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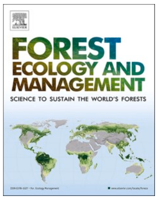

Tree-cavity survival for biodiversity in temperate forests of South America: A multi-scale approach

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ABSTRACT

Tree cavities are critical habitat attributes for a diversity of species that use them for reproduction and shelter. Worldwide, their availability has shown an intense decline in forests because of the loss of old-growth stands and the reduction in cavity recruitment. These disturbance processes are influenced by factors occurring across different scales: from cavities to landscapes. We analyzed the survival of 613 cavities in 455 trees in old-growth and second-growth forests over 10 years in Andean temperate forests in southern South America, Chile. Kaplan–Meier and Cox proportional hazards models were used to determine median cavity survival and its influencing factors at the cavity, tree, stand and landscape scales. The median survival was six years. Non-excavated cavities (6 years) survived longer than excavated cavities (4 years), with a significantly longer life-span in large decaying trees. Cavities' survival was strongly influenced by cavity- and tree-scale factors, including their origin, the vertical cavity depth, tree decay class, tree branch order and tree diameter class. In old-growth forests, most cavities were found in live decaying trees, while in second-growth forests they were mostly in long-dead trees (snags). We suggest that management should maintain forest structural complexity, retaining dead wood and trees in different stages of decay to permit a continuous supply of substrates over time for the formation of cavities.

1. Introduction

In recent decades, there has been an increase in the adoption of practices that minimize the negative impacts of forest harvest (e.g. retention forestry, agroforestry, selective harvesting; Fedrowitz et al., 2014; Gustafsson et al., 2012). However, quantitative and multi-scale evaluations of the effectiveness of these approaches are still required, particularly in the case of those habitat attributes that are critical for biodiversity (Koch et al., 2018; Mori and Kitagawa, 2014). Old-growth forests, unlike second-growth forests, can provide numerous cavities in large, old trees for use by a wide diversity of species for nesting and shelter (Ibarra et al., 2020; Lindenmayer et al., 2012). Globally, at least 1,878 bird species (18 % of the total) are tree-cavity nesters (van der Hoek et al., 2017). Cavity-nesting birds include those known as "excavators" or primary cavity nesters (PCNs), which make their own cavities, and those known as "non-excavators" or secondary cavity nesters (SCNs), which use cavities that have been previously excavated or formed by decomposition processes (Martin et al., 2004; Altamirano

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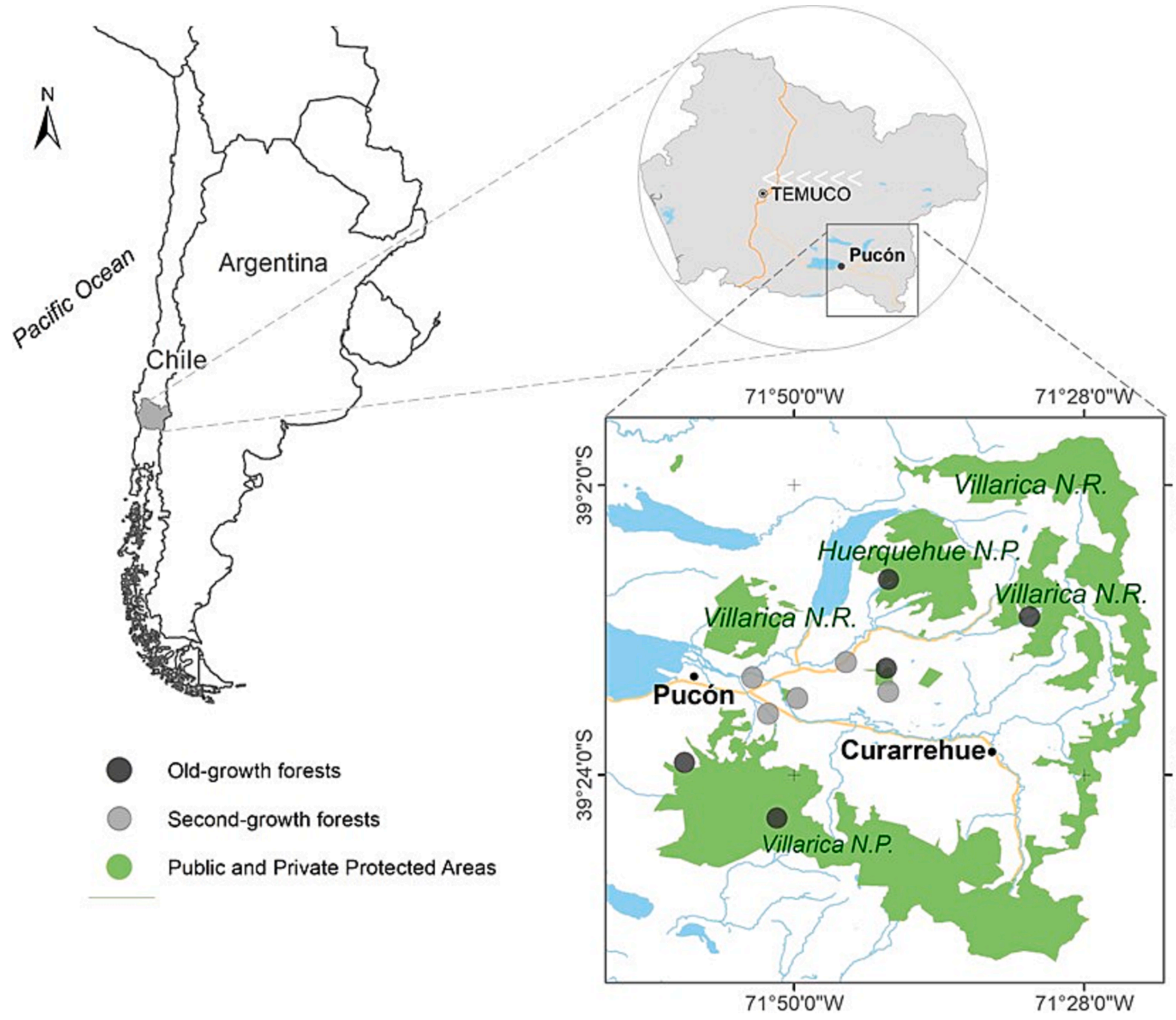

Fig. 1. Study area and location of the ten sampling sites in Andean temperate forests of the La Araucanía Region, southern Chile.

et al., 2017; Wesołowski and Martin, 2018). The main causes of cavity loss are the destruction of the tree segment where they are located, falling of trees, the deterioration of both the sides and floor of the inner chamber, and the narrowing or collapse of the entrance (Sedgwick and Knopf, 1992; Wesolowski, 2011).

Tree-cavity survival dynamics vary depending on the ecosystem and the region of the world (Cockle et al., 2017, 2011a; Edworthy et al., 2012; Edworthy and Martin, 2013; Hardenbol et al., 2019; Lindenmayer and Wood, 2010; Pakkala et al., 2022, 2019,2018; Wesołowski, 2012, 2011). Their survival over time is influenced by factors that occur at multiple spatial scales. At the cavity scale, for example, survival has been reported as a function of the cavity's origin (i.e. non-excavated or excavated; Lindenmayer et al., 2012; Wesołowski and Martin, 2018). Non-excavated cavities have been found to survive longer than excavated ones in subtropical forests in Argentina (median = 10 and median = 2 years, respectively) as well as in temperate forests in Poland (median = 12 and median = 6 years; Cockle et al., 2017; Wesolowski, 2012). By contrast, in temperate forests in Canada, no differences were found depending on origin (median = 14 years; Edworthy et al. 2012) while, in the boreal forests of Finland, survival varied depending on the species of woodpecker that excavated the cavity (Pakkala et al., 2018, 2019). Furthermore, SCNs often modify the internal dimensions of excavated cavities, affecting both their survival and occupation rates (Wiebe et al., 2020).

Cavity survival can also vary with the characteristics of the tree, such as its species and diameter (Hardenbol et al., 2019; Wesołowski, 2012), its decay class (Edworthy et al., 2012; Pakkala et al., 2022) as well as the wood's hardness and durability (Cockle et al., 2017; Wesołowski, 2012). In general, cavities appear to survive longer if they are in live, relatively larger trees (Hardenbol et al., 2019), in the trunk rather than the branches (Cockle et al., 2017) and in slow-growing species with a higher wood density (Barbosa et al., 2017). Most of the cavities excavated in Canada were in the trunks of live trees (55 %) with a low wood density (e.g. *Populus tremuloides*) and remained available for over a decade (Martin et al., 2004). In Poland and Argentina, cavities are created mainly in branches or dead trees, which fall and decay rapidly (Cockle et al., 2011). Finally, habitat attributes at the stand and landscape levels can also influence cavity survival (Edworthy and Martin, 2013; Pakkala et al., 2018). In forests with less canopy cover, trees with cavities near the edge of a stand may be more susceptible to being blown over by the wind (Laurance et al., 2000). In addition, cavity survival may be longer in old-growth stands than second-growth forests (Lindenmayer et al., 2012) and depend on management history (Edworthy and Martin, 2013).

The temperate forests of South America (35–55 S) are considered a Global Biodiversity Hotspot because of its high rates of species endemism and human disturbances. Here, old-growth forests have been greatly reduced by anthropogenic fires, indiscriminate exploitation and

Table 1
Measurements of (non-excavated and excavated) cavities at multi-scale levels.

Scale	Attribute	Type of factor	Description
Cavity	Origin (ORI)	Nominal	Non-excavated: formed by decay or damage, with min. entrance diameter $\geq$ 2.5 cm (Ibarra et al., 2020) and max. entrance diameter $\leq$ 40 cm and horizontal depth $\geq$ 4 cm. All fissures with min. width > 2.5 cm. Excavated: formed by excavator birds, more regular in shape than non-excavated cavities, oval or round.
	Internal dimensions (HD and VD)	Continuous	HD: horizontal depth (cm), measured between the entrance and the opposite wall, considering only the internal edge of the former. VD: vertical depth (cm), measured from the bottom of the cavity to the lower edge of the cavity entrance, closest in direction of the forest floor.
Tree	Species (SPP)	Nominal	Species of tree.
	Density (BWD)	Discrete	Index of amount of woody material in a certain volume of wood for each species of nesting tree (kg/m^3).
	Natural durability of wood (NDW)	Ordinal	Capacity of the wood to withstand different destructive biological agents without application of any preservative treatment (Chilean Standard 789/1 Of. 87). 1: Very durable, 2: Durable, 3: Moderately durable, 4: Not durable.
	Diameter at breast height (DBH)	Continuous	Diameter at breast height (cm). DBH class: DBH intervals $\leq$ 20, 20–50, 50–80 and $\geq$ 80 cm.
	Diameter at cavity height (DCH)	Continuous	Diameter of branch or trunk at cavity height (cm).
	Branch order (BO)	Ordinal	Degree of branching where cavity is located: 1: trunk; 2: 2nd branch order; 3: 3rd branch order.
	Decay class (DEC)	Ordinal	2: Live unhealthy (e.g. fungi, feed for woodpeckers or White-throated treerunner, borers, broken top, dead branches); 3: Recently dead, but still has branches, with partial loss of bark, hard and/or soft parts; 4: Long-dead, without branches or bark, broken top and soft wood; 5: Fallen, tree fallen naturally (e.g. wind or snow). Over the study period, we had no records of nestings cavities in decay class 1: Live healthy trees.
Stand	Canopy cover (COV)	Ordinal	Proportion of ground covered by projection of crown of the tree, calculated using photo-interpretation and physiognomic characterization (adapted from Etienne and Prado, 1982). Open (COV < 10 %), clear (10 < COV < 50 %) and dense (COV > 50 %).
	Number of trees (NHA)	Discrete	N of live and dead trees with DBH > 10 cm per ha, obtained from plots around nesting tree (radius = 11.2 m).
	Basal area (BA)	Continuous	Area of trunk projected to the hectare (live and dead trees with DBH > 10 cm, measured at 1.3 m), obtained from plots around nesting tree (radius = 11.2 m).
Landscape	Type of forest (FT)	Nominal	Old-growth and second-growth forest.
	Distance to edge (DE)	Ordinal	Distance (m) to interface between forest and non-forest ecosystems or between two forests with contrasting composition or structure (Harper et al., 2005), in intervals of 0 m, < 50 m, 51–100 m, 101–200 m and > 200 m.

replacement by exotic-tree plantations and, in many places, have regenerated as second-growth forests (Armesto et al., 2009; Donoso et al., 2022; Gutiérrez et al., 2009). One of the highest proportions of cavity-nesting birds in forests globally (57 % of the bird community) has been reported in these forests, with a total of 25 species of SCNs and four species of PCNs (Altamirano et al. 2017). In addition, there is a higher density of cavities in old-growth forests than in second-growth ones, giving cavity availability rates above the global median (Ibarra et al., 2020; Remm and Lõhmus, 2011).

For the first time for southern temperate forests, and as the second cavity longevity study in South America (Cockle et al., 2017), we evaluated the survival of excavated and non-excavated cavities used by cavity-nesting birds. Using a long time series (10 years), we tested the hypothesis that cavity survival will be influenced by characteristics that operate at four different scales: cavity, tree, forest stand, and landscape. We predicted that cavities will survive longer when they: (i) are created by decay, rather than by excavation (cavity-scale); (ii) are in larger, less decayed trees, with fewer branches (tree-level); and (iii) are in stands with relatively higher canopy cover and at a greater distance from the edge of the forest stand (stand- and landscape-level) in this Global Biodiversity Hotspot of southern South America.

2. Materials and methods

2.1. Study area

The study took place in Andean temperate forests in the watershed of Lake Mallolafquen (39 S, 71 W) in the Pucón municipal district of southern Chile's La Araucanía Region, ancestral land of the Mapuche Indigenous People. The area has a temperate climate with dry summers (January-March) and an average annual rainfall of 1,945 mm (Luebert and Pliscoff, 2006). The project studied five sites of old-growth forest (>200 years) at high altitudes (900–1,500 masl) and at medium altitudes (500–900 masl) and five sites of second-growth forest (40–80 years) at low altitudes (200–500 masl) (Fig. 1) (Ibarra et al., 2014; Altamirano et al., 2017; Caviedes and Ibarra 2017). In the old-growth, high-altitude forests, *Nothofagus pumilio* and *Araucaria araucana* predominated while the old-growth, medium-altitude forests had a mixed conifer-broadleaf composition, with a predominance of *Saxegothaea conspicua*, *Laureliopsis philippiana* and *Nothofagus dombeyi*. In the case of the second-growth forests, broadleaf species predominated, including *Nothofagus obliqua, Laurelia sempervirens*, *Gevuina avellana* and *Persea lingue* (Altamirano et al., 2017; Ibarra et al., 2020).

2.2. Field methods

We monitored the survival of excavated and non-excavated cavities in old-growth and second-growth Andean temperate forests. An active search for nests in tree cavities took place during the reproductive season (October-January) from 2010 to 2020.

Cavity scale. We georeferenced cavities with nests and determined

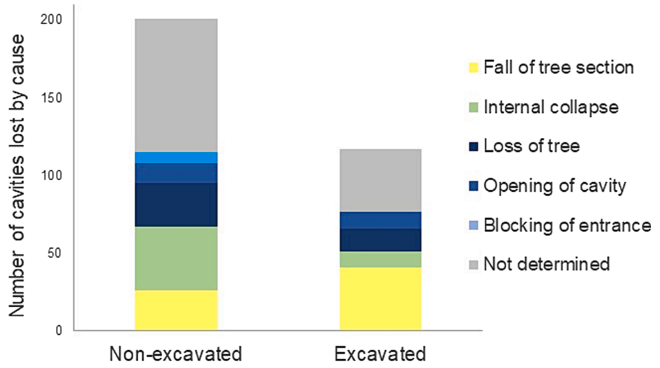

Fig. 2. Number of cavities lost by cause of failure and type of origin (non-excavated and excavated). Fall of the section within the tree that contains the cavity ("fall of tree section"), the internal collapse of the cavity ("internal collapse"), whether floor or walls, loss of the entire tree ("loss of tree"), opening of the cavity to the outside due to its collapse or depredation ("opening of cavity"), blocking of the entrance ("blocking of entrance") and natural loss, without an identified cause ("not determined").

their origin (ORI). The latter was done visually because non-excavated cavities were natural openings or fissures, of different sizes and shapes, but with dimensions that allow nesting and refuge (Table 1; Ibarra et al., 2020), while excavated cavities were identified by their oval or rounded entrance, with a regular and symmetrical shape. In some cases, the excavator could be observed creating the cavity or remains of wood chips were found under the trees. Each cavity, that was used at least once for nesting over the ten-year period, was monitored annually from the year it was found to the end of this study (January 2020), or until the cavity was unavailable. A cavity was considered unavailable when the segment of the tree where it was located fell, the tree fell down, the internal chamber was deteriorated (walls and/or floor), or the entrance collapsed or narrowed (Edworthy et al., 2012). After the reproductive season, we used a telescopic pole with a height of up to 15 m, equipped with a camera and graduated bar, to determine the cavity's origin and two scale variables: horizontal depth (HD) of the cavity (distance between the inner edge of its entrance and the opposite wall) and its vertical depth (VD) (from the bottom of the cavity to the lower edge of the cavity-entrance; Table 1).

Tree scale. We recorded i) the species of tree (SPP) where possible (in some cases, the level of decay made this impossible), ii) diameter at breast height (DBH), iii) diameter at cavity height (DCH), iv) branch order (BO) (i.e. trunk, 2nd and 3rd branch orders) and v) decay class (DEC), based on externally observable characteristics and categorized into 4 classes (decay class: 1: live, healthy tree; 2: Live unhealthy e.g. fungi, feed for woodpeckers or White-throated treerunner, borers, broken top, dead branches; 3: Recently dead, but still has branches, with partial loss of bark, hard and/or soft parts; 4: Long-dead, without branches or bark, broken top and soft wood; 5: Fallen, tree fallen naturally (e.g. wind or snow); Altamirano et al., 2017; Ibarra et al., 2020; Table 1). To evaluate wood mechanical resistance we determined vi) basic wood density (BWD) by species, based on samples of live trees at the height of the DBH and on the different stands. The samples were submerged in water for 72 h to obtain the green volume using the water immersion method and were subsequently dried in a forced-air oven

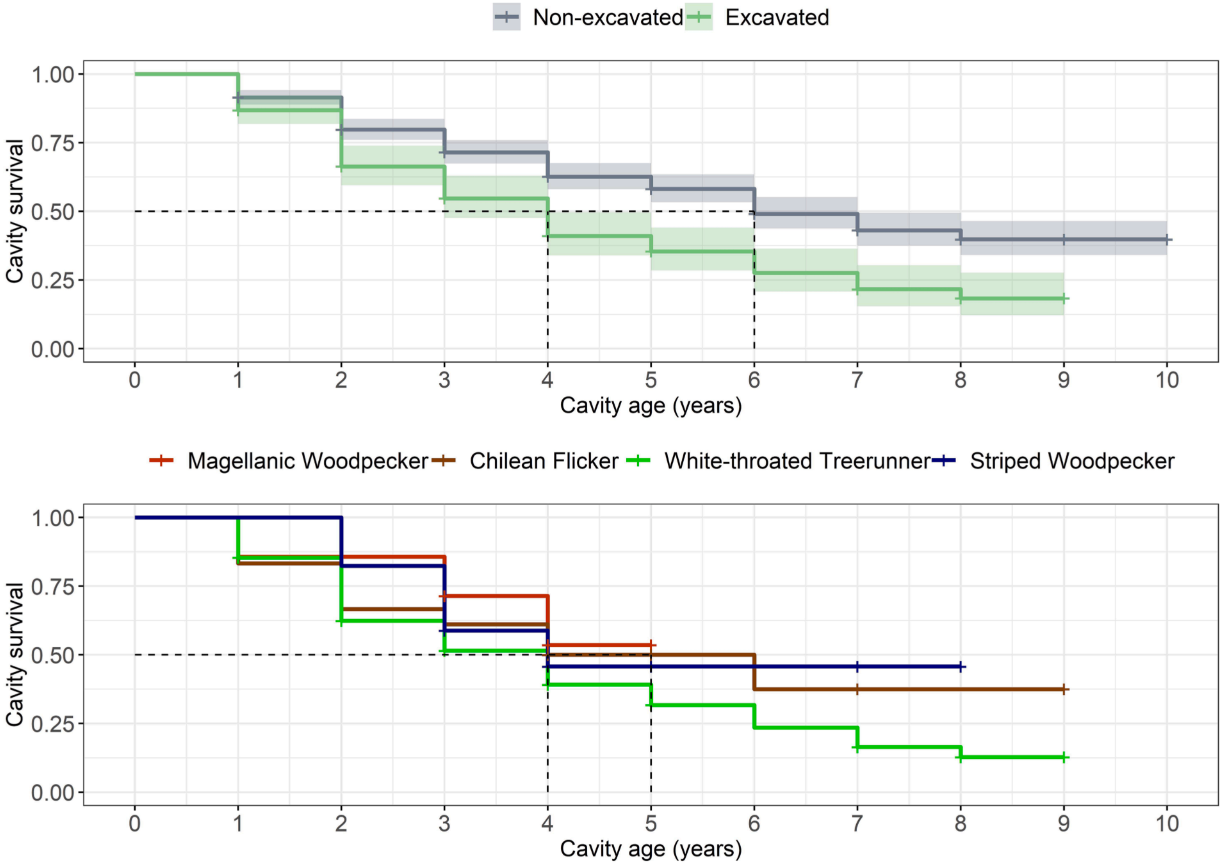

Fig. 3. (a) Kaplan-Meier curves (unbroken lines) and 95 % confidence intervals (shaded area) for excavated and non-excavated cavities. The X axis shows the time in years and the Y axis the probability of cavity survival while a vertical drop in the curves indicates the loss of a cavity. The difference in survival between the two groups is significant ($p < 0.01$; excavated: $n = 167$, median = 4 years; non-excavated: $n = 435$, median = 6 years). (b) Probability of survival of cavities excavated by four excavator species found in the temperate forests of the Araucanía Region. The difference in cavity lifespan between the different excavator species is not statistically significant.

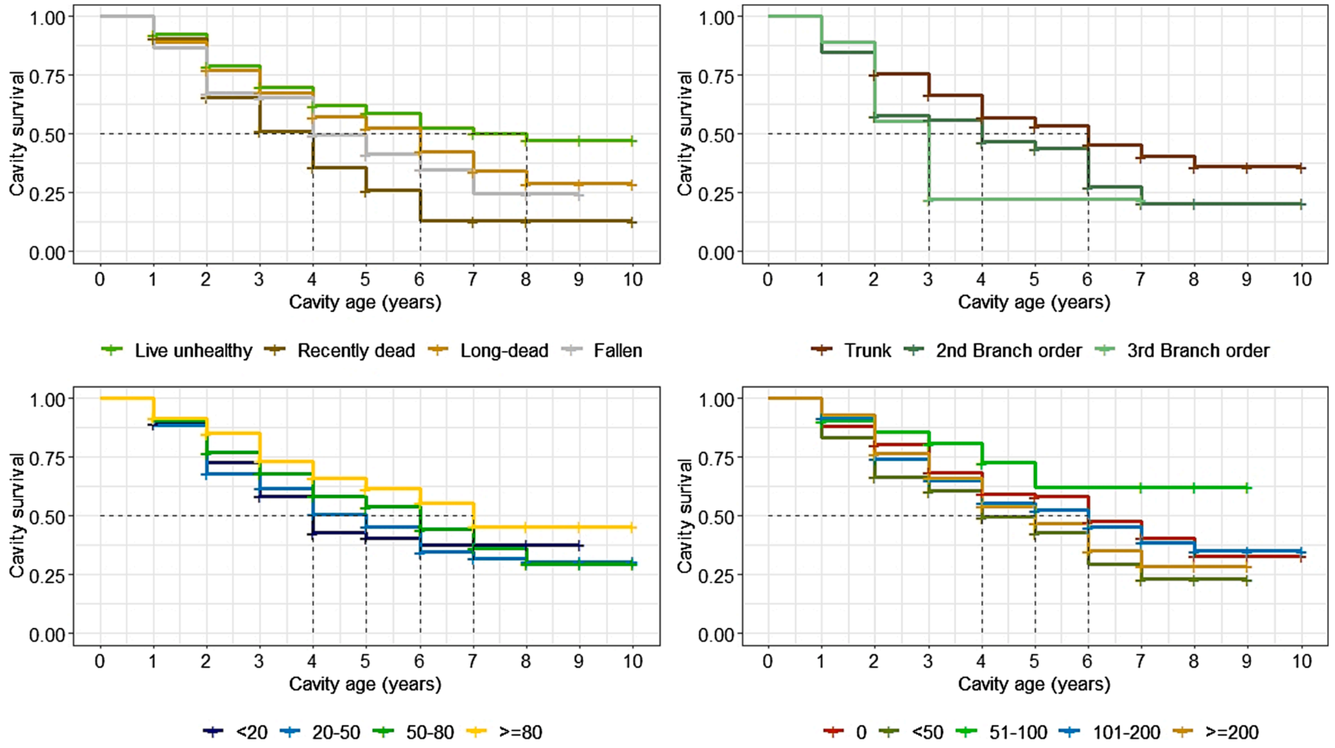

Fig. 4. Kaplan-Meier curves showing the probability of cavity survival by: (a) decay class; b) branch order; c) DBH in intervals from 9.5 to 245 cm (average = 56.8 cm); d) intervals of distance to stand edge in meters.

until their dry weight was obtained to calculate the density (24 h at 105C), and vii) the natural durability of the wood (NDW) (i.e. n ≥ 10 trees per tree species with cavities), defined based on the literature and the classification of the corresponding Chilean Standard (Hernández and Pinilla, 2010; INN, 1987).

Stand and landscape scales. Stands were classified by color, texture and structure using photo-interpretation (Etienne and Prado, 1982) and we determined i) canopy cover (COV), ii) number of trees per hectare (NHA) and iii) basal area per hectare (BA), using circular plots (radius = 11.2 m) around the nesting tree. At the landscape scale, we classified i) forest type (FT) based on management history and the structure of the stands (i.e. old-growth or second-growth forest), and ii) the shortest linear distance from each tree with cavities, to the interface between the forest and non-forest ecosystems or two forests of contrasting composition or structure (DE) (Harper et al., 2005), using the QGIS program version 2.18.23.

2.3. Statistical analysis

To estimate survival functions of cavities, we used Kaplan-Meier models (Kaplan and Meier, 1958), under which censored data (i.e. unknown year of cavity loss or cavities with discontinued monitoring) can be taken into account, the cavities mean survival was calculated as the year in which survival reached 0.50 (50 %) (Cockle et al., 2017; Rao and Schoenfeld, 2007).

To understand how factors at the cavity, tree, stand and landscape scales are related to cavity loss times and predict the rate of failure or risk, we used Cox proportional hazards models (Cox, 1972), which permit the incorporation of multiple covariates (Courbaud et al., 2017) and provide hazard ratios (HR=$(e^{coef})^{b}$) that represent the proportional risk of cavity loss compared to a risk level used as a reference defined on each model, where hazard ratio (HR) > 1 means that exposure to the factor increases the rate of occurrence of the event (cavity lost), and HR < 1 decreases the rate. If the HR = 1 we will say that the factor does not influence survival (Kleinbaum and Klein, 2012). After fitting the models to explore the relevance of the predictor variables within the scale of analysis (i.e., cavity, tree, stand, and landscape), we tested more complex models containing different combinations of the best-supported factors, depending on the model weights and estimated coefficients (from previously tested models). From these models and considering each their AIC values and their relative weights, we considered models within two sets of Cox models: the first to explore the multi-scale characteristics that affect cavity survival and the second to evaluate the characteristics of the trees where there were at least ten trees with cavities for each type of tree species (i.e. taxonomic species, density, natural durability, factors at cavity and tree scales). A linear correlation threshold was considered (r > 0.5 Akoglu, 2018) to keep one variable with strong biological influence from each pair of assessed variables (DBH and DCH; NHA and BA; BA and DE, were strongly correlated).

To verify the assumption that risks were constant over time, we evaluated Schoenfeld residuals plots (Schoenfeld, 1982) and checked that the continuous factors followed a linear form when tested against martingale residuals (Therneau et al., 2016). When this was not the case, the factor was categorized and, in some cases, we applied the cubic smoothing splines method to segment the data into intervals. Cox models were selected using the Akaike information criterion corrected for small sample sizes (AICc) and Δi AICc values, which measure the distance between the ith model and the best model (with Δ AICc ≤ 2), as well as the Akaike weights, ω i (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). All the analyses were performed using the the survfit and coxph functions from "Survival", "Survminer" and "survMisc" packages of the R statistical program (version 3.2.2) (Therneau et al., 2016; R Core Team, 2021).

3. Results

3.1. Cavity survival patterns

We monitored 613 cavities in 455 trees of which 169 (28 %) were excavated and 444 (72 %) were non-excavated, found in both second-

Table 2

Candidate models for predicting the risk of loss of tree cavities in temperate Andean forests. The table shows: (a) Set A of models that consider combinations of factors at different scales (i.e. cavity, tree, stand and landscape) and (b) Set B of models that also consider the characteristics of the principal species of tree in which the cavities are found. The rows in bold indicate the best models, with Δ AIC ≤ 2 and a cumulative Akaike weight $\sum$wi ≥ 90 %.

	Factor Code	k	LL	Δ AICc	w_i
(a) Set A: Multi-scale models					
1	**ORI + VD + DBH + BO + DEC + DBHxORI**	**9**	−1228.19	0.00	**0.9**
2	VD + DBH + BO + DEC	7	−1240.71	20.88	1.0
3	ORI + BO + DCH** + DEC	20	−1289.06	145.22	1.0
4	ORI + DCH** + COV	17	−1434.78	430.01	1.0
5	ORI + DCH + DEC + COV	7	−1449.34	438.10	1.0
6	ORI + DBH + BO + ORIxDBH	7	−1501.21	541.84	1.0
7	ORI + DBH + BO + DEC	5	−1503.76	542.84	1.0
8	ORI + DBH + BO + DEC + COV + FT	10	−1500.37	546.37	1.0
9	ORI + DBH + BO + FT	5	−1512.54	560.40	1.0
10	ORI + BO + DEC + BA + FT	8	−1512.9	567.29	1.0
11	ORI + BO + DEC + NHA + FT	8	−1514.32	570.12	1.0
12	DBH + BO + COV + BA	6	−1520.69	578.75	1.0
13	ORI + DEC + ORIxDEC + COV + ORIxCOV	11	−1792.08	1131.83	1.0
14	ORI + FT + DB + FTxDE	4	−1803.72	1140.71	1.0
15	ORI + COV + FT + DE	5	−1805.98	1147.27	1.0
(b) Set B: Tree species models, excluding UKN trees and with n ≥ 10 trees per species					
1	**SPP + ORI + VD + DBH** + BO + DEC**	**14**	**−733.61**	**0.00**	**1.0**
2	NDW + ORI + DCH* + ORIxDCH	20	−833.80	213.60	1.0
3	SPP + DBH** + DEC + BWD* + ORI	22	−862.30	274.55	1.0
4	SPP + DEC + BO + DBH + ORI	11	−886.08	298.29	1.0

Note: Each model is presented with k = number of parameters, LL = maximum log likelihood value, Δ AICc = difference in the AIC between each model and the best model, and wi = Akaike weight. The factors considered are: ORI: origin of the cavity; VD: vertical depth; HD: horizontal depth; DBH: diameter at breast height; DCH: diameter at cavity height; BO: branch order; DEC: decay class; BWD: basic wood density; NDW: natural durability of wood; SPP: tree species; COV: canopy cover; number of trees per hectare (NHA); BA: basal area; FT: type of forest; DE: distance to edge; *cubic smoothing splines method; ** DBH in intervals of ≤ 20, 20–50, 50–80 and ≥ 80 cm.

growth (n = 433) and old-growth (n = 180) forests (Appendix 1 and 2). The cavities were mainly in large trees (i.e. DBH of 50–80 cm; second-growth forests: n = 211, 72 %; old-growth forests: n = 82, 28 %). Trees with DBH of 50–80 cm accounted for 46 % of the trees with cavities studied, but only 16 % and 9 % of trees per hectare present in old-growth and second-growth forests, respectively. In old-growth forests, cavities were predominately in live unhealthy trees (DEC = 2; 60 % for excavated cavities and 54 % for non-excavated cavities) and 93 % were in only two species (*N. pumilio*, n = 136; *N. dombeyi*, n = 31) while, in second-growth forests, cavities were mostly in old dead trees (DEC = 4; 56 % for excavated cavities and 54 % for non-excavated cavities) and, as a result, most trees were of a non-identified species (n = 165), followed by *N. obliqua* (n = 111).

Excavated cavities were found mainly in second-growth forests (79 %), in old dead trees (47 %, n = 80, DEC = 4) and in the trunk (64 %, n = 189, in both types of forest) while excavated cavities in old-growth forests were mainly in live unhealthy trees (60 %, n = 21, DEC = 2). In the case of non-excavated cavities, these were also found more frequently in trunks (77 %, n = 341) and in old dead trees (56 %, n = 168, in second-growth forest) and in live unhealthy trees (54 %, n = 78, old-growth forest).

The median survival time was six years (n = 602, 95 % CI = 5–6 years) and the mean was 3.2 years. Out of the total number of cavities, 284 remained in the tree at the end of the sampling period and nine trees (n = 11 cavities) were cut and excluded from the models (Fig. 2). The lifespan of the cavities differed significantly depending on their origin, reaching six years for non-excavated cavities (median 95 % CI = 6–7 years) and four years for excavated cavities (median 95 % CI = 4–3 years) (log-rank test: $X^2 = 25.8$, $p < 0.001$, gl = 1; Fig. 3a and Appendix 3). In excavated cavities, no differences in mean cavity survival were found for the different excavator species (Fig. 3b). Cavities in live unhealthy trees survived longer than those in trees in other decay classes and remained available twice as long as those in recently dead trees (median was 8 years versus median 4 years, $p < 0.001$) and those in fallen trees (median 4 years, n = 52). Cavities in old dead trees survived longer than those in recently dead trees (median 6 years, n = 276, p = 0.013) and those in fallen trees (Fig. 4a). Cavities also survived longer when in the trunks of larger trees, although the differences were not significant (Fig. 4c and Fig. 4d). In the case of the type of forest, canopy cover and distance to the forest edge (Fig. 4d), no significant differences were observed between the Kaplan-Meier curves.

3.2. *Factors influencing cavity survival*

Out of all the candidate models (Table 2), we selected two as the best predictors (Table 3). In the first set, the *Multi-scale Model 1* had the greatest weight in predicting risk (likelihood ratio, Wald and log-rank tests $p \leq 0.001$). At the cavity level, origin was an important factor in loss risk, with excavated cavities having a 323 % greater likelihood of loss than non-excavated ones (HR = 4.23, 95 % CI = 2.35–7.62). In all the candidate models of the first set where vertical depth was included, it was significant, with each 1 cm increase implying a 1.5 % reduction in the probability of cavity loss.

Compared to cavities in trunks, the greater the branching the worse the survival outlook: cavities in the 2nd and 3rd branch orders were 109 % and 389 % more likely to be lost, respectively. Taking cavities in healthier and more vigorous trees (DEC = 2) as a baseline, cavities in recently dead trees increased their risk of loss by a 77 % (95 % CI = 1.08–2.90) while, in old dead trees, the increase was 66 % (95 % CI = 1.18–2.36) and, in fallen trees on the forest floor, 138 % (95 % CI = 1.38–4.10).

Among the models in the second set, the *Species Model 1* was selected as the best for the available data. At the tree species level, there were only significant differences at an alpha level of 0.05 between *Nothofagus obliqua* and *Gevuina avellana*, with the latter representing a 58 % decrease in the risk of cavity loss compared to the former (HR = 0.411, 95 % CI = 0.20–0.84). However, 67 % (n = 34) of *G. avellana* were live unhealthy trees and 88 % (n = 45) had a DBH of < 30 cm; all were located in the lower strata of the canopy as suppressed trees. Similarly to the finding of the model selected from the first set, a higher level of tree decay increased the risk of cavity loss by 88 % for cavities in recently dead trees and by 292 % for those in fallen trees. The exception was old dead trees where the increase was not significant. In addition, the risk of loss decreased significantly with the size of the tree: compared to trees with DBH ≤ 20 cm, the risk decreased by 39 % for a DBH of 20–50 cm, by 45 % for a DBH of 50–80 cm and by 83 % for DBH ≥ 80 cm.

There were not significant differences in cavity lifespan or loss risk depending on the excavator species: white-throated treerunner (*P. albogularis,* n = 125 cavities, 20 %), Chilean flicker (*Colaptes pitus*, 18 cavities, 2.9 %), striped woodpecker (*Dryobateslignarius*, n = 17 cavities, 2.8 %) and Magellanic woodpecker (*Campephilus magellanicus*, n = 7 cavities, 1.1 %) (Fig. 3b). The cavities of the white-throated treerunner were the only ones showing a higher loss risk than those of other excavators (HR = 1.65 times compared to the Chilean flicker, 95 % CI = 0.81–2.9, p = 0.18).

4. Discussion

Our results for a Global Biodiversity Hotspot indicate that both cavity and tree scales' attributes may have strong effects on the survival patterns of cavities, which are a crucial resource for biodiversity of temperate forests of South America. In contrast, characteristics at stand

Table 3
Cox proportional hazards models selected previously based on the Akaike information criterion. In the case of the hazard ratio (HR), HR ≤ 1 indicates a negative association between the factor and the risk of cavity loss (lower risk, longer lifespan) while HR ≥ 1 indicates a positive association (greater risk, shorter lifespan) and HR $= 1$ indicates no change in the level of risk.

Name of model		Coefficient	HR	SE coefficient		Z	P	95 % CI	
(a) Multi-scale model - Model 1									
Origin of cavity									
ORI 1		0.00	1.00						
ORI 2		1.44	4.23	0.30		4.80	< 0.001***	2.35	7.62
VD (cm)	–	0.02	0.995	0.01	–	2.30	0.02*	0.97	0.99
DBH (cm)	–	0.001	0.99	0.003	–	0.48	0.63	0.99	1.00
Branch order									
BO 1		0.00	1.00						
BO 2		0.74	2.089	0.21		3.44	< 0.001***	1.37	3.17
BO 3		1.59	4.89	0.48		3.32	< 0.001***	1.92	12.48
Decay class									
DEC 2		0.00	1.00						
DEC 3		0.57	1.782	0.25		2.28	0.02*	1.08	2.90
DEC 4		0.51	1.67	0.18		2.91	0.004**	1.18	2.36
DEC 5		0.87	2.38	0.28		3.12	0.002**	1.34	4.10
DBHxORI1		0.000		1.000					
DBHxORI2	–	0.02	0.98	0.01	–	3.21	0.001**	0.97	0.99
(b) Models of species characteristics, excluding UKN trees and with n ≥ 10 trees by species - Model 1									
Tree species									
N. obliqua (roble beech)		0.00	1.00						
G. avellana (gevuina nutt)	–	0.89	0.41	0.37	–	2.46	0.014 *	0.20	0.84
N. dombeyi (coigue beech)	–	0.25	0.79	0.28	–	0.86	0.39	0.45	1.37
N. pumilio (lenga beech)	–	0.09	0.92	0.22	–	0.38	0.71	0.59	1.43
P. lingue (lingue)	–	0.41	0.67	0.37	–	1.09	0.27	0.32	1.38
Origin of cavity									
ORI 1		0.00	1.00						
ORI 2		0.81	2.24	0.20		4.01	< 0.001***	1.51	3.32
VD (cm)	–	0.02	0.97	0.01	–	2.91	< 0.001**	0.96	0.99
Branch order									
BO 1		0.00	1.00						
BO 2		0.71	2.03	0.23		3.10	0.001**	1.30	3.17
BO 3		1.37	3.92	0.54		2.54	0.01*	1.37	11.24
DBH class									
< 20		0.00	1.00						
20–50	–	0.51	0.60	0.26	–	1.98	0.05*	0.36	0.99
50–80	–	0.60	0.55	0.31	–	1.97	0.05*	0.30	0.99
> 80	–	1.78	0.17	0.45	–	3.92	< 0.001***	0.07	0.41
Decay class									
DEC 2		0.00	1.00						
DEC 3		0.63	1.89	0.25		2.55	0.01*	1.15	3.06
DEC 4		0.34	1.40	0.22		1.55	0.12	0.89	2.12
DEC 5		1.37	3.93	0.33		4.19	< 0.001***	2.07	7.45

and landscape scales did not have a significant influence on cavity survival in these forests.

4.1. Survival patterns and associated factors

Supporting our predictions, cavities formed by decay processes survived longer than excavated cavities. This is in line with results in other latitudes such as the European temperate forests and the subtropical humid Atlantic Forests of South America (Cockle et al., 2011). Highly decayed and smaller diameter trees are often more likely to collapse than larger ones and may be an important cause of cavity loss, a pattern that has been reported in other studies that have evaluated survival patterns (Cockle et al., 2017; Edworthy et al., 2012; Hardenbol, et al., 2019; Lindenmayer et al., 2012; Lindenmayer et al.,1997; Lindenmayer and Wood 2010; Wesołowski 2011, 2012). Many of the cavities at our sites were in live unhealthy trees and they had a longer lifespan than those in dead trees. Our cavities in old dead trees had a lower loss risk than cavities in recently dead trees, which may be because the former no longer had branches with cavities that can break off; the latter is the main cause of cavity loss in these forests. Cavities in fallen trees had a > 130 % higher loss risk than those in live unhealthy trees because they were located in substrates that disintegrate quickly, possibly due to higher humidity near the forest floor. This may be relevant for cavity-nesting birds that breed chiefly in fallen trees, such as the chucao tapaculo (*Scelorchilus rubecola*) and the Magellanic tapaculo (*Scytalopus magellanicus*) (Altamirano et al., 2017; Altamirano et al., 2012). While some previous studies have found that cavity survival is positively correlated with DBH (Cockle et al., 2017; Edworthy et al., 2012; Lindenmayer and Wood, 2010), we did not find this association in our study system. However, when tree DBH interacted with cavity origin, the excavated ones at a relatively larger diameter tree had a significantly lower loss risk than non-excavated cavities at larger diameters.

Some characteristics of the trees evaluated (i.e. species, wood density and natural durability of the wood) were not important predictors of survival. Wood hardness, or the presence of extractable compounds, might be better indicators of cavity lifespan than durability; however, for logistical reasons it was not possible for us to explore this in detail. Birds may be sensitive to subtle features that are not always apparent in the tree's external appearance as, for example, how hard it is to excavate (Schepps et al., 1999). *Nothofagus* species have relatively high rates of decay in the face of attacks by wood-boring insects and the presence of Basidiomycota fungi (Baldini and Pancel, 2000; Veblen et al., 1996). Because *Nothofagus* trees represented nearly 90 % of the trees with cavities in old-growth forests and around 40 % in second-growth forests (Ibarra et al., 2020), the role of the saproxylic network in cavity survival needs further study.

The study area has a relatively high density of cavities in old-growth and second-growth forests, with 60 % of the cavities occurring in live unhealthy trees (Ibarra et al., 2020). We knew that, in second-growth forests, snags left by fires contained a disproportionate number of cavities compared to their relative availability and that when they are lost, there is a dramatic decrease in cavity density because many of the live trees lack the size or level of decay required for cavities (Caviedes and Ibarra, 2017; Ibarra et al., 2020). At the stand and landscape scales, the factors evaluated in this study did not affect cavity survival or loss risk. Although we expected to find significant differences in cavity survival between old-growth and second-growth forests (Edworthy and Martin, 2013; Hardenbol et al., 2019), this was not supported by our data. In stands with a relatively low tree cover, 69 % of cavities were in old dead trees and mainly in isolated trees, which are more vulnerable to the wind and weathering. In dense forests, the vegetation surrounding a tree may favor moisture retention by the tree with cavities and this may, in turn, facilitate its decay and vulnerability to collapse (Lindenmayer and Wood, 2010).

4.2. *Implications for conservation and forest management*

The formation of non-excavated cavities is a relatively slow process which may take several decades to create cavities suitable for cavity-nesting wildlife (Lindenmayer and Wood, 2010). In second-growth forests, the trees generally must reach a certain diameter and decay class to be suitable for excavation. The elimination of dead trees in these forests may, therefore, be harmful to wildlife, particularly if mean cavity survival is low. As well as the total availability of cavities in the ecosystem, it is necessary to consider their occupancy rate and changes in their quality as they get old and deteriorate. This may affect the number of birds that nest in cavities, even when the ecosystem seems to be rich in cavities (Lõhmus and Remm, 2005; Pakkala et al., 2022).

Conventional forestry management practices in Chile include activities subsidized by the National Forest Service (CONAF) that reduce the abundance of tree cavities. They include the elimination of isolated trees or unwanted remnants of the upper canopy, the authorization of “salvage logging”, under which dead specimens or those damaged by forest fires can be felled at any stage of their development, and the authorization and financing of the sanitary logging of trees affected or likely to be affected by pests that may pose a threat to forest stability. In managing temperate forests of South America, it is necessary to bear in mind that cavities are relatively short-lived multi-annual attributes (median = 6 years, $\overline{X}$=3.2 years) and that their temporal, as well as spatial, persistence must be ensured in order to provide a continuous supply of a crucial resource to at least 57 % of the bird community, four mammals, three reptiles and one amphibian (Altamirano et al. 2017).

In southern temperate forests and beyond, we need to ensure cavities over time through a diversity of live trees in different stages of senescence, accompanied by a stock of dead wood (Edworthy and Martin, 2013; Ibarra et al., 2017, Ibarra et al., 2020; Lindenmayer and Wood, 2010). In addition, it is important to consider different strata within the canopy (i.e. fallen, suppressed, intermediate, co-dominant and dominant strata). Forests where one or more decay classes are absent may suffer severe cavity shortages in the future (Cockle et al., 2011). It is paramount that forests be managed in a way that maintains habitat attributes that are critical for biodiversity and that the practices adopted recognize cavities as critical attributes of the ecosystem, considering their dynamics of formation and loss as well as the related biological interactions.

CRediT authorship contribution statement

Mariangela Paratori: Investigation, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Fernando J. Novoa:** Investigation, Data curation, Formal analysis, Visualization. **Tomás A. Altamirano:** Conceptualization, Investigation, Methodology, Project administration, Writing – review & editing. **Cristian Bonacic:** Supervision, Writing – review & editing. **José Tomás Ibarra:** Conceptualization, Investigation, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jose Tomas Ibarra reports financial support was provided by National Commission for Scientific and Technological Research.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

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