From Tree-cavity to Landscape: Habitat Preferences and Fitness Operates Across Scales for an Old Relict Species of Southern South-america

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Abstract

Animals select their habitats from available resources in a way that should maximize fitness, and thus habitat preferences are generally predicted to be adaptive. However, there may be a mismatch between habitat preferences and fitness due to factors such as limited availability or disturbance of breeding habitats. In this study, we examine whether preferred nesting habitat attributes are linked to fitness (nesting success and number of fledglings) of White-throated treerunner (*Pygarrhichas albogularis*), an obligate excavator and tree cavity nester across four spatial scales: (1) cavity, (2) nest-tree, (3) forest-stand, and (4) landscape. During eight breeding seasons (October to February), between 2010 and 2018, we found and monitored 65 treerunner nests in Andean Temperate Forests, Chile. Our results show a multiscale response for both habitat preferences and fitness: both nest-tree and landscape scales were the most influential variables for nesting habitat preferences, while all habitat scales influenced fitness. The probability that a given habitat is used for nesting increased with larger trees, advanced tree decay classes, and forest cover. Nesting success was positively related with cavity entrance diameter, height, and distance from the forest edge. On the other hand, the number of fledglings decrease with larger trees and increase with decay class. Our findings suggest a match between habitat preferences and fitness. Finally, treerunners prefer areas with a relatively high forest cover and their nesting success increased with relatively lower tree density, suggesting that old-growth forests comprise the best integration of multiscale habitat attributes for this species.

INTRODUCTION

Animals select their habitats from available resources in a way that should maximize fitness [1]. Thus, it is expected that habitat attributes associated with habitat selection will also be those most strongly linked to fitness [2]. Habitat preferences (i.e. the final pattern of habitat used with respect to its availability) will generally be adaptive, under the pressures of natural selection, if a species obtains maximum fitness [3,4]. However, there may be a mismatch between habitat preferences and fitness by factors such as temporal changes in habitat features after territory establishment [5] and rapid disturbance of reproductive habitats [6,7].

Habitat attributes influence fitness via the costs (e.g. predation risk) and benefits (e.g. food availability) of habitat preferences[8]. There is evidence that avian habitat preferences are scale-dependent and hierarchical phenomena [9]. Scales at which habitat selection may occur range from microsites selected for nesting or foraging to the entire geographic range of a species [10]. Thus, differences between nesting and available sites reported for excavators (i.e. species that excavate their nesting cavities in trees) may be because there are multiple scales operating in nesting site selection processes, from fine to coarse scales [11,12]. Excavators should assess, for example, the tradeoff between a secure nesting substrate for excavation and the distance to a foraging area [13]. Multiscale studies allow identifying important scales concerning individual perception of their habitats, otherwise difficult to detect when knowledge of the ecology of the study species is limited [14].

The White-throated treerunner (*Pygarrhichas albogularis* King 1831), is a poorly known Furnariid endemic to South American temperate and Mediterranean ecosystems, mainly found in central and southern regions of Chile and Argentina [15]. This species is considered a “living fossil” or “old relict” as it is the only living species of the genus *Pygarrhichas* [16,17]. White-throated treerunner is one of the four species of tree cavity excavators in these ecosystems [18]. As an excavator, this species relies on habitats with presence of trees suitable for excavation [19]. Although this species has been suggested as a key habitat facilitator for several avian and mammalian cavity-nesting species in southern South America [20,21], there is only one study on the ecology of treerunners and focused on foraging use of tree species [22]. There are occasional community level studies that included treerunners as part of an avian assemblage [23–32]. Thus, this research advances the knowledge exploring nesting habitat preference and fitness of treerunners in the centre of its distribution.

In this study we examine the nesting tree preference of treerunners and whether their preferred habitat attributes are linked to fitness through a two-step modelling approach. First, we assess habitat preferences analyzing the link between habitat attributes and preferences of nesting sites at three spatial scales: (1) nest-tree scale, (2) forest-stand scale, and (3) landscape scale. Second, we assess whether habitat attributes of preferred reproduction sites are linked to fitness (represented as nesting success and number of fledglings) at the same three spatial scales, adding cavity characteristics as a fourth smaller spatial scale in the analysis. We hypothesize that (1) preferred reproductive habitat attributes differ to those of surrounding available habitat and that (2) habitat attributes at each spatial scale are linked to improved fitness, and (3) there is a match between attributes of habitat preferred and fitness. This study delivers better understanding of forests attributes that must be maintained to ensure habitat for this and other coexisting cavity nester species in south temperate forests [31].

Results

Between 2010 and 2018, we located and monitored 65 White-throated treerunner’nests (273 to 1,342 m of elevation), 84.6% of which were excavated in *Nothofagus* trees (Table 2). In average, treerunners used mid-size trees for nesting (DBH = 40.6 cm) within a broad range of trees (DBH range: 14.1 - 123.1 cm). Old dead trees with advanced decay (55%) and live unhealthy trees (35%) contained the great majority of its nests, with only 8% and 2% for recently dead and live healthy trees, respectively (Table 2). When we look at the specific substrate decay, 80% of the nests where in old dead substrates, and only 14% and 6% in live unhealthy and recently dead substrates, respectively. Fifty-eight nests (89.2%) were in freshly excavated cavities. White-throated treerunner laid an average of 3 eggs (range: 1 – 5 eggs). The overall nest survival was 75.03% (95% CI = 62.77 – 89.62%; n = 61 including only nests with known outcome). Regarding unsuccessful nests (n = 10), 6 failed because of predation, 3 were abandoned, and 1 nest failed because eggs were not viable (Table 2).

Breeding habitat preferences across spatial scales

Variation in the use of breeding habitat was best predicted by a model that included two tree-nest scale variables (DBH and tree decay), one forest-stand scale variable (basal area), and one landscape scale variable (forest area; Table 3). However, basal area was not significant ($b = 4.64 \pm 3.04$, $p > 0.05$). The probability that a given habitat is used for nesting increased with larger trees, advanced tree decay, and forest area. Tree decay was the strongest predictor of nest presence, followed by forest area, and DBH. Treerunners avoided healthy living trees ($b = -10.10 \pm 2.86$, $p < 0.01$), and the probability of nesting in a tree increased positively with each increasing decay class (Fig. 2A): unhealthy living trees ($b = 3.53 \pm 1.26$, $p < 0.01$), recently dead trees ($b = 3.76 \pm 1.46$, $p = 0.01$), and old dead trees ($b = 7.35 \pm 1.64$, $p < 0.01$). Even when both forest area and DBH are positively associated with preferred breeding habitats, GLMMs showed that the extension of forest area ($b = 4.09 \pm 2.11$, $p = 0.05$, marginally significant; Fig. 2B) influenced 82 times more than DBH ($b = 0.04 \pm 0.02$, $p = 0.01$).

Fitness outputs

For nesting success, there were two spatial scales included in the best models: cavity scale (entrance diameter and height) and landscape scale (forest edge, Table 3). Entrance diameter and forest edge had a positive effect on nesting success (daily survival rate). Nests with bigger entrances and further from the forest edge were more successful. Height was positively and marginally associated with nesting success ($b = 1.093$ 95% CI = 0.241 – 2.837, $p = 0.05$; Fig. 3A).

Regarding the number of fledglings produced, the final model only had parameters at the tree scale (DBH and decay class). DBH was negatively associated with number of fledglings ($b = -0.263$; CI = -0.508 – -0.021; Table 3; Fig. 3B). Decay class had an important effect on number of fledglings, being positively associated with unhealthy living trees ($b = 3.180$) and with recently dead trees ($b = 0.798$), while long dead trees were negatively associated with the number of fledglings ($b = -0.403$) (Fig. 3C).

Discussion

We found that both habitat preferences for nesting and nesting success measures for White-throated treerunner operate across multiple spatial scales. Similar to previous studies using multiscale approaches [7,13,33], at least one variable at each scale influenced nest site preferences and/or fitness (number of fledglings and nesting success) for our study species. Both tree and landscape scales were the most important variables influencing nesting habitat preferences, while cavity, forest-stand, and landscape scale variables were the most important in our assessment of nesting success (daily survival rate and number of fledglings). White-throated treerunner showed preferences for areas with a relatively high forest cover and that their nesting success increased in forests with a relatively low density of trees. This may suggest that old-growth forests, with extensive areas of forest with relatively less, but larger, trees compared to second-growth forests [34], contain the best complement of multiscale variables for this species.

White-throated treerunner tends to excavate new cavities (89%) every nesting season, with the remaining 11% consisting of reused cavities, all of which were excavated by this species during previous years. Thus, we have determined that this is a primary cavity-nester (i.e. obligate excavators; mainly excavates their own cavities, but occasionally use existing excavated cavities; [35]. Breeding pairs might use existing cavities depending on food and/or nest predation risk (e.g. in case their breeding attempt failed in their fresh cavity). Similarly to Red-naped Sapsuckers (*Sphyrapicus nuchalis*), which mostly excavate their own cavities, but about 11–12% reuse existing cavities, mainly cavities that were excavated in previous years [36]. White-throated treerunner are considered to have similar breeding behavior to nuthatches in North America, but Red-Breasted nuthatch (*Sitta canadensis*) tend to be facultative excavators (i.e. excavate about 50% of their nests, excavation rates vary annually; Aitken et al. 2002, Norris & Martin 2012) [38,39]. Thus, based on our study, treerunners are more extensively primary cavity excavators like Red-naped Sapsuckers or Downy Woodpeckers (*Dryobates pubescens*) rather than nuthatches that are facultative excavators [19].

White-throated treerunner nesting habitat preferences were mainly associated with variables acting at both tree and landscape scales, preferring relatively larger trees in advanced decay classes present in forested areas. This partially agrees with the results found for functionally similar species in the northern Hemisphere, such as Red-naped Sapsucker (*Sphyrapicus nuchalis*) [13]. The latter species preferred nesting habitats associated with landscape scale attributes, similar to treerunners, but only tree scale attributes were linked to fitness [13]. This suggests a hierarchical process of habitat selection in White-throated treerunner [40], in which several factors, at different spatial scales, influence the decision of choosing a given nest-site [7]. For example, the main trophic resource for treerunners are forest-dwelling arthropods in adult and larvae states [41,42], which are probably more abundant in multi-stratified forested landscapes with presence of all tree decay classes [43]. On the other hand, this species is choosing variables at finer scale for nesting too. Like other cavity-nesting species in the study area [29], tree scale attributes are the most influential factors for treerunners. This finding is similar to results reported for several primary cavity nesters such as woodpeckers in temperate forests of North America[19] and in tropical Atlantic forests of South America [44], where excavators strongly select live unhealthy and standing dead trees as nesting sites.

White-throated treerunner showed high values of nesting success, with 75% of its nests being successful. This high percentage strongly contrasts with the overall nesting success of avian communities in tropical forests of Brasil (42%)[45] and Dominican Republic (34%) [46], but similar to other cavity nesters and excavators such as Red-Breasted nuthatch (84%) [47], and Red-naped Sapsuckers (91%) [13]. We found that the entrance diameter of cavities was positively associated with nesting success, a counterintuitive finding, which might be associated with adult ability to successfully breed; and thus, stronger adults might be able to protect the nest and excavate larger cavities. Furthermore, cavity-nest predator assemblage in our study area is diverse but composed by relatively large animals, with *Leopardus guigna*, *Dromiciops gliroides, Milvago chimango, Caracara plancus, Glaucidium nana*, and *Rattus rattus* being the main predators [48]. Thus, even when predation was the main cause of nest failure, small differences in entrance diameter may not increase predation risk. On the other hand, and because the nesting substrate that treerunners choose for excavation is usually soft, excavate cavities higher in the forest might reduce the predation risk by terrestrial predators. Nesting success increased with the distance from the forest edge, suggesting that the selection of breeding habitats (selecting sites with high forest cover) is adaptive, and that decision is being translated in more breeding success [13]. Second-growth forests contain a larger number of trees and more chance to be close to edge compared to old-growth forests, as well as less options to nests higher in the canopy, suggesting that the first may not be ideal habitats to breed for White-throated treerunners.

The number of fledglings of White-throated treerunners was associated only with tree scale attributes (i.e. DBH and decay). The latter is partially similar to the productivity of Red-naped Sapsuckers in the United States [13], where cavity and tree scales were the most important attributes associated with the number of fledglings. Breeding outputs were positively related to southeastern orientation of cavity entrance for Red-naped Sapsuckers, while we did not find any relation between cavity aspect and fitness for treerunners. Our finding showing a lack of association between cavity orientation and fitness matches with recently published results for South American excavators, in which there is no general pattern of cavity orientation [49]. Instead, and unlike nesting success, the number of fledglings was associated with tree scale, being negatively associated with tree DBH. This can be responding to elevation, due to larger trees are present mainly at high elevations, where shorter breeding seasons can be translated in smaller clutch sizes [50]. On the other hand, we found that unhealthy live trees and recently dead trees increased the number of fledglings, while long dead trees negatively affected the number of fledglings. This might be also responding to adult ability to generate more breeding outputs; perhaps stronger adults select stronger substrate to excavate, leaving softer trees and brunches to the weaker pairs.

Within forest biodiversity, cavity-nesters have globally become seriously threatened by deforestation [51] and conventional silviculture [44,52,53], in which old and large cavity-bearing trees are often removed. This might also be the case for White-throated treerunners, and also for other cavity-nester species that nest in large decaying and standing dead trees in south temperate forests [29]. Despite their importance, these important large decaying and standing dead trees are not protected by current forestry laws in Chile [54]. Here, temperate forests are threatened by fragmentation, degradation, and deforestation [55,56], as nearly 70% of its original extent has been lost [57]. Our reported relationship between habitat preferences and fitness could be crucial information to conserve White-throated treerunners and multiple coexisting species, as this excavator is known to play an important role structuring forest-dependent communities by providing cavities for other small-size vertebrates, including birds, marsupials, and bats [21,58].

Methods

Study area and focal species

We studied White-throated treerunners in Andean temperate forests of La Araucanía Region, Chile (39°16’S, 71°48’W, see Altamirano et al. 2017a for a full description of the study area). This area presents a mean daily temperature of 6.0°C and an average annual precipitation > 2.000 mm distributed throughout the year [21,59]. We surveyed 20 forest stands (20–40 ha each), corresponding to nine second-growth forest stands between 40 to 80 years old subjected to selective logging, and 11 old-growth forest stands over 200 years old. Broadleaf species dominated second-growth forests stands include *Nothofagus obliqua*, *Nothofagus dombeyi*, and *Laurelia sempervirens*, while old-growth stands were mixed conifer-broadleaf forests dominated by broadleaf species such as *Laureliopsis philippiana* and *Nothofagus dombeyi* associated with the conifer *Saxegothaea conspicua* al lower elevations (500–900 m). At higher elevations (900-1,600 m) of old-growth stands include *Nothofagus pumilio* (broadleaf) and *Araucaria araucana* (conifer). The understory of second- and old-growth forests were dominated by bamboo species (*Chusquea* spp.), *Azara* spp., *Berberis* spp., and tree saplings.

In Chile, White-throated treerunner is distributed between Santa Inés hill (32° 9'31.51"S; 71°29'32.76"O) and the Cape Horn Archipelago (55°58`59.61” S; 67°16´00.69” O, Martínez & González 2004). Because of its size, morphology, and habits, White-throated treerunner has been compared to “Nuthatches” (Sittidae, genus *Sitta*) from North America, Europe, and Asia [60,61]. White-throated treerunner is strictly arboreal, does not fly long distances, and similar to nuthatches moves from tree to tree, climbing them vertically with its legs and tail [62,63]. It actively feeds on larvae, adult insects [15,64] and other arthropods [65], by removing small pieces of bark along tree trunks and branches [15,62]. At early stages of the reproductive season, naturalist records indicate that treerunner excavates its nesting-cavities on highly decayed or burned trees [63,66], and standing dead trees of small diameter at breast high (15 cm) [66].

Nest searching and monitoring

During eight breeding seasons (October to February), between 2010 and 2018, we searched (6 h per day, 6 days per week) for occupied cavities of White-throated treerunner in each of the 20 forest stands. To find and monitor nests, we employed the protocol described in Martin and Geupel (1993), observing adult behavior such as repeated visits to the same tree, long periods out of sight after knowing its position on a tree or sudden flight out of a tree-cavity [68].

Nests in cavities lower than 2 m height were checked directly using a Ridgid camera, while a wireless monitoring system [69] mounted on a 15 m long telescopic pole [29,44,68] was used for cavities above 2 m height. A nest was considered active after we confirmed it contained at least one egg or nestling. Then, we obtained geographic coordinates for each nest using a handheld GPS with ± 10 m accuracy. Unique code was given to every nest, cavity, and tree containing a nest for monitoring (every 3 to 4 days) until fate to determine number of hatched eggs and fledglings, signs of depredation, or cavity availability for further nesting attempts.

Habitat sampling across spatial scales

Following Sadoti and Vierling (2010), we used a paired used-availability study design to infer habitat preference at four spatial scales (Table 1, Fig. 1). At (1) cavity-scale, we measured entrance diameter (cm), diameter at cavity height (DCH, m), cavity height above the ground (m), aspect (°), internal cavity volume (cm^3), branch order (order of tree branches where excavated cavity was located; 1: main trunk; 2 secondary branch; 3: tertiary branch; and so forth), and substrate decay class (degree of decomposition of the specific substrate where a given nest was located, associated with the branch order). At (2) nest-tree scale, we recorded tree species, diameter at breast height (DBH), and decay class of nest-trees (1: live healthy tree; 2: live unhealthy tree; 3: recently dead tree; 4: old dead tree; and 5: naturally fallen tree; for details see [29]). At (3) forest-stand scale, we established vegetation plots of 11,2 m radius (0,04 ha), with the nest-tree at the center of the plot and recorded both DBH and decay classes for every tree with DBH > 12.5. These data allowed us to calculate habitat attributes including tree density, mean DBH and standard deviation, decay class mode, and stand basal area [14]. At (4) landscape scale, we used a 3 ha buffer for analysis with nest-trees at the center. We choose a 3 ha buffer because other studies reported home ranges of 3 ha for Brown-headed nuthatch (*Sitta pusilla*)[71]and Eurasian nuthatch (*Sitta europaea*)[72]; species of comparable size and habits to White-throated treerunner. At this scale, we measured the nearest distance to a forest edge and forest area [14] (Table 1). We determined forest cover area through remote sensing combining Remap [73] and QGIS 3.6 Noosa [74]. Remap is an online mapping platform that allowed us to classify land cover. At an approximate 120.000 ha buffer area containing all 130 plots (65 corresponding to White-throated treerunner nests and 65 to control trees, i.e. random trees without nests of the study species), we established a set of training points through photointerpretation. This set of training points feeds an algorithm that based on a set of biophysical, spectral, and climatic predictors classifies the entire area in the different classes of land cover types that were defined with the training set points. The image of reference corresponded to a 2014–2017 Landsat composite image. The resulting classified image was downloaded and corrected with QGIS, determining the forest cover at 3 ha plots for every nest. Forest edge was established when there was a > 50 m distance between forests, as Eurasian nuthatch shows a maximum distance of 50 m in open spaces [75].

Table 1
Spatial scales (cavity, nest-tree, forest-stand and landscape) assessed to explore habitat preference and fitness of White-throated treerunner (*Pygarrhychas albogularis*).

Spatial scale	**Variable**	**Description**
Cavity	Fresh	1: Cavity excavated during the observation year; 0: Cavity excavated in previous seasons.
	Entrance diameter	Horizontal diameter entrance of the excavated cavities (cm)
	DCH	Diameter at cavity height of nest trees (cm)
	Height	Height above the ground of the excavated cavities on tree (m)
	Aspect	Cardinal orientations of the excavated cavities in degrees (0° – 360°)
	Cavity volume	Internal cavity volume calculated as volume of cylinder (cm^3)
	Branch order	Order of tree branches where excavated cavity was located. 1: main trunk; 2 secondary branch; 3: tertiary branch; and so forth.
	Subdecay class	Degree of decomposition of the tree branch where excavated cavity was located
Nest-tree	Tree species	Tree species where nests were found.
	Tree DBH	Diameter at breast height of nest trees
	Decay class	Degree of decomposition of the nest trees. Decay classes assigned were 1 (live healthy tree); 2 (live unhealthy tree); 3 (recently dead tree); and 4 (long dead tree; modified from Thomas et al. 1979; Edworthy et al. 2012).
Forest-stand	Tree density	Density of total trees in one hectare
	Average DBH	Mean DBH of total trees in forest-stand
	Standard deviation DBH	Standard deviation of DBH in total trees on forest-stand
	Decay class mode	Mode of degree decomposition of the total trees in forest-stand
	Basal area	Basal area of forest-stand (cm^2/ha)
Landscape	Forest edge	Nearest distance to forest edge from to nest tree (m).
	Forest area	Forest area in circular buffer of 3 ha with nest tree in the center (m^1)

Statistical Analysis

Breeding habitat preferences

We used a stratified case-control sampling design [76] to examine habitat attributes, across spatial scales, associated with nest-site preferences and fitness. We had 65 nests of White-throated treerunner, and thus randomly selected 65 control sites from a large data base we have collected throughout the years (2008–2018). For the random selection of control sites, we excluded plots were treerunner nests were found and we selected control vegetation plots and trees from the same forest site and season of its paired treerunner nest.

To examine habitat preferences we used generalized linear mixed effect models (R package lme4 v1.1-31)[77] with site and season as random effects and White-throated treerunner nest presence (1) or absence (0) as the response. We assessed possible preferences at three spatial scales (nest-tree scale, forest-stand scale, and landscape scale. Table 1). The modelling algorithm was considered keeping all random effect variables as a basis, and manually adding fixed effect variables one at a time from smaller to larger scales. Eighteen models were built, and the best model was selected through Akaike criterion and variable significance.

Fitness

To investigate whether habitat attributes of preferred reproduction sites are linked to fitness we looked at two different aspects: nesting success and number of fledglings. For nesting success we estimated daily nest survival rate (DSR) using the logistic exposure method [78] with generalized linear mixed effect models, including site and season as random effects. The response variable was either 1 (nest survived between nest visits) or 0 (nest did not survive). For the number of fledglings produced, we used linear mixed effect models, with number of fledglings as the response variable and included site and season as random effects. As for the fixed effects, we used the same three spatial scales used in the habitat preference assessment, but also added cavity-scale covariables in the analysis (Table 1). This was done only for fitness and not habitat selection because, as an excavator, cavity attributes are generated by the excavation process; thus, those attributes are not “preferred” or “avoided”. We fitted all possible combinations of covariables, excluding interactions. For most covariables we looked at their linear effect only. However, for Aspect, we looked at its linear and quadratic effect. We then ranked the models by AICc and selected the model with the lowest value. We assessed parameter importance in the final model by determining whether or not their 95% confidence interval (CI) included zero [79].

We estimated overall nest survival rate using Mayfield-derived daily failure rates [80]. Before fitting nest survival models we investigated a potential effect of researcher on DSR derived from frequent nest visitations. We created a continuous variable of cumulative nest visitations, and assessed its effect on DSR using logistic exposure method, as described above. Before fitting any model, we checked for outliers with Cook's distance (D), and for correlation among covariates to assess multicollinearity ($r > 0.75$). We replaced missing values with the mean of the variable and standardized all continuous variables to a mean of zero with one unit of standard deviation [81]. We assessed the goodness of fit of the final models with χ^2 tests, rejecting the model if $p < 0.05$. All analysis were performed in R 4.2.1 [82].

Declarations

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Data Availability Statement. The data that support the findings of this study are available from the corresponding author upon reasonable request.

Additional information (Competing interests Statement). The authors declare no competing interests. This research was carried out under a Chilean permit to develop science in protected areas (N° 018/2023), also it did not involve either animal captures or the collection of any plan material.

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Tables

Table 1. Spatial scales (cavity, nest-tree, forest-stand and landscape) assessed to explore habitat preference and fitness of White-throated treerunner (*Pygarrhychas albogularis*).

Spatial scale	Variable	Description
Cavity	Fresh	1: Cavity excavated during the observation year; 0: Cavity excavated in previous seasons.
	Entrance diameter	Horizontal diameter entrance of the excavated cavities (cm)
	DCH	Diameter at cavity height of nest trees (cm)
	Height	Height above the ground of the excavated cavities on tree (m)
	Aspect	Cardinal orientations of the excavated cavities in degrees (0° - 360°)
	Cavity volume	Internal cavity volume calculated as volume of cylinder (cm^3)
	Branch order	Order of tree branches where excavated cavity was located. 1: main trunk; 2 secondary branch; 3: tertiary branch; and so forth.
	Subdecay class	Degree of decomposition of the tree branch where excavated cavity was located
Nest-tree	Tree species	Tree species where nests were found.
	Tree DBH	Diameter at breast height of nest trees
	Decay class	Degree of decomposition of the nest trees. Decay classes assigned were 1 (live healthy tree); 2 (live unhealthy tree); 3 (recently dead tree); and 4 (long dead tree; modified from Thomas et al. 1979; Edworthy et al. 2012).
Forest-stand	Tree density	Density of total trees in one hectare
	Average DBH	Mean DBH of total trees in forest-stand
	Standard deviation DBH	Standard deviation of DBH in total trees on forest-stand
	Decay class mode	Mode of degree decomposition of the total trees in forest-stand
	Basal area	Basal area of forest-stand (cm^2/ha)
Landscape	Forest edge	Nearest distance to forest edge from to nest tree (m).
	Forest area	Forest area in circular buffer of 3 ha with nest tree in the center (m^1)

Table 2. Characteristics of nesting habitats (cavities and tree scales) and fitness (measured as nesting success and the number of fledglings) of White-throated treerunners (*Pygarrhychas albogularis*; n = 65).

Values are presented as percentages or mean ± standard deviation (range).

Variable	White-throated treerunners' nests
Landscape scale	
Forest edge (m)	482.1 ± 807.7 (0 - 2851.8)
Forest area (m^1)	25882.1 ± 4403.4 (9880 - 29499)
Forest-stand scale	
Tree density (tree/ha)	771 ± 366 (25 - 1550)
Average DBH (cm)	31.4 ± 7.7 (20.2 - 59.8)
Standard deviation DBH (cm)	16.2 ± 11.2 (6.9 - 86)
Decay class mode	2 ± 0.6 (1 - 4)
Tree scale	
Tree species (%)	*Nothofagus obliqua*: 61.5 *Nothofagus dombeyi*: 12.3 *Nothofagus pumilio*: 10.8 *Persea lingue*: 9.2 *Eucryphia cordifolia*: 6.1
Tree DBH (cm)	40.7 ± 20.3 (14.1 - 123.1)
Decay class	3.2 ± 1.0 (1 – 4)
Cavity scale	
Fresh (%)	Fresh cavities: 89.2 Non-fresh cavities: 10.8
Entrance diameter (cm)	3.8 ± 0.6 (2.5 – 5)
DCH (cm)	21.5 ± 11.5 (9 – 60)
Height (m)	9.6 ± 4.1 (1.1 – 17.1)
Aspect (°)	145.4 ± 106.5 (4 – 348)
Cavity volumen (cm^3)	1,349.1 ± 755.2 (147.3 – 4,417.9)
Branch order (%)	Main trunk: 64.6 2nd order branch: 30.8 3rd order branch: 4.6

Substrate decay class	3.7 ± 0.7 (2 – 4)
Fitness	
Clutch size (# eggs)	3.2 ± 0.8 (1 – 5)
Nesting success (%)	Successful: 75.03 (CI = 62.77 – 89.62) unsuccessful: 24.97
Number of fledglings (# chicks)	3.0 ± 1.2 (1 – 5)

Table 3. Model rankings (for White-throated treerunners (*Pygarrhychas albogularis*) habitat preference, number of fledglings, and nest success in relation to the four spatial scales assessed in its nesting sites in south temperate forests, Chile. Season and site were random terms in all models. Bold indicates best-supported models. [a] Number of parameters estimated. [b] Difference in AICc values between each model and the lowest AICc model (we show the list of models until the first one with ΔAIC > 2). [c] AICc model weight. [d] Log likelihood.

Model	**K^a**	**AICc**	**ΔAIC^b**	**W_i^c**	**LL^d**
(a) Habitat preference					
DBH + Decay + Basal area + Forest area	**9**	**113.7**	**0.00**	**0.34**	**-47.8**
DBH + Decay + Basal area + Forest area + SD DBH	10	117.26	2.06	0.12	-47.67
(b) Nesting success					
Entrance diameter + forest edge + height	**6**	**95.1**	**0.00**	**0.07**	**-41.44**
Entrance diameter + height	5	95.4	0.26	0.06	-42.61
Forest edge + height	5	95.9	0.81	0.05	-42.88
Height	4	96.1	0.98	0.05	-44.00
DBH + entrance diameter	5	96.4	1.27	0.04	-43.11
Entrance diameter + forest edge + height + tree density	7	96.7	1.77	0.03	-41.29
Entrance diameter + DBH + height	6	97.0	1.84	0.029	-42.36
Forest edge + height + tree density	6	97.0	1.92	0.03	-42.40
DBH	4	91.1	1.97	0.03	-44.49
DBH + Forest edge + height + entrance diameter	7	97.19	2.06	0.03	-41.43
(c) Number of fledglings					
DBH + decay class	**7**	**102.2**	**0.00**	**0.35**	**-42.28**
Intercept	4	103.5	1.28	0.19	-47.14
Decay class	6	103.6	1.47	0.17	-44.50
DBH	5	103.6	1.47	0.17	-45.91
ASP + ASP^2 + DBH + decay clas	9	104.3	2.08	0.12	-40.02

Figures

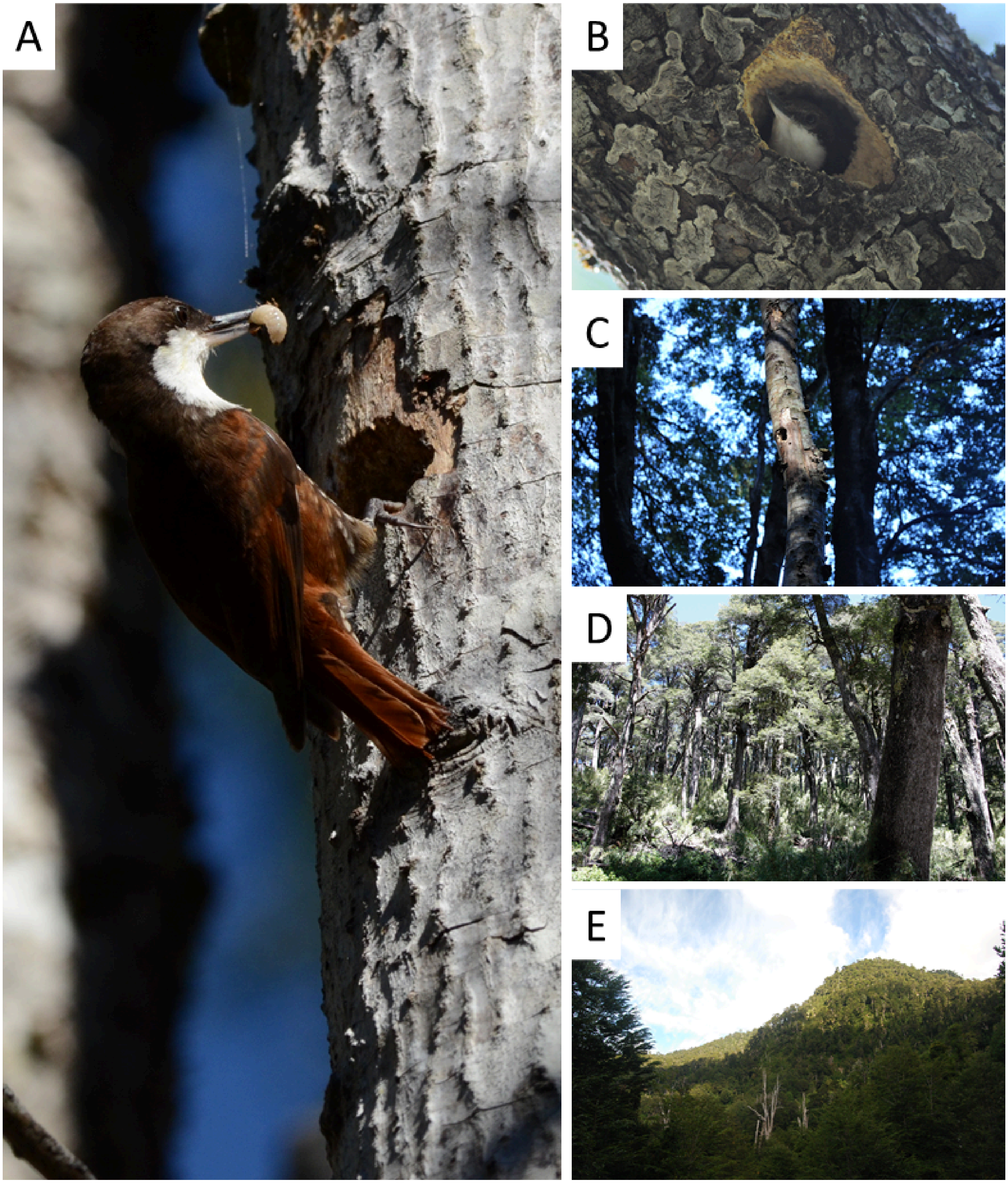

Figure 1

Study species White-throated treerunners (*Pygarrhychas albogularis*) (A) and the spatial scales assessed for breeding habitat preferences and fitness in temperate forests of South America: cavity scale (B), tree scale (C), forest-stand scale (D), and landscape scale (E).

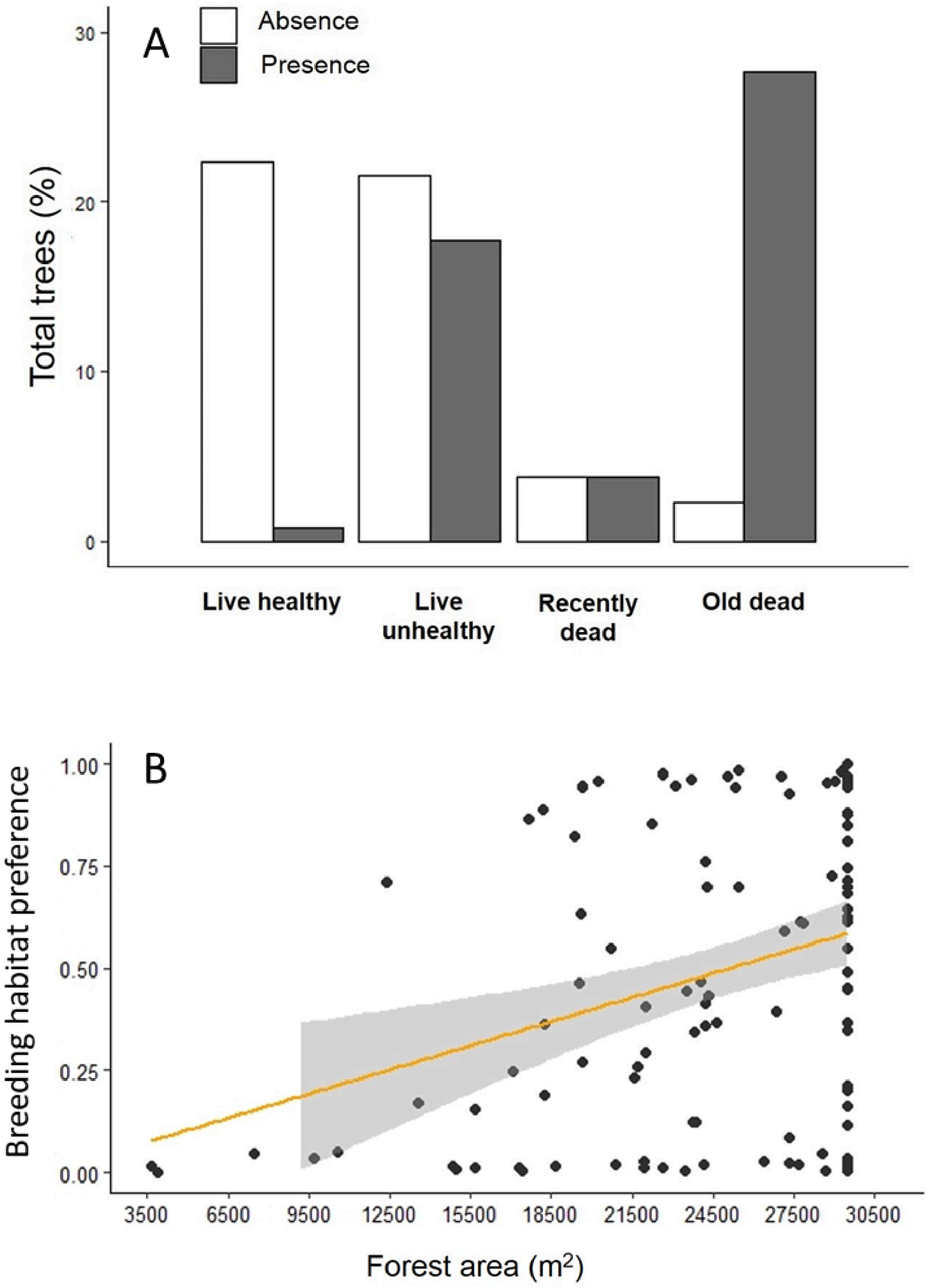

Figure 2

Most influential variables, at different spatial scales, on nesting habitat preferences of White-throated treerunners (*Pygarrhichas albogularis*) in temperate forest of South America: (A) Tree-decay (tree scale) and (B) forest area (landscape scale).

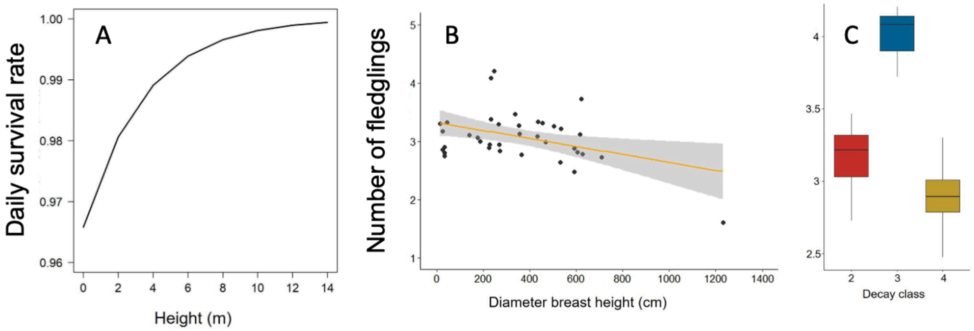

Figure 3

Most influential variables (significant and marginally significant), at different spatial scales, on fitness (daily survival rate and number of fledglings) of White-throated treerunner (*Pygarrhichas albogularis*) in temperate forest, South America: (A) Height (cavity scale), (B) Diameter at breast heigh (tree scale), and (C) decay class (tree scale).