). Dominant tree species are *Calycophyllum multiflorum* and *Phyllostylon rhamnoides* (Brown et al., 2001). Other tree species such as *Handroanthus impetiginosus*, *Anadenanthera colubrina*, *Myroxylon peruiferum*, *Cordia trichotoma*, *C. americana,* and *Astronium urundeuva* that constitute a closed-canopy of 25–35 m (Brown et al., 2001). Also, PF host a high proportion of endemic (almost 30%) and deciduous (70–80%) tree species, as well as a great diversity of vines and epiphytes (Brown et al., 2001, 2009; Prado, 2000).

We conducted field work in two sites located in the Jujuy province, NW Argentina (23°56′02.3″S, 64°54′34.3″W; 23°45′23″S, 64°48′49.3″W). These sites have not been subject to human activities for at least 45 years, and have a tree species composition typical of PF. Thus, our results can be considered as a reference for forest restoration and/or conservation actions.

2.2. Field work

Field work took place in both sites from July to February, between the years 2005–2006, 2006–2007, and 2014–2015. At each site, a 100 ha plot was delimited, where we randomly established 20 variable length with no fixed width transects to maximized the area searched. We looked for tree cavities in a total of 6 km per site. Every cavity-tree encountered was marked, and cavities were inspected with a camera system attached to a 15 m extensible pole (Richardson et al., 1999), reaching cavities as high as 16.8 m. Less than 1% of all cavities detected were above this height (Politi, 2007). All reachable cavities were monthly inspected with the camera system during each period to determine use; i.e., those cavities with evidence of current (adults, eggs, chicks, etc.) or past (egg shells, feathers, or finished excavated cavities) use. For each used cavity the following characteristics were measured or assessed: tree species, tree diameter at breast height (DBH), tree height, cavity height from the ground, cavity location in the tree (i.e. main trunk, primary branch, secondary branch, and tertiary branch), tree condition (i.e. alive or standing dead trees) and cavity origin (i.e. excavated or decayed). An interaction between a tree species and a bird species was considered to occur when we found signals of breeding or roosting inside cavities (i.e., feathers, eggs, nestlings, parental food bouts). Excavated cavities were assigned to a woodpecker species according to the body size of the four woodpeckers present in the study area: excavated cavities with an entrance >10 cm in diameter to *Campephilus leucopogon*, the largest woodpecker (28 cm); excavated cavities with entrances of 5–10 cm in diameter to *Colaptes rubiginosus* and *Veniliornis frontalis* (medium-sized woodpeckers, 20 and 15 cm, respectively); and excavated cavities with entrances <5 cm in diameter to *Picumnus cirratus,* the smallest woodpecker (8–10 cm). Cavity entrance diameters of medium-sized woodpeckers overlap. Therefore, we assumed that their ecological requirements for cavity excavation would be similar, and thus, they were treated as only one species. Identification of non-excavator bird species was determined by visual observation of adults entering or leaving the cavity. We