Lifetime productivity of tree cavities used by cavity-nesting animals in temperate and subtropical forests

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Abstract. Tree cavities are a critical multi-annual resource that can limit populations and structure communities of cavity-nesting vertebrates. We examined the regional and local factors influencing lifetime productivity (number and richness of occupants) of individual tree cavities across two divergent forest ecosystems: temperate mixed forest in Canada and subtropical Atlantic Forest, Argentina. We predicted that (1) species would accumulate more rapidly within cavities in the species-rich system (Argentina: 76 species) than the poorer system (Canada: 31 species), (2) cavity characteristics associated with nest-site selection in short-term studies would predict lifetime cavity productivity, and (3) species would accumulate more rapidly across highly used cavities than across cavities used only once, and in Argentina than in Canada. We monitored and measured nesting cavities used by birds and mammals over 22 breeding seasons (1995–2016) in Canada and 12 breeding seasons (2006–2017) in Argentina. Cavities were used an average of 3.1 times by 1.7 species in Canada and 2.2 times by 1.4 species in Argentina. Species richness within cavities increased with number of nesting events at similar rates in Canada and Argentina, in both cases much slower than expected if within-cavity species assemblages were random, suggesting that lifetime richness of individual cavities is more strongly influenced by local ecological factors (nest site fidelity, nest niche) than by the regional species pool. The major determinant of lifetime cavity productivity was the cavity's life span. We found only weak or inconsistent relationships with cavity characteristics selected by individuals in short-term nest-site selection studies. Turnover among (vs. within) cavities was the primary driver of diversity at the landscape scale. In Canada, as predicted, species accumulation was fastest when sampling across high-use cavities. In Argentina, the rates of species accumulation were similar across high- and low-use cavities, and fastest when both high- and low-use cavities were pooled. These findings imply that biodiversity of cavity nesters is maintained by a mix of long-lived (highly productive, legacy trees) and many high-turnover (single-use, fast decaying) tree cavities. Conservation of both long-lasting and single-use cavities should be incorporated into decisions about stand-level forest management, regional land use policies, and reserve networks.

Key words: beta diversity; cavity-nesting vertebrates; nest-site selection; occupancy; resource quality; species pool; species richness; species turnover; tree cavity; tree hole; tree hollow.

Introduction

Nearly 2,000 bird species and a wide diversity of mammals and insects require tree cavities for nesting and roosting, comprising a key component of forest communities globally (van der Hoek et al. 2017). These species interact locally in nest webs: commensal interspecific networks linking cavity producers (avian excavators, such as woodpeckers; decay organisms, such as heart rot fungi) and users (non-excavators, including many songbirds, raptors, ducks, and mammals; Martin and Eadie 1999, Gibbons and Lindenmayer 2002, Martin et al. 2004). Nest cavity requirements often limit the distribution and abundance of cavity-nesters, making these communities highly susceptible to human interventions (such as logging); in response, many conservation efforts

aim to maximize the quantity and quality of tree cavities in the landscape (Gibbons and Lindenmayer 2002, Poonswad et al. 2005, Monterrubio-Rico and Escalante-Pliego 2006, Munks et al. 2009).

To identify important tree and cavity characteristics for conservation of cavity-nesting animals, short-term nest-site selection studies (e.g., Lindenmayer et al. 1990, Li and Martin 1991, Politi et al. 2009) can provide critical information about nesting requirements at the scale of individual organisms. For example, birds may select cavities that are high above the ground, with small entrance diameters and large interior volumes to avoid predation and provide enough space for developing young (Nilsson 1984, Wiebe and Swift 2001, Gibbons et al. 2002, Wesołowski 2017). However, tree cavities are a multiannual resource that can remain available for a few weeks to several decades (Lindenmayer and Wood 2010, Wesołowski 2011, 2012, Edworthy et al. 2012, Cockle et al. 2017, Pakkala et al. 2018). As they age, cavities undergo structural changes (such as increasing interior volume; Edworthy and Martin 2014). Some cavities rapidly lose their value to secondary cavity users (Pakkala et al. 2018), but others become suitable for different suites of species (e.g., larger vertebrates) and could potentially fledge multiple broods over their lifetimes (Edworthy et al. 2018).

The number and richness of occupants are likely to vary according to both the regional species pool and the local cavity characteristics. Highly productive cavities, with many nesting events (hereafter, "nests") and species across multiple years, may contribute disproportionately to populations and communities of cavity-nesting animals at the landscape scale. If we could identify such cavities, they could be spared from logging operations to support diverse communities of cavity nesters. Here we follow cavities over time to assess their lifetime productivity (number of nests and species in the cavity across its life span, Fig. 1). This approach provides a unique perspective on the multi-annual resource value of cavities and is somewhat analogous to the lifetime reproductive success or fitness measured for individual animals.

We aim to evaluate how the regional species pool and local factors influence lifetime productivity (number of nests and species) of individual tree cavities across two widely separated forest ecosystems that differ in species richness (higher in subtropical Argentina), community composition, cavity supply (higher in temperate Canada), length of the breeding season (longer in Argentina), and key processes responsible for cavity formation (woodpeckers in Canada, decay processes in Argentina; Table 1; Appendix S1: Table S1). At a regional scale, we assess the contribution of the regional species pool to lifetime productivity of tree cavities. We use

TABLE 1. Characteristics of cavity-nesting communities at our study areas in north temperate forest (Canada) and subtropical Atlantic Forest (Argentina).

Characteristic	Canada	Argentina
Biome	temperate mixed forest	subtropical mixed forest
Latitude	52°	27°
Length of breeding season	3 months	5 months
Cavity-nester species	31	>76
Excavator birds	12	16
Non-excavator birds	17	54
Mammals	9	>4
Social insects		>2
Tree species available	10	>116
Primary source of cavities	excavation	decay
Cavity density (no./ha)	aspen groves, 16; coniferous forest, 1.2	primary forest, 4.5; logged forest, 0.5
Relationship between cavity abundance and nest density	positive	positive
Median cavity life span (yr)	14	6
Nest-site features selected by individual birds	low, excavated cavities, near open area	high, deep cavities in large-diameter trees

Sources: Martin et al. (2004), Ríos et al. (2010), Aitken and Martin (2004, 2007, 2012), Cockle et al. (2010, 2011, 2017), Edworthy et al. (2012).
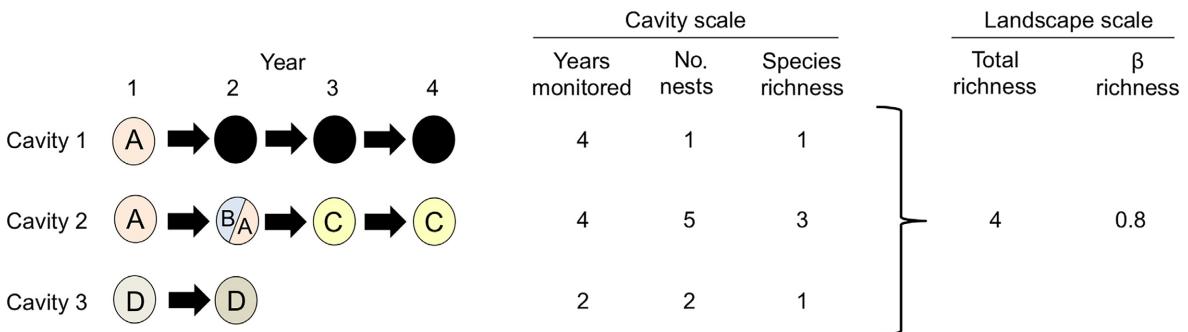

FIG. 1. Hypothetical set of three nesting cavities and their measures of productivity at cavity and landscape scales. Each year they were available (ovals), cavities were unoccupied (black) or contained a nest of a given species (letters, colored). Because cavities occasionally support more than one nest per breeding season, cavity 2 is shown to contain two nests in year 2.

Connor and McCoy's (1979) random sampling hypothesis as a neutral model in which cavity occupants are a random draw from the regional species pool, and then examine differences between expected vs. observed species richness of individual tree cavities. We predict that, after accounting for years available, species richness of individual cavities will be higher, and species will accumulate more rapidly as the number of nests increases, in the species-rich community (Argentina) than in the more species-poor community (Canada). Additionally, given the lower regional cavity supply (limiting the number of cavities available for nesting) and longer breeding season (allowing multiple nests per season) in Argentina, we predict that individual cavities will be occupied more frequently with a faster accumulation of nests in Argentina than in Canada. At a local scale, nest-site characteristics of tree cavities identified in short-term studies are often the only data available to conservation managers for sparing high-quality cavity trees from harvesting. The underlying assumption with the use of such characteristics is that they are suitable surrogates for lifetime productivity of tree cavities. Here, we examine the extent to which characteristics from short-term nest-site selection studies (Aitken and Martin 2004, Cockle et al. 2011; Table 1) are associated with lifetime cavity productivity. Finally, given the neutral model in which cavity occupants are a random draw from the regional species pool, we predict that when sampling across cavities, species will accumulate more rapidly (1) in cavities with many nests than in cavities with few nests and (2) in Argentina vs. Canada.

METHODS

Study systems

We studied tree cavities and cavity-nesting birds over 22 breeding seasons (1995–2016) in a north temperate forest (Canada) and 12 breeding seasons (2006–2017) in subtropical Atlantic forest (Argentina). The north temperate study area was in the Cariboo-Chilcotin region of interior British Columbia, Canada, within 100 km of Williams Lake (52°09′ N, 122°09′ W), and included trembling aspen (*Populus tremuloides*) groves surrounded by native grassland, as well as continuous forest dominated by lodgepole pine (*Pinus contorta*) or Douglas-fir (*Pseudotsuga menziesii*), with hybrid spruce (*Picea* spp.) and trembling aspen (Wiebe 2001, 2016, Martin et al. 2004). Elevation was 930 m above sea level and annual precipitation was 460 mm. Eleven of the continuous forest sites were harvested between 1998 and 2010. Aspen and most large-sized fir trees were retained in harvested sites to provide nesting habitat for cavity-nesting vertebrates and winter habitat for ungulates, but most pine and spruce were removed in a "partial cut" or "clear cut with retention patches" harvest plan (see Drever et al. 2008 and Edworthy and Martin 2013 for further details). Over the study period, this harvest plan

led to stable or increasing populations of cavity-nesting vertebrates (Drever and Martin 2010). The subtropical study area was in the Atlantic forest of Misiones, Argentina, within 30 km of San Pedro (26°38′ S, 54°07′ W), and included primary (unlogged) forest, selectively logged forest, and small farms with remnant native vegetation. Selectively logged areas had few large trees and very few suitable nesting cavities (Cockle et al. 2010). The vegetation was semideciduous Atlantic mixed forest with laurels (Lauraceae), guatambú (*Balfourodendron riedelianum*), and Paraná pine (*Araucaria angustifolia*; Cabrera 1976). Elevation was 520–700 m above sea level and annual rainfall was 1,900 mm distributed evenly throughout the year.

Nest monitoring and cavity occupancy

We searched for active nests by following adult birds and inspecting cavities using mirrors and flashlights, or small (1.8–5.0 cm diameter) video cameras. In Canada, we accessed cavities by ladder (1995–2016, up to 6.8 m above ground) and extendable poles (2003–2016, up to 15 m). In Argentina, we accessed cavities by ladder (2006–2017, up to 9 m), extendable pole (2006–2015, up to 15 m; 2016–2017 up to 22 m), and single-rope tree-climbing (2006–2017, up to 25 m). A cavity was considered occupied if it contained one or more eggs (excluding dumped eggs) or young. A few cavities were inaccessible; these cavities were observed from the ground and only considered occupied if adult behavior indicated the presence of eggs or nestlings. After a cavity was first recorded as occupied, we continued to check it every subsequent breeding season until it was destroyed, usually when the tree or the cavity-bearing limb fell (90% of cavity losses in Canada, 83% in Argentina; Edworthy et al. 2012, Cockle et al. 2017), or we stopped monitoring the area. Each breeding season, cavities were checked regularly for signs of nesting activity (Canada, every 4–5 d during May–July; Argentina, every 1–20 d during August/September–December/January). Insect nests (Hymenoptera) were confirmed from the ground by observing many adults entering and exiting the cavity. Cavities were only included in the present study if they were monitored for at least two breeding seasons.

Cavity characteristics

In the year a cavity was first found, we recorded cavity, tree, and habitat characteristics. We determined cavity producer (excavator species or non-excavated) by observing excavation or discovering fresh cavities (with woodchips) occupied by excavators. Cavities formed by decay or damage, often in knotholes or cracks, were designated as non-excavated. We used tapes to measure cavity height above ground (m), entrance diameter (horizontal, cm), vertical depth (cm, from the entrance sill to the cavity bottom), and nest-tree diameter at

breast height (DBH, in cm) GPS to measure distance from the tree to the nearest open area/forest edge (m).

Statistical analysis

For each cavity, we calculated two measures of productivity that became the response variables for our models: (1) total number of nests and (2) species richness (total number of species that used the cavity for nesting), both of which are counts (Fig. 1). All analyses were performed in R version 3.2.2 (R Core Team 2015). Where our data met the assumption of equidispersion, we fit generalized linear models (Poisson family) using the glm command in the stats package. Where data were underdispersed, we fit Conway-Maxwell-Poisson (COM-Poisson) regression models (which include an additional dispersion parameter to handle underdispersed count data) using the glm.cmp command in the COMPoissonReg package (Sellers and Shmueli 2010, Sellers et al. 2012, 2017).

Our first set of models predicted species richness from ln(number of nests), study area (Canada, Argentina), and their interaction. We generated a null expectation for species accumulation within cavities at each study area by calculating species richness of 1,000 random samples of i nests drawn from each of our data sets, for $i = 1$ to 22. Our second set of models predicted, for each of the two study areas, (1) number of nests and (2) species richness, from the following predictor variables: number of years the cavity was available and monitored (plus second- and third-order quadratics), cavity origin (excavated or non-excavated), entrance diameter, cavity depth, cavity height (above ground), tree diameter (DBH), distance to edge, and all two-way interactions between years available and cavity, tree, and habitat features. Excavator species was not included in models because of its correlation with entrance diameter and depth in Canada (Edworthy et al. 2018), and because this information was not available for a large portion of excavated cavities in Argentina. We re-ran the models omitting nonsignificant interaction terms, and finally nonsignificant quadratic terms, to achieve four final models: one for each of the two measures of productivity (number of nests, species richness) at each of the two study areas (Canada, Argentina).

To explore the contribution of individual cavities to overall species richness, across each study area we explored beta diversity of incidence matrices (presence/absence of species in each cavity) using the function beta.multi in the package betapart (Baselga et al. 2018). Beta diversity was calculated as Sørensen's index of dissimilarity across multiple cavities (β_{SOR}), partitioned into two components: dissimilarity due to species turnover (replacement of one species by another; β_{SIM}) and dissimilarity due to nestedness (poorer assemblage is a subset of richer assemblage; β_{SNE}; Baselga and Orme 2012). Sørensen's index ranges from 0 (all species shared) to 1 (no species shared). Finally, we used the specaccum command in package vegan (method = exact;

Oksanen et al. 2017) to generate species accumulation curves across (1) all cavities, (2) high-use cavities, and (3) low-use cavities within each study area.

RESULTS

Overview of cavity productivity

Individual cavities were monitored for a mean of 6.7 yr (range: 2–20 yr, $N = 2,146$ cavities) in Canada and 3.9 yr (range, 2–12 yr; $N = 245$) in Argentina (minimum 2 yr to enter our data set). Within these cavities we found 6,647 nests of 33 taxa (25 bird species, 8 mammal species) in 14,350 cavity-years in Canada (0.46 nests/cavity-year), and 545 nests of 44 taxa (42 bird species, 1 mammal species, 1 insect order) in 957 cavity-years in Argentina (0.57 nests/cavity-year; Appendix S1: Table S1). Over their life span, cavities were used an average of 3.1 ± 0.57 [1–22] (mean $\pm$ SE [range]) times by 1.7 ± 0.19 [1–7] species in Canada and 2.2 ± 0.12 [1–14] times by 1.4 ± 0.48 [1–5] species in Argentina. In both study systems, number of nests and species per cavity were strongly skewed, with most cavities occupied only one or two times, and few cavities used many times (Fig. 2).

In COM-Poisson glm models predicting species richness of individual cavities ($N = 2,391$), we did not find a significant interaction between study area (Canada vs. Argentina) and ln(number of nests) ($b = -0.057$, SE = 0.20, $Z = -0.28$, $P = 0.78$), nor a significant effect of study area itself ($b = 0.34$, SE = 0.22, $Z = 1.52$, $P = 0.13$). Instead, contrary to our predictions, species richness increased with ln(number of nests) at similar rates in Canada (COM-Poisson glm, $b = 2.86$, SE = 0.10, $Z = 29.5$, $P < 0.001$, N = 2,146) and Argentina ($b = 3.04$, SE = 0.32, $Z = 9.5$, $P < 0.001$, N = 245; Fig. 3). In both study areas, species accumulation within cavities was much slower than predicted by random sampling of nests from our data, and this was particularly unexpected in species-rich Argentina (Fig. 3).

Factors influencing cavity productivity

For each system, we considered the top 5% of cavities with the greatest number of nests and the top 5% of cavities with the greatest number of species to be "exceptionally productive" (Canada, 131 cavities with 9–22 nests or 4–7 species, 37 cavities of which met both of the cut-offs; Argentina, 21 cavities with 7–14 nests or 3–5 species, 5 of which met both cut-offs). We compared these with "exceptionally unproductive cavities" (single use, only 1 known nest; Table 2). As would be expected based on differences in sampling effort, exceptionally productive cavities had been monitored, on average, for over twice as long as single-use cavities (12.6 yr vs. 4.9 yr); they were also significantly deeper and more likely to be in living trees. Compared to single-use cavities, exceptionally productive cavities were more often excavated by Northern Flickers in Canada but more often of
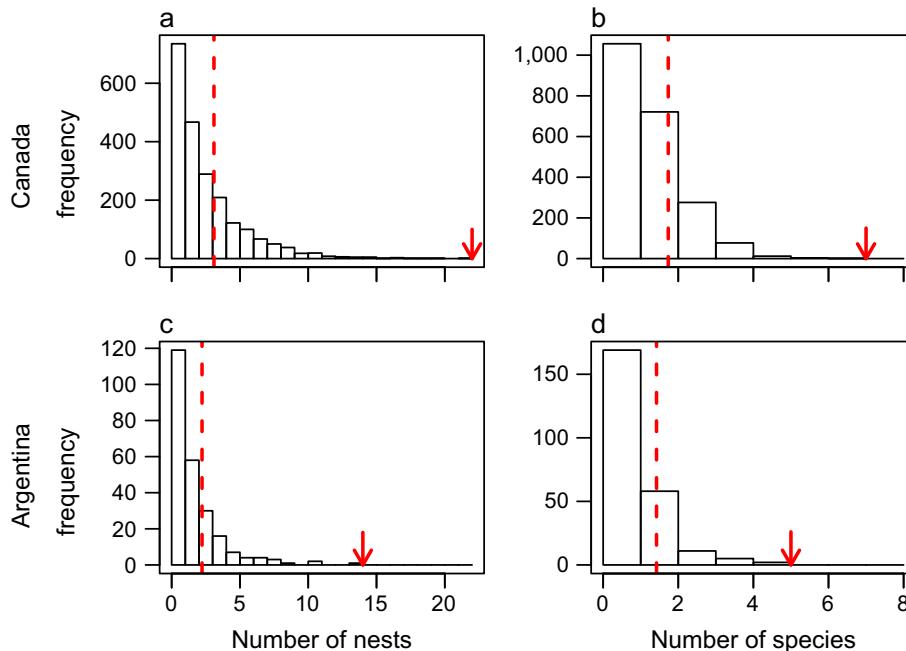
Fig. 2. Frequency distribution of (a, c) number of nests over the lifetime of a cavity and (b, d) the species richness per cavity at study areas in (a, b) Canada and (c, d) Argentina. Broken vertical red lines indicate means; red arrows indicate maxima.
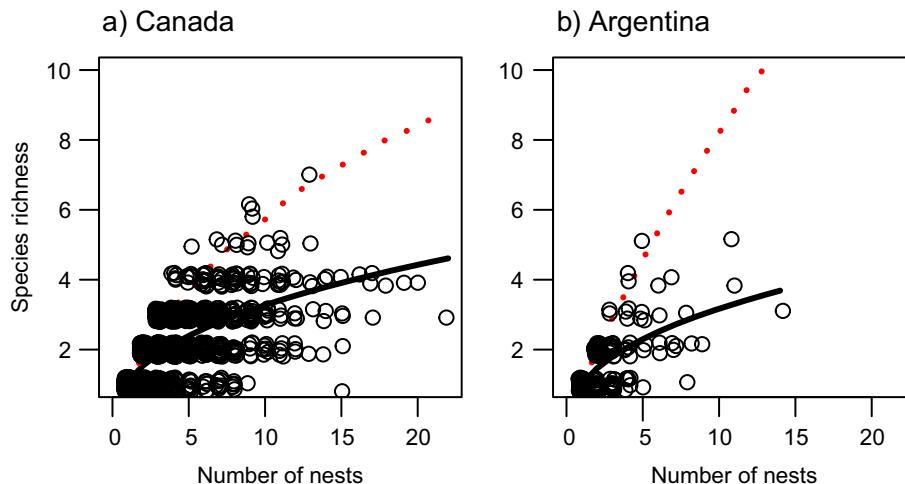

Fig. 3. Relationships between two measures of within-cavity productivity (number of nests, species richness across all years monitored) for tree cavities in (a) Canada and (b) Argentina. Jittered points indicate observations of individual cavities. Red dotted lines represent the null expectation (mean of 1,000 random draws of i nests from our nest data set). Solid lines represent predicted values of COM-Poisson models.

non-excavated origin in Argentina. In Canada, exceptionally productive cavities also had larger entrances, and were lower on the tree, in larger trees, and closer to forest edge, compared to single-use cavities (Table 2).

Years available, a proxy for longevity of the cavity, was the strongest predictor of number of nests and species richness within cavities in both study areas (Table 3, all $P < 0.001$). The relationships between years available and cavity productivity were similar in Canada and

Argentina, although the quadratic effect was stronger in Canada where species accumulation eventually tapered off (Fig. 4). Thus, cavities available for five years were predicted to support 2.7 nests of 1.7 species in Canada and 2.7 nests of 1.6 species in Argentina, whereas cavities available for 10 yr were predicted to support 5.1 nests of 2.3 species in Canada, and 7.0 nests of 2.8 species in Argentina (Fig. 4). Models combining the two study areas indicated only a marginally significant

TABLE 2. Characteristics (mean ± SE) and comparisons (univariate statistical tests) between exceptionally productive (Canada, 9 –20 nests or 4–7 species; Argentina, 7–14 nests or 3–5 species) and low use (1 nest) cavities.

	Canada				Argentina			
Characteristic	Productive	Low use	Test statistic	P	Productive	Low use	Test statistic	P
Number of cavities (N)	131	269			21	94		
Number of nests	9.7 ± 0.3	1 ± 0			6.7 ± 0.6	1 ± 0		
Number of species	3.6 ± 0.09	1 ± 0			3.1 ± 0.2	1 ± 0		
Years available	**12.6 ± 0.3**	**4.9 ± 0.2**	$t = 21.6$	<0.001	**7.1 ± 0.6**	**3.1 ± 0.1**	$t = 6.5$	<0.001
Cavity producer	**88% NOFL**	**51% NOFL**	$\chi^2 = 55.4$	<0.001	**14% exc.**	**51% exc.**	$\chi^2 = 8.0$	0.005
Entrance diameter (cm)	**6.2 ± 0.1**	**5.3 ± 0.1**	$t = 6.3$	<0.001	6.6 ± 0.5	7.6 ± 0.4	$t = -1.6$	0.11
Cavity depth (cm)	**33.8 ± 1.0**	**27.6 ± 0.9**	$t = 4.7$	<0.001	**66.3 ± 6.2**	**38.6 ± 3.2**	$t = 4.0$	0.0004
Height above ground (m)	**2.9 ± 0.1**	**3.3 ± 0.1**	$t = -2.9$	0.004	12.2 ± 1.2	10.1 ± 0.5	$t = 1.6$	0.11
Decay class	**79% living**	**49% living**	$t = 31.9$	<0.001	**86% living**	**63% living**	$\chi^2 = 19.3$	<0.001
Tree DBH (cm)	**35.8 ± 0.7**	**31.2 ± 0.6**	$t = 4.6$	<0.001	63.0 ± 5.6	55.9 ± 2.4	$t = 1.2$	0.25
Tree taxon	At: 97%	At: 95%	$\chi^2 = 3.7$	0.16	Gr: 19%	Gr: 7%	$t = 10.8$	0.21
Distance to edge (m)	**7.3 ± 0.6**	**28.1 ± 3.5**	$t = -5.9$	<0.001	527 ± 89	663 ± 54	$t = -1.3$	0.20

Notes: NOFL, Northern Flicker (*Colaptes auratus*); exc., excavated; At, trembling aspen (*Populus tremuloides*); Gr, Grapia (*Apuleia leiocarpa*). Bold values indicates that differed significantly between exceptionally productive and low use cavities at α = 0.05.

interaction between study area and years available in predicting number of nests (relationship between number of nests and years available had a slightly more positive slope in Argentina), and a significant effect of study area on number of nests (higher in Canada; Table 4). Contrary to our predictions, neither study area nor its interaction with years available was a significant predictor of species richness (Table 4).

After controlling for years available, each of the cavity, tree and habitat features we studied, except cavity depth, was related to at least one of our measures of cavity productivity in Argentina or Canada; however, most of the effects were weak and did not coincide with our earlier short-term studies of nest-site selection (Table 3; Aitken and Martin 2004, Cockle et al. 2011). In alignment with our nest-site selection studies, height-above-ground had

TABLE 3. Effect of cavity, tree, and habitat characteristics on nest-site selection (characteristics selected (+) vs. avoided (−); Aitken and Martin 2004, Cockle et al. 2011) and lifetime cavity productivity (total number of nests and species richness across the lifetime of individual cavities; this study) in (A) North Temperate (interior Douglas-fir) forest, Canada, and (B) subtropical Atlantic forest, Argentina.

		Number of nests		Species richness	
Predictor variable	Nest-site selection	b	P	b	P
(A) Canada					
Years available		**0.20 ± 0.015**	**<0.001**	**0.35 ± 0.038**	**<0.001**
(Years available)^2		**−0.0045 ± 0.00073**	**<0.001**	**−0.011 ± 0.002**	**<0.001**
Cavity origin (excavated)	+	−0.043 ± 0.105	0.69	0.27 ± 0.27	0.31
Entrance diameter (cm)		**0.039 ± 0.013**	**0.002**	0.045 ± 0.031	0.14
Cavity depth (cm)		−0.00063 ± 0.0013	0.62	0.0020 ± 0.0032	0.52
Height above ground (m)	−	0.005 ± 0.012	0.65	**0.11 ± 0.028**	**<0.001**
Tree DBH (cm)		0.003 ± 0.0017	0.13	**0.0094 ± 0.0041**	**0.023**
Distance to edge (km)	−	0.46 ± 1.42	0.74	−1.13 ± 1.22	0.36
Years available × distance to edge		**−0.65 ± 0.22**	**0.0036**		
(B) Argentina					
Years available		**0.25 ± 0.034**	**<0.001**	**0.44 ± 0.067**	**<0.001**
Cavity origin (excavated)		**−0.39 ± 0.15**	**0.008**	0.11 ± 0.29	0.71
Entrance diameter (cm)		−0.022 ± 0.012	0.082	−0.0053 ± 0.025	0.83
Cavity depth (cm)	+	0.0013 ± 0.0011	0.23	0.0000 ± 0.0026	0.998
Height above ground (m)	+	−0.0044 ± 0.013	0.73	**0.068 ± 0.028**	**0.017**
Tree DBH (cm)	+	−0.0020 ± 0.0026	0.45	−0.0075 ± 0.0058	0.19
Distance to edge (km)		−0.0012 ± 0.12	0.99	**−0.66 ± 0.27**	**0.014**

Notes: Parameter estimates (b, with associated standard errors in parentheses) and probabilities (P) are given for generalized linear models predicting number of nests and species richness within individual cavities. Effect of each predictor on each measure of cavity productivity is highlighted in boldface type if the slope parameter differs significantly from 0 (Z test, α = 0.05). Reference level for cavity origin is non-excavated.

TABLE 4. Predictions, parameter estimates (b, with associated standard errors in parentheses) and probabilities (P; associated with Z test) for generalized linear models predicting two measures of productivity (number of nests, Poisson family; species richness, COM-Poisson) in tree cavities in north temperate (interior Douglas-fir) forest, Canada, and subtropical Atlantic forest, Argentina.

Response and predictor variables	b	SE	P
Number of nests			
Years available	**0.16**	**0.012**	**<0.0001**
(Years available)^2	**−0.0025**	**0.00061**	**<0.0001**
Study area	**−0.40**	**0.20**	**0.041**
Years available × study area	0.13	0.070	0.064
(Years available)^2 × study area	−0.0050	0.0052	0.334
Species richness			
Years available	**0.28**	**0.030**	**<0.0001**
(Years available)^2	**−0.0068**	**0.0016**	**<0.0001**
Study area	−0.18	0.41	0.66
Years available × study area	−0.046	0.16	0.77
(Years available)^2 × study area	0.013	0.013	0.30

Notes: Reference level for study area variable is Canada. Effect of each predictor on each measure of cavity productivity is highlighted in bold if the slope parameter b differs significantly from 0.

a positive effect on species richness in Argentina (but unexpectedly, also in Canada; Table 3). Contrary to the results of nest-site selection studies, productivity was not higher in excavated cavities than in non-excavated

cavities in Canada, and excavated cavities supported fewer nests than non-excavated cavities in Argentina (Table 3). Distance-to-edge, which was negatively associated with nest-site selection in Canada (Aitken and Martin 2004), diminished the strength of the positive relationship between years available and number of nests in Canada, and had a negative effect on species richness in Argentina (Table 3).

Contributions to landscape-scale diversity

At the scale of the study area, the 20% most highly used cavities (5–22 nests/cavity in Canada, $N = 429$; 3–14 nests/cavity in Argentina, $N = 49$) accounted for 48% of nests and 74% of species in Canada and 46% of nests and 47% of species in Argentina. Cavities used only once ($N = 735$ cavities in Canada, 119 cavities in Argentina) accounted for 34% of cavities, 11% of nests and 55% of species in Canada, and 49% of cavities, 22% of nests, and 71% of species in Argentina. Sampling across cavities, species accumulation was (1) faster in Argentina than in Canada, (2) faster in high-use cavities than single-use cavities in Canada, but (3), unexpectedly, similar between high-use and single-use cavities in Argentina (Fig. 5). Thus, a random sample of 49 single-use cavities in Argentina would harbor 22.5 species (vs. 20 species for high-use cavities in Argentina, 15.2 species for high-use cavities in Canada, and 10.6 species for single-use cavities in Canada; Fig. 5). In Canada, single-use
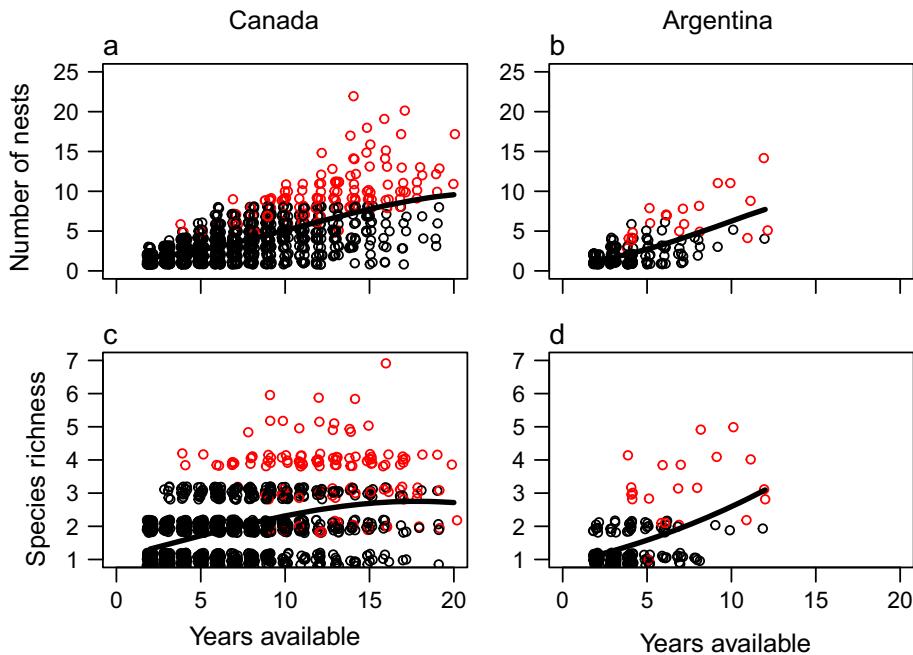

FIG. 4. Relationship between (a, b) number of nests or (c, d) species richness within tree cavities, and the number of years these cavities were available and monitored, in (a, c) Canada and (b, d) Argentina. Jittered points indicate observations of individual cavities. Red points indicate cavities in the top 5% for either number of nests or species richness. Solid lines indicate the predicted values of generalized linear models that included only years available and (years available)^2 as predictors: (a) Poisson, (b–d) COM-Poisson.
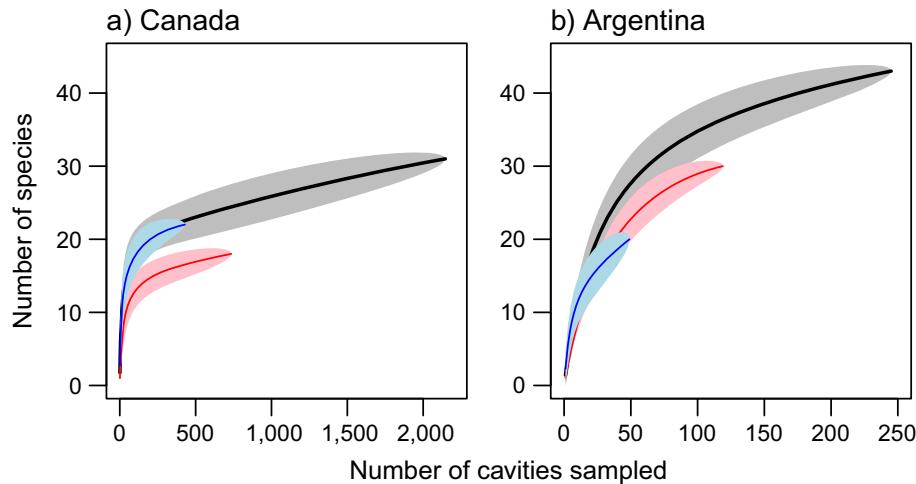
FIG. 5.   Estimated landscape-level species accumulation curves with 95% confidence intervals for (a) interior Douglas-fir forest, Canada and (b) Atlantic forest, Argentina, constructed by sampling across all cavities (black), single-use cavities (cavities with only one recorded nest; red), and the 20% most highly used cavities (5–22 nests/cavity in Canada; 3–14 nests/cavity in Argentina; blue).

cavities were occupied by a perfectly nested subset of 18 of the 22 species found in high-use cavities (including 8 of 8 excavator species; Appendix S1: Table S1). In Argentina, in contrast, 30 species were found in single-use cavities, 20 in high-use cavities, and only 12 of these in both (including only 2 of the 11 excavators found in single-use cavities). Because we found lifetime richness within cavities to be similar between study areas, despite large differences in the regional species pool, we explored species turnover among cavities within each study area. Beta diversity (among cavities) was very high for both study areas (β_{SOR}, Canada 0.999, Argentina 0.994), driven almost entirely by species turnover (β_{SIM}, Canada 0.998, Argentina 0.992).

DISCUSSION

Despite large regional differences in the two species pools, species did not accumulate more rapidly within cavities in our species-rich system (Argentina) than in the poorer system (Canada), suggesting that local ecological and behavioral factors are more important than the regional species pool in determining the richness within individual cavities. In both regions, many cavities were used only once, and within-cavity species richness was much lower than predicted by null models. Productivity was consistently explained mainly by the length of time that the cavity was available (i.e., its life span). Unexpectedly, measures of lifetime productivity showed weak or inconsistent relationships with characteristics identified in short-term nest-site selection studies (Aitken and Martin 2004, Cockle et al. 2011), supporting the finding by Lindenmayer et al. (2011) that short-term (cross-sectional) studies are inadequate to identify resources that will be used consistently by fauna over the long term. At the landscape scale, we observed high

species turnover among cavities (high beta diversity) in both study systems. In Canada, as predicted, species accumulated most rapidly when sampling across high-use cavities. In contrast, in Argentina species accumulated at similar rates in high- vs. single-use cavities, and more rapidly when all cavities were included in the sample. We suggest that biodiversity of species-rich cavity-nesting communities is maintained by the combination of a few highly productive cavities and many low-use cavities.

Regional species pool does not predict within-cavity richness

As expected (given the longer breeding season and lower cavity availability in Argentina), occupancy of cavities was somewhat higher in Argentina (0.57 nests/cavity-year) than in Canada (0.46 nests/cavity-year), although this only became evident for the cavities monitored longest (e.g., ≥10 yr; Fig. 4). Unexpectedly, neither lower cavity availability nor the larger species pool resulted in faster accumulation of species within cavities in Argentina, suggesting that local ecological factors may depress cavity-level species richness in Argentina more than in Canada. The following local ecological factors are not expected to reduce the number of nests per cavity, but might explain low within-cavity species richness in Argentina. First, the pool of species that can use a given cavity is constrained by species-specific traits, such as body size and habitat preference (Saunders et al. 1982, Martin et al. 2004, Renton et al. 2015, Bonaparte and Cockle 2017). Cavity-nesters exhibited a similar range of body sizes between our two systems (Appendix S1: Table S1), so variation in body size is not likely to explain the unexpected low richness of cavities in Argentina. However, structurally complex subtropical

forest may allow greater niche differentiation than temperate forest (Terborgh and Weske 1969, Monteiro Vieira and Monteiro-Filho 2003, Lamanna et al. 2014). For example, emergent trees with large branches, high in the canopy, offer a 35% greater range of nest heights in our study system in Argentina (1–32 m; Cockle et al. 2017) compared to the system in Canada (0–23 m; K. Martin, *unpublished data*), possibly allowing greater vertical segregation (i.e. lower nest niche overlap) and reducing the pool of species that will use any individual cavity, despite lower cavity availability in Argentina than in Canada. Second, high year-to-year nest-site fidelity in subtropical forests (e.g., 63% cavity reuse across years for Turquoise-fronted Parrots, *Amazona aestiva*, in subtropical Chaco forest [Berkunsky and Reboreda 2009]) would maintain a high number of nests in some cavities, but strongly reduce the number of species using each cavity. Third, by restricting access of subordinate species to high-quality cavities, dominant species might reduce cavity-level richness (again, while maintaining a high number of nests in some cavities; e.g., Renton and Brightsmith 2009, Strubbe and Matthysen 2009, Brazill-Boast et al. 2011). We currently lack evidence regarding the relative strength of interspecific competition for cavities in temperate vs. subtropical forests. Niche overlap, nest-site fidelity, sequential use of cavities, and resource competition are important avenues for future comparative research among cavity-nesting communities across forest types, to understand mechanisms of species coexistence and functioning of complex nest webs.

Short-term studies are insufficient to characterize highly productive cavities

High productivity (many nests and/or species) was associated predominantly with long cavity life span, and additionally with (1) excavation by Northern Flickers, in large living trees near forest edge, in Canada, and (2) deep non-excavated cavities in living trees, in Argentina. Short-term nest-site selection studies did not generally identify the cavity characteristics associated with high productivity, but they can still provide critical data on cavity requirements in systems where both high- and low-productivity cavities contribute to cavity-nester diversity. In particular, approaches that combine nest-site selection and analyses of species-specific nest niche can help ensure that forestry policies include measures to conserve the range of tree cavity requirements for whole nest webs.

Conserving high- and low-productivity cavities in the landscape

Relative to the number of species that coexist at a single time over the space of a forest landscape (Table 1), we found fewer than expected cavity-nester species using individual cavities across time in even our most productive cavities, meaning that diversity of cavity-users at the landscape scale is maintained primarily by turnover among (vs. within) cavities. When sampling multiple cavities across the landscape, in Canada, species accumulation was faster in high-use than in single-use cavities, and single-use cavities were occupied by a nested subset of the species found in high-use cavities. In contrast, in Argentina, the rate of species accumulation was similar across high- and single-use cavities (despite 3–14 times more nests in high-use cavities), and many species, including nine species of excavators, were found in single-use cavities but not in high-use cavities. Thus, a few long-lasting, high-quality cavities can contribute disproportionately to cavity-nester populations (and thus communities), and should be especially targeted for conservation, but many single-use cavities are also needed to conserve the most diverse nest webs.

Because the longest-lasting cavities outlived our study, we have provided minimum estimates of the number of nests and species across their lifetimes. Long-lasting cavities occur primarily in large, living trees, often in slow-growing old-growth species, but also in some faster-growing early successional species such as trembling aspen (Lindenmayer and Wood 2010, Wesołowski 2011, 2012, Edworthy et al. 2012, Cockle et al. 2017). Harvesting large living trees (e.g., through minimum diameter cutting limits) has led to disproportionate reductions in cavity availability, as well as the abundance, taxonomic and functional diversity of cavity nesters (Politi et al. 2012, Ruggera et al. 2016, Ibarra et al. 2017). For example, following the current policy of minimum diameter cutting limits in our study system in Argentina, harvesting one-half of the basal area of trees resulted in nine times fewer cavities and 17 times fewer nests (Cockle et al. 2010). The large living trees that are removed under such policies are the same trees most likely to harbor long-lasting (Cockle et al. 2017) and therefore highly productive cavities (this study), resulting in disproportionate impacts on the diversity, structure, and function of cavity-nesting communities. Instead of minimum diameter cutting limits, we suggest that sparing some large living trees from harvest (as occurred at our study site in Canada) can help maintain highly productive cavities, their role in the nest web, and their connections to other above-ground (e.g., epiphytes, seed dispersal) and below-ground networks (e.g., mycorrhizae; Diaz et al. 2012, Sáyago et al. 2013, Simard et al. 2013, Filotas et al. 2014, Lindenmayer and Laurance 2017).

Unexpectedly, low productivity cavities (used only once) harbored more than one-half of all species, and, in Argentina, combining all types of cavities produced the highest rates of species accumulation overall. Thus, conserving only highly productive legacy trees will not be sufficient to maintain landscape-scale cavity-nester diversity in all systems. Some bird species (e.g., many trogons), specialize on single-use cavities in short-lived substrates such as highly decayed wood or rapidly decaying palms, which contribute significantly to beta

diversity (among cavities) at the landscape scale (Brightsmith 2005, Renton and Brightsmith 2009, Steward et al. 2013). Ensuring the long-term availability of such substrates in managed landscapes, such as pastures, poses a significant challenge, as their short life span (e.g., 1–2 yr) necessitates constant recruitment. However, a single large living tree could provide both long-lasting cavities (e.g., in the main stem) and a series of short-lived, single-use cavities (e.g., in dead branches). Just as a long-lived cavity can become suitable for a changing suite of species across its lifetime, a single tree can support a succession of cavities and cavity nesters if it is permitted to grow, decay, and die over the course of several decades (Blanc and Martin 2012). Forest policies should include measures to conserve large standing dead and senescing trees, to promote an ongoing supply of short-lived cavities. Ultimately, landscapes with a high structural diversity of trees (variety of sizes and decay stages) are needed to support diverse communities of tree cavity-nesting organisms (Cadieux and Drapeau 2017). Harvesting plans should promote retention of a range of tree sizes to allow for future recruitment of cavity-bearing trees and maintenance of structural diversity over time. A continuous supply of large trees with decaying sections will ensure a supply of long-lived non-excavated cavities (particularly important in Argentina, where non-excavated cavities form almost exclusively in large trees; Cockle et al. 2011). Managing for abundant and diverse excavator populations will help ensure a continual supply of fresh, single-use, excavator-formed cavities. Landscape-level planning to include both long-lasting and single-use cavities should be incorporated into regional-level policy decisions, reserve networks, and criteria for sustainable forest certification.

Given widespread loss and degradation of mature forest globally, conservation of cavity-nesting communities will increasingly rely on an understanding of nest web dynamics in secondary forest and agroforestry landscapes (Regos et al. 2018). To understand and maintain complex nest web dynamics, longitudinal approaches can be used to integrate demography of cavity nesters with production and loss of tree cavities at the landscape scale (Lindenmayer et al. 2011, Cockle and Martin 2015). Future research should evaluate the extent to which different types of cavities (e.g., woodpecker vs. decay-formed; low- vs. high-productivity) can compensate for one another, providing redundancy and resilience to cavity-nesting communities in the face of increasing levels of local and regional disturbance.

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