Ornithological
Applications

OXFORD

Ecosystem engineers show variable impacts on habitat availability for cavity nesters in South American temperate forests

Cecilia Cuatianquiz Lima,[1,2,3,]* (iD) **Tomás A. Altamirano,**[4,5,6] **Rocío Jara,**[1,6] **Edwin R. Price,**[7] **Fernando J. Novoa,**[1,6] **and José Tomás Ibarra**[1,6,8]

[1]ECOS (Ecosystem-Complexity-Society) Co-Laboratory, Center for Local Development (CEDEL) & Center for Intercultural and Indigenous Research (CIIR), Villarrica Campus, Pontificia Universidad Católica de Chile, Villarrica, Chile
[2]Departamento de Biología Celular y Fisiología, Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, Unidad Foránea Tlaxcala, Tlaxcala, México
[3]Centro Tlaxcala de Biología de la Conducta, Estación Científica La Malinche, Universidad Autónoma de Tlaxcala, Tlaxcala, México
[4]Austral Mountain Conservation and Research (CIMA) Laboratory, Center for Local Development (CEDEL), Villarrica Campus, Pontificia Universidad Católica de Chile, Villarrica, La Araucanía Region, Chile
[5]Audubon Americas, National Audubon Society, Pucón, Chile
[6]Cape Horn International Center for Global Change Studies and Biocultural Conservation (CHIC), Universidad de Magallanes, Puerto Williams, Chile
[7]Green Godwit Consulting LLC, Cleveland, Ohio, USA
[8]Department of Ecosystems and the Environment, Faculty of Agriculture and Natural Systems & Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
*Corresponding author: cecilia.cuatianquiz.l@uatx.mx

ABSTRACT

Ecosystem engineers are organisms that impact their environment and co-existing species by creating or modifying habitats, and thus they play important roles as drivers of community assembly. We examined whether cavity characteristics and/or habitat attributes associated with cavities provided by 4 ecosystem engineers influence the presence of nests of 3 secondary cavity-nesting birds—*Aphrastura spinicauda* (Thorn-tailed Rayadito), *Tachycineta leucopyga* (Chilean Swallow), and *Troglodytes aedon* (Southern House Wren)—and whether these variations influence their reproductive success. We tested this by: (1) assessing nest presence in cavities supplied by ecosystem engineers and (2) quantifying the reproductive success of secondary cavity nesters as a function of cavity characteristics and habitat attributes supplied by ecosystem engineers. Between 2009 and 2022, we recorded 757 cavities in 546 trees in old-growth and second-growth forests in a Global Biodiversity Hotspot in the Andes of southern Chile. Insect/fungi and *Pygarrhichas albogularis* (White-throated Treerunner) play a key role as the primary producers of cavities. Insect/fungi generated the cavities for 82% of *A. spinicauda* nests and 95% of *T. aedon* nests; in contrast, 57% of *T. leucopyga* nests were cavities excavated by *P. albogularis*. Characteristics of cavities (size of cavity entrance, volume, and height above ground) were associated with nest presence of secondary cavity nesters and with reproductive success of *A. spinicauda* and *T. aedon*. Habitat attributes such as tree density and canopy cover influenced nest presence for *A. spinicauda* and *T. leucopyga*, but did not correlate with the reproductive success of any secondary cavity nester. Bamboo density and forest type were related to reproductive success of *A. spinicauda* and *T. aedon*. Diameter at Breast Height of trees was related to the reproductive success of *T. leucopyga*. This study contributes to understanding the importance of various ecosystem engineers for the conservation of secondary cavity-nesting birds in temperate forests and beyond.

Keywords: cavity characteristics, Chile, ecosystem engineers, habitat attributes, native birds, secondary cavity nesters

LAY SUMMARY

- Ecosystem engineers are organisms that impact their environment and co-existing species by creating or modifying habitats, and thus they play important roles as drivers of community assembly.
- We examined the presence of nests of 3 species of secondary cavity nesters and their reproductive success in cavities supplied by 4 ecosystem engineers.
- Between 2009 and 2022, we recorded 757 cavities in 546 trees in old-growth and second-growth forests in a Global Biodiversity Hotspot in the Andes of southern Chile.

- Insect/fungi and *Pygarrhichas albogularis* played a key role as the primary producers of cavities for secondary cavity nesters. The characteristics of cavities were associated with the presence of nests and showed a weaker association with the reproductive success of secondary cavity nesters.
- Habitat attributes showed a weak association with the presence of nests and the reproductive success of 3 secondary cavity nesters.
- This study contributes to understanding the importance of various ecosystem engineers for the conservation of secondary cavity-nesting birds.

Los ingenieros de ecosistemas muestran impactos variables en la disponibilidad de hábitats para los nidificadores de cavidades en los bosques templados de Sudamérica

RESUMEN

Los ingenieros de ecosistemas son organismos que influyen en su entorno y en las especies coexistentes creando o modificando hábitats, por lo que desempeñan un papel importante como impulsores de la formación de comunidades. Examinamos si las características de las cavidades y/o los atributos de hábitat asociados con las cavidades proporcionados por cuatro ingenieros de ecosistemas influyen en la presencia de los nidos de tres aves que anidan en cavidades secundarias (*Aphrastura spinicauda*, *Tachycineta leucopyga* y *Troglodytes aedon*), y si estas variaciones influyen en su éxito reproductivo. Esto se comprobó: i) evaluando la presencia de nidos en cavidades suministradas por los ingenieros de ecosistemas y ii) cuantificando el éxito reproductivo de los nidificadores secundarios en función de las características de las cavidades y los atributos del hábitat suministrados por los ingenieros de ecosistemas. Entre 2009 y 2022, registramos 757 cavidades en 546 árboles de bosques antiguos y de segundo crecimiento a lo largo de un Hotspot de Biodiversidad Global en los Andes del sur de Chile. Los insectos/hongos y el *Pygarrhichas albogularis* desempeñaron un papel clave como principales productores de cavidades. Los insectos/hongos generaron el 82% de los nidos de *A. spinicauda* y el 95% de los nidos de *T. aedon*; en contraste, el 57% de los nidos de *T. leucopyga* fueron cavidades excavadas por *P. albogularis*. Las características de las cavidades (tamaño de la entrada de la cavidad, volumen y altura sobre el suelo) se asociaron con la presencia de nidos de los nidificadores secundarios y con el éxito reproductivo de *A. spinicauda* y *T. aedon*. Los atributos del hábitat, como la densidad de árboles y la cobertura del dosel, influyeron en la presencia de nidos de *A. spinicauda* y *T. leucopyga*, pero no de *T. aedon*, y no afectaron el éxito reproductor de ninguno de los nidificadores secundarios. La densidad de bambú y el tipo de bosque se relacionaron con el éxito reproductivo de *A. spinicauda* y *T. aedon*. El Diámetro a la Altura del Pecho de los árboles se relacionó con el éxito reproductivo de *T. leucopyga*. Este estudio contribuye a comprender la importancia de varios ingenieros de ecosistemas para la conservación de aves que anidan en cavidades secundarias en el bosque templado y más allá.

Palabras clave: Atributos del hábitat, aves nativas, características de cavidades, Chile, ingenieros de ecosistemas, nidificadores secundarios de cavidades

INTRODUCTION

Ecosystem engineers are organisms that directly or indirectly impact the availability of resources for other organisms by modifying or maintaining habitats, causing changes in the biophysical state of a given ecosystem (Jones et al. 1994, 1997). Thus, ecosystem engineers play important roles as drivers of community assembly and can improve ecosystem functions directly, by enhancing microhabitat conditions and resources, as well as indirectly, by increasing diversity at the community level (Wright and Jones 2006, Chapman et al. 2013, Romero et al. 2014, Losapio et al. 2021). Examples of empirically validated ecosystem engineers include *Alligator mississippiensis* (American alligator) that creates wallows (Finlayson and Moser 1991), *Geomys bursarius* (pocket gopher) and ants (Formicidae) that move soil (Dauber et al. 2008, Huntly and Inouye 1988), *Colaptes auratus* (Northern Flicker) that produce cavities (Martin et al. 2004), and *Castor canadensis* (American beaver) that alter the successional dynamics of riparian communities (Wright et al. 2002). Ecosystem engineers are often considered keystone species if their effects on communities and ecosystems are much larger than would be predicted from their abundance (Power et al. 1996). However, the variation among resource attributes provided by ecosystem engineers—and their selection by resource users—are poorly understood in most ecosystems. Elucidating the potential importance of ecosystem engineering as a structural force influencing ecological communities (Wright and Jones 2006, Boogert et al. 2006) is crucial for implementing management actions oriented to conserve biodiversity (Machiote et al. 2004).

In forest ecosystems, numerous bird species rely on tree cavities to fulfill their life history requirements, such as reproductive success (Newton 1994, Monterrubio-Rico and Escalante-Pliego 2006, Wesolowski 2007, Aitken and Martin 2008). These bird communities are hierarchically structured within nest webs according to their strategies for obtaining cavities (Martin and Eadie 1999). Primary cavity nesters are species that produce their own nesting cavities, whereas secondary cavity-nesting birds depend on finding preexisting cavities generated either by primary cavity nesters or through the decay caused by insects and fungi (Swallow et al. 1986, Martin et al. 2004, Lohmus and Remm 2005, Remm et al. 2006). Insects and fungi can indeed be considered tree-cavity producers because they have the ability to bore into wood, generating cavities within trees (Robles et al. 2007). Wood-boring beetles and termites, for example, can tunnel into trees to create nests or to feed on the wood, while fungi can decompose the wood, softening it and making it easier for insects or primary cavity nesters to excavate (Jones et al. 1997). Therefore, primary cavity nesters, insects, and fungi might play a significant role in the process of creating habitats within trees as ecosystem engineers (Jones et al. 1994, Wright and Jones 2006, Robles et al. 2011, Robles and Martin 2013, 2014). In temperate forests of North America, cavities generated by insects/fungi have relatively lower importance compared to those provided by primary cavity nesters, which represent 70% to 90% of all cavities (Aitken and Martin 2007, Blanc and Walters 2008, Cockle et al. 2011a, Cuatianquiz Lima and Macías Garcia 2016). In contrast, studies conducted in subtropical and temperate forests of South America have shown that nesting sites selected by secondary cavity nesters were mostly produced by insects/fungal decay (accounting for 75% to 80% of cavities; Cockle et al. 2011b, Altamirano et al. 2017). These studies suggest that habitat attributes may mediate interspecific associations between cavity producers and secondary cavity nesters.

Habitat attributes such as tree species, together with the age and decay of trees, can significantly influence the generation and survival of cavities (Brightsmith 2005, Remm et al. 2006, Koch et al. 2008, Ibarra et al. 2020, Medina-Estrada et al. 2022, Paratori et al. 2023). Also, cavity characteristics may play a crucial role in habitat selection of secondary cavity nesters (Gibbons et al. 2002, Altamirano et al. 2017, Pakkala et al. 2018). For instance, previous studies found positive associations between nest survival and selection of higher cavities by secondary cavity-nesting birds in forests of both North and South America (Li and Martin 1991, Cockle et al. 2015). Other studies suggest that the availability of suitable cavities is the main factor limiting populations of secondary cavity-nesters (eg, Aitken and Martin 2008, Cockle et al. 2010, Cuatianquiz Lima and Macías Garcia 2016, Altamirano et al. 2024), and together with breeding behavior, are significant predictors of nesting success (Kozma and Kroll 2010, Zhu et al. 2012). Moreover, several studies have indicated that tree and cavity characteristics are the main factors driving depredation and interspecific competition, and thus they strongly influence the selection of cavities by secondary cavity nesters (Li and Martin 1991, Martin et al. 2004, Cockle et al. 2017). By examining patterns of utilization of cavities with different characteristics (eg, cavity volume, cavity entrance size, height above ground), in contrast to their availability, we can discern preferences for specific attributes of nesting habitats (Jones 2001). Identifying these preferences can provide valuable insight into the habitat requirements and nesting behavior of avian species, aiding conservation efforts and habitat management strategies. In this study, our aim was to investigate whether cavity characteristics and/or cavity-associated habitat attributes provided by different ecosystem engineers influence the nest presence of 3 secondary cavity nesters, and whether these variations influence their reproductive success. Specifically, we tested 2 hypotheses: (1) There is variation in the presence of nests in cavities supplied by ecosystem engineers in relation to cavity characteristics and habitat attributes; and (2) cavity characteristics and habitat attributes influence reproductive success. We tested these hypotheses by (1) investigating the relationship between nest presence of the 3 most abundant secondary cavity-nesting birds in southern Chile—*Aphrastura spinicauda* (Thorn-tailed Rayadito), *Tachycineta leucopyga* (Chilean Swallow), and *Troglodytes aedon* (Southern House Wren)—and the cavities provided by 4 ecosystem engineers—*Colaptes pitius* (Chilean Flicker), *Dryobates lignarius* (Striped Woodpecker), *Pygarrhichas albogularis* (White-throated Treerunner) and decay insect/fungi—in old-growth and second-growth forests; and (2) quantifying the reproductive success of secondary nesters as a function of both the cavity characteristics and habitat attributes supplied by different ecosystem engineers.

METHODS

### Study Area and Focal Species
We conducted our study in Andean temperate rainforests of South America in the La Araucanía Region, Chile (39°16′S–71°48′W). The main weather characteristics of the area are cool summers and average annual precipitation >2,000 mm distributed throughout the year. The surveyed sites included 8 old-growth forests (>200 years) within public and private protected areas and 7 second-growth forest sites

(40 to 100 years) on private land (Ibarra et al. 2012, Caviedes and Ibarra 2017), each with a mean area of 40 ha (Figure 1). Old-growth forest sites were mixed conifer-broadleaf forests dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *Nothofagus dombeyi* (500 to 1,000 meters above sea level [m.a.s.l.]) or by the conifer *Araucaria araucana* and *Nothofagus pumilio* (1,000 to 1,400 m.a.s.l.). Second-growth forest sites were dominated by broadleaf species including *Nothofagus obliqua*, *N. dombeyi*, and *Laurelia sempervirens* (Díaz et al. 2005, Altamirano et al. 2017). The understory in both old-growth and second-growth forest sites was mostly dominated by bamboo species (*Chusquea* spp.), *Rhaphithamnus spinosus*, different species of *Azara* and *Berberis*, and tree saplings of species found in both types of forest (Díaz et al. 2006, Altamirano et al. 2017).

Aphrastura spinicauda, *Tachycineta leucopyga*, and *T. aedon* are strictly dependent on cavities for nesting, and they are among the most abundant secondary cavity nesters in the temperate forests of South America (Ridgely and Guy 2009, Altamirano et al. 2017). *A. spinicauda* and *T. leucopyga* are forest specialists and typically prefer to use large trees for nesting, while *T. aedon* is considered a generalist and can be found in both forests and shrublands (Díaz et al. 2005, Cornelius et al. 2000). The diet of all 3 species consists mainly of insects (Arayo and Chester 1993, Altamirano et al. 2012). Nests of these species are typically located at heights ranging from 0 to 29 m above the ground (Cornelius 2008, Altamirano et al. 2012). These species exhibit the highest degrees of habitat specialization among the avian community in southern temperate rainforests, and they are known to be strongly affected by habitat loss and degradation in this region (Ibarra and Martin 2015).

Nest Searching, Monitoring, and Cavity Characteristics
Between 2009 and 2022, we conducted systematic nest monitoring from October to February throughout the breeding season. We worked 6 hr day⁻¹ and 6 days per week in 15 stands encompassing both old-growth and second-growth forests. We found and monitored as many active cavity-nests as possible (Figure 1). The authors and field assistants searched for nests mostly from preexisting trails in each stand. We located active bird nests by stopping frequently to observe the behavior of adult birds using binoculars. We were alerted to potential nests if adults visited the same tree or flew out of a tree suddenly, by evidence of recent wear at the entrance of the cavity, or if adults perched near or entered/exited cavities (Martin et al. 2004, Cockle et al. 2011b, Altamirano et al. 2017). Nest searching was alternated between stand and days. We checked lower cavities (<2 m in height) directly using a flashlight with a mirror. For higher cavities (>2 m in height), we checked the interior using a wireless monitoring system with a telescopic pole reaching up to 15 m high (Martin et al 2004, Huebner and Hurteau 2007, Cockle et al 2011b). We considered a cavity as active when at least one egg or nestling was present inside. We identified nests >15 m high as active by observing adult nesting behavior (eg, active feeding nestling or removing fecal sacs). We assigned a unique number code for each nest, cavity, and nest-tree and recorded the nesting bird species, origin of the cavity (excavated or produced by fungal/insect decay) and excavator species (in the case the cavity was excavated). We monitored each occupied cavity
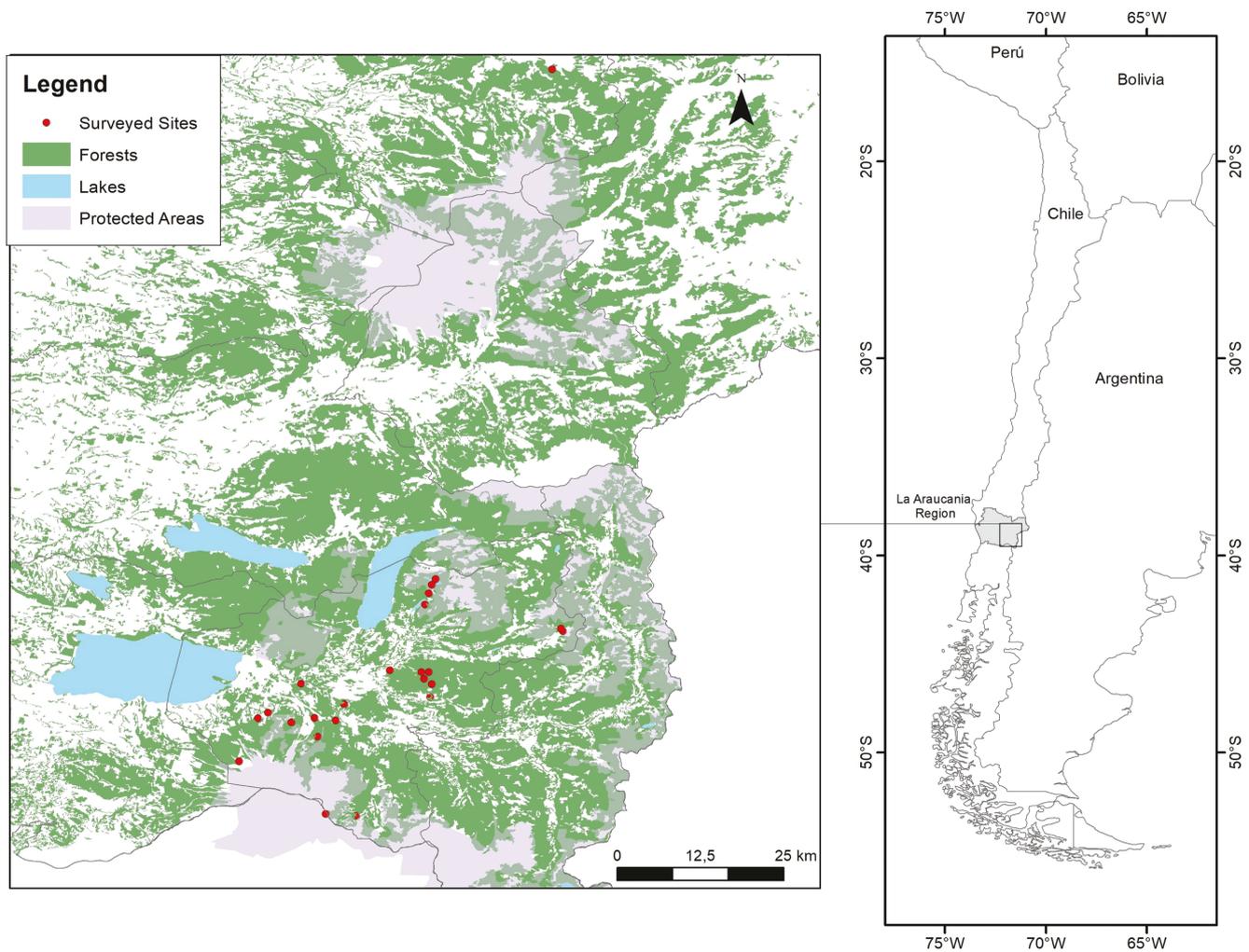
FIGURE 1. Location of the 15 surveyed sites in Andean temperate rainforests in the La Araucanía Region, Chile (39°16′S–71°48′W); each site had a mean area of 40 ha.

every 3 to 4 days to determine nest fate (number of hatched eggs, number of fledglings) and to record when cavities were available again for additional nesting attempts. For all surveyed cavities that were accessible, we recorded cavity characteristics: cavity volume (cm³), size of cavity entrance (cm), and cavity height above ground (m). As a proxy to assess the cavity volume, we use a cylindrical-shape volume formula: $V = \pi r^2 d$, where r is half of cavity width and d is cavity depth (Koch et al. 2012, Robles and Martin 2013).

Habitat Attributes

At the end of each nesting season, we quantified habitat attributes through vegetation plots (0.04 ha, radius = 11.2 m) around each nest-tree found in old-growth and second-growth forests (Ibarra et al. 2014, Caviedes and Ibarra 2017). We established 0.04-ha plots with a radius of 11.2 m around each nest-tree, under the assumption that secondary nesters would concentrate their activities, such as foraging and territory defense, within this area (Ibarra et al. 2014, Altamirano et al. 2015). Within each plot, we measured both site-level and tree-level attributes. Site-level attributes included (1) tree density: the density of all trees with a diameter at breast height (DBH) greater than 12.5 cm; (2) tree DBH: the diameter of trees measured at breast height; (3)

canopy cover: the proportion of the sky covered by canopy, estimated from the center of the plot; and (4) density of bamboo understory: the density of bamboo vegetation up to 3 m in height. For tree-level attributes, trees were assigned to 1 of 5 decay classes: class 1, live healthy trees; class 2, live unhealthy trees; class 3, recently dead trees; class 4, long-dead trees; and class 5, naturally fallen trees (modified from Edworthy et al., 2012).

Statistical Analyses

Nest presence and cavity selection

To assess the relationships between the nest presence of *A. spinicauda, T. leucopyga,* or *T. aedon* and the cavities supplied by ecosystem engineers, we first assigned a "1" to cavities with nest presence of any of these 3 secondary cavity nesters and "0" for cavities found empty or with the presence other nesting birds. For all analyses, we excluded years 2010 and 2022 because of a lack of data. We used generalized linear mixed models (GLMMs) with binomial error distributions and logit link functions. The identity of the ecosystem engineer, along with forest type (old-growth and second-growth forests), cavity volume (cm³), size of cavity entrance (cm), cavity height above ground (m), tree density,

average DBH, canopy cover (%), and bamboo density, were incorporated as fixed terms in our analysis. Year and site identity were fitted as a random term to control for variability among years and sites (Bates 2010). We tested all possible combinations of variables, excluding interactions. We used an information-theory approach to assess which characteristics better describe cavity selection; such an approach allows consideration of non-exclusive candidate models, which is particularly relevant when many factors may influence the dependent variable (Burnham and Anderson, 2002). For each species we ranked all candidate models based on AIC, averaged all models within ΔAIC ≤ 2, and we calculated model-averaged parameter estimates and standard errors.

### Reproductive success of secondary cavity nesters

We used the logistic exposure method (Shaffer 2004) to assess the influence of habitat on daily nest survival rate for each of the 3 focal species. Similar to the analyses conducted for nest presence, we tested all possible combinations of variables, excluding interactions. In this model, the identity of the ecosystem engineer, along with forest type (old-growth and second-growth forests), cavity volume (cm³), size of cavity entrance (cm), cavity height above ground (m), tree density, average DBH, canopy cover (%), and bamboo density, were included as fixed terms. For each species we ranked all candidate models based on AIC, averaged all models within ΔAIC ≤ 2, and we calculated model-averaged parameter estimates and standard errors. This approach allowed us to assess the relative importance of each variable on the reproductive success and provided insights into the cavity and habitat preferences and requirements of avian species within the study area.

We used GLMMs (package *lme4* v1.1.3, Bates et al. 2015, R software version 4.0.3) using Year and Site as random term and nest fate (successful = 1, failed = 0) as the response variable. We had to exclude, from the analysis, the nests in cavities excavated by *D. lignarius* for both *T. leucopyga* and *T. aedon*. We also excluded the nests of *T. aedon* in the cavities excavated by *C. pitius*, because there was no variability in the response (these nests were all successful) preventing the assessment of how external variables may affect their survival (ie, quasi-complete separation of data points). For all analyses, we standardized all continuous variables to a mean of zero with one unit of standard deviation (Schielzeth 2010).

RESULTS

Ecosystem engineers produced a total 757 nest-cavities (82% by insects/fungi and 18% by primary cavity nesters [14% by *P. albogularis*, 2% by *D. lignarius*, and 2% by *C. pitius*]), located in 546 trees. We counted a total 23,554 trees, corresponding to 5,718 trees in old-growth and 17,836 in secondary forest stands. Cavities produced by insects/fungi were more likely to be occupied by secondary cavity nesters (80% of nests), followed by cavities formed by *P. albogularis* (16% of nests), *D. lignarius* (2% of nests), and *C. pitius* (2% of nests). The tree decay classes where the cavities with nests were found were mostly long-dead trees (47%), followed by live unhealthy trees (46%), fallen trees (3.9%), recently dead trees (3%), and live healthy trees (0.1%) (Figure 2).
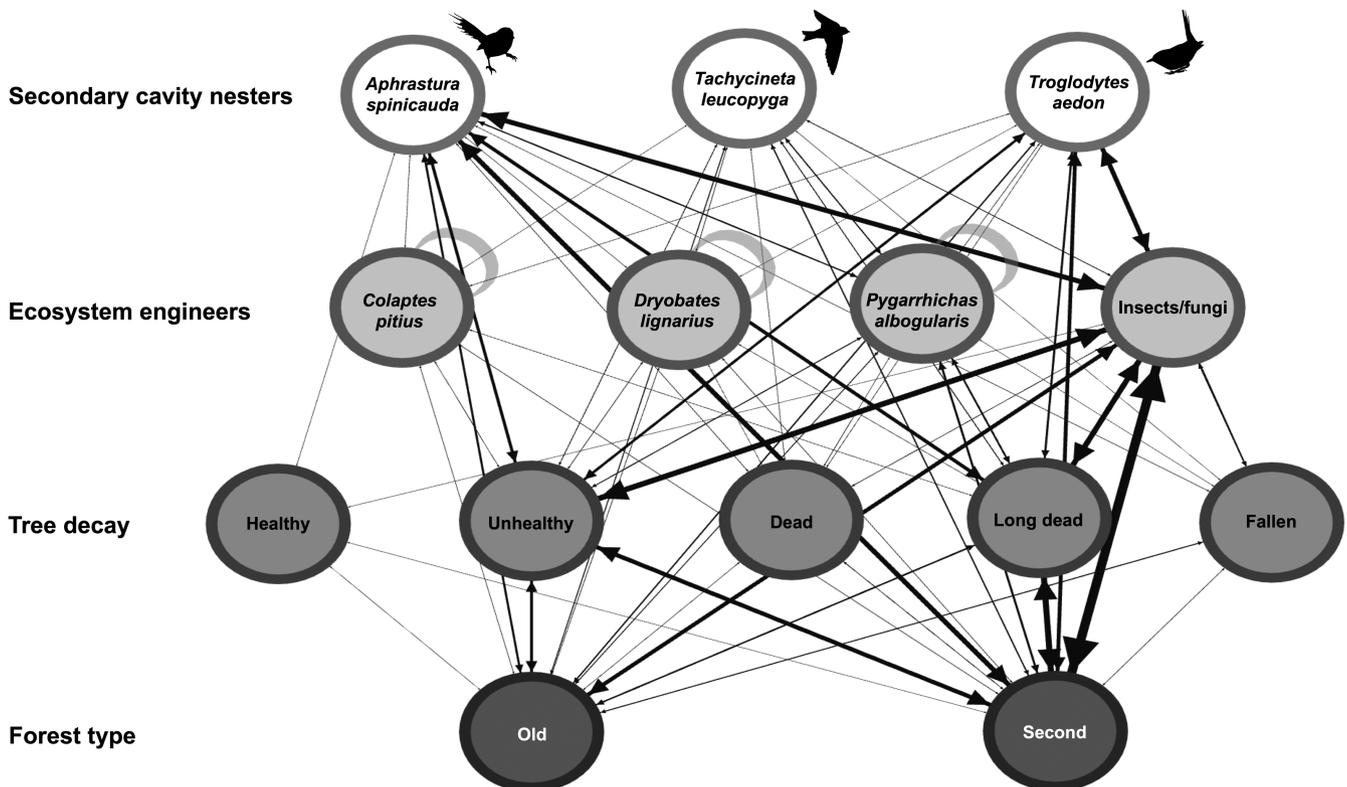
FIGURE 2. Interspecific associations of 3 of the most common and abundant secondary cavity-nesting birds in temperate forests of South America (*Aphrastura spinicauda*, *Tachycineta leucopyga*, and *Troglodytes aedon*). The strength of relationship is shown by the thickness of lines. Analysis includes nests of 3 secondary cavity nesters and cavities supplied by 4 ecosystem engineers (*Colaptes pitius*, *Dryobates lignarius*, *Pygarrhichas albogularis*, and insects/fungi) in different substrate and forest type.
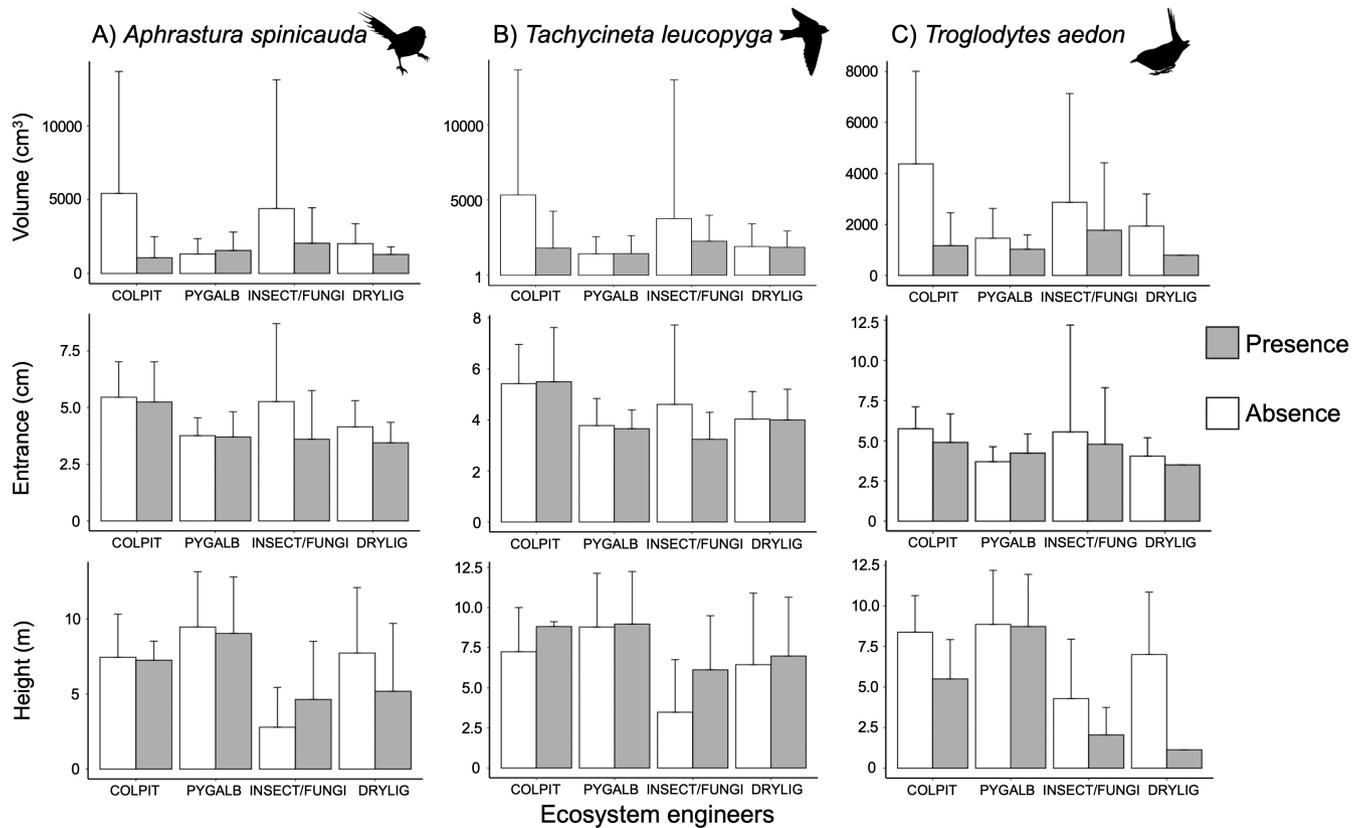
FIGURE 3. Cavity characteristics and nest presence. (**A**) *Aphrastura spinicauda*: cavities used for nesting had smaller entrance sizes, lower volume/depth, and were higher off the ground. (**B**) *Tachycineta leucopyga*: cavities used for nesting had smaller entrance sizes and were higher off the ground. (**C**) *Troglodytes aedon*: cavities used were shallower/lower volume and closer to the ground. Ecosystem engineers are *Colaptes pitius* = COLPIT, *Pygarrhichas albogularis* = PYGALB, Insects/fungi, and *Dryobates lignarius* = DRYLIG. Grey boxes indicate cavities with nests of the 3 focal secondary cavity-nesting birds and white boxes indicate cavities found empty or with presence of other birds.

Aphrastura spinicauda

Nest presence

The best model for nest presence included ecosystem engineer identity, cavity entrance size, cavity volume, cavity height, tree density, and canopy cover ($\Delta AIC_c = 0.00$, $w_i = 0.24$, df = 12). *A. spinicauda* was more likely to nest in cavities formed by insects/fungi (82% of 496 nests) and they avoided cavities formed by *C. pitius* (0.6% of 496 nests). Cavities with smaller entrances size (mean ± SD: 3.62 ± 2.02 cm vs. not used 6.07 ± 6.54 cm) and smaller internal volumes (mean ± SD: 1,970.32 ± 2,265.01 cm³ vs. not used 4,388.78 ± 10,621.71 cm³) were more likely to be used for nesting. Further, nests were placed in cavities higher off the ground compared to cavities without nests (mean ± SD: 5.34 ± 4.14 m vs. 3.99 ± 4.12 m) (Figure 3A). *A. spinicauda* nests were associated with plots with higher tree density (mean ± SD: 21.96 ± 16.02 vs. 19 ± 15.12) and higher canopy cover (mean ± SD: 55 ± 34% vs. 49 ± 33%) (Table 1).

Reproductive success

We analyzed 326 *A. spinicauda* nests. Nest success was higher in cavities in second-growth forests (model-averaged parameter estimate ± SE: 0.38 ± 0.30) and in cavities with a relatively lower depth (model-averaged parameter estimate ± SE: −0.17 ± 0.10). Nesting success was negatively associated with bamboo density (model-averaged parameter estimate ± SE: −0.10 ± 0.07) (Table 2).

Tachycineta leucopyga

Nest presence

The best model included ecosystem engineer identity, cavity entrance size, cavity height, and canopy cover ($\Delta AIC_c = 0.00$, $w_i = 0.14$, df = 9). *T. leucopyga* was more likely to nest in cavities formed by *P. albogularis* (57% of 108 nests) and they rarely used cavities formed by insects/fungi (29% of 108 nests). Cavities with relatively smaller entrance size (mean ± SD: 3.62 ± 0.98 cm vs. not used 5.20 ± 5.55 cm) and those higher off the ground (mean ± SD: 8.19 ± 3.84 m vs. 4.21 ± 4.06 m) were more likely to be used for nesting (Figure 3B). *T. leucopyga* nests were more likely to be associated with open canopies (mean ± SD: 48 ± 30% vs. 51 ± 34%) (Table 1).

Reproductive success

We analyzed 48 *T. leucopyga* nests. Nesting success was negatively associated with average DBH (model-averaged parameter estimate ± SE: −1.01 ± 0.43) (Table 2).

Troglodytes aedon

Nest presence

The best model included ecosystem engineer identity, cavity volume, and cavity height ($\Delta AIC_c = 0.00$, $w_i = 0.05$, df = 9). *T. aedon* was more likely to nest in cavities formed by insects/fungi (95% of 339 nests). Cavities with relatively lower depths (mean ± SD: 1,829.14 ± 3,018.87 cm³ vs. 4,100 ± 9,793.20 cm³) and lower height off the ground

TABLE 1. Binomial GLMMs analyses explaining nest presence of 3 secondary cavity-nesters in relation to the cavity characteristics and habitat attributes in forest of southern Chile, between 2009 and 2022. We showed model-averaged parameter estimates and standard errors for *Aphrastura spinicauda* (496 nests), *Tachycineta leucopyga* (108 nests), and *Troglodytes aedon* (339 nests). Significant values ($P \leq 0.05$) are highlighted in bold.

Parameters	Estimate	SE	z	P
Aphrastura spinicauda				
Intercept	–2.798	9.188	3.042	**0.002**
Ecosystem engineer (insects/fungi)	2.259	0.831	2.71	**0.006**
Ecosystem engineer (*Pygarrhichas albogularis*)	1.067	0.836	1.27	0.202
Ecosystem engineer (*Dryobates lignarius*)	0.590	1.01	0.57	0.562
Forest (secondary)	0.292	0.288	1.015	0.310
Cavity volume	–0.00005	0.00001	2.86	**0.004**
Cavity entrance	–0.229	0.039	5.84	**0.000**
Cavity height	0.167	0.027	6.03	**0.000**
Canopy cover (%)	0.005	0.002	2.19	**0.028**
Tree density	0.016	0.006	2.79	**0.005**
DBH average	–0.0001	0.002	0.04	0.960
Bamboo density	–0.140	0.127	1.09	0.273
Tachycineta leucopyga				
Intercept	–0.661	1.113	0.59	0.553
Ecosystem engineer (insects/fungi)	–1.735	–0.85	2.02	**0.043**
Ecosystem engineer (*Pygarrhichas albogularis*)	1.016	0.837	1.21	0.225
Ecosystem engineer (*Dryobates lignarius*)	1.556	0.971	1.60	0.109
Forest (secondary)	–0.049	0.248	0.20	0.841
Cavity volume	–0.000001	0.00001	0.11	0.905
Cavity entrance	–0.262	0.118	2.21	**0.026**
Cavity height	0.106	0.042	2.53	**0.011**
Canopy cover (%)	–0.014	0.004	2.97	**0.002**
Tree density	–0.0009	0.004	0.20	0.835
DBH average	–0.0002	0.004	0.05	0.953
Bamboo density	–0.004	0.071	0.06	0.951
Troglodytes aedon				
Intercept	2.663	0.729	3.60	**0.0003**
Ecosystem engineer (insects/fungi)	–1.824	0.668	2.72	**0.006**
Ecosystem engineer (*Pygarrhichas albogularis*)	–2.326	0.730	3.18	**0.001**
Ecosystem engineer (*Dryobates lignarius*)	–4.037	1.275	3.16	**0.001**
Forest (secondary)	–0.006	0.068	0.09	0.923
Cavity volume	–0.0001	0.00002	4.86	**0.000**
Cavity entrance	0.010	0.019	0.52	0.601
Cavity height	–0.353	0.043	8.201	**0.000**
Canopy cover (%)	–0.002	0.002	0.93	0.347
Tree density	–0.002	0.005	0.50	0.613
DBH average	–0.0001	0.001	0.10	0.912
Bamboo density	0.018	0.053	0.33	0.734

(mean ± SD: 2.30 ± 2.10 m vs. 5.45 ± 4.47 m) were more likely to be used for nesting (Table 1, Figure 3C).

Reproductive success

We analyzed 119 *T. aedon* nests. Nest success was higher in cavities in second-growth forests (model-averaged parameter estimate ± SE: 0.42 ± 0.30) with smaller entrances (model-averaged parameter estimate ± SE: –0.28 ± 0.10) (Table 2).

DISCUSSION

Ecosystem engineers are expected to have an influence on co-existing species by creating or modifying habitats. Our results demonstrate that there is variation in nest presence in cavities provided by ecosystem engineers in relation to cavity characteristics and habitat attributes. This, in turn, influences the reproductive success of secondary nesters. Cavities produced by insects/fungi, followed by cavities formed by *P. albogularis*, played an outstanding role as the main nesting-cavity providers for 3 species of secondary cavity nesters. Consistent with Altamirano et al. (2017), we found a high percentage of cavities located in long-dead trees and live unhealthy trees for our focal species. The presence of nests of 3 species of secondary cavity nesters was strongly associated with cavity characteristics. Contrary to previous studies in which habitat at local spatial scales determined the variation in the association between multiple ecosystem engineers and resource users in ecological communities (Machicote et al.

TABLE 2. Model selection of analyses examining reproductive success of *Aphrastura spinicauda*, *Tachycineta leucopyga*, and *Troglodytes aedon* in relation to the cavity characteristics and habitat attributes. We used GLMMs using nest fate (successful = 1, failed = 0) as the response variable. Models with ΔAICc < 2 from the best model within the set of candidate models examined are indicated. Models are ranked according to their Akaike weight (w), higher weights indicating better explanatory power. AIC corrected for small smaple size and ΔAICc: difference in AICc to the best model. df = degrees of freedom.

Selected models	df	LogLik	AIC_c	ΔAIC_c	w_i
Aphrastura spinicauda					
Bamboo density, forest type, canopy cover, cavity volume	7	–307.5	627.24	0	0.034
Bamboo density, forest type, cavity volume	6	–307.93	627.92	0.682	0.024
Bamboo density, cavity volume	5	–309.11	628.26	1.024	0.020
Bamboo density, canopy cover, cavity volume	6	–308.14	628.35	1.108	0.019
Forest type, canopy cover, cavity volume	6	–308.24	628.54	1.321	0.017
Bamboo density, cavity entrance, forest type, canopy cover, cavity volume	8	–306.27	628.65	1.409	0.016
Forest type, cavity volume	5	–309.36	628.78	1.539	0.015
Bamboo density, forest type, canopy cover	6	–308.41	628.90	1.657	0.014
Bamboo density, forest type, canopy cover, cavity height, cavity volume	8	–306.49	629.10	1.865	0.013
Tachycineta leucopyga					
DBH average	4	–41.356	90.947	0	0.042
DBH average, tree density	5	–40.840	92.036	1.089	0.024
DBH average, cavity height	5	–40.878	92.111	1.640	0.023
Bamboo density, DBH average	5	–41.144	92.644	1.697	0.018
DBH average, canopy cover	5	–41.201	92.758	1.810	0.017
DBH average, cavity entrance	5	–41.290	92.935	1.988	0.015
Troglodytes aedon					
DBH average, cavity entrance, forest type, cavity volume	7	–264.99	544.13	0	0.036
DBH average, ecosystem engineer, cavity entrance, forest type, cavity volume	9	–263.28	544.79	0.661	0.026
DBH average, cavity entrance, forest type	6	–266.36	544.84	0.710	0.025
DBH average, ecosystem engineer, cavity entrance, forest type	8	–264.57	545.32	1.194	0.199
DBH average, cavity entrance, cavity volume	6	–266.73	545.58	1.449	0.017
DBH average, ecosystem engineer, cavity entrance, forest type, cavity height, cavity volume	10	–262.69	545.66	1.527	0.016
DBH average, cavity entrance, forest type, canopy cover, cavity volume	8	–264.83	545.84	1.707	0.015
Bamboo density, DBH average, cavity entrance, forest type, cavity volume	8	–264.87	545.91	1.783	0.014
DBH average, cavity entrance	5	–267.94	545.96	1.827	0.014
DBH average, cavity entrance, forest type, cavity height, cavity volume	8	–264.93	546.05	1.918	0.013

2004, Robles and Martin 2014), our findings reveal that *A. spinicauda*, *T. leucopyga,* and *T. aedon* exhibit a preference for specific cavity characteristics over habitat attributes surrounding the nest-tree.

The strong preference for cavities supplied by insects/fungi showed by *A. spinicauda* and *T. aedon* may be partially associated with the high number of cavities available in live unhealthy and long-dead trees. The latter substrate, prior to falling down, supports a disproportional number of cavities compared to their relative availability (Altamirano et al. 2017, Caviedes and Ibarra 2017, Ibarra et al. 2020). Tomasevic and Estades (2006) suggested that *A. spinicauda* exhibit a preference for large dead trees in southern beech forests in south-central Chile. This may be related to the strong preference for cavities produced by insect/fungal decay observed in our study. Conversely, *T. leucopyga* showed a preference for excavated cavities. These differences in cavity use, produced by different ecosystem engineers, may indicate niche differentiation (Boogert et al., 2006). In addition, it is consistent with studies in North America, where the *Tachycineta* genus selects cavities formed by woodpeckers (Robles and Martin 2013, 2014). *Troglodytes aedon* in North America show a strong preference of dead trees for nesting (Li and Martin 1991), suggesting that the *Troglodytes* genus could have a

general preference for nesting in decayed wood in forest habitats (Taylor 2003, Kaluthota and Rendall 2017). In addition, cavities supplied by *D. lignarius* and *C. pitius* were less likely to be used by *A. spinicauda* and *T. aedon* (< 2 % of use) but not by *T. leucopyga*, which used 12% of cavities formed by *D. lignarius*. The low importance of cavities supplied by both *D. lignarius* and *C. pitius* may be associated with their greater home ranges and relatively low densities. On the other hand, our study was conducted in forests dominated by trees of the *Nothofagus* genus, which are more susceptible to insect attacks, presence of wood-decay fungi, mistletoe infections, wind, and drought, which promote wood decay (Ojeda et al. 2007, Ibarra et al.2020). Our data support the assumption that dead trees in temperate forests of South America play an important role providing cavities and thus maintaining vertebrate diversity, including birds; this suggests that old and dead standing trees are highly valuable for conservation (Altamirano et al. 2017, Ibarra et al. 2020, Moreira-Arce et al. 2021).

Similar to other studies, cavity preference was species-specific (Politi et al. 2009, 2010, Cockle et al. 2011b, 2015, 2019, De la Parra Martínez et al. 2015). This selection may be related to individual requirements for thermo-regulation by nestlings and/or protection from predators

(Nilsson 1984, Li and Martin 1991, Wiebe 2001, Wesolowski 2002, Wesolowski and Rowiński 2006, Remm et al. 2006, Berkunsky et al. 2016). *A. spinicauda* and *T. aedon* showed preferences for shallow cavities, while *A. spinicauda* and *T. leucopyga* preferred cavities with smaller entrance sizes and higher placement above the ground. Possibly these characteristics promote heat retention inside the nest and avoiding predation (Wiebe 2001). Predators attacking nests is the primary reason for avian nest failure (Ricklefs 1969). Concealing nests helps minimize the visual, chemical, and auditory signals that attract predators and is a crucial consideration for many bird species when choosing nesting sites. Nests located higher above ground are less exposed to terrestrial predators; conversely, one may expect nests that are lower in height to be less exposed to aerial predators (Nilsson 1984, Sofaer et al. 2013, Dias and Lima 2015). Therefore, nest height may be a relevant parameter affecting nest fate, although it does not always influence nest survival (Sadoti and Vierling 2010, Dias and Lima 2015). On the other hand, the selection of habitat with different characteristics might facilitate the coexistence of ecologically similar species by overcoming potential negative effects of interspecific competition (Ricklefs 1990, Odling-Smee et al. 1996). Since they share nesting habitats, it is possible they also share feeding habitats. This may reflect behavioral decisions to avoid interspecific competition for food (Martin 1988, Saab et al. 2004, Hardin et al. 2021). Therefore, identifying key ecosystem engineers may necessitate evaluating resource quality by assessing the factors that impact resource utilization and reproduction for each resource user.

Reproductive success of our 3 cavity nesters varied between 50 and 65%; these results are similar to those reported in other studies (Wiebe and Swift 2001, Mahon and Martin 2006, Renton and Brightsmith 2009). Contrary to our predictions, the cavity characteristics and habitat attributes that were preferred for nesting did not necessarily determine the reproductive success of our focal cavity nesters. The relatively weak effect of site-level and cavity characteristics on the reproductive success of our focal species suggests that reproductive success is limited, partially or completely, by ecological factors that are uncorrelated to cavity characteristics and habitat attributes (Bonnot et al. 2008, Kozma and Kroll 2010, Zhu et al. 2012, Holt and Martin 1997, Kus et al. 2008, Jara et al. 2020). Although cavity height was an important parameter that had a positive effect on nest cavity selection by the 3 secondary nesters, it was not significant in reproductive success. On the other hand, higher vegetation density also had no effect on the reproductive success of our focal cavity-nesting species. Our data suggest that reproductive success may be associated with other characteristics such as cavity microclimate, predation, or food intake provided by parents (Wiebe and Swift 2001, Mahon and martin 2006, Sadoti and Vierling 2010, Zhu et al. 2012, Dias and Lima 2015), variables that were not measured in this study. Our results also suggest that some ecosystem engineers may be functionally similar for *A. spinicauda*, *T. leucopyga,* and *T. aedon*. While *T. leucopyga* appeared to prefer the less common *P. albogularis* cavities even more than the abundant and frequently-used cavities produced by insect/fungi, the reproductive success of *A. spinicauda*, *T. leucopyga,* and *T. aedon* were similar regardless of ecosystem engineer, suggesting that the importance of cavities produced by insect/fungi was at least as high as that of produced by *P. albogularis*.

We conclude that insect/fungi decay plays an outsized role as the main ecosystem engineers for *A. spinicauda* and *T. aedon*, while *P. albogularis* are the main source of cavities for *T. leucopyga*. Differences in cavity use and reproductive success may explain, at least in part, the difference in niche and coexistence of the 3 secondary nesters, which are ecologically similar, and they share foraging and nesting sites (Ridgely and Guy 2009), but exhibit cavity use with different habitat characteristics and attributes. We reveal variations in the significant role of ecosystem engineers concerning the characteristics of the resources they provide, and their preference by secondary cavity nesters, which may impact their reproductive success. Therefore, the conservation of secondary cavity nesters may require the development of different management actions for each ecosystem engineer and associated resource users. In line with the Bird Conservation Strategy in Chile (MMA–ONU Medio Ambiente, 2022), we recommend the retention and recruitment of a variety of trees, including live unhealthy trees, large-decaying trees, and standing dead trees, which promote the production of a variety of cavities that are required by the 3 secondary cavity nesters that are most abundant in South American temperate forests.

Supplementary material

Supplementary material is available at *Ornithological Applications* online. A Spanish version of this article is available in Supplementary Material 1 (Spanish) and the authors' reflexivity statement is available in the Supplementary Material.

Ethical statement

We followed the IOU Code of Ethics (https://www.internationalorniyhology.org/iou-code-ethics).

Conflict of interest statement

The authors declare that they have no conflicts of interest.

Author contributions

C.C.L., J.T.I., and T.A.A. conceived the idea, design, and experiment. C.C.L., J.T.I., T.A.A., and F.N. performed the experiments (collected data, conducted the research) and

designed the methods. C.C.L., R.J., and E.R.P. analyzed the data. C.C.L., J.T.I., and T.A.A. wrote the manuscript with substantial contributions from R.J. and E.R.P.

Data availability

Analyses reported in this article can be reproduced using the data provided by Cuatianquiz Lima et al. (2024).

LITERATURE CITED

Aitken, K. E. H., and K. Martin (2007). The importance of excavators in hole nesting communities: availability and use of natural tree holes in old mixes forest of Western Canada. *Journal of Ornithology* 148 (Supplement 2):S425–S434.

Aitken, K. E. H., and K. Martin (2008). Resource selection plasticity and community responses to experimental reduction of a critical resource. *Ecology* 89:971–980.

Altamirano, T. A., J. T. Ibarra, F. Hernández, I. Rojas, J. Laker, and C. Bonacic (2012). *Hábitos de nidificación de las aves del bosque templado Andino de Chile*. Serie Fauna Australis, Facultad de Agronomía e Ingeniería Forestal, Pontificia Universidad Católica de Chile, Santiago, Chile.

Altamirano, T.A., J. T. Ibarra, M. de la Maza, S. A. Navarrete, and C Bonacic (2015). Reproductive life-history variation in a secondary cavity-nester across an elevational gradient in Andean temperate ecosystems. *The Auk: Ornithological Advances* 132:826–835.

Altamirano, T. A., J. T. Ibarra, K. Martin, and C. Bonacic (2017). The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforest. *Biodiversity and Conservation* 26:2453–2472.

Altamirano, T. A., F. Novoa, J. T. Ibarra, S. A. Navarrete, C. Bonacic, and K. Martin (2024). Tree cavity density is a limiting factor for a secondary cavity nester in second-growth Andean temperate rainforests. *Ornithological Applications* 126:duae031.

Arayo, B., and S. Chester (1993). *The Birds of Chile: A Field Guide*. Latour, Santiago, Chile.

Bates, D. (2010). *lme4: Mixed-effect modeling with R*. Springer. doi: 10.1002/9780470061602.eqf08016

Bates, D., M. Mächler, B. Bolker, and S. Walker (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–47.

Berkunsky, I., L. N. Segura, R. M. Aramburú, R. A. Ruggera, W. S. Svagelj, and J. C. Reboreda (2016). Nest survival and predation in Blue-fronted Parrots Amazona aestiva: Effects of nesting behaviour and cavity characteristics. *Ardea* 104:143–151.

Blanc, L. A., and J. R Walters (2008). Cavity-nest webs in a longleaf pine ecosystem. *The Condor* 110:80–92.

Bonnot, T. W., M. A. Rumble, and J. J. Millspaugh (2008). Nest success of Black-backed Woodpeckers in forests with mountain pine beetle outbreaks in the Black Hills, South Dakota. *The Condor* 110:450–457.

Boogert, N. J., D. M. Paterson, and K. N. Laland (2006). The implications of niche construction and ecosystem engineering for conservation biology. *BioScience* 56:570–578.

Brightsmith, D. J. (2005). Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. *The Wilson Bulletin* 117:296–305.

Burnham, K. P., and D. R Anderson (2002). *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY, USA.

Caviedes, J., and J. T. Ibarra (2017). Influence of anthropogenic disturbances on stand structural complexity in Andean temperate forest: Implications for managing key habitat for biodiversity. *PLoS One* 12:e0169450.

Chapman, C. A., T. R. Bonnell, J. F. Gogarten, J. E. Lambert, P. A. Omeja, D. Twinomugisha, M. D. Wasserman, and J.M. Rothman (2013). Are primates ecosystem engineers? *International Journal of Primatology* 34:1–14.

Cockle, K., K. Martin, and M. Drever (2010). Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation* 143:2851–2857.

Cockle, K. L., K. Martin, and T. Wesolowski (2011a). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities world. *Frontiers in Ecology and the Environment* 9:377–382.

Cockle, K., K. Martin, and K. Wiebe (2011b). Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. *Biotropica* 43:228–236.

Cockle, K. L., A. Bodrati, M. Lammertink, and K. Martin (2015). Cavity characteristics, but no habitat influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biological Conservation* 184:193–200.

Cockle, K. L., K. Martin, and A. Bodrati (2017). Persistence and loss of tree cavities used by birds in the subtropical Atlantic Forest. *Forest Ecology and Management* 384:200–207.

Cockle, K. L., M. K. Trzcinski, K. L. Wiebe, A. B. Edworthy, and K. Martin (2019). Lifetime productivity of tree cavities used by cavity-nesting animals in temperate and subtropical forests. *Ecological Applications* 29:e01916.

Cornelius, C. (2008). Spatial variation in nest-site selection by a secondary cavity-nesting bird in a human-altered landscape. *The Condor* 110:615–626.

Cornelius, C., H. Cofré, and P. A. Marquet (2000). Effects of habitat fragmentation on bird species in a relict temperate forest in semiarid Chile. *Conservation Biology* 14:534–543.

Cuatianquiz Lima, C., and C. Macías Garcia (2016). Pre- and post-experimental manipulation assessments confirm the increase in number of birds due to the addition of nest boxes. *PeerJ* 4:e1806.

Cuatianquiz Lima, C., T. A. Altamirano, R. Jara, E. R. Price, F. J. Novoa, and J. T. Ibarra (2024). Ecosystem engineers show variable impacts on habitat availability for cavity nesters in South American temperate forests. *Ornithological Applications* 126:duae000. https://doi.org/10.5061/dryad.qjq2bvqqv.

Dauber, J., R. Niechoj, and H. Baltruschat (2008). Soil engineering ants increase grass root arbuscular mycorrhizal colonization. *Biology and Fertility of Soils* 44:791–796.

Dias, R. I., and M. R. Lima (2015). Breeding biology and nest survival in Tropical Screech-Owls (*Megascops choliba*) in the Brazilian Cerrado. *The Wilson Journal of Ornithology* 127:432–440.

Díaz, I. A., J. J. Armesto, S. Reid, K. E. Sieving, and M. F. Willson (2005). Linking forest structure and composition: Avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation* 123:91–101.

Díaz, I. A., J. J. Armesto, and M. F. Willson (2006). Mating success of the endemic Des Murs' Wiretail (*Sylviorthorhynchus desmursii*, Furnariidae) in fragmented Chilean rainforests. *Austral Ecology* 31:13–21.

De la Parra Martínez, S. M., K. Renton, A. Salinas-Melgoza, and L. G. Muñoz-Lacy (2015). Tree-cavity availability and selection by a large-bodied secondary cavity-nester: The Military Macaw. *Journal of Ornithology* 156:489–498.

Edworthy, A. B., K. L. Wiebe, and K. Martin (2012). Survival analysis of a critical resource for cavity-nesting communities: Patterns of tree cavity longevity. *Ecological Applications* 22:1733–1742.

Finlayson, M., and M. Moser (1991). *Wetlands*. International Waterfowl and Wetlands Research Bureau, Oxford, UK.

Gibbons, P., D. B. Lindenmayer, S. C. Barry, and M. T. Tanton (2002). Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation* 103:1–12.

Hardin, F. O., S. Leivers, J. K. Grace, Z. Hancock, T. Campbell, B. Pierce, and M. L. Morrison (2021). Secondhand homes: The multi-layered influence of woodpeckers as ecosystem engineers. *Ecology and Evolution* 11:11425–11439.

Holt, R. F., and K. Martin (1997). Landscape modification and patch selection: The demography of two secondary cavity nesters colonizing clearcuts. *The Auk* 114:443–455.

Huebner, D. P., and S. R. Hurteau (2007). An economical wireless cavity-nest viewer. *Journal of Field Ornithology* 78:87–92.

Huntly, N., and R. Inouye (1988). Pocket gophers in ecosystems: Patterns and mechanisms. *BioScience* 38:786–793.

Ibarra, J. T., N. Gálvez, A. Gimona, T. A. Altamirano, I. Rojas, A. Hester, J. Laker, and C. Bonacic (2012). Rufous-legged owl (*Strix rufipes*) and Austral pygmy owl (*Glaucidium nanum*) stand use in a gradient of disrupted and old growth Andean temperate forests, Chile. *Studies on Neotropical Fauna and Environment* 47:33–40.

Ibarra, J. T., K. Martin, M. C. Drever, and G. Vergara (2014). Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: A multi-scale approach. *Forest Ecology and Management* 331:281–291.

Ibarra, J. T., and K. Martin (2015). Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests. *Biological Conservation* 192:418–427.

Ibarra, J. T., F. J. Novoa, H. Jaillard, and T.A Altamirano (2020). Large trees and decay: Suppliers of a keystone resource for cavity-using wildlife in old-growth and second Andean temperate forests. *Austral Ecology* 45:1135–1144.

Jara, R. F., R. D. Crego, M. D. Samuel, R. Rozzi, and J. E. Jiménez (2020). Nest-site selection and breeding success of passerines in the world's southernmost forests. *PeerJ* 8:e9892.

Jones, J. (2001). Habitat selection studies in avian ecology: A critical review. *The Auk* 118:557–562.

Jones, C. G., J. H. Lawton, and M. Shachak (1994). Organisms as ecosystem engineers. *Oikos* 69:373–386.

Jones, C. G., J. H. Lawton, and M. Shachak (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.

Kaluthota, C. D., and D. Rendall (2017). Nest site selection and breeding biology of House Wrens (*Troglodytes aedon parkmanii*) using natural cavities in Western Canada. *Canadian Journal of Zoology* 95:505–514.

Koch, A. J., S. A. Munks, D. Driscoll, and J. B. Kirkpatrick (2008). Does hollow occurrence vary with forest type? A case study in wet and dry *Eucalyptus obliqua* forest. *Forest Ecology and Management* 255:3938–3951.

Koch, A. J., K. Martin, and K. E. H. Aitken (2012). The relationship between introduced European Starlings and the reproductive activities of Mountain Bluebirds and Tree Swallows in British Columbia, *Canada*. *Ibis* 154:590–600.

Kozma, J. M., and A. J. Kroll (2010). Nest survival of Western Bluebirds using tree cavities in managed ponderosa pine forests of central Washington. *The Condor* 112:87–95.

Kus, B. E., B. L. Peterson, and D. H. Deutschman (2008). A multiscale analysis of nest predation on Least Bell's Vireos (*Vireo bellii pusillus*). *The Auk* 125:277–284.

Li, P., and T. E. Martin (1991). Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *The Auk* 108:405–418.

Lohmus, A., and J. Remm (2005). Nest quality the number of hole-nesting passerines in their natural cavity-rich habitat. *Acta Oecologica* 27:125–128.

Losapio, G., B. Schmid, J. Bascompte, R. Michalet, P. Cerretti, C. Germann, J.P. Haenni, R. Neumeyer, F. J. Ortiz-Sánchez, A. C. Pont, P. Rousse, J. Schmid, D. Sommaggio, and C. Schöb (2021). An experimental approach to assessing the impact of ecosystem engineers on biodiversity and ecosystem functions. *Ecology* 102:e03243.

Machicote, M., L. C. Branch, and D. Villarreal (2004). Burrowing owls and burrowing mammals: Are ecosystem engineers interchangeable as facilitators? *Oikos* 106:527–535.

Mahon, C. L., and K. Martin (2006). Survival of chickadees in management forests: Habitat, predator, and year effects. *The Journal of Wildlife Management* 70:1257–1265.

Martin, T. E. (1988). On the advantage of being different: Nest predation and the coexistence of bird species. *Proceedings of the National Academy of Sciences USA* 85:2196–2199.

Martin, K., K. Aitken, and K. Wiebe (2004). Nest site and nest web for cavity-nesting communities in interior British Columbia, Canada: Nest characteristics and niche partitioning. *The Condor* 106:5–19.

Martin, K., and J. M. Eadie (1999). Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243–257.

Medina-Estrada, J., D. Remolina-Figueroa, P. Ramírez-Bastida, and L. D. Vázquez-Reyes (2022). Nesting resources availability for cavity adopter birds in a tropical dry forest of Central Mexico. *Revista Mexicana de Biodiversidad* 93:e933836.

MMA–ONU Medio Ambiente (2022) *Estrategia Nacional de Conservación de Aves 2021–2030. Elaborada por Tomás A. Altamirano, consultor proyecto GEF/SEC ID: 9766 "Conservación de Humedales Costero de la Zona Centro-Sur de Chile."* Ministerio del Medio Ambiente, Santiago, Chile.

Monterrubio-Rico, T. C., and P. Escalante-Pliego (2006). Richness, distribution and conservation status of cavity nesting birds in Mexico. *Biological Conservation* 128:67–78.

Moreira-Arce D., P. M. Vergara, A. Fierro, E. Pincheira, S. J. Crespin, A. Alaniz, and M. A. Carvajal (2021). Standing dead trees as indicators of vertebrate diversity: Bringing continuity to the ecological roles of senescent trees in austral temperate forests. *Ecological Indicators* 129:107878.

Newton, I. (1994). The role of nest-sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation* 70:265–276.

Nilsson, S. G. (1984). The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scandinavica* 15:167–175.

Odling-Smee, F. J., K. N. Laland, and M. W. Feldman (1996). Niche construction. *The American Naturalist* 147:641–648.

Ojeda, V. S., M. L. Suarez, and T. Kitzberger (2007). Crown dieback events as key processes creating cavity habitat for Magellanic Woodpeckers. *Austral Ecology* 32:436–445.

Pakkala, T., J. Tiainen, P. Markus, and J. Kouki (2018). Nest tree characteristics of the old-growth specialist Three-toed Woodpecker *Picoides tridactylus*. *Ornis Fennica* 95:89–102.

Paratori, M., F. J. Novoa, T. A. Altamirano, C. Bonacic, and J. T. Ibarra (2023). Tree-cavity survival for biodiversity in temperate forests of South America: A multi-scale approach. *Forest Ecology and Management* 530:120769.

Politi, N., M. Hunter, Jr., and L. Rivera (2009). Nest selection by cavity-nesting birds in Subtropical Montane Forests of the Andes: Implications for sustainable forests management. *Biotropica* 41:354–360.

Politi, N., M. Hunter, Jr., and L. Rivera (2010). Availability of cavities for avian cavity nesters in selectively logged subtropical montane forests of the Andes. *Forest Ecology and Management*. 260:893–906.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R.T. Paine (1996). Challenges in the Quest for Keystones: Identifying keystone species is difficult—but essential to understanding how loss of species will affect ecosystems. *BioScience*. 46:609–620.

Remm, J., A. Lohmus, and K. Remm (2006). Tree cavities in riverine forests: What determines their occurrence and use by hole-nesting passerines? *Forest Ecology Management*. 221:267–277.

Renton, K., and D. J. Brightsmith (2009). Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. *Journal of Field Ornithology* 80:1–8.

Ricklefs, R. E. (1969). *An Analysis of Nesting Mortality in Birds*. Smithsonian Contributions to Zoology, Number 9, Smithsonian Institution Press, U.S. Government Printing Office, Washington, D.C., USA.

Ricklefs, R. E. (1990). *Ecology*, third edition. Freeman, New York, NY, USA.

Ridgely, R. S., and T. Guy (2009). *Field Guide to the Songbirds of South America: The Passerines. University of Texas Press, Austin, TX*, USA.

Robles, H., C. Ciudad, R. Vera, P. P. Olea, F. J. Purroy, and E. Matthysen (2007). Sylvopastoral management and conservation of the Middle-spotted Woodpecker at the south-western edge of its distribution range. *Forest Ecology Management* 242:343–352.

Robles, H., C. Ciudad, and E. Matthysen (2011). Tree-cavity occurrence, cavity occupation and reproductive performance of secondary

cavity-nesting birds in oak forests: The role of traditional management practices. *Forest Ecology and Management*. 261:1428–1435.

Robles, H., and K. Martin (2013). Resource quantity and quality determine the inter-specific associations between ecosystem engineers and resource users in a cavity-nest web. *PLoS One* 8:e74694.

Robles, H., and K. Martin (2014). Habitat-mediated variation in the importance of ecosystem engineers for secondary cavity nesters in a nest web. *PLoS One* 9: e90071.

Romero, G. Q., T. Gonçalves-Souza, C. Vieira, and J. Koricheva (2014). Ecosystem engineering effects on species diversity across ecosystems: A meta-analysis. *Biological Reviews* 90:877–890.

Saab, V. A., J. Dudley, and W. L. Thompson (2004). Factors influencing occupancy of nest cavities in recently burned forests. *The Condor* 106:20–36.

Sadoti, G., and K. T. Vierling (2010). Nonideal habitat selection by a North American cavity excavator: Pecking up the wrong tree? *Canadian Journal Zoology* 88:527–535.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.

Shaffer, T. L. (2004). A unified approach to analyzing nest success. *The Auk* 121:526–540.

Sofaer, H. R., T. S. Sillett, S. I. Peluc, S. A. Morrison, and C. K. Ghalambor (2013). Differential effects of food availability and nest predation risk on avian reproductive strategies. *Behavioral Ecology* 24:698–707.

Swallow, S. K., R. J. Gutierrez, and R.A. Howard (1986). Primary cavity-site selection by birds. *The Journal of Wildlife Management* 50:576–583.

Taylor, R. V. (2003) Factors influencing expansion of the breeding distribution of Bewick's wren into riparian forests of the Rio Grande in central New Mexico. *The Southwestern Naturalist* 48:373–382.

Tomasevic, J. A., and C. F. Estades (2006). Stand attributes and the abundance of secondary cavity-nesting birds in southern beech (*Nothofagus*) forests in south-central Chile. *Ornitología Neotropical* 17:1–14.

Wesolowski, T. (2002), Anti-predators adaptations in nesting Marsh Tits *Parus palustris*: The role of nest-site security. *Ibis* 144:593–601.

Wesolowski, T., and P. Rowiński (2006). Timing of bud burst and tree-leaf development in a multispecies temperate forest. *Forest Ecology and Management* 237:387–393.

Wesolowski, T. (2007). Lessons from long-term hole-nester studies in primeval temperate forest. *Journal of Ornithology* 148:395–405.

Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in Northern Flickers? *The Auk* 118:412–421.

Wiebe, K. L., and T. L. Swift (2001). Clutch size relative to tree cavity in Northern Flickers. *Journal of Avian Biology* 32:167–173.

Wright, J. P., C. G. Jones, and A. S. Flecker (2002). An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101.

Wright, J. P., and C. G. Jones (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience* 56:203–209.

Zhu, X., D. S. Srivastava, J. N. M. Smith, and K. Martin (2012). Habitat selection and reproductive success of Lewis's Woodpecker (*Melanerpes lewis*) at its northern limit. *PLoS One* 7:e44346.