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.

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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

did not record cases in which the same or different individuals of a given cavity-user species used the same cavity through the study period.

Scientific names of birds follow South American Classification Committee of the American Ornithologist Union (www.museum. lsu.edu/Remsen/SACCBaseline.html), and of trees follow Instituto de Botánica Darwinion (www.darwin.edu.ar/Proyectos/Flora Argentina/Especies.asp) recommendations.

2.3. Data analyses

Bird-tree cavities interactions were arranged in matrices with bird species in rows and tree species in columns. Standing dead trees of all species were grouped into a separate, single category. Interactions for which the cavity-user species could not be identified were pooled and treated as one cavity-user species for all the analyses. Cell values corresponded to the interaction frequency (i.e. number of active nests found) between bird and tree species. As previously stated, *C. rubiginosus* and *V. frontalis* were treated as one species and the number of their excavated cavities were pooled. These matrices were then used to draw the quantitative network with Pajek Software (Batagelj and Mrvar, 1998) and to estimate several parameters with 'Bipartite' package of R (R Development Core Team, 2012).

Determination of keystone tree species was based on the calculation of two indices: the Species Importance index, *I*, and the Species Strength index, *S*. The former is a qualitative index, meaning that it does not take into account the interaction frequency data, so each link between a given tree-bird species pair is considered 1 (species seen interacting) or 0 (no interaction recorded) (Murray, 2000). It weights the contribution of a tree species *j*, considering how many bird species use its cavities and how many other tree species with cavities are used by the same bird species. I_j index is given by the following equation:

$$I_j = \sum_{i=1}^{P} \left(\frac{C_{ij}/T_i}{P} \right)$$

where C_{ij} = 1 if the tree species *j* is used by the bird species *i*, otherwise it is 0; T_i is the total tree species with cavities used by the bird species *i*; and *P* is the total number of cavity-user bird species. *Ij* index ranges from 0 (a tree species whose cavities are not used at all) to 1 (when that tree species is the only one species with used cavities).

The second index S_j is a quantitative extension of the former index, and can be defined as the sum of dependences of all cavity-user bird species relying on the tree species *j* (Bascompte et al., 2006).

$$S_j = \sum_{i=1}^{E} d_{ij} \text{ and } d_{ij} = \frac{f_{ij}}{\sum_{m=1}^{J} f_{im}}$$

E indicates the bird species number that used cavities of the tree species *j*; d_{ij} is the dependence of the bird species *i* on the cavities of (or to excavate cavities in) the tree species *j*, and can be defined as the fraction of all the tree species with cavities used by that bird species *i*, going only to (or excavating) cavities of the tree species *j* (Bascompte et al., 2006; Vázquez et al., 2007); f_{ij} corresponds to the interaction frequency between the bird species *i* and the tree species *j*; *J* is the tree species number interacting with the bird species *i*. This index was divided by the number of cavity-user species so that it goes from 0 (i.e. a negligible role of a given tree species in providing substrate for cavity excavation or an usable cavity for bird species) to 1 (i.e. a high dependence of cavity-user bird species on the cavities supplied by a particular tree species).

We also report three network parameters: (I) the network connectance, which is the proportion of possible links between cavity user and tree species that actually occur; (II) the *H′* index, which is a measurement of how specialized is a network, ranging from 0 to 1 for extreme generalization and specialization, respectively (Blüthgen et al., 2006); and (III) the network evenness estimated through the Hurlbert's PIE (Probability of Interspecific Encounter) index, which calculates the probability that two randomly sampled individuals from the assemblage represent two different species. In a network context, it is the diversity of cavity-user-tree links that is estimated. Values closer to 1 indicate a high diversity of bird-tree links with a relatively homogeneous interaction frequency (i.e. a high network evenness), and values closer to 0 indicate the existence of one or few links with a relatively high interaction frequency (i.e. a low network evenness).

Modular structure of the nest web, and species composition of modules were assessed with the '*computeModules*' function of Bipartite package for R (R Development Core Team, 2012). This function applies the Quantitative Bipartite Modularity algorithm, which computes modules in weighted, bipartite networks, based on a hierarchical representation of species link weights and optimal allocation to modules. The higher is the modularity value (*Q*), the higher will be the support for a division of the network in the modules proposed (range = 0–1). Specifically, this function first builds a dendrogam joining species at random, which will likely have a very low *Q*. After that, the function starts to sequentially swap branches through a procedure known as Simulated Annealing, resulting in dendrogams with growing *Q*'s. The algorithm stops when after a predefined number of branch swaps (which we set in 1000000) a dendrogram with a higher *Q* is not found. For a more detailed description of this method, see Dormann and Strauss (2013).

We assessed the nest web modularity in two different forms, not exclusive but complementary: (I) the taxonomic approach considered the identity of tree species; and (II) the functional approach considered the tree condition (i.e. alive or dead), and the cavity origin (i.e. excavated or decay-formed). In both cases, the statistical significance of *Q* was determined by comparing it with the mean *Q* obtained from 100 simulated networks. This simulation was performed with the '*vaznull*' algorithm of the 'Bipartite' package of R (R Development Core Team, 2012), which generates networks with the same number of species, interactions and connectance as the observed network, but allows for variations in marginal totals (i.e. the interaction number that each species carried out). We considered that the observed *Q* was statistically significant when z_Q was higher than 2, where:

$$z_Q = \frac{Q_{\text{observed}} - \overline{\overline{Q}}_{\text{null}}}{\sigma_{Q_{\text{null}}}}$$

Simulations of tree species extinctions were performed with the '*secondextinct*' function of 'Bipartite' package of R (R Development Core Team, 2012). It sequentially eliminates a tree species (primary extinction) and assesses the effect of this disappearance on the bird assemblage. If a given bird species was only seen using cavities from the extinct tree species, it is assumed that this bird species also goes to extinct (secondary extinction) (see Memmott et al., 2004). This implies that cavity-user species remaining after the extinction of a tree species do not excavate or use cavities in alternative tree species. This method fit a hyperbolic curve to the extinction sequence, and calculates the area under the curve. This measurement, *R*, is known as the network robustness against species extinction (Burgos et al., 2007). *R* ranges from 0 (i.e. very weak system in which the curve decreases abruptly when just a few tree species are eliminated) to 1 (i.e. very robust system in which the curve decreases smoothly until all tree species are eliminated).

When the exponent of the fitted hyperbolic model is higher than 1, the curve has a gradual fall at the beginning (i.e. for the lowest values in the x-axis), but close to the end (i.e., the highest values in the x-axis) the species disappearance is accelerated. This situation reflects a very robust system in which most of the bird species survive even if a large fraction of the tree species is extirpated. On the other hand, when the exponent is lower than 1 the pattern is the opposite, this is, an abrupt die-off of species at the beginning and then the curve becomes progressively flatter. This scenario indicates a very weak system in which most of bird species go extinct even when a very small number of tree species is eliminated.

We conducted two simulations: in the first, the sequence of tree species extinction was at random; in the second, the sequence of tree species extinction followed an order given by a decreasing ranking of the S index (see above), i.e., the most important tree species were eliminated first.

3. Results

3.1. General characteristics of the nest web

We recorded 109 interactions between 15 bird and 11 cavity-tree species; 22 of these interactions were between decay-formed cavities and non-excavator cavity-users that could not be identified (Fig. 1). Identified non-excavators were three parrots, three owls, three woodcreepers, one falcon, and one tyrant fly-catcher species. Fifty-eight percent of the total number of interactions recorded was made by four woodpecker species: 20 excavated cavities by C. leucopogon (32% of total excavated cavities); 12 excavated cavities (19%) by medium-sized woodpeckers (i.e., C. rubiginosus and V. frontalis); and 31 excavated cavities (49%) by P. cirratus. Non-excavator cavity-user species barely used these excavated cavities; instead, 91% (N = 46 interactions) of

non-excavator interactions were made with decay-formed cavities (Fig. 1, Table 1).

The most used tree species was C. multiflorum (35% of total interactions) (Table 2). Cavities in standing dead trees accounted for 25% of the total interactions and were predominantly performed by woodpeckers (85%; N = 27 interactions in standing dead trees) (Table 2). Decay-formed cavities used by birds were mostly in the main trunk (74%, N = 42 cavities) of living trees (90%), at a mean height of 8.4 ± 3.5 m (N = 42 cavities; range = 1.9–16.8 m). Trees holding used decay-formed cavities had a mean height of 18 ± 4.9 m (N = 41 trees; range = 6.7–28.8 m), and a mean DBH of 48.2 ± 21.8 cm (N = 42 trees; range = 22.3–124.1 cm). The majority (62%; N = 63 cavities) of excavated cavities were in the main trunk of trees, 14% in primary, 18% in secondary, and 6% in tertiary branches. Mean height of excavated cavities was 11.4 ± 4.6 m (N = 62 cavities; range = 3–20 m), in trees with a mean height of 19.7 ± 6.9 m (N = 62 trees; range = 6.7–30 m), and a mean DBH of 51.1 ± 18.6 cm (N = 62 trees; range = 20.0–90.0 cm).

According to the Importance (I) and Strength (S) indices, the most significant cavity-tree species for the nest web were C. multiflorum (I = 0.286, S = 0.353), A. colubrina (I = 0.211, S = 0.193), and Cedrela balansae (I = 0.113, S = 0.106) (Table 2). Interactions recorded were distributed homogenously among species, and no links had a disproportionately high interaction frequency. The nest web connectance was 0.22, the H' index was 0.27, and the evenness was 0.96 (Table 1).

3.2. Modules

Nest web modularity was relatively low (Q = 0.33), but statistically significant (z_{Qnull} = 2.66; p = 0.004) when considering bird and tree species (taxonomic approach). Nest web was split into five modules, two of them included only one and two bird species and were supported by 1 and 2 interactions, respectively
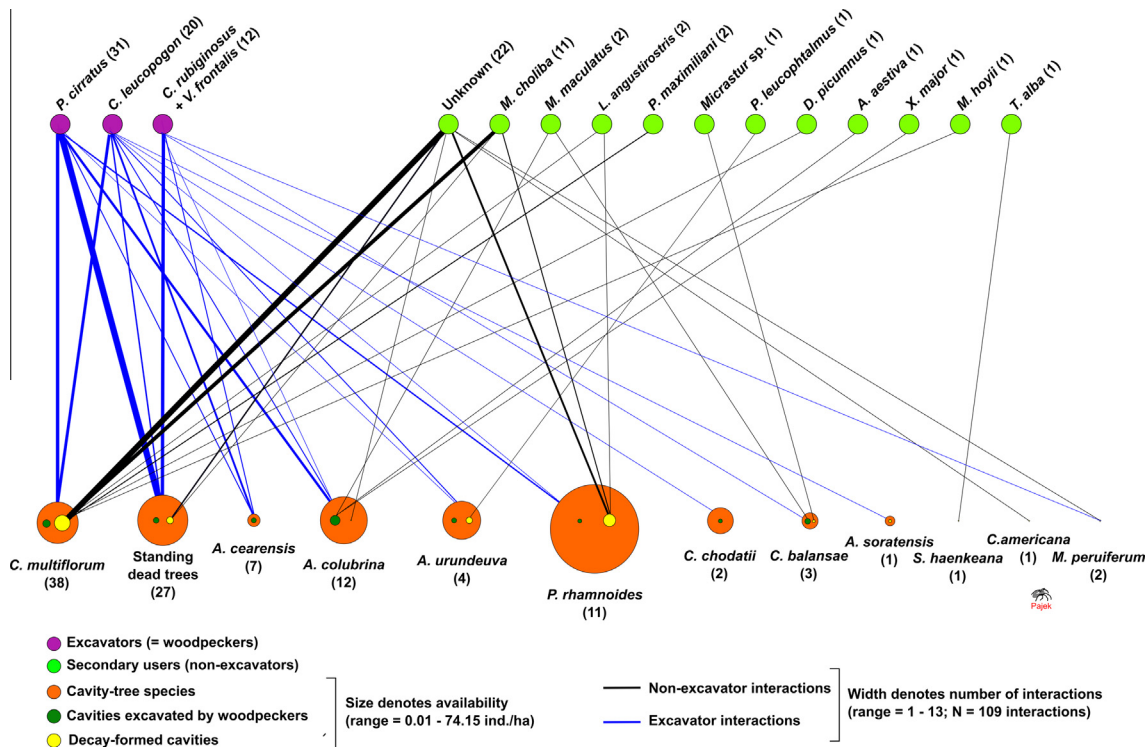
Fig. 1. Nest-web of birds and cavity-trees in well-conserved piedmont forests of northwestern Argentina. Medium-sized woodpeckers (i.e. Colaptes rubiginosus and Veniliornis frontalis) are treated as a unique species (see Methods). "Unknown" refers to all the unidentified non-excavator cavity-user species, whose interactions were grouped. Number of interactions performed by each species is in brackets after the names.

Table 1
Nest web characteristics observed in four studies carried out in South and North American forests.

Parameters	Piedmont Forest (this study)	Atlantic Forest Cockle et al. (2012)	Longleaf pine forest Blanc and Walters (2008a)	Mixed coniferous/deciduous forest Martin et al. (2004)
Number of tree species used	12	28	2	5
Number of bird cavity-user species (+ other vertebrate users)	15	35	13	20 (+6 mammals)
Number of excavator species – i.e., Woodpecker (+ other excavators)	4	8 (+1 trogon)	7 (+2 passerines)	7 (+2 passerines)
Number of interactions recorded	109	137	733	1692
Percentage of interactions with cavities in standing dead trees	24.8	21.2	70.8	45
Percentage of woodpecker (+ other excavator) interactions in the nest-web	57.8	23.4 (+5.1 of *Trogon surrucura*)	73.7 (+1.4 of passerines)	31.2 (+11.9 of passerines)
Percentage of non-excavator interactions with excavated cavities	8.7	17	99.1	92.6
Dominance	0.119	0.028	0.370	0.155
Evenness PIE	0.971	0.997		

(Fig. 2A). Two other modules included woodpeckers, separating large- from medium- and small-sized woodpeckers. These modules also included one and two non-excavator bird species, respectively, that used excavated cavities. Finally, another module had five non-excavator bird species (plus unknown species). Non-excavators in this module intensively used cavities of *C. multiflorum* (25 out of 34 interactions recorded for the four tree species in this module). Cavities in *A. colubrina* and standing dead trees were important for the small- and medium-sized woodpecker module. Large-sized woodpeckers used a wide range of tree species (Fig. 2A).

In the functional approach of modularity (i.e., considering if tree individuals were alive or dead, and if cavities were excavated or decay-formed) the nest web was divided into three modules ($Q = 0.52$; $z_{Qnull} = 2.29$; $p = 0.01$). One module was composed of woodpeckers, which used excavated cavities in living and dead trees. Another module was composed by non-excavator birds that used decay-formed cavities primarily in living trees, and in a lesser extent in standing dead trees (38 vs. 4 interactions, respectively). The third module included three non-excavator bird species using excavated cavities in living trees (Fig. 2B). Excavated cavities used by non-excavators were made by *C. leucopogon* (three interactions) and by a medium-sized woodpecker (one interaction).

3.3. Nest web robustness against random and deterministic tree species extinctions

Nest-web was more robust when tree species were randomly extinct ($R = 0.65$) than when the most important tree species were first removed ($R = 0.39$) (Fig. 3). Random extinctions of cavity-bearing tree species caused a gradual (exponent = 1.83) disappearance of cavity-users, until approximately 80% of tree species were eliminated; then, the cavity-user species extinction was accelerated (red points and curve in Fig. 3). Randomly removing three tree species (i.e. 25% of tree species used) triggered the extinction of two bird species (i.e. 15% of cavity-user species) (red dotted line in Fig. 3). Deterministic extinction simulation of the three most important tree species (i.e., *C. multiflorum*, *A. colubrina*, and *C. balansae*; Table 2) resulted in a rapid (exponent = 0.62) extinction of seven bird species (i.e. 47% of cavity-user species) (blue dotted line in Fig. 3).

4. Discussion

Our results show that in the PF avian cavity users interact with cavity-bearing tree species in distinct modules, and that some tree species are key in the nest-web since they harbor a high proportion of interactions with avian cavity-users. Modular structure and

knowledge of key tree species can be critical for the outlining of sustainable forest management guidelines aimed at the conservation of all the components interacting in nest-webs. Information on modular structure will ensure that such guidelines will impact on the whole nest-web, whereas a proper management of key tree species can prevent cascading effects on the persistence of most avian cavity-user species.

According to the functional approach of modularity, forest management in PF should consider two modules: woodpeckers that rely in living and dead standing trees, and non-excavator species that use decay-formed cavities mainly in alive trees. Conservation strategies directed towards the woodpecker module would have an indirect positive impact on the module conformed by the few non-excavator species that rely on excavated cavities in alive trees. These strategies are quite different to what has been suggested for North American forests where conservation efforts should be focused to the requirements of a few woodpecker species, which would strongly and positively impact on a large number of non-excavator bird species (Blanc and Walters, 2008b; Martin et al., 2004). Furthermore, the maintenance of standing dead trees in a wide range of North American forests has been suggested to be crucial for the persistence of the bulk of the cavity-nester community, given that they constitute a heavily used resource (references in Table 1; see also Raphael and White, 1984). However, in South American forests, focusing conservation and management actions

Table 2
Number of interactions, Importance (*I*) and Strength (*S*) indices of trees whose cavities were used by bird species in piedmont forests of northwestern Argentina.

Family	Species	Number of interactions	*I*	*S*
FABACEAE	*Amburana cearensis*	7	0.033	0.025
FABACEAE	*Anadenanthera colubrina*	12	0.211	0.193
FABACEAE	*Myroxylon peruiferum*	2	0.024	0.009
ULMACEAE	*Phyllostilon rhamnoides*	11	0.086	0.067
ANACARDIACEAE	*Astronium urundeuva*	4	0.086	0.075
ANACARDIACEAE	*Schinopsis haenkeana*	1	0.067	0.067
MELIACEAE	*Cedrela balansae*	3	0.113	0.106
BOMBACACEAE	*Ceiba chodatii*	2	0.008	0.007
RUBIACEAE	*Calycophyllum multiflorum*	38	0.286	0.353
BORAGINACEAE	*Cordia americana*	1	0.011	0.003
ARALIACEAE	*Aralia soratensis*	1	0.008	0.003
	Standing dead trees	28	0.066	0.092

Fig. 2. Modularity (Q) of the bird-tree cavity nest web, in a piedmont forest of northwestern Argentina. Modules are groups of bird species and tree species (A; taxonomic approach) or tree condition (B; functional approach), that interact more frequently between them than with species/conditions in other groups. Cell colour denotes the interaction frequency recorded between a given bird species with a cavity of, or excavating a cavity in, a given tree species. The darker it is the blue, the higher the interaction frequency recorded. White cells indicate no interactions between a bird-tree species pair. 'Medium-sized woodpeckers' includes *Colaptes rubiginosus* and *Veniliornis frontalis* data. "Unknown" refers to all the non-excavator cavity-user species that could not be identified, whose interactions were grouped. Number of interactions performed by each species is in brackets after the names. Superscript *a* = brand new, unused cavity recently excavated by a woodpecker; *e* = cavity used and excavated by a woodpecker; *d* = decay-formed cavity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 3. Simulation of tree species extinctions in a bird-tree cavity nest-web in piedmont forests from northwestern Argentina. When a tree species is eliminated (= primary extinction), cascading extinctions (= secondary extinctions) of bird species that interacted only with the extinct tree species occur. In red, random tree species extinction; in blue, tree species extinction follows the strength index (from highest to lowest values; see Table 2). Dotted lines indicate the proportion of cavity-user bird species remaining alive after the extinction of three tree species (25% of all cavity-bearing tree species used). Exp.: exponent of the hyperbolic function with which is fitted the curve to the simulated extinctions; *R*: nest-web robustness against tree species extinctions given by the area below the curve. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

on standing dead trees would have a comparatively smaller, positive impact restricted almost exclusively to the woodpecker module (Cockle et al., 2011b, 2012; Pereira et al., 2009; this study; see also Remm et al., 2006). Therefore, in South American forests it is probably necessary to address conservation efforts on certain alive tree species, as much or even more than on standing dead trees. It is worth to note that target tree species will differ according to the module intended to conserve. Undoubtedly, a greater sampling effort is required to verify if weakly supported modules are held or if they are co-opted onto the more strongly supported modules.

In the area in which this study was carried out, cavity conservation is not a trivial issue. Twenty-one obligated cavity nester bird species are frequently recorded in the PF (Politi et al., 2012). Moreover, Politi et al. (2010) determined that only 4% of all the trees harbored cavities in PF, and only 1% contained potentially usable cavities by birds (Politi et al., 2010). Additionally, cavity density significantly decreased in logged forests, which was not simply explained by a lower density of standing trees (Politi et al., 2010). Logged trees held a higher proportion of potentially usable cavities. In fact, the three more important tree species for cavity-using birds (i.e. *C. multiflorum*, *A. colubrina* and *Cedrela balansae*; Table 2) are among the most commercially valuable tree species (Balducci et al., 2012). Unsustainable logging of key tree species can have a pervasive effect on the nest-web, as was reflected in the deterministic extinction of tree species (blue points and curve in Fig. 3), with a negative impact on the cavity-using bird assemblage three times stronger than that seen when tree species extinctions were at random. In this sense, the remarkably high proportion of cavities harbored on *C. multiflorum* individuals, in relation with the abundance of this species (Fig. 1), makes it a conservation priority species in which management strategies should be focused on. The assumption made in this analysis -i.e., that cavity-users are not able to shift to other tree species to excavate or use cavities after the used tree species was extirpated-, may

be an overestimation of the negative impact of tree species extinction on the nest-web. Our ongoing research in PF sites with selective logging will hopefully provide in the future the answer if this assumption is realistic or if, alternatively, avian cavity-user assemblage in logged sites use a spectrum of cavity-bearing tree species that are not so extensively logged, and that were not used in unlogged sites, such as *Ceiba chodatii* (Politi et al., 2010).

In this study non-excavator bird species made little use of excavated cavities. This is similar to results from other forests in South America (Cockle et al., 2012; Pereira et al., 2009) and opposite to the pattern described for North America (Blanc and Walters, 2008a; Martin et al., 2004). The higher frequency of use of excavated cavities by non-excavators bird species might be explained by the longer persistence of excavated cavities in North America than in South America (Cockle et al., 2011a). Overall, woodpeckers excavate cavities in standing dead trees very often (Martin et al., 2004), and sometimes even more frequently than in living trees (Blanc and Walters, 2008a; Boyle et al., 2008; Cockle et al., 2012; Politi et al., 2009; this study). In the PF, cavities in standing dead trees have a higher loss rate (>40% per year) (Politi et al., 2010) than in temperate forests, which was also seen in other South American forests (Cockle et al., 2011a). Therefore, excavated cavities in standing dead trees in South American forests remain available for a short time rendering a ephemeral resource for non-excavators bird species (Cockle et al., 2011a; Gibbs et al., 1993).

Additionally, the scarce use of excavated cavities by non-excavator bird species in our study might be related to our finding that 49% of the excavated cavities were created by *P. cirratus*, the smallest species in the nest-web (8–10 cm, 6.8–12 g; Winkler et al., 2013). These small, excavated cavities probably do not meet the size requirements of most non-excavator bird species in the PF; for example, the smallest non-excavator species recorded in the PF nest-web was *Lepidocolaptes angustirostris*, which is 18–22 cm long and weighs 21.5–37.5 g (Marantz et al., 2016). In fact, the few excavated cavities used by non-excavators (Table 1) were created by medium- and large-sized woodpeckers. Therefore, in the PF woodpeckers do not seem to play a key role in provisioning cavities to the nest-web, a pattern also shown for other South American and some European forests, and contrary to the findings in North America (Cockle et al., 2011a,b; Pereira et al., 2009; Wesołowski, 2007). However, in logged forests medium- and large-sized woodpeckers might have a significant role in creating the few available cavities for the nest-web (Cockle et al., 2015; Drever and Martin, 2010; Politi et al., 2009), since trees with suitable decay-formed cavities in logged forests are likely to be extracted (Cockle et al., 2010; Edworthy and Martin, 2013; Politi et al., 2010, 2012). A study in North American forests, where non-excavators usually nest in excavated cavities, showed that non-excavator cavity preferences changed according to forest types and availability of cavities excavated by particular woodpecker species (Robles and Martin, 2014; see also Norris and Martin, 2010). It remains to be properly corroborated if South American non-excavator cavity-users, which apparently prefer decay-formed cavities (Cockle et al., 2012; Pereira et al., 2009; this study), are plastic enough to widely adopt excavated cavities in logged forests (Politi et al., 2009). Indeed, cavity availability experiments in both North and South America found that non-excavators chose cavities based on their suitable characteristics rather than the cavity formation type (excavated or decay-formed, Aitken and Martin, 2007; Cockle et al., 2010). Nevertheless, it would be advisable to periodically monitor the nesting success of non-excavators when using these non-preferred, excavated cavities, since some European secondary-users had higher predation rates in non preferred excavated than in decay-formed cavities (Remm et al., 2006; Wesołowski, 2002).

Through the application of simple tools already used in other interaction networks, we have explored more in detail nest-webs

in the PF. With the results of these analytical methods forest recommendations should be based on retaining two tree species (*C. multiflorum* and *A. colubrina*) as well as standing dead trees. Combining this information with that from previous studies (Politi et al., 2009, 2010) we recommend to retain at least 4 standing dead trees/ha, as well as 4 live *C. multiflorum*/ha > 40 cm DBH, and 4 live *A. colubrina*/ha > 30 cm DBH. For *A. colubrina* the recommendation is less restrictive since it is pioneer species with moderate density (40 ind/ha > 20 cm DBH) that regenerates well in logged stands (Brown et al., 2009). We consider that these recommendations, even when simple, are imperative for conservation of the cavity-user bird assemblage, and lastly, for the stability of the whole nest-web, given the great threat that PF (as many other forests around the world) faces due to unsustainable logging operations.

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