RESEARCH ARTICLE

Unravelling the cavity-nesting network at large spatial scales: The biogeographic role of woodpeckers as ecosystem engineers

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Abstract

Aim: Primary cavity nesters (e.g. woodpeckers) act as ecosystem engineers by providing tree cavities to several vertebrates that use them as nests or refuges. Although diverse assemblages of primary excavators are assumed to increase the number of tree cavities, environmental factors can limit populations of primary excavators, thus weakening their ecological function. We aim to test the biogeographical-scale relationships between primary excavators and cavity users by distinguishing the contribution of environmental variables.

Location: Southern South America.

Materials and Methods: We used species distribution models, which combine bioclimatic and remote sensing derived variables, to map the richness of vertebrates composing the cavity-network of temperate and Mediterranean forests of South America. Based on a resampling procedure for ensuring spatial independence, we fitted structural equation models to estimate relationships between forest characteristics and cavity user vertebrates.

Results: Richness of secondary cavity users (mammals, obligated, habitat generalists and forest specialists) were positively and strongly influenced by the richness of primary excavators. Environmental variables affected differently the richness of primary and secondary cavity users. The richness of primary cavity users responded to tree richness and height while that of habitat specialist secondary users was positively affected by primary productivity and negatively by sclerophyll forests.

Main Conclusions: Our results confirm the role of primary excavators as ecosystem engineers but highlight the importance of considering large spatial scales when analysing cavity-nesting networks. Biogeographical patterns of tree diversity and forest structure can be important drivers of cavity nesting networks that remain hidden when studies are conducted over fine spatial scales.

KEYWORDS
ecosystem engineers, forest cavity networks, primary cavity excavators, secondary cavity users, species distribution modelling

1 | INTRODUCTION

The amount and variability of microhabitat resources shape species abundance and diversity, with effects that spread though ecological networks (Brown et al., 2020; Sobral et al., 2017; Tylianakis et al., 2008). A typically limiting resource in forests ecosystems are the tree cavities animals use for reproduction or refuge (Maziarz et al., 2017; van der Hoek et al., 2017), whose quantity affects individual fitness, population size, and intraspecific competition (Maziarz et al., 2016; Wiebe, 2011). A reduced number of cavities may also strengthen interspecific competition because tree cavities are used by different species, such as small mammals, birds, reptiles, and amphibians (Edworthy, 2015; Hernández-Brito et al., 2020; Wiebe, 2016). The number of cavities within a forest usually increases as trees become older and die due to natural or anthropogenic disturbances (Andersson et al., 2018; Zawadzka et al., 2016) but also depends on species acting as primary cavity excavators, such as woodpeckers (Cockle et al., 2017; Gutzat & Dormann, 2018). Thus, the provision of cavities may increase as primary cavity excavators generate new cavities for nesting or roosting in living and dead trees, which are added to those generated without the intervention of animal species (i.e. non-excavated or decay cavities) (Cockle et al., 2011; Pakkala et al., 2018; Tarbill et al., 2015). The assemblages of non-excavating species that either obligatory or facultatively use cavities (hereafter referred to as secondary cavity users) comprise a series of vertebrate and invertebrate species (Cockle et al., 2011; Jusino et al., 2015; Mikusiński et al., 2001). Primary cavity excavators, secondary cavity users and cavity-trees interact through facilitation networks whose complexity is inherent to multiple ecological interactions, dynamics and processes acting from single tree to biome (Ibarra et al., 2020).

Woodpecker species are the quintessential primary cavity excavators and indicator species of forest biodiversity (Martin et al., 2021; Mikusiński et al., 2001). Species-specific differences in preferences for tree species, nest height, and activity times make a larger diversity of woodpecker species to provide a larger number and diversity of cavities (in terms of size, shape, height, and substrate) (Nappi et al., 2015; Vergara & Schlatter, 2004). Although the diversity of secondary cavity users may depend on the diversity of cavity excavators in forest patches (Mikusiński et al., 2001), other factors such as feeding resources, interspecific interactions (e.g. predation, parasitism, competition), structural forest complexity, tree species diversity and disturbances (e.g. fires, logging) may also limit population of these organisms (Baral et al., 2018; Baroni et al., 2021; Vaillancourt et al., 2009). Environmental conditions could limit the role of primary excavators as ecosystem engineers either when the availability of non-excavated cavities is high enough or when the habitat conditions are not suitable for primary excavators.

The distribution patterns of woodpecker species at biogeographical scales are an increasingly studied topic in the fields of conservation and protected area planning (Ilsøe et al., 2017; Moradi et al., 2019; Vergara-Tabares et al., 2018). These studies have revealed that the richness of woodpecker species is globally shaped by forest cover and climatic properties (Ilsøe et al., 2017). The use of species distribution models (SDM) to map the distribution of woodpecker assemblages has provided a framework for identifying areas where either excavated cavities may be a limiting resource or great diversity of primary excavators species coexists (Moradi et al., 2019; Virkkala et al., 2022). SDMs have been related to a Grinellian niche approach, using environmental variables to predict the potential distribution of species (Soberón, 2007; Soberon & Nakamura, 2009). However, biotic variables, and in particular, interspecific interactions, are usually not considered by SDMs, despite the well-known fact that the geographical patterns of species distribution are affected by the presence of and the interaction with other species (Anderson, 2017; Gherghel et al., 2018; Godsoe et al., 2017; Stephens et al., 2020). When compared with climate-based approaches, studies on how ecological interaction shapes the distribution of species assemblages at biogeographical scales have remained neglected (Anderson, 2017; Zurell, 2017). A few studies have evaluated the positive relationship between the diversity of prey species and predators at the biogeographical scale (Alaniz et al., 2020; Gherghel et al., 2018) as well as the overlap of niche requirements and geographical distribution among mutualistic species (Vasconcelos et al., 2017). Even less studied are the macroecological processes that shape the facilitation networks of cavity users under a niche modelling approach.

In this study, we address the relationship between primary excavators and secondary cavity users of southern South American temperate and Mediterranean forests. In these biomes, a few species act as primary cavity excavators with some of them, such as woodpeckers, being considered indicator species (Ojeda, 2004; Ojeda & Chazarreta, 2006). However, the community-level impact of woodpeckers may also be influenced by the environmental characteristics of those temperate forests, such as tree species diversity, structural heterogeneity, and tree decay stage (Alaniz et al., 2021; Soto et al., 2018; Vergara et al., 2021). Disentangling the role of woodpeckers as ecological engineers structuring cavity-nesting networks at broad spatial scales remains a challenging topic. In this study, we faced the biogeographic ecological interactions among woodpeckers and secondary cavity users by developing a novel approach combining multiple methodological tools. This approach was used to assess the potential of primary excavators as biogeographic indicator species across temperate and Mediterranean forests of southern South America. Particularly, we aim to test the following two hypotheses:

1. The richness of secondary cavity users is influenced by primary excavators, while forest characteristics are less relevant (the excavated cavity limitation hypothesis). This effect is predicted to be stronger for obligated cavity users.
2. The richness of secondary cavity users is influenced by forest characteristics, while the effect of primary excavators is less relevant (the habitat limitation hypothesis). This effect is predicted to be stronger for forest specialists than for habitat generalists.

2 | MATERIALS AND METHODS

2.1 | Study area and target species

Our study area encompasses southern South American forests found from 30°S to 56°S in Chile and western Argentina, an area comprised of three ecoregions: the Chilean matorral or sclerophyll forest in the North, the Valdivian temperate forest, and the Magellanic subpolar forest in the southernmost part of the continent (Olson et al., 2001). The cavity-nesting network in these biomes is formed by four primary excavators: the Magellanic woodpecker (*Campephilus magellanicus*), Chilean flicker (*Colaptes pitius*), striped woodpecker (*Dryobates lignarius*), and white-throated treerunner (*Pygarrhichas albogularis*), while the number of secondary users estimated by different studies (Altamirano et al., 2017; Ibarra et al., 2017) amounts to 28 species of birds, 7 of mammals, 2 reptiles, and one amphibian. Previous studies have suggested that the presence of these woodpeckers is highly linked with the diversity of other bird species, granting them the status of forest ecosystem engineers (Ojeda, 2004).

We identified secondary cavity users and host trees through a systematic literature review of indexed scientific articles on Web of Science, combining the following key words: 'cavity', 'users', 'nesters', 'secondary', 'Chile', 'Temperate', 'Mediterranean', and 'forest ecosystems'. We also reviewed previous studies that have listed the number of secondary cavity user species (Altamirano et al., 2017; Ibarra et al., 2017). To classify species, we used published information about dependence on cavities (Altamirano et al., 2012) and habitat preferences (Vergara & Armesto, 2009). Information of species-specific ecological traits was systematized as: (A) level of dependence on cavities, (B) level of dependence on forest ecosystem, (C) type of cavity used (non-excavated/excavated) and behaviour of cavity (nest/refuge), and (D) host tree species. In this analysis, we only included vertebrate species including bird, mammal, reptile, and amphibian species (Table S1). However, we did not group species based on the type of cavities they use to breed or rest (excavated vs. non-excavated) due to the following reasons: (1) more than a quarter of species lacked information about the cavity type; (2) some studies reported data from one or a few individuals per species; and (3) most studies did not report the number of nests observed. In particular, some bird species known to be open nesters (e.g. *Turdus falcklandii*, *Phrygilus catatonic's*, *Elaenia albiceps*) were assigned as secondary cavity nesters because they behave marginal cavity nesters (Jara et al., 2019; Ojeda & Trejo, 2002).

2.2 | Analytical framework

In order to estimate the geographic distribution of primary cavity excavators, secondary cavity users and host tree species, we used SDM based on the Maximum Entropy technique (Phillips et al., 2017). With this technique, we generated a series of species
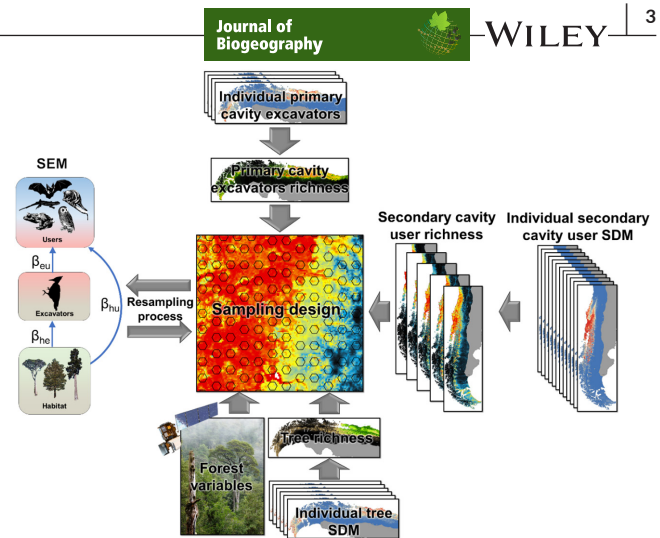

FIGURE 1 Methodological chart showing the sequence of analyses used in this study.

richness maps for each species group, distinguishing among forest specialists, habitat specialists, obligated cavity users, and mammals. Additionally, we generated a characterization of forest variables relevant for secondary cavity nesters based on the literature review. We used a sampling design based on non-neighbouring hexagon units, in which species assemblages and forest variables were characterized. We selected equal-area hexagon cells for our analysis because they minimize edge effects, their shape and dimensions are consistent across space, and their dimensions encompass in most cases both fine and course input datasets, as previous studies have shown (La Sorte et al., 2019). Finally, we developed structural equation models (SEMs) based on the sampled data to evaluate the effects of primary cavity excavators and forest characteristics across the nesting-cavity network (Figure 1).

2.3 | Species inputs

To fit SDMs, we compiled a series of species occurrence records from different sources for each species. In the case of animals, we included occurrences from: (A) Global Biodiversity Information Facility (GBIF), considering occurrences with specific geographical coordinates and deleting duplicated records, (B) Ebird database, (C) previously published studies and (D) our own records from trap cameras, systematic sampling and censuses accumulated in the last 10 years. In the case of trees, we included occurrences from GBIF and Scherson et al. (2017), considering occurrences with specific geographical coordinates and deleting duplicated records. The list of occurrences appears in Table S2, completing 121,699 occurrences of which 117,746 are animals and 3953 are trees (Table S2). Then, to reduce the impact of spatial autocorrelation between occurrences, we applied the spatial rarefy function in a geographic information system (Brown, 2014). We maintained points more than 15 km apart, deleting the points with less than this distance, which prevents some occurrences to be excessively weighted in model training

(Brown, 2014); this procedure reduced the number of occurrence records to 14,179 and 2292 non-autocorrelated occurrences for animals and trees, respectively.

2.4 | Environmental inputs

The second input used by SDM corresponds to environmental predictor variables, which are used to estimate the potential distribution based on the niche requirements of species (Elith et al., 2011). We included variables associated with climate and biophysical characteristics (Table S3). Climate variables included the 19 bioclimatic variables from the WorldClim 2 project plus wind speed (Fick & Hijmans, 2017). Biophysical variables were processed in the Cloud-based platform Google Earth Engine (Gorelick et al., 2017; code available in supplementary data) and included elevation, Evenness Vegetation Index, Normalized Difference Water Index, Net Primary Productivity (NPP), Vegetation Continuous Fields (VCF), Soil Organic Carbon, the topographic diversity index, Net Evapotranspiration and aboveground biomass (AGB). All the variables were estimated at 1 km of pixel resolution, considering the coarser pixel of the used products (WorldClim 2). We also distinguished forest habitats in terms of the forest type (evergreen, sclerophyll, and deciduous) and successional stage (mature or secondary). The cover percentage of each forest type, and successional stage was estimated from the National Vegetation Resources Cadaster (CONAF, 2011).

2.5 | Modelling procedure

We modelled each species independently, generating an initial exploratory model that included the non-spatially autocorrelated occurrences and the complete set of environmental variables as inputs. This model was run considering cross validation or bootstrap techniques in MaxEnt 3.4.1 depending on the number of occurrences (Table S3), using the jackknife technique to calculate permutation importance (PI) and the percent contribution (PC) of each variable to the model (Tables S4 and S5). The background modelling area considered 100 km from forest vegetation reported by Olson et al. (2001) from 30°S to 56°S. We estimated the correlation between pairs of variables using the Spearman correlation index (*rho*). Then, to avoid a potential model overfitting due to the collinearity among environmental variables, we selected the variables with highest PI and PC, as well as low correlation index (*rho* < |0.7|), from the initial exploratory models. Finally, we ran a final model including the non-autocorrelated occurrences and the selected environmental variables after checking for collinearity and considering cross validation or bootstrap techniques depending on the number of occurrences. We assessed the accuracy of the model using the area under the curve (AUC) of the receiver operating characteristic curve (Table S3). This process was performed independently for each modelled species.

2.6 | Data analysis

To estimate species richness (S), we summed the median suitability values from each species per group, considering that a *proxy* for richness (Alaniz et al., 2020). These groups corresponded to different guilds of cavity excavators (*n* = 4 species), secondary cavity users (*n* = 36 species) and host trees (*n* = 34 species). Additionally, based on our literature review, we grouped the secondary users in four sub-categories, namely obligated cavity user birds (*n* = 13), habitat generalist birds (*n* = 13), forest specialist birds (*n* = 6) and mammals (*n* = 7) (Table S1; data available at: https://doi.org/10.5061/dryad.zs7h44jdj). These groups (guilds) were not exclusive as the traits of some species led them to be classified into more than a single group.

We calculated habitat variables that are known to affect forest birds and mammals based on previous studies (Díaz et al., 2005; Estades & Temple, 1999; Quilodrán et al., 2012; Soto et al., 2017). To characterize forest decay, we included the Plant Senescence Reflectance Index (PSRI), which was calculated as the median of all Sentinel-2 PSRI derived images for each summer season between 2014 and 2020, considering less than 5% of cloud cover between 30°S and 42°S and less than 40% at south of 42°S (*n* = 1016). To characterize forest maturity, we included the tree canopy height for the year 2005 based on Simard et al. (2011). Additionally, we added NPP, AGB and VCF as important variables related to succession and forest dynamics (Table S2). We also included the richness of *Nothofagus* trees because some primary cavity nesters (e.g. Magellanic woodpeckers) have preferences for *Nothofagus* trees by providing woodpeckers with a large diversity and abundance of wood-boring insects (Fierro et al., 2023; Vergara et al., 2022).

We used 25 km^2 hexagonal grid cells to quantify each estimate of species richness (trees and vertebrates) and forest characteristics using the zonal function in the 'Raster' package in R (Hijmans & Etten, 2012) (*n* = 4320). Sampling and analytical methodology involved the following steps:

(A) Selection of non-neighbouring hexagonal cells separated by more than 20 km between them. We considered a unit surface of 25 km^2 based on the area requirements (ca. 1 km^2 home range) of the Magellanic woodpecker (Ojeda & Chazarreta, 2014; Soto et al., 2012), the largest primary cavity user in the studied cavity-nesting network. Thus, we assumed ca. 25 non-overlapped territories of Magellanic woodpeckers (25 pairs ~50 individuals) could be found in a cell of 25 km^2 covered by continuous native forest, which is consistent with theoretical expectancies of minimum viable population size (Shoemaker et al., 2013). The distance between hexagons centroids was estimated using the *spThin* library in R, which provides a minimum distance to avoid spatial autocorrelation in sampling design (Aiello-Lammens et al., 2015).

(B) A resampling procedure to draw spatially independent samples of species diversity and forest characteristics to be analysed later. We assumed that each sample represents a spatially independent realization of the nesting-cavity network within the geographical range of

the biome. We randomly drew 30 spatially independent samples of 150 units each from a total of 4320 possible units.

(C) The sampling data were fitted to SEMs using the PiecewiseSEM R package (Lefcheck et al., 2016). We developed a single path model representing the potential relationships among primary cavity users, secondary cavity users, and environmental variables from a bottom-up perspective, where secondary cavity users are at the upper levels, primary cavity users at intermediate levels, and environmental variables at the bottom. SEMs were developed using the *psem* function, which deals with variables that have different distributions of errors and random effect structures. We used linear mixed-effect model (LME) regressions through the *lme* package in R. The richness of secondary cavity user and primary cavity excavators were specified as response variables, while environmental variables and excavator diversity were considered predictor variables. SEMs dealt with the correlated error between predictor variables by incorporating the correlation between predictors, using a d-separation test to assess the conditional independence assumption. Response variables were previously log-transformed to adjust a Gaussian distribution, and environmental variables were standardized to have unit variance and mean zero. We included a latitudinal random factor controlling for latitudinal gradient in species distribution. We also explored interactive effects between predictors but avoided interactions between pairs of collinear variables. However, we did not find significant interactions to be retained in the final SEM. Spatial autocorrelation in the residuals of SEM was assessed using Mantel test. We computed model-averaged coefficients based on the Akaike information criterion weights of the 30 SEMs using the RMark package in R. The effect of each relationship was interpreted based on the averaged standardized coefficients value and their confidence intervals (CI), with CI values different from zero considered significant effects. We reported the conditional and marginal regression coefficients. Fisher's *C* statistic was used to assess the goodness-of-fit of SEM, with significant ($p<0.05$) *C* values indicating that the model fails to fit data due to missing links (Shipley, 2013).

3 | RESULTS

3.1 | Species distribution models

All the models reached a good degree of fit level with a median AUC of 0.837, 0.927, 0.941 and 0.954 for birds, mammals, herptiles and trees, respectively (Table S2). For birds, mammals, and herptiles the most important variables were VCF, annual precipitation and elevation with a median PC of 20.0, 13.4, and 9.2, respectively (Tables S4 and S5). The variables with the highest median PI for these groups corresponded to elevation, wind speed, and VCF with 10.4, 6.8, and 4.3, respectively (Tables S4 and S5). The variables with the highest PC were seasonal precipitation, precipitation of wettest month, and VCF, with a PC of 27.9, 10.6 and 10.6, respectively. The variables with the highest PI were seasonal precipitation, wind speed and precipitation of wettest month with 19.3, 16.9, and 8.4, respectively.
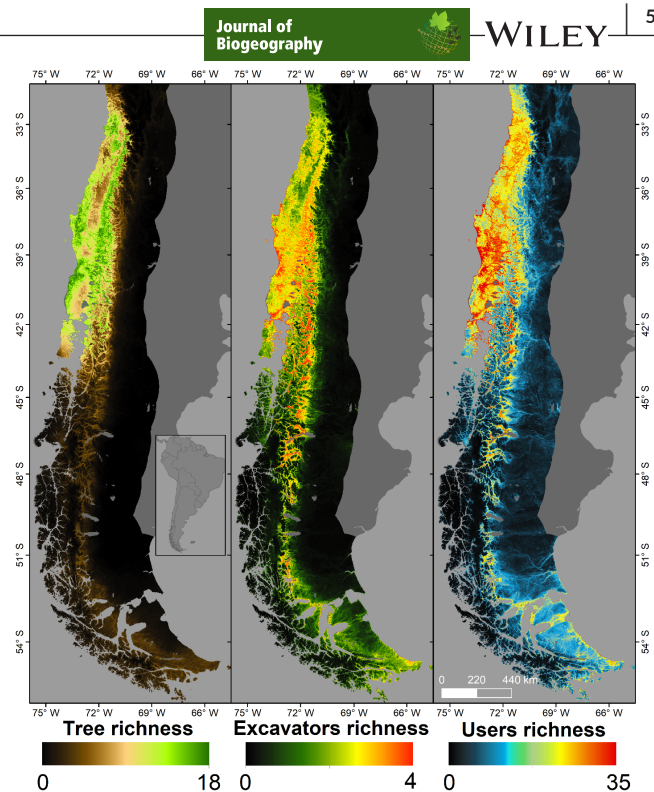

FIGURE 2 Richness (S) of cavity tree hosts (a), cavity excavators (b) and total secondary cavity users. (c) Based on SDMs (individual SDM in Figures S1–S3). SDM, species distribution models.

The central zone of Chile (32°S to 42°S) concentrated the highest richness of trees, primary excavators, and secondary users (Figure 2), decreasing to the southern zone until 56°S (individual species SDMs in Figures S1–S3). The central valley from 32°S to 37°S has a low richness of trees and primary excavators in contrast to secondary cavity users, which have a higher richness (Figure 2). A similar pattern is present in habitat generalist birds, which had a higher richness between 32°S and 34°S, while obligated cavity user birds achieved their highest richness between 34°S and 37°S (Figure S4). Forest specialists have a higher richness between 37°S and 41°S, while mammals were mainly concentrated on the coastal zone between 32°S and 39°S (Figure S4).

3.2 | Nesting-cavity network

The richness of secondary cavity user groups was associated with that of primary excavators but also was affected by forest characteristics (Figure 3; see details in Tables S6 and S7). The richness of primary excavators had a strong positive relationship (standardized coefficient >0.77) over all the guilds of secondary users except for mammals (standardized coefficient=0.4) (Figure 4 and Figure 5a–e). The richness of the different guilds of secondary cavity users was differently affected by habitat variables, except for vegetation biomass, which negatively affected all species, obligated cavity users, habitat generalists, and habitat specialists (Figures 4 and 6a–d). Habitat specialists were richer as net primary productivity increased
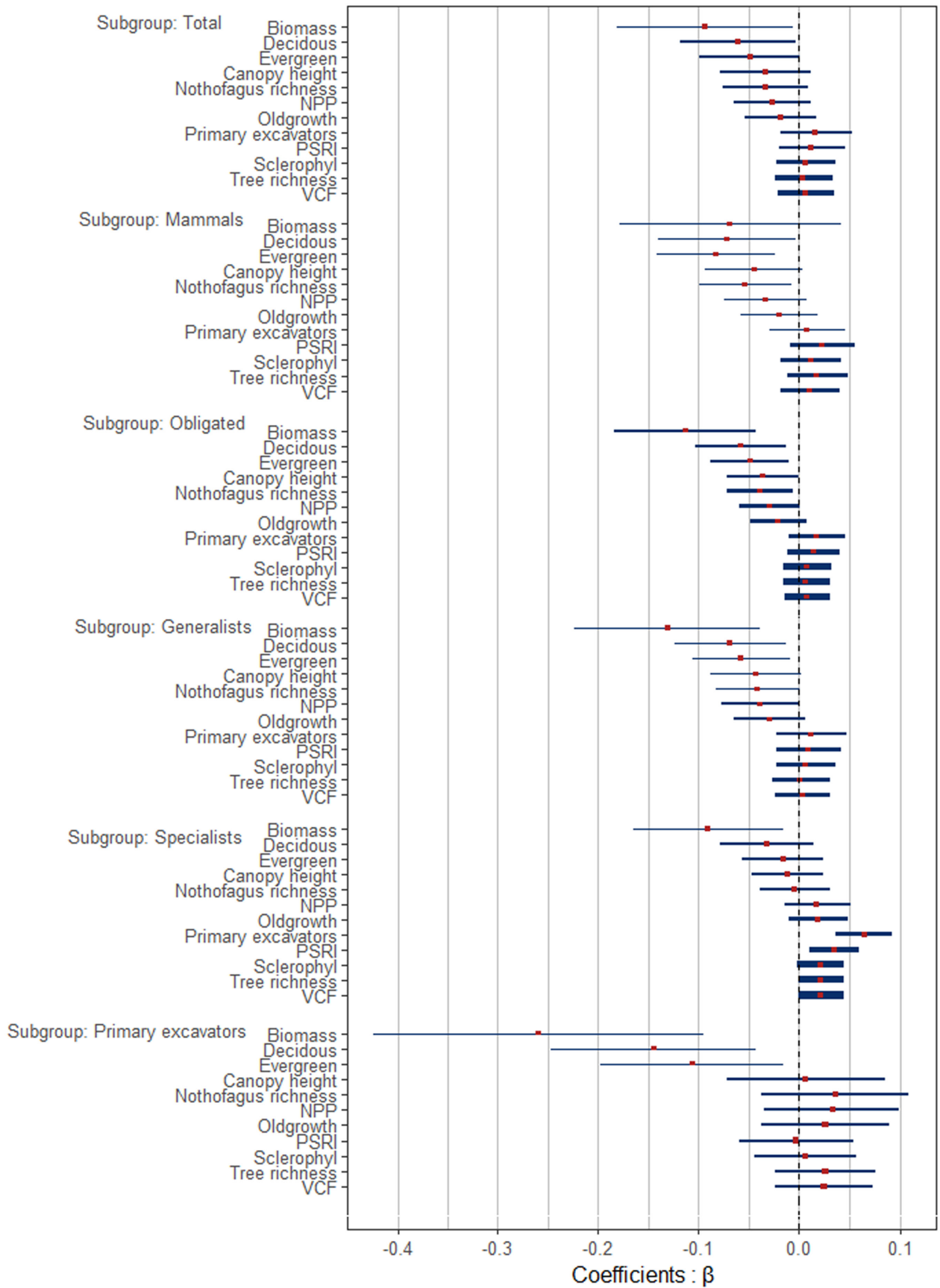
FIGURE 3 Model-averaged coefficients (±95% confidence intervals) included in the supported structural equation model. Coefficients represent the relationships of environmental variables with primary cavity users and secondary cavity user groups, as well as the relationships of primary cavity users and secondary cavity user groups.

(Figure 6e) but also decreased in diversity as the cover of sclerophyll forest cover increased (Figure 6f). Mammals were richer when the PSRI (Figure 6g) and the richness of trees increased (Figure 6h). Primary excavators were less diverse as biomass increased (Figure 7a) but became richer when the tree height (Figure 7b), the richness of *Nothofagus* tree species (Figure 7c), and the richness of tree species increased (Figure 7d).

4 | DISCUSSION

Our findings provide evidence for the biogeographic facilitation limitation hypothesis, according to which primary cavity excavators play an important role in structuring the cavity-nesting network in Southern South American Forests. Most groups of cavity users (not only the obligated ones) were strongly affected by primary excavators, thus supporting the excavated cavity limitation hypothesis. Mammals were an exception as they were better supported by environmental variables, as stated by the habitat limitation hypothesis. Mammals may be influenced by other resources different from cavities such as seeds and insects, which are more abundant in forests with a high diversity of trees or structural complexity (Delciellos et al., 2015; Schlinkert et al., 2016). In fact, the native marsupial *Dromiciops gliroides* exhibits high phenotypic plasticity in selecting nesting substrates, which if present in other small mammal species would make them less influenced by primary excavators (Vazquez et al., 2020). However, except for mammal species, we did not find support for the positive
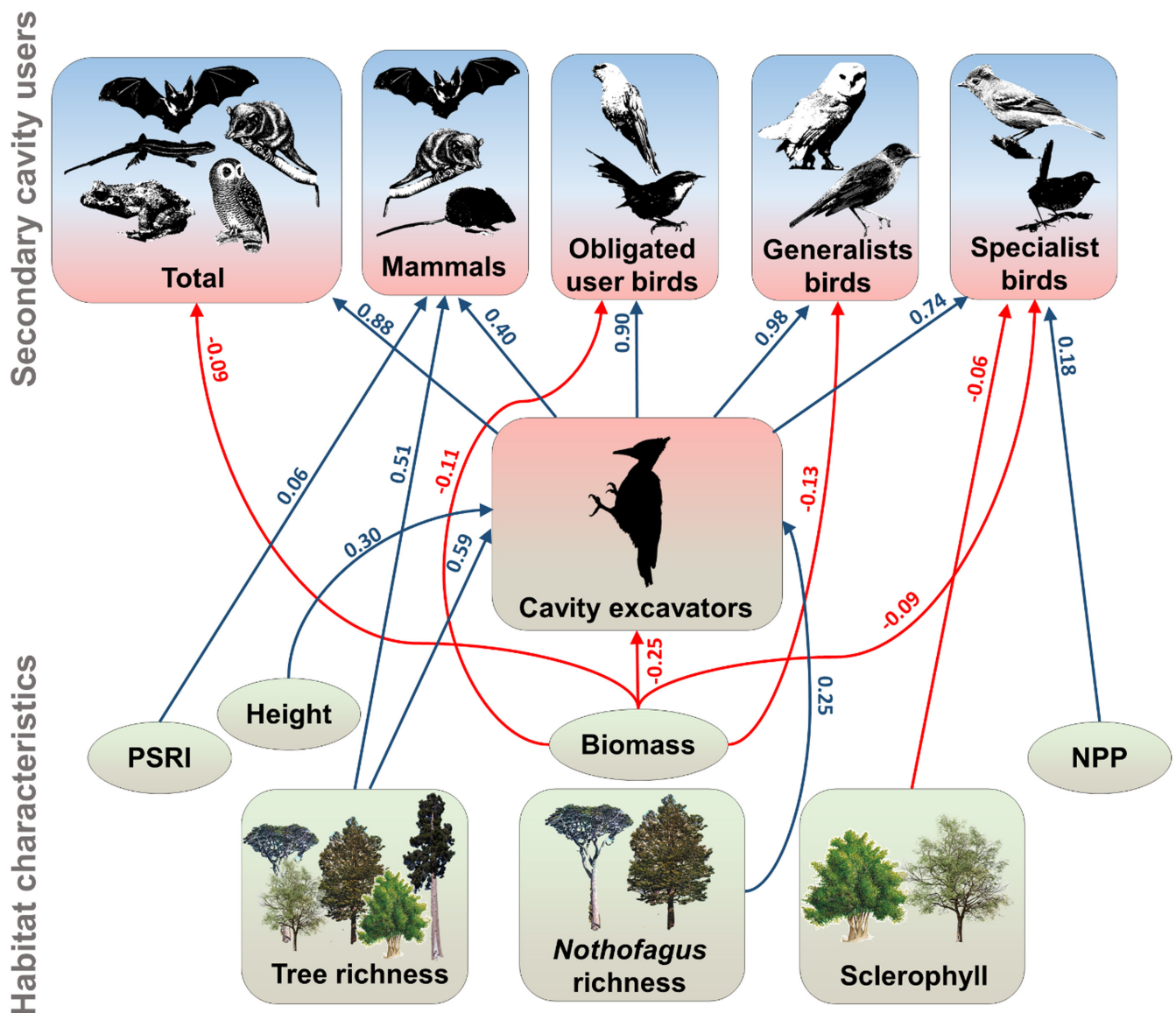

FIGURE 4 Path diagram representing the supported structural equation model testing for relationships between cavity excavators, the different groups of secondary cavity users and habitat characteristics (Figure 3). Only significant paths between variables are shown, each being labelled with its standardized coefficient (higher values indicate stronger relationships). The relationships between all the evaluated variables are present in Figure S4 and Table S5. Correlations were not included in the path diagram but are available in Table S6.
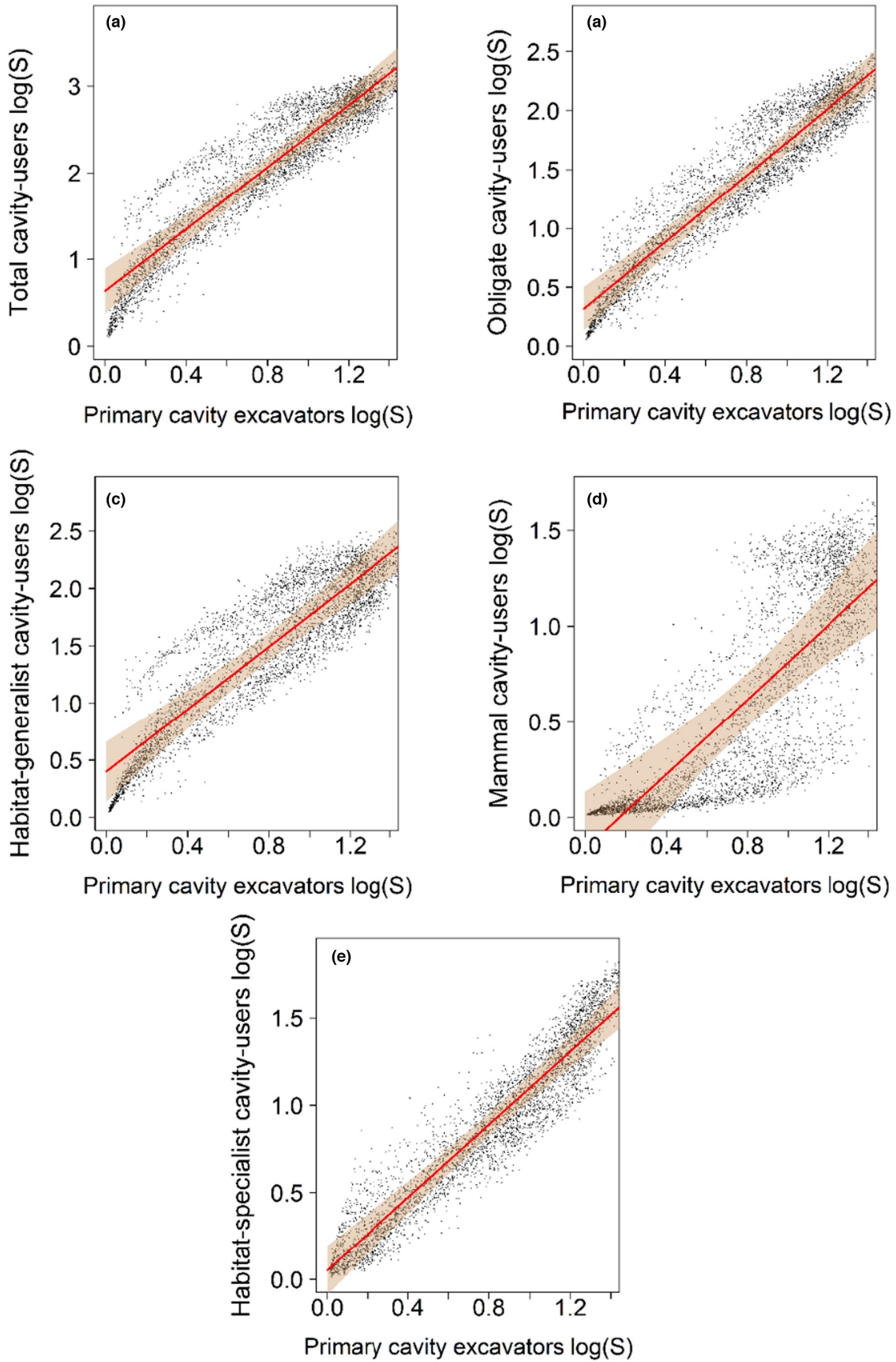
FIGURE 5 Predicted positive relationships between the log-transformed species richness (S) of primary cavity excavators with the log-transformed species richness (S) of total cavity users (a), obligated cavity users (b), habitat-generalist cavity users (c), mammal cavity users and habitat-specialist cavity users (e).
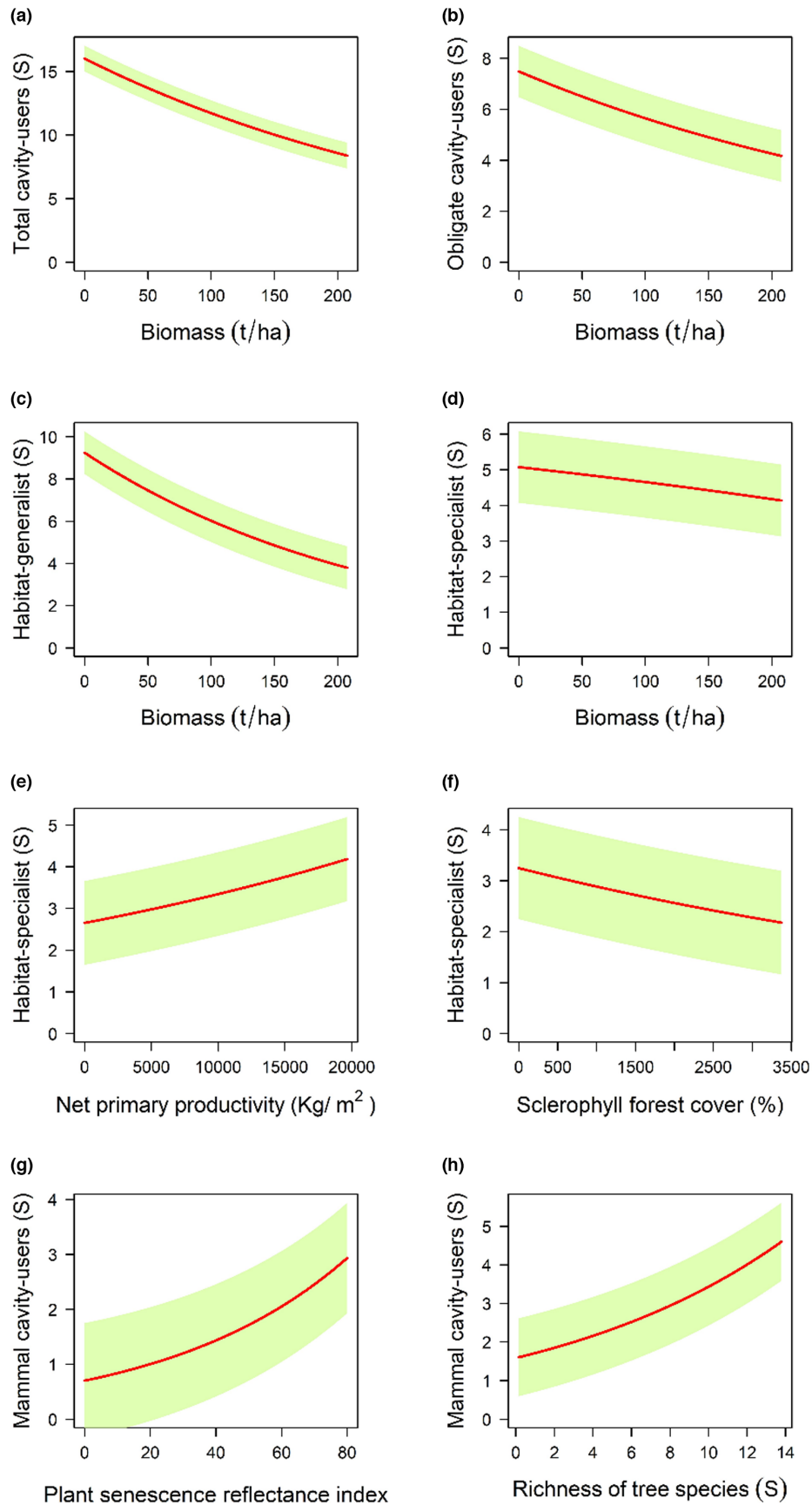
FIGURE 6 Predicted relationships between environmental variables and the richness (S) of secondary cavity users, including all species (a), obligated cavity users (b), habitat generalists (c), habitat specialists (d–f), and mammals (g, h).
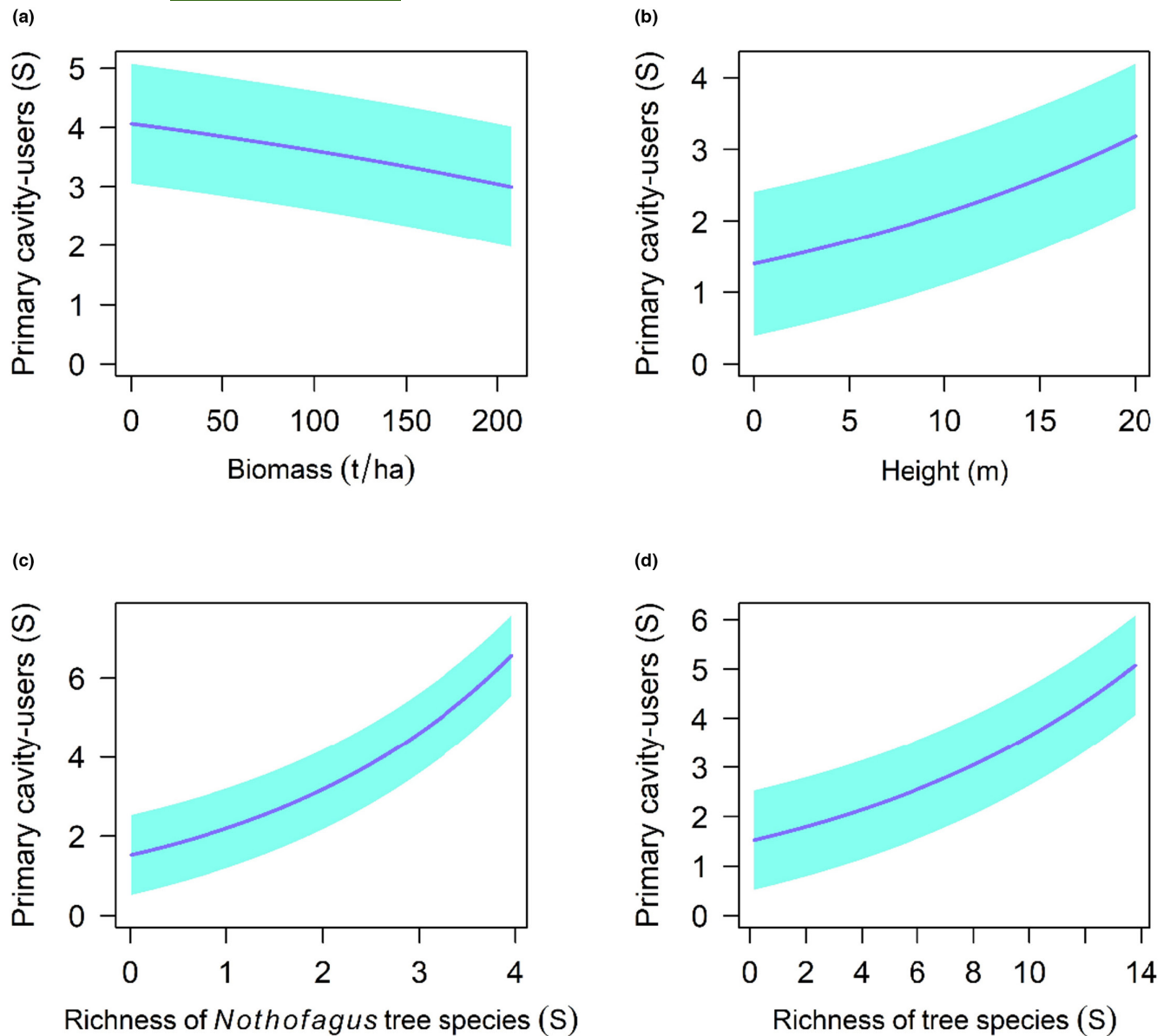
FIGURE 7 Predicted relationships between environmental variables and the richness (S) of primary cavity users.

relationship of mature forests and tree senescence (PSRI) on the richness of secondary cavity users, both variables proximately related to the creation of non-excavated (decay) cavities in trees (Boyle et al., 2008; Moreira-Arce et al., 2021). Primary cavity nesters also were neither affected by PSRI nor mature forest cover. Thus, the lack of relationships with forest characteristics could be considered as evidence of the ecological role of primary cavity users but also prevented us from drawing conclusions about the relative importance of woodpecker cavities on non-excavated cavities. We suggest more studies are necessary to discriminate which species select woodpecker cavities against decay cavities in the Mediterranean and temperate forests of South America, which may involve long-term field experiments and large sample sizes. In addition, the uncertainty inherent to broad-scale assessment, as in this study, can lead to the misinterpretation of some

relationships, especially when analysing species interactions. Although SEMs deal with multiple intercorrelated variables, the mechanistic interpretation of our results needs additional support to be considered legitimate causal relationships.

The contribution of primary excavator richness to the diversity of secondary cavity users was influenced by forest attributes that act as biogeographic filters of primary excavator diversity. The negative relationship of biomass on the richness of primary excavators and tree cavity users could arise from two reasons: (A) Since exotic forest plantations in central Chile have high biomass and do not provide tree cavities (Goded et al., 2019; Quilodrán et al., 2012), the broad-scale negative relationship of biomass could result from the extensive area planted with exotic forests in central Chile (Uribe et al., 2020); (B) the latitudinal gradient of tree species richness is inverse to that of forest biomass. A decreasing latitudinal pattern

in species richness has been identified south of 35°S, which is associated with the presence of glaciers during the last glacier maximum (Samaniego & Marquet, 2009; Segovia et al., 2013; Villagran & Hinojosa, 1997). We suggest that a combination of both relationships could explain the negative link between the species groups and biomass at the biogeographical scale.

We found a positive relationship between primary cavity excavators with tree richness, Nothofagus tree richness, and canopy height, suggesting primary cavity excavators benefit from forest stands composed of multiple species of large mature trees (Fierro et al., 2023; Vergara et al., 2017). Previous studies have evidenced that the abundance of Magellanic woodpeckers is positively associated with large-diameter senescent trees and dead trees by providing woodpeckers with feeding resources (e.g. woodboring larvae of saproxylic beetles) but also by being used as substrates for cavity excavation (Vergara et al., 2017; Vergara & Schlatter, 2004). In particular, Nothofagus trees offer a variety of resources for primary and secondary cavity users, such as a high abundance of invertebrates (Espinosa et al., 2016; Vergara et al., 2022). In contrast, we found a negative association between sclerophyll forest cover and habitat specialists resulting from the structure and composition of sclerophyll forests, which are less diverse in tree species and have a less developed canopy than that of southern temperate forests (Alaniz, 2019). The most specialized birds of Southern South American forests are understory and foliage-canopy specialists by feeding on insects and having populations that fluctuate depending on forest productivity. From a network perspective, environmental variables that affected the richness of primary cavity users only (i.e. tree height and Nothofagus tree richness) could have exerted bottom-up control on the richness of secondary cavity users, with effects propagating to the highest trophic levels. Moreover, some environmental variables (NPP, sclerophyll forest, and PRSI) had additive and direct effects on the upper levels (richness of secondary cavity users). Finally, the richness of primary and secondary cavity users shared their responses to some environmental variables (biomass and tree species richness), suggesting those variables exerted control on multiple levels. This interpretation is consistent with a previous study testing how the effects of environmental variables on invertebrates transmit to insectivorous birds in temperate Chilean forests (Vergara et al., 2020) and provide evidence of the importance of bottom-up forces in cavity-nesting networks.

The important role of woodpeckers has been highlighted at a local scale, where positive feedback with animal and fungus diversity has been found in different forest ecosystems worldwide (Lõhmus, 2016; Mikusiński et al., 2001; van der Hoek et al., 2017). However, their role on the spatial patterns of cavity-nesting networks has remained less explored, with a few studies exploring patterns of co-occurrences among cavity excavators and secondary users (van der Hoek et al., 2020), and discussing the influence of climate and biomes on nesting-cavity network at regional scales (Ibarra et al., 2020). In regions with a low richness of woodpecker species, like southern South America (Ilsøe et al., 2017), the local loss of a few woodpecker species may cause important impacts on the facilitation networks of cavity users. In this study, we unravelled these relationships at a biogeographic scale, using an approach that is not exempt from limitations. First, our analyses are based on the potential spatial distribution of organisms, implying that our results should be taken with caution since other factors could be playing an important role in the modulation of the actual distribution of species (i.e. food distribution, disturbances, predation, competition; Hof et al., 2012, Palacio & Girini, 2018). Additionally, we estimated the correlation of richness at a spatial dimension based on suitability. However, actual species richness could vary depending on other factors associated with dispersal or disturbances (Del Toro et al., 2019). Studies have identified that currently SDM and other methods such as Macroecological Models are able to estimate species richness with similar results (Biber et al., 2020; Grenié et al., 2020; Moradi et al., 2019). Another source of uncertainty is related to the estimation of biophysical variables representing ecosystem processes and vegetation characteristics, such as primary productivity, canopy cover, and biomass density. We recommend evaluating these dynamics at finer spatial scales, comparing zones with different species richness in other ecosystem types and integrating other methodological approaches. It should be borne in mind that our representation of the cavity-nesting network is a simplification of the true complexity of this network, which also involves other organisms such as insects and wood-decaying fungi (Jusino et al., 2015, 2016; Micó, 2018). Fungi are known to be important in facilitating cavity generation, and in using birds for dispersal between cavities (Jusino et al., 2015, 2016). Saproxylic insects also are an important group for cavity-nesting network by representing a trophic resource for primary excavators and secondary cavity users, but also by contributing to wood decomposition through the activity of their larvae in dead trees (Fierro & Vergara, 2019; Micó, 2018). Unfortunately, no information on these species is available for the region under study. Future studies on the role of these taxa in the cavity-nesting network would be a great contribution to better understand the complexity of this network.

Woodpeckers have been considered forest ecological engineers as their tree excavation activity facilitates the presence of several species (Mikusiński et al., 2001). In this study, we provide evidence in support of this claim and in particular find that ecological assemblages of secondary cavity users are highly influenced by the richness of cavity excavators at a broad spatial scale. Our results highlight the usefulness of the development of new approaches for analysing ecological networks and their underlying processes from a macroecological perspective.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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BIOSKETCH

The team of authors is a group of researchers specialized in the study of the distribution, abundance and conservation of animal and plant species in southern South America, including birds, mammals, reptiles and trees, with recognized experience in macroecology, forest ecology and landscape ecology, as well as with advanced knowledge on geospatial tools and statistic models.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.