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Secondary Amazon rainforest partially recovers tree cavities suitable for nesting birds in 18–34 years

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ABSTRACT

Passive restoration of secondary forests can partially offset loss of biodiversity following tropical deforestation. Tree cavities, an essential resource for cavity-nesting birds, are usually associated with old forest. We investigated the restoration time for tree cavities suitable for cavity-nesting birds in secondary forest at the Biological Dynamics of Forest Fragments Project (BDFFP) in central Amazonian Brazil. We hypothesized that cavity abundance would increase with forest age, but more rapidly in areas exposed to cutting only, compared to areas where forest was cut and burned. We also hypothesized that cavities would be lower, smaller, and less variable in secondary forest than in old-growth forest, which at the BDFFP is part of a vast lowland forest with no recent history of human disturbance. We used pole-mounted cameras and tree-climbing to survey cavities in 39 plots (each 200 × 40 m) across old-growth forests and 11–34-year-old secondary forests. We used generalized linear models to examine how cavity supply was related to forest age and land-use history (cut only vs cut-and-burn), and principal components analysis to compare cavity characteristics between old-growth and secondary forest. Cavity availability increased with secondary forest age, regardless of land-use history, but the oldest secondary forest (31–34 years) still had fewer cavities (mean ± SE = 9.8 ± 2.2 cavities ha^{-1}) than old-growth forest (20.5 ± 4.2 cavities ha^{-1}). Moreover, secondary forests lacked cavities that were high and deep, with large entrances—characteristics likely to be important for many species of cavity-nesting birds. Several decades may be necessary to restore cavity supply in secondary Amazonian forests, especially for the largest birds (e.g., forest-falcons and parrots > 190 g). Retention of legacy trees as forest is cleared might help maintain a supply of cavities that could allow earlier recolonization by some species of cavity-nesting birds when cleared areas are abandoned. A Portuguese version of this article is available in Supplementary Material 1.

Keywords: Amazon, cavity-nesting bird, cavity supply, fire, forest age, secondary forest, tree hole, tropical

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LAY SUMMARY

- Conserving cavity-nesting birds outside of old-growth reserves requires an understanding of how long it takes for cavities to develop in secondary forest.
- We investigated the passive restoration time for tree cavities in the Central Amazon by surveying cavities in 39 plots across old-growth forests and 11–34-year-old secondary forests.
- Cavity availability increased with forest age, but the oldest secondary forest still had fewer cavities than old-growth forest, and secondary forests lacked cavities suitable for the largest cavity-nesting birds.
- Several decades may be necessary to restore cavity supply in secondary Amazonian forests.
- Cavity-nesting birds might be able to recolonize secondary forest more quickly if legacy trees are retained when old-growth forest is cleared.

A floresta tropical secundária da Amazónia recupera parcialmente as cavidades das árvores adequadas para a nidificação de aves em 18–34 anos

RESUMO

A perda de biodiversidade após o desmatamento de florestas tropicais pode ser parcialmente compensada pela recuperação de florestas secundárias. As cavidades das árvores são um recurso essencial para as aves que nidificam em cavidades, mas geralmente estão associadas a florestas primarias. Investigamos o tempo de recuperação de cavidades em árvores, adequadas para aves que fazem ninhos em cavidades,

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na floresta secundária no Projeto Dinâmica Biológica de Fragmentos Florestais (PDBFF) da Amazônia Central do Brasil. Nossa hipótese era de que a abundância de cavidades aumentaria com a idade da floresta, mas esta aumentaria mais rapidamente em áreas expostas apenas ao corte, em comparação com áreas onde a floresta havia sido cortada e queimada. Também levantamos a hipótese de que as cavidades seriam mais baixas, menores e menos variáveis na floresta secundária do que na floresta primária, que no PDBFF faz parte de uma vasta floresta de planície sem histórico recente de perturbação humana. Utilizamos câmeras montadas em postes e escalamos árvores para pesquisar cavidades em 39 parcelas (cada uma com 200 × 40 m) em florestas primárias e florestas secundárias de 11 a 34 anos de idade. Utilizamos modelos lineares generalizados para examinar como o suprimento de cavidades estava relacionado à idade da floresta e ao histórico de uso da terra (somente corte vs. corte e queima) e análise de componentes principais para comparar as características das cavidades entre florestas primárias e secundárias. A disponibilidade de cavidades aumentou com a idade da floresta secundária, independentemente do histórico de uso da terra, mas a floresta secundária mais antiga (31–34 anos) ainda teve menos cavidades (média ± SE = 9,8 ± 2,2/ha) do que a floresta primária (20,5 ± 4,2 cavidades/ha). Além disso, as florestas secundárias não tiveram cavidades altas e profundas, com entradas grandes - características que provavelmente são importantes para muitas espécies de aves que fazem ninhos em cavidades. Podem ser necessárias várias décadas para recuperar o suprimento de cavidades nas florestas secundárias da Amazônia, especialmente para as aves maiores (e.g., *Micrastur* spp. e Psittacidae > 190 g). A retenção de árvores legadas (quando as florestas são desmatadas) pode ajudar a manter um suprimento de cavidades que poderia permitir a recolonização precoce por algumas especies de aves florestais que fazem ninhos em cavidades, quando essas pastagens são abandonadas permitindo o crescimento da floresta secundária. Uma versão em português deste artigo está disponível no Material Suplementar 1.

Palavras chave: Amazônia, Aves que nidificam em cavidades, Abundância de cavidades, Fogo, Idade da floresta, Floresta secundaria, Cavidade, Tropical

INTRODUCTION

Globally, ~72% of cavity-nesting bird species are non-excavators that rely, for their reproduction, on pre-existing tree cavities expected to develop slowly over time with forest succession (Newton 1998, van der Hoek et al. 2017, Ibarra et al. 2020). Observational studies and nest-box addition experiments suggest that populations of these non-excavators are often limited by cavity supply in areas with few large trees (Holt and Martin 1997, Newton 1998, Cockle et al. 2010, Politi et al. 2010, 2012; Warakai et al. 2013, Cuatianquiz Lima and Macías Garcia 2016, Nyirenda et al. 2016, Schaaf et al. 2021, 2022; Niringiyimana et al. 2022). Newton (1998) proposed that during the earliest stages of forest succession, cavities and cavity-nesting birds are absent; as the forest grows, both cavities and cavity-nesting birds increase; and finally, in mature forest, the number of cavities passes a critical threshold, whereby other factors begin to limit populations of cavity-nesting birds. Nest box experiments support the idea that in some older forests an abundant supply of tree cavities releases birds from nest site limitation (Wiebe 2011), but few empirical studies have examined how cavity supply develops during forest succession.

Whether cavities are facilitated by excavators (e.g., woodpeckers) or formed by decay and damage alone, the process of tree cavity formation begins with wood decay. Decay fungi colonize wood cells, modifying chemical and physical properties and softening the wood, usually at the center of the tree (i.e., heartwood), at a rate of a few centimeters per year (Robledo and Urcelay 2009, Cockle et al. 2012, Bednarz et al. 2013, Zheng et al. 2016). For a suitable nest cavity to form in this decayed wood, an external agent, such as a woodpecker, branch breakage, or other mechanical damage, must perforate the outer wood, which is usually harder (e.g., Conner and Locke 1982, Gibbons and Lindenmayer 2002, Lorenz et al. 2015). Thus, for a tree to contain a nesting cavity, it first requires a core of decayed wood with a volume approximating the minimum size of a suitable nest chamber (Jackson and Jackson 2004). The smallest cavity-nesting birds can occupy cavities in trees as small as 11 cm in diameter, but larger species require much larger trees (Pichorim 2006, De Labra-Hernández and Renton 2016, Wesołowski and Martin 2018). Tree cavities thus develop on a timescale of years or even centuries, and there is a well-established positive association between tree age, tree size, and cavity development, whereby most cavities are found in the largest, oldest trees (Koch et al. 2008, Cockle et al. 2010, Warakai et al. 2013, Niringiyimana et al. 2022).

Tree-cavity nesters reach their peak diversity in tropical forests, particularly the Amazon, the largest tropical forest biome globally, where some sites are estimated to support up to 145 species of cavity-nesting birds (van der Hoek et al. 2017). Ongoing deforestation and wildfires in the Amazon and other tropical biomes have led many researchers to propose legal protection of secondary forests to capture carbon and meet reforestation targets, which might also benefit biodiversity (Bongers et al. 2015, Heinrich et al. 2021). In a meta-analysis of 600 tropical and subtropical secondary forest sites globally, tree species richness recovered after ~50 years and above-ground biomass recovered after ~80 years, but epiphyte richness (associated with the presence of large trees) did not recover even after a century (Martin et al. 2013). Studying structural elements of a tropical moist forest chronosequence in central Panama, DeWalt et al. (2003) concluded that many cavity nesters may find adequate nesting sites only in forests at least 70 years old. Burning after clearing may exacerbate the time lag to develop cavities: intentional burning in the Amazon led to early forest succession involving fewer tree species, of smaller diameter, probably slowing the process of forest recovery compared to unburned areas (Mesquita et al. 2001). Secondary forests are already growing on approximately 150,000 km^2 or 21% of deforested land in the Brazilian Amazon (Almeida et al. 2016). It remains unclear how quickly or how much these secondary tropical forests can contribute to biodiversity targets, including the cavities required by many nesting birds (Dunn 2004, Wright and Muller-Landau 2006, Barlow et al. 2007, Omeja et al. 2016).

Most community-level research on birds in tropical secondary forest has grouped species by feeding guild, rather than nesting guild (Renner et al. 2006, Santamaría-Rivero et al. 2016, Acevedo-Charry and Aide 2019), in part because the nesting habits of so many tropical species remain undescribed (Crozariol 2016). Nevertheless, there is evidence that cavity nesters are less abundant in secondary than in old-growth tropical forest, and that the difference may be related to cavity availability. In tropical Mesoamerica, secondary forest supported half the number of suitable nesting cavities and almost six times lower density of cavity-nesting Northern Mealy Amazon (*Amazona farinosa guatemalae*) compared to old forest (De Labra Hernández and Renton 2016, 2017). Secondary forest was also avoided by Collared Forest-Falcons (*Micrastur semitorquatus*), which require large, non-excavated cavities in live trees for nesting

TABLE 1. Number of plots and number of cavities ha^{-1} (mean ± SE) in old-growth and secondary forest. Age indicates forest age since abandonment (beginning of passive restoration). Plots are divided by land-use history (cut and burned vs cut only).

Forest type	Age (yr)	Number of plots			Cavities ha^{-1} (mean ± SE)
		Cut only	Cut and burned	Total	
Secondary	11–15	4	4	8	0 ± 0
Secondary	18–20	6	4	10	5.5 ± 2.1
Secondary	25–27	4	4	8	5.3 ± 2.1
Secondary	31–34	5	0	5	9.8 ± 2.2
Old-growth	Unknown	0	0	8	20.5 ± 4.2

(Martínez-Ruiz 2021). In the central Amazon, researchers recorded lower abundance of canopy-dwelling parrots and confirmed breeding in fewer species of understory cavity-nesters in < 35-year-old secondary forest compared to old-growth forest (Figueira et al. 2015, Rutt et al. 2021). All of these studies inferred scarcity of tree cavities to be a likely driver of the differences in birds' use of secondary vs. old-growth forest.

The presence, diversity, and recruitment of non-excavator birds depends not only on the abundance of cavities but also on their characteristics. A diversity of cavity characteristics can be important for maintaining a diversity of cavity-nesting species (e.g., large and small-bodied birds; Li and Martin 1991, Martin et al. 2004, Datta and Rawat 2004, Bonaparte and Cockle 2017, Di Sallo and Cockle 2022). Large, decay-formed cavities, high above the ground, can be especially critical for maintaining large-bodied, canopy-dwelling species (e.g., macaws, Renton and Brightsmith 2009; hornbills, Poonswad 1995, Manikandan and Balasubramanian 2018). However, such cavities are strongly associated with mature forest (De Labra Hernández and Renton 2016, Ibarra et al. 2020, Schaaf et al. 2020). Compared to old tropical forests, logged and secondary forests are expected to harbor lower, smaller, and shallower cavities, suitable for small birds (Cockle et al. 2011, Bonaparte et al. 2020).

Here, we studied tree cavity abundance and diversity in old forest and secondary forest undergoing natural succession (passive restoration) in the central Amazon. We considered old forest to represent the baseline, then used a space-for-time substitution to examine the restoration of tree cavities in secondary forest aged 11–34 years. If passive restoration of tree cavities occurs in 11- to 34-year-old secondary forest in the central Amazon, we predicted that the abundance of cavities would increase with forest age. If burning of clearcut sites slows cavity restoration during early succession, we predicted that the increase with age would occur more rapidly in areas exposed to cutting only, compared to areas where the forest had been cut and then intentionally burned. Finally, we compared cavity characteristics and diversity between old-growth and secondary forest. Given that trees must reach a certain size before they can support a large, high cavity, we expected that cavities in secondary forest might be lower, smaller, and less variable than cavities in old-growth forest.

METHODS

Study Area

We surveyed tree cavities in upland Terra Firme forest at the Biological Dynamics of Forest Fragments Project (BDFFP), north of Manaus in central Amazonas, Brazil (02°20′S, 60°5′W). Although the nests of several species remain undescribed, we estimate that the study area harbors approximately 15 species of avian excavators, including woodpeckers (Picidae), trogons (Trogonidae), and Plain Xenops (*Xenops minutus*), and 47 species of non-excavators, including passerines (Passeriformes), toucans (Ramphastidae), parrots (Psittacidae), and raptors (Falconidae and Strigidae; Johnson et al. 2011, Rutt et al. 2017, van der Hoek et al. 2017). The non-excavators vary in size by two orders of magnitude (e.g., from the 14-g Wedge-billed Woodcreeper [*Glyphorynchus spirurus*] to the 1.5-kg Red-and-green Macaw [*Ara chloropterus*]).

The study area comprised approximately 90% old-growth rainforest (not cut or substantially disturbed by humans within recent memory), with the remaining area including secondary growth, experimentally isolated forest fragments, and small areas of pasture (Rutt et al. 2019; Supplementary Material Figure 1). Isolation of the BDFFP reserves began in 1979. Some areas were cut without burning, giving rise to secondary forest dominated by *Cecropia sciadophylla*; other areas were cut and then intentionally burned, giving rise to secondary forest initially dominated by *Vismia* spp. (Mesquita et al. 2001). When *Cecropia* and *Vismia* stands were studied at 6 years of age, they had similar heights (approximately 1.5 m) but the young *Cecropia* stands had more trees > 5 cm in diameter, higher basal area, and a diversity of old-forest species in the understory, whereas *Vismia* stands had only *Vismia* in the understory, suggesting that *Vismia* may inhibit the regeneration of old forest tree species (Mesquita et al. 2001).

At the time of our study, the area comprised a mosaic of old-growth forest, grasslands, and regenerating forest of different ages. Within this mosaic, we placed 39 plots: 8 in old-growth forest and 31 in secondary forest aged 11–34 years (Supplementary Material Figure 1). Each plot measured 200 × 40 m (0.8 ha). For each stand age, we aimed to balance the number of plots in secondary forest that grew after cutting only vs. cutting and burning, but this was not always possible (Table 1). Plots were centered along established linear transects or mist-net lines from other projects, with 200 m length and 20 m extension to each side. We spaced plots as well as was feasible given the existing trail network, which was limited, especially in secondary forest. There were no existing trails through most of the secondary forest, and the youngest forest was clumped because of the management that created it (Supplementary Material Figure 1).

Field Methods

From July to October 2013, 2 observers searched for cavities by examining each tree within each plot, with the aid of binoculars. To inspect the interior of cavities, we used a 2-cm diameter video camera, which was either mounted on a 15-m telescoping fibreglass pole, or carried up to the cavity using single-rope tree-climbing (Politi et al. 2009, Di Sallo and Cockle 2022). Cavities were only included in our dataset if they had a sufficient diameter to permit the passage of a bird (>2 cm), and an internal chamber capable of offering protection to eggs (i.e., with a floor, walls, and some overhead protection, at minimum; Politi et al. 2009). We excluded cavities that contained water. We measured the height of each cavity from the lower sill of the entrance to the ground, using the 15-m pole, marked every 10 cm. For cavities above 15 m, we used the climbing rope to measure cavity height. Entrance dimensions and horizontal depth were measured to the nearest centimeter using a tape measure (if we climbed to the cavity) or a 35-cm ruler attached to the top of the 15-m pole. We used a tape measure to determine vertical depth of cavities to the nearest centimeter. In the few cases in which it was not possible to climb to the cavities (e.g., dead trees in decomposition), but where we could access the cavity with the pole-mounted camera, we estimated vertical depth using the camera image, after first practicing on cavities that were measured with a tape measure. Using either tree climbing or the pole, we were able to measure 93% of cavities found in secondary forest and 92% of cavities found in primary forest.

Analyses

We used R version 4.2.0 (R Core Team 2022) for all statistical analyses. To evaluate the effect of forest age and land-use history on cavity availability in secondary forests, we used the stats package to create a generalized linear model (GLM, quasi-Poisson family, log link). The full model included the number of cavities per plot as the response variable, and forest age, land use history (i.e., cutting only vs cutting and burning), and their interaction, as predictor variables. We chose the quasi-Poisson family for the error structure because preliminary visualization of the data and analyses with a Poisson distribution revealed overdispersion in the data. Analyses using a negative binomial distribution gave similar results to the quasi-Poisson distribution, but we opted for a quasi-Poisson distribution because we wanted to put more weight on higher values of cavity abundance than on values near zero (Ver Hoef and Boveng 2007). We removed a non-significant interaction term and present the parameters for the model with all main effects in the Results. For simplicity, we removed a non-significant main effect to produce a final model for prediction. We also built a constant (intercept-only) model. We compared generalized linear models using analysis of deviance and present their parameters in Supplementary Material Table 1. The relationship of cavity abundance to forest age was not expected to be linear, and we observed some probable non-linearities in the data, so we additionally used the *nls* function to fit a self-starting logistic growth curve (Fox and Weisberg 2010) and a quasi-Poisson family generalized additive model with up to 3rd-order polynomials (Wood 2017), considering forest age as the single predictor variable. More information and code are provided in Supplementary Material 2.

We evaluated whether the density of suitable cavities in the oldest secondary forest could be distinguished statistically from that of old-growth forest. To do so, we used a Wilcoxon rank sum test (with continuity correction) to compare the number of suitable cavities found in the 8 old-growth forest plots to the number found in the 5 plots in 31- to 34-year-old secondary forest (data did not follow a normal distribution). Because of our small sample size, for this test we used $\alpha = 0.1$ to avoid type II errors.

We used Wilcoxon rank sum tests with continuity correction to compare cavity characteristics between old-growth and secondary forests. To explore how cavity characteristics vary among forests of different ages, we used the prcomp command (stats package) to perform a principal components analysis (PCA). We stipulated scale = TRUE to use the correlation matrix, thus weighting each variable equally. We used PCA to find linear combinations of cavity height, vertical diameter, horizontal diameter, vertical depth, and horizontal depth that best represent the variation in cavity characteristics. We followed the Kaiser Guttman criterion (Jackson 1993) and interpreted the principal components with eigenvalues > 1. The principal component values for each cavity were plotted to visually assess possible differences in centroids and variability of cavity characteristics between young secondary forest (<20 years), older secondary forest (>20 years) and old-growth forest.

RESULTS

We recorded 131 cavities suitable for nesting birds in our 8 old-growth forest plots (mean ± SE = 20.5 ± 4.2 cavities ha^{-1}, range: 9–38) and 117 in our 31 secondary forest plots (4.7 ± 1.1 cavities ha^{-1}, range: 0–17; Table 1, Figure 1). We did not find any cavities in the 8 plots in secondary forest 11–15 years old, but we found cavities in 8 of the 10 plots in forest 18–20 years old, in 7 of the 8 plots in forest 25–27 years old, in all 5 plots in forest 31–34 years old, and in all 8 plots in old-growth forest. We found about twice the density of cavities in old-growth forest compared to the oldest secondary forest (31–34 years; Table 1). However, this difference was only marginally statistically significant ($W = 34$, $p = 0.055$) and several plots in secondary forest (age 18 and older) had higher cavity availability than many plots in old-growth forest (Figure 1).

All of our models indicated that cavity availability increased with forest age (Figure 1, Supplementary Material Table S1 and Figure S5). None of the models explained the large variation in cavity abundance within forest 18–20 and 25–27 years old, and all of the models overestimated cavity abundance in the youngest forest (Supplementary Material Figures S2–S5). Cavity abundance was positively related to secondary forest age but not related to land use history (Figure 1A, Table 2, and Supplementary Material Table S1). We explored non-linearities in the relationship between forest age and cavity abundance via generalized additive models, but these models did not improve fit over the generalized linear model (Supplementary Material Figure S5). A non-linear logistic-growth curve also produced predictions similar to those of the generalized linear model, indicating an inflection point at 36 years and an asymptote of 22 cavities per 0.8-ha plot (Supplementary Material Figure S5).

We measured 109 cavities in secondary forest and 120 cavities in old-growth forest. Overall, cavities were significantly smaller in secondary forest than in old-growth forest (Table 3). Additionally, multivariate analysis suggested that cavity characteristics were less diverse in secondary forest than in old-growth forest (Figure 2). The first two principal

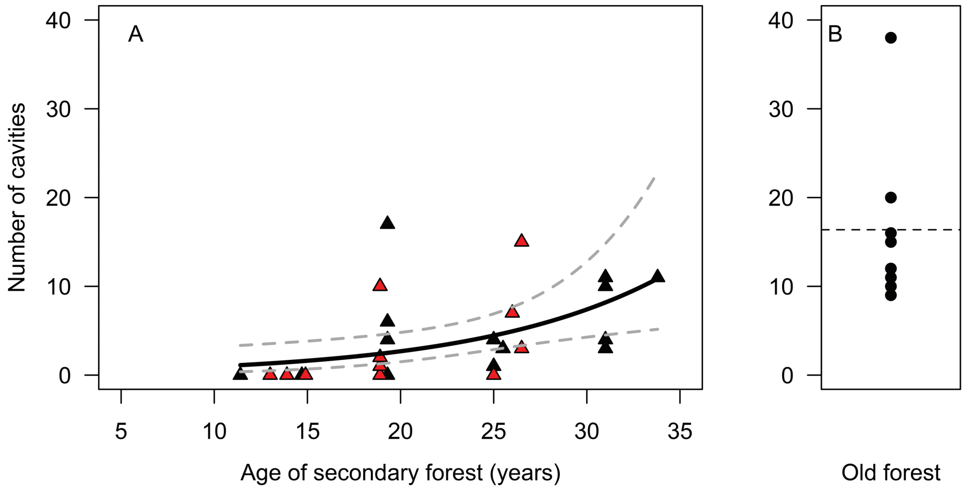

FIGURE 1. Cavity supply increases with forest age in 0.8-ha forest plots in the central Amazon (31 plots in secondary forest, 8 plots in old forest). (**A**) Number of cavities vs. forest age, in secondary forest regenerating after cutting and burning (red triangles) or cutting only (black triangles). Solid line indicates predicted values of the quasi-Poisson family generalized linear model: cavities ~ forest age. Dashed grey lines indicate 95% confidence intervals on the predicted values. (**B**) Number of cavities in eight plots in old-growth forest. Broken horizontal line indicates mean.

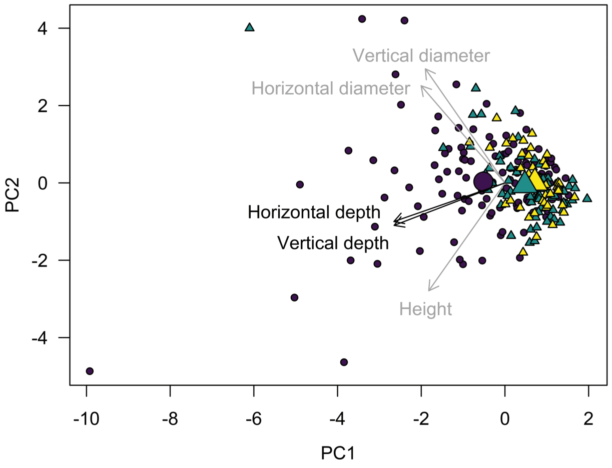

FIGURE 2. Cavity characteristics are more variable in old-growth forest than in secondary forest. Principal components analysis (PCA) showing the variation in characteristics of 120 cavities measured in old-growth forest (dark purple), 42 in secondary forest 18–20 years old (yellow triangles), and 67 in secondary forest 25–34 years old (turquoise triangles). Large symbols indicate centroids for each forest type. PC1 is negatively correlated with horizontal and vertical depth (black arrows), and PC2 is positively correlated with entrance diameter and negatively correlated with cavity height above ground (grey arrows). Cavities in old-growth forest occupy most of the ordination space, whereas cavities in secondary forest cluster to the right, signifying low variability in their characteristics.

TABLE 2. Forest age is important in predicting cavity supply. Parameters of a generalized linear model (quasi-Poisson family) predicting the number of cavities in 31 0.8-ha plots in secondary Amazon forest aged 11–34 years.

Parameter	*b* ± SE	*t*	*P*
Intercept	−1.17 ± 1.12	−1.04	0.31
Forest age	0.10 ± 0.04	−2.60	0.01
History (cut-and-burned)	0.13 ± 0.52	0.25	0.80

components had eigenvalues > 1 and were interpreted following the Kaiser Guttman criterion (Jackson 1993). PC1 explained 42% of the sample variance and was negatively correlated with horizontal depth ($r = -0.53$) and vertical depth ($r = -0.53$). PC2 explained 24% of the sample variance and was positively correlated with vertical diameter ($r = 0.59$) and horizontal diameter ($r = 0.50$) and negatively correlated with cavity height ($r = -0.56$; Figure 2). Cavities in old-growth forest were dispersed along both axes, demonstrating a wide range of cavity characteristics in old-growth forest (e.g., cavities that ranged from small to large and from low to high). In contrast, cavities in secondary forest, and particularly those in young secondary forest (<20 years old), clustered to the center-right of the multivariate space (Figure 2), signifying low variability (small, low, shallow cavities).

DISCUSSION

Tree cavities suitable for nesting birds were initially absent in secondary forests of the central Amazon, first appearing 16–20 years after the land was abandoned. Although burned areas generally exhibit slower regeneration than unburned areas in the Amazon (Mesquita et al. 2001) and the forests we studied were still young, we found no evidence to support the idea that land-use history (cutting only vs. cutting and burning) influenced cavity availability. After 31–34 years these secondary forests had not quite reached the levels of cavity availability found in old-growth forest, and they lacked large, deep, and high cavities suitable for many large-bodied birds (such as toucans, large raptors and macaws); nevertheless, they were clearly on the path to recovery, and harbored cavities that were likely suitable for several species of non-excavating passerines (e.g., woodcreepers). We surmise that absence of tree cavities will exclude cavity-nesting birds from breeding in secondary forest for the first approximately 15–20 years of succession in the central Amazon. An important direction for future research is the extent to which passive restoration of cavities

TABLE 3. Measurements (mean ± SE [range]) of 109 cavities in secondary forest and 120 cavities in old-growth forest of the central Amazon, with associated statistics for Wilcoxon rank sum test (with continuity correction).

Cavity measurements	Secondary (mean ± SE [range])	Old-growth (mean ± SE [range])	Test statistic (*W*)	*P*
Height (m)	4.8 ± 0.2 [1.4–10.7]	5.7 ± 0.4 [1.6–22.0]	6090	0.37
Horizontal entrance diameter (cm)	7 ± 0.4 [2–35]	8 ± 0.4 [3–25]	5032	0.0021
Vertical entrance diameter (cm)	10 ± 1 [3–35]	15 ± 0.8 [3–60]	3796	<0.0001
Horizontal depth (cm)	15 ± 0.3 [10–35]	18 ± 0.8 [10–80]	4755	0.0003
Vertical depth (cm)	18 ± 1 [5–50]	27 ± 2 [12–90]	3414	<0.0001

results in the restoration of cavity-nesting bird communities, as proposed by Newton (1998) under the hypothesis that nest sites limit populations of cavity-nesting birds in young forests.

Our finding from the central Amazon, that cavity abundance in 31- to 34-year-old secondary forest approached the levels found in old-growth forest, suggests, as expected, a relatively short lag-time for cavity development in tropical forest compared to subtropical and temperate forests. In subtropical southeastern Brazil, 35-year-old secondary Atlantic forest harbored less than half as many cavities per hectare compared to old-growth forest (Katayama et al. 2017). In temperate Poland, secondary pine forest harbored only 0.6 cavity trees ha^{-1} at 70–100 years of age, increasing to 3.3 trees ha^{-1} in stands > 130 years of age, still dramatically lower than the density of cavity trees in a primeval forest (12.5 cavity trees ha^{-1}; Zawadzka et al. 2016). In the midwestern USA, old-growth forest supported nearly 5 times the density of cavity trees compared to forests ≥ 110 years old (Fan et al. 2003). We caution that in our study and others, detectability of cavities may decline with forest age and complexity, such that we may be underestimating the differences in cavity abundance between young forest and old-growth forest. Additionally, some tree-cavity-nesting bird species in the Amazon can also use cavities excavated in arboreal termitaria, epiphytic root balls and wasp nests (Brightsmith 2004, 2005; Vasconcelos et al. 2015), which were not included in our study, and might increase overall resource availability. Given the warm and humid climate of the Amazon, conducive to rapid tree growth and decay (Poorter et al. 2016, Chambers et al. 2000), we suggest that approximately 18–34 years is about the fastest passive restoration of tree-cavities we are likely to see in secondary forest globally, an order of magnitude faster than in temperate forest.

Our analysis of cavity supply over time did not include information about how cavities were produced (i.e., by decay alone, or facilitated by avian excavators). In mature forests of the Neotropics, the predominant mode of cavity production is wood decay and breakage (Cornelius et al. 2008, Cockle et al. 2011, De Labra-Hernández and Renton 2016, Ruggera et al. 2016, Altamirano et al. 2017, Di Sallo and Cockle 2022, Soares et al. 2023). Nevertheless, woodpeckers and other excavators may speed up the restoration of tree cavities in disturbed systems such as secondary forest, before there is time for the slower formation of cavities by decay alone (Cockle et al. 2017, Bonaparte et al. 2020). Future studies should examine the role of excavators in providing cavities in the Amazon and other tropical rainforests, with particular attention to how this role varies with forest age and disturbance.

An 18–34-year lag is considerably longer than the lifespan of most secondary forest in the Brazilian Amazon, which is often subject to repeated cutting and regrowth (e.g., on a 5–10 year cycle; Yang et al. 2020). We did not find any cavities in secondary forest 11–15 years old. Although secondary forest is widespread in the Brazilian Amazon, most of it is currently < 10 years old (Yang et al. 2020), and remains unprotected (Vieira et al. 2014). Given that rates of biomass accumulation and other forest properties vary regionally within the Amazon (Baker et al. 2004, Esquivel-Muelbert et al. 2018), rates of cavity development merit further study across a range of Amazonian forests. However, even considering this possible variation in cavity formation rates, secondary forest seems unlikely to provide nest sites for cavity-nesting birds unless cutting cycles are extended by at least a decade.

Although burning of pastures strongly impacted vegetation and bird communities for the first decade of secondary forest growth in the central Amazon, bird communities (Stouffer 2020) and cavity availability (this study) converged soon after. In temperate forests, fire can both eliminate existing cavities and facilitate development of future cavities (e.g., by killing trees or breaking limbs; Lindenmayer et al. 1993, Stojanovic et al. 2016). Almost nothing is known about how fire affects habitat for cavity-nesting birds in tropical forests, and its effect will likely depend on the presence of remnant trees as well as the intensity of the burn.

Our findings that cavity characteristics, such as size and height, were much more variable in old-growth forest than in secondary forest, and that secondary forest only supported small, low cavities, likely indicate that 34 years is not enough time for secondary forest trees to develop large, high cavities. Likewise, in other parts of the Neotropics, cavities were lower and smaller in secondary forest, open farmland, and selectively logged forest, compared to old, well-conserved forest (De Labra Hernández and Renton 2016, Katayama et al. 2017, Bonaparte et al. 2020, Schaaf et al. 2020, 2022). High cavities are restricted to tall trees, and cavities with a large internal volume are restricted to large-diameter trees where fungi have had sufficient time to progressively colonize and decompose the heartwood (Koch et al. 2008, Warakai et al. 2013, Zheng et al. 2016). In the first decades of tropical secondary forest succession, trees are young and small; large trees, suitable for large cavities, may take many more decades to grow (Makelele et al. 2020), potentially limiting the sizes and heights of cavities for many years.

We expect that the restricted size and height of cavities represents an important filter limiting the diversity of cavity-nesting birds breeding in secondary tropical forest. Cavity diversity has a positive effect on abundance of cavity-nesting birds (Remm et al. 2008). In tropical and subtropical forests, many cavity nesting species select large, high cavities, which tend to occur in large old trees (Olah et al. 2014, de la Parra-Martínez et al. 2015). For example, in our study area, 4 species of forest-falcons (*Micrastur* spp.) range in size from the Barred Forest-Falcon (*Micrastur ruficollis*), with a mean female body mass of 196 g, to the Collared Forest-Falcon (739 g; Dunning 2007). Barred Forest-Falcons in Guatemala and Argentina nested in cavities 10–30 m high, 8–18 cm in horizontal entrance diameter, 30–40 cm in horizontal depth and 3–200 cm in vertical depth (Thorstrom et al. 1990, Thorstrom et al. 2000b, Thorstrom 2001, Bonaparte and Cockle 2017, K. Cockle personal observation). Collared Forest-Falcons in Guatemala and Venezuela nested in cavities 12–24 m high, 23–100 cm in vertical depth, 60 cm in horizontal depth, and with entrance diameters of 16–60 cm (Mader 1979, Thorstrom et al. 1990, 2000a; Thorstrom 2001). In old-growth forest within our study area, a pair of Lined Forest-Falcons (*Micrastur gilvicollis*; female: 209 g) nested in a cavity 4 m high, 24 cm in entrance diameter, 100 cm in horizontal depth and 180 cm in vertical depth (C. Dantas Oliveira personal observation). Taking 3.5 m as the minimum height, 25 cm as the minimum horizontal depth, and 8 cm as the minimum entrance diameter (16 cm for the largest species), our 6.4 ha of old-growth forest harbored 15 cavities large and high enough for a small forest-falcon (2.3 ha^{-1}). One of these cavities (0.2 ha^{-1}) was large enough for a Collared Forest-Falcon. In contrast, the 24.8 ha of secondary forest harbored only 2 cavities suitable for a small forest-falcon (0.1 ha^{-1}), 1 of which would also be suitable for a Collared Forest-Falcon (0.04 ha^{-1}). Cavities suitable for forest-falcons are approximately similar in dimensions to those used by *Amazona* spp. parrots (Rodríguez Castillo and Eberhard 2006, De Labra-Hernández and Renton 2016, Bonaparte and Cockle 2017, Di Sallo and Cockle 2022), of which 2 species, Mealy Amazon (*Amazona farinosa*, 626 g) and Red-lored Amazon (*Amazona autumnalis*, 416 g) are present in our study area. We surmise that for forest-falcons, *Amazona* parrots, and other large-bodied birds, including Red-and-Green Macaws, Blue-and-yellow Macaws (*Ara ararauna*, 1.2 kg), Red-billed Toucan (*Ramphastos tucanus* 595 g), Channel-billed Toucan (*Ramphastos vitellinus*, 363 g), Spectacled Owl (*Pulsatrix perspicillata*, 908 g), and Crested Owl (*Lophostrix cristata*, 620 g), potential nest cavities remain very rare or absent in secondary forest.

The barriers related to scarcity and small size of cavities in secondary forest could be studied and partly overcome through nest-box programs that might help bridge the approximately 18-year gap between pasture abandonment and cavity development in protected secondary forest. Some of the species in our study area have been recorded using nest boxes in other parts of their distributions (e.g., Barred Forest-Falcon in Argentina, Cockle et al. 2008; Black-banded Woodcreeper [*Dendrocolaptes picumnus*] in Colombia, Botero-Delgadillo and Olaciregui 2011). Nest box programs offer interesting research potential (Lambrechts et al. 2010, Warakai et al. 2013) but nest boxes are expensive and management intensive, they are often used by only a small subset of cavity-nesting species, and they can have unexpected negative impacts on birds (Lindenmayer et al. 2009, Le Roux et al. 2016a,b; Pedro 2023, Zhang et al. 2023). A more effective conservation strategy would probably be to retain old-growth forest patches and large legacy trees (trees of an older generation that persist in early successional forest), but studies are needed to examine the feasibility of legacy tree and old-growth retention in the Amazon and other Neotropical forests. Even when it does not offer nest sites, secondary Amazon forest can be important for movement, foraging, and roosting of cavity-nesting and other birds (Powell et al. 2015, Mokross et al. 2018, Stouffer 2020, Rutt and Stouffer 2021). Importantly, as Acevedo-Charry and Aide (2019) have remarked, although a large proportion of tropical forest vertebrates can colonize and survive in secondary forests, in many cases this process requires > 100 years, and if secondary forests are to contribute to the conservation of these groups, they need to be protected from future deforestation over the long term.

Our study provides a robust assessment of cavity availability in old-growth and secondary forest of the central Amazon, but little is known about the nesting requirements of Amazonian birds, and many nests remain undescribed. Previous work in our study area has shown that cavity-nesting birds are absent or scarce in young secondary forest (Figueira et al. 2015, Rutt et al. 2021), and our results support the idea that this pattern could be driven by the limited availability and sizes of cavities; however, we do not have direct evidence that increasing the supply or diversity of cavities leads to increased use of secondary forest by non-excavators. Other factors, such as food availability, predation risk, and environmental conditions (such as ambient light) are also known to constrain the presence, abundance, and recruitment of cavity-nesting birds (Renton et al. 2015, Seixas and Mourão 2022). Though challenging in tropical forests (Stouffer et al. 2013, Rutt et al. 2021), studies of nest-site selection, nest-site limitation, and recruitment are important to explore the factors that influence recolonization of secondary forest. Such studies would inform conservation and restoration of bird communities, including cavity-nesters, and allow researchers to take full advantage of fast-growing tropical forest to test models of resource limitation and restoration.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Field activities were approved by SISBIO authorization 52655-1. This is publication 0869 of the BDFFP Technical Series and publication 76 of the Amazonian Ornithology Technical Series of the INPA Collections Program. The manuscript was approved by the Director of the Louisiana State University Agricultural Center as manuscript number 2024-241-39168.

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

C.D.C. was responsible for conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization, writing (original draft, writing - review & editing). C.C. was responsible for conceptualization, funding acquisition, methodology, resources, supervision, writing (original draft, writing - review & editing). P.C.S. was responsible for conceptualization, funding acquisition, methodology, supervision, writing (review & editing). K.L.C. was responsible for conceptualization, formal analysis, funding acquisition, methodology, resources, supervision, visualization, writing (original draft, writing - review & editing).

Reflexivity statement

Were local/in-country researchers or community members involved in the study design?

Yes.

How will research products be shared to address local needs?

This publication will be part of the technical series of the Biological Dynamics of Forest Fragments Project (BDFFP) at Instituto Nacional de Pesquisas da Amazonia in Manaus, Brazil. Results in BDFFP technical series are available for synthesis and can be applied for land-use planning and public policies in the Central Amazon region.

Are researchers within the region (particularly women, gender minorities, and early career researchers) included as authors?

Yes. At the time of the research, C.D.O. was a master's student and C.C. a professor at Universidade Federal do Amazonas in Manaus, Brazil.

Did the authors search for relevant publications in regional journals, including those in languages other than English?

Yes.

If the study includes researchers from high income countries, how has the project developed their capacity to work collaboratively and equitably with colleagues within the region of study?

K.L.C. was a post-doctoral fellow affiliated in the USA at the time of the research. The project developed her capacity for mentorship of graduate students in Latin America, improved her Portuguese, and helped spark a series of collaborations to reduce barriers to ornithologists based in Latin America.

How has the project influenced the means and ability of the researchers from within the region to implement their research agenda?

The project resulted in C.D.O. obtaining her Master's Degree and contributed to C.C.'s ongoing research agenda.

Data Availability

Analyses reported in this article can be reproduced using data in Dantas Oliveira et al. (2024).

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