



# Palm snags are a critical nesting resource for woodpeckers in an urbanized tropical region

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## Abstract

Critical resources for birds nesting in cities can support populations in spite of the challenges imposed by urbanization, and the identification of such resources can shed light on how species are able to adapt to novel environments. In the case of woodpeckers, these resources also support the conservation of secondary cavity-nesters. Woodpecker nesting has been well-studied in temperate regions, including within urban areas, but in subtropical and tropical regions, less is known. Here we ask what types of trees and what habitats woodpeckers use most, and which species of woodpeckers create the most nest cavities. We recorded information from 967 woodpecker nest trees in the region surrounding Miami, Florida, USA, which contained 1864 nest cavities excavated by four woodpecker species. Palm trees were used more than all other tree categories, and royal palms (*Roystonea regia*) were the most-used species overall. Woodpeckers preferentially excavated palm snags in every habitat where they were available and three of the four woodpecker species used palms snags over all other categories of trees. Red-bellied Woodpeckers (*Melanerpes carolinus*) were the most prolific cavity excavators, creating 78.1% of holes. Remnant patches of two native forest types contained the highest densities of woodpecker nest trees. We found a higher density of nest trees in moderately-developed suburban areas than either rural, agricultural areas or in the highly-developed urban core. We consider how these results can inform conservation efforts in the developing tropics, and especially within similar urbanizing environments in the nearby Caribbean.

**Keywords** Hole nests · Cavity nest webs · Miami-Dade County · Palms · Urban forestry · Birds

## Introduction

Woodpeckers are globally distributed birds, absent only from Australasia, Antarctica, Madagascar, remote islands, and treeless environments (Mikusiński 2006; Ilsøe et al. 2017). The tropics have the greatest richness of woodpecker species, as

well as the greatest richness of imperiled woodpecker species (Mikusiński 2006; Lammertink 2014). Woodpeckers are considered keystone species due to their role in excavating holes, creating breeding habitat for secondary cavity users (Martin et al. 2004; Blanc and Walters 2008; Roberge et al. 2008; Robles and Martin 2013; Cockle and Martin 2015). Despite the great threats to conservation in the tropics, most research on imperiled woodpeckers have focused on three temperate North American species, the Red-headed (*Melanerpes erythrocephalus*), Red-cockaded (*Picoides borealis*) and Ivory-billed Woodpeckers (*Campephilus principalis*) (Lammertink 2014). Woodpecker conservation is needed in tropical regions, where deforestation and urbanization follow rapid population growth (Meyer and Turner 1992; Cincotta et al. 2000). Much human population growth in Latin America and the Caribbean occurs in coastal or lowland regions. Researchers project low elevation coastal zones in these countries to grow by up to 20 million people by 2060 over 2000 baseline populations (Neumann et al. 2015). Half of the woodpecker species red-listed by IUCN occur in Latin America (Lammertink 2014).

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Managing expanding urban areas for woodpeckers will be a major conservation challenge. As urban regions grow to cover more land area in the tropics, policy makers need more information to conserve species within the heterogeneous mix of developed areas, urban parks, and conservation lands that comprise the urban landscape. The effects of urbanization on species richness and abundance of cavity-nesting birds is a topic of some debate. Strong negative effects are observed in some environments (Luck and Smallbone 2010; Myczko et al. 2014) and positive effects in others (Chace and Walsh 2006; Kajtoch and Figarski 2017). Generally, land birds are excellent indicators of the effects on urbanization, due to their mobility and rapid response to changes in the landscape (Hutto 1998; Marzluff et al. 1998; Alberti 2008). Researchers have studied the ecology of urban woodpeckers in many temperate regions. Managers have identified critical resources such as the characteristics and densities of snags (standing dead trees), and green space requirements (Moulton and Adams 1991; Bütler et al. 2004; Morrison and Chapman 2005; LaMontagne et al. 2015; Anderson and LaMontagne 2016; Tomasevic and Marzluff 2017, 2018; Figarski and Kajtoch 2018). In some environments, specific tree taxa may be important for nesting woodpeckers, such as aspen, poplar, willow, cactus, bamboo, or pines (Kerpez and Smith 1990; Kratter 1998; Martin and Eadie 1999; James 2001; Walankiewicz and Czeszczewik 2005; Blanc and Martin 2012; Figarski 2014). For example, resource managers in Arizona, USA, have legally protected the saguaro cactus (*Carnegiea gigantea*) in part because of its importance to cavity-nesting birds (Brush et al. 1983; Pavek 1993). In some tropical and subtropical regions, woodpeckers are less important to cavity nest webs due to availability of natural cavities (Cockle et al. 2011a, b). Resource managers in the tropics need more information on the ecology of urban woodpeckers, as well as tropical woodpeckers more broadly.

South Florida (USA), centered on Miami-Dade County resembles other Caribbean cities in its size and mixture of land uses. Its location is subtropical in latitude but tropical in climate given its low elevation and proximity to the warm currents flowing through the Straits of Florida and up the eastern US coast. Native forest communities and developed areas of the county are both dominated by tropical vegetation, and the environments and biota are more similar to the Caribbean than to temperate North America (Lee and West 2011). In Miami and other tropical cities, palm trees (Arecaceae) are a major presence in both urban forests and natural plant communities. A study in adjacent Broward County, Florida found a preference among residents for non-shade trees like palms in urban tree distribution programs (Dawes et al. 2018). In densely packed urban environments, trees with small canopies are horticulturally preferred over spreading shade trees, and palms are often valued for this morphology. Several exotic palms have escaped cultivation through wide use as landscape trees,

such as coconut palm (*Cocos nucifera*) and queen palm (*Syagrus romanzoffiana*) (Florida Exotic Pest Plant Council 2017). The County's street tree master plan calls for increasing tree canopy cover to a countywide average of 30% by 2020, up from 10% in 1996 (Miami-Dade County 2007). These actions thus provide habitat for woodpeckers to excavate in most terrestrial environments, and at every level of urban development.

The objectives of this paper are to determine (1) what tree species and physical attributes are important for woodpecker nesting, (2) what habitat cover types (including urbanized areas at different levels of development) woodpeckers most frequently use for nesting, and (3) which temperate woodpecker species are the most prevalent in the southernmost portion of their range? We also consider how preferences for specific types of nest trees in urban regions can help conservation efforts elsewhere in the tropics, especially within the Caribbean.

## Methods

### Study area

The modern landscapes of Miami-Dade County uplands are predominantly developed. The county itself has nearly three million residents, but much of its ca. 5000 km<sup>2</sup> is wetland occupied by national, state, or local preserves. Most prominent is Everglades National Park, a Category 2 protected area, World Heritage Site, Biosphere Reserve, and Wetland of International Importance (Heinen 1995). The broader Miami metropolitan area has over six million residents, and is the seventh most populous metropolitan area in the United States (United States Census Bureau 2010). Despite high property values and development pressures, significant portions of urban Miami-Dade have been preserved in natural or semi-natural states, including county and state parks and conserved private forests (Alonso and Heinen 2011; Giannini and Heinen 2014). We primarily conducted our surveys in the county, which composed our core study area. We surveyed less frequently outside Miami-Dade County, making one visit each north to West Palm Beach, the northern limit of the metropolitan region, and southwest to Key West, the southernmost point of the continental USA.

The uplands of the region were historically covered with pine rockland forest, an open, savanna-like community dominated by South Florida slash pine (*Pinus elliottii* var. *densa*) in the canopy, but containing a diverse mixture of tropical understory plants (Possley and Maschinski 2008; Maschinski et al. 2011; Trotta et al. 2018). As they occur on the highest elevations in this hurricane and flood-prone region, pine rocklands were the first areas developed for permanent human settlements. Even where development avoided

pine rocklands, the condition of these forests declined greatly due to fire suppression. Isolated patches remain throughout the southern, less-developed portion of Miami-Dade County, where fire can be used more effectively for management (Diamond and Heinen 2016). In the absence of fire, hardwood trees grow in the understory, pine regeneration is stifled, and tropical hardwood hammock forest (hereafter hardwood hammocks) develops. These are closed-canopy tropical dry forests dominated by a variety of broadleaved trees. Native Florida hardwood trees are primarily of West Indian origin. Pine trees remaining from early seral stages can persist in hammocks. Native palms are a major component of some relict natural areas in Miami-Dade County, including upland forests and wetlands.

### Field methods and data analysis

We developed methods for locating woodpecker nest trees based on prior studies, with modifications for an urban environment. Dudley and Saab (2003) developed a protocol for locating and monitoring cavity-nesting birds, frequently used in both intact and disturbed forests. We based key methods on this protocol for temperate montane forests and adapted it to a flat, tropical, urban landscape. Belt transects searching for snags and cavities are not possible in an urban environment, so we used a random walk search following whatever paths would allow us to investigate safely. Although this method introduces some subjectivity, it kept observers safe in areas that were not pedestrian-friendly or were otherwise dangerous. We changed metrics for comparing responses to habitat modification from comparisons of nests per unit area to nests per unit distance searched, as total area sampling is not possible in developed areas.

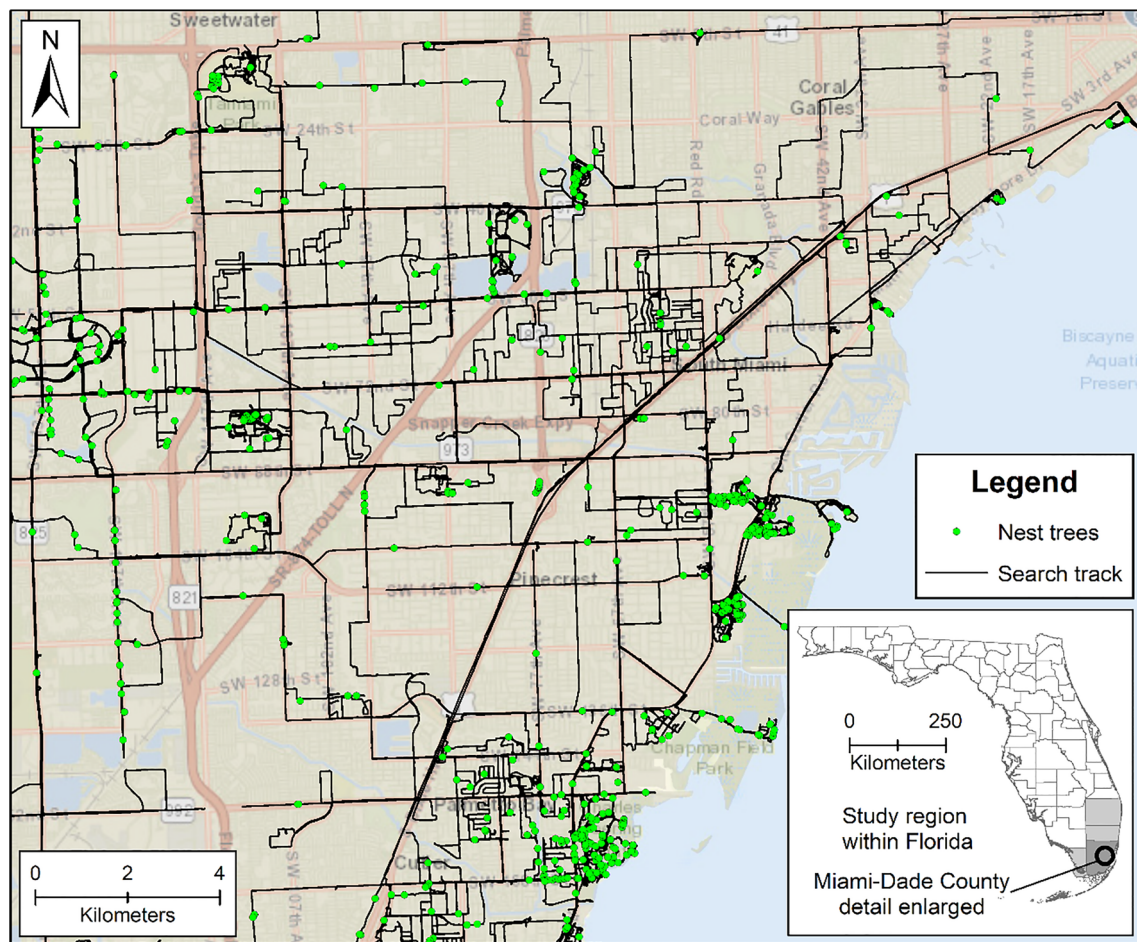
We located almost all nests by search image, meaning we looked for visual cues to woodpecker activity. Our visual cues were snags, dead tops, fungal conks, discolored wood, defoliation, and absent crownshafts or petiole bases. Search images for burned and unburned forests are distinctly different from each other and from urban forests. Some visual cues described for nest searches are uncommon due to tree morphology or urban forestry practices. We used dead tops of trees as a search image, but bayonet tops (new growth around broken tops) described in Bull et al. (1997) rarely form in the Caribbean ecoregion. We developed our local search image before the first field season began to identify potentially suitable nest trees. We stopped to examine any snag tree, and any live tree appearing to have decayed portions, as long as it was safe and permissible to do so. We examined any tree with fungal conks, the fruiting body of a fungus, including both live trees and snags. Fungal conks of *Ganoderma* spp. (particularly *G. zonatum* and *G. lucidum*), were an important visual cue (Elliott and Broschat 2000). *G. lucidum*, which infects oak trees, was useful for finding

sufficiently decayed branches and portions of the bole in live trees (Lloyd et al. 2017). In the absence of fungal conks, we also looked for discolored wood suggesting decay, and defoliated portions of hardwood trees that have lost most of their fine branches. Among palm tree species which have a crownshaft, an elongated leaf base at the treetop, the complete absence of a crownshaft indicates the tree is a snag more likely than partial defoliation (Stevenson 1996). We used the absence of old petiole bases in palms without a crownshaft as a visual cue indicating decay. Based on our review of literature, we initially concentrated search efforts on larger diameter live trees and snags, but upon finding nest cavities in urban palm trees as small as 8 cm diameter at breast height (DBH), we inspected any tree that satisfied other visual cues.

During the breeding season, we located some nests by following woodpeckers or secondary-cavity nesters. We located a few nests by hearing nestlings beg. However, auditory clues were minimally useful in Miami's developed areas. Between omnipresent vehicle noise and loud music played outdoors, many of the urban and suburban areas of Miami are particularly difficult for acoustic searches. Red-bellied Woodpeckers are our most common urban woodpecker, and they are a particularly vocal species (Gorman 2014). However, other than alarm calls, they are quiet during the breeding season, especially near nest trees. As a result, our search methods were primarily visual, especially while driving, which completely excluded auditory methods.

We used GPS tracking to determine search distances in each habitat type, and recorded all nest trees. We conducted searches by driving, bicycling, and/or walking through various urban and natural habitats (Fig. 1). We assumed a difference in detectability in searches, with the highest likelihood of detection walking, intermediate by bicycle, and lowest by motor vehicle. In order to avoid overly searching native upland forests by foot and bicycle, we selected additional sites outside of our core area to search exclusively by motor vehicle. We occasionally observed nest trees behind fences or on private property. When unable to obtain permission to access the nest tree, we observed and recorded as much data as we could from public walkways, resulting in some incomplete observations of nest trees. We searched for nests from October 2016 to August 2018, encompassing two full breeding seasons. A single observer collected all data, with the assistance of over two dozen volunteers.

The City of Miami Beach and the Village of Palmetto Bay, two urbanized municipalities within Miami-Dade County, had recently collected street tree inventories. Arborists collected the inventories, which contain species identification of every tree that intersects the public right-of-way. These two tree surveys contained over 55,000 trees. Our field observations suggest they are highly representative of the tree composition of the urban county as a whole. These municipal inventories



**Fig. 1** Search track and nests found within the core study area, Miami-Dade County, Florida. Searches were made by bicycle, foot, and automobile. Large clusters of woodpecker nest trees were found in urban parks and natural areas along the coastline

cover mixed urban/suburban area with mowed parkland included in the Miami Beach inventory. We used the inventories to compare the species of woodpecker nest trees in developed areas to the overall urban forest composition.

We recorded data for each nest tree: tree species, habitat type, tree height, decay class, and DBH (Dudley and Saab 2003). We recorded 20 different habitat types in our surveys. These included multiple native forest types, herbaceous wetlands, and different densities of urban development. We describe key characteristics for each habitat in Appendix 1. We pooled habitats with less than 50 km of distance searched for analysis as “other habitats.” We divided tree species into four categories: palms, pines, hardwoods, and wooden telephone/utility poles (hereafter referred to as poles). We also recorded the decay class for each snag on a scale from zero to ten, where decay class one appears recently dead and stable, and decay class nine is disintegrating and appears unsteady and ready to fall. We assigned living trees a value of zero and they were not included in the analyses of snags, even if a portion of the tree was dead. Some trees had already fallen when first located but had observable nest holes. We assigned these a value of ten

and we did not include in the analysis of snags. We did not assign poles a decay class, and we excluded them from analysis of snags. Snags are particularly important for woodpeckers, as these standing dead trees provide ample opportunities for cavity excavation (Drapeau et al. 2009). By contrast, a live tree may not have any dead branches suitable for excavation. For each woodpecker cavity, we recorded the height, entrance hole diameter, and the species of woodpecker that was the original excavator (e.g. Dudley and Saab (2003)), using cues of cavity size and shape when direct observations were unavailable. We observed woodpeckers excavating cavities in the year before data collection began to familiarize ourselves with the appearance of different species holes.

We inspected the interior of woodpecker nest cavities using a wireless video camera designed for the study of cavity-nesting birds (Luneau and Noel 2010). We mounted the camera probe on a collapsible fiberglass pole capable of reaching nests up to approximately 15 m above the ground. We inspected cavities in non-breeding and breeding seasons to determine which cavities were sufficiently large and suitable for nesting.

We completed all statistical analyses using IBM SPSS version 20.0, Microsoft Excel 2016, and ArcMap GIS version 10.4. Using univariate analysis of variance, we compared the four categories of tree species for mean height, mean DBH, number of woodpecker nest holes per tree, amount of decay, and nest height ratio, the nest height as a proportion of tree height. The tree categories were the explanatory and attributes were response variables. We used chi-square tests for differences in the proportions of excavated trees that were snags or living trees, and in the proportions of trees available in developed regions to the trees excavated by woodpeckers. We used univariate analysis of variance to compare the four woodpecker excavators for tree height, tree DBH, nest height proportion of tree height, and nest entrance hole diameter. The woodpecker species were the explanatory variable and the tree attributes were the response variables. We used aerial photographs in combination with field notes and GPS tracks to measure search distance in each habitat in ArcMap. Mean values reported in the results are  $\pm 1$  standard deviation (SD).

## Results

We searched more than 50 km of 13 different habitats across developed and wildland areas (Table 1). The two native upland forest types, pine rocklands and hardwood hammocks, contained the greatest concentrations of woodpecker nest trees (Fig. 2). Habitats dominated by pine trees are the major exception to the trend towards the use of palms. Nests in pine rocklands were exclusively in *P. elliotii* var. *densa* trees, at a density of 0.38 nest trees per km searched. Despite their importance to woodpeckers in these forests, pines were only

0.1%, and all coniferous trees were only 0.2%, of trees recorded in the two urban tree inventories. We found nest trees in hardwood hammocks every 0.34 km and were evenly split between palms and hardwoods. Parks and botanical gardens also featured high concentrations of nests, 0.33 and 0.31 per km respectively, mostly in palm trees. The inventories for Miami Beach and Palmetto Bay contained 55,101 trees: 53.6% palms, 46.2% hardwoods, and 0.2% conifers. Within those developed areas, palms were 83.0% of nest trees, hardwoods were 12.2%, telephone poles were 3.9%, and conifers were 0.8% of nest trees.

We recorded data on 967 nest trees throughout the study, although we removed 17 from some analyses due to incomplete data beyond species identification. Of the nest trees in the sample, 63.1% were palms, 18.8% were hardwoods, 11.4% were pines, and 6.7% were poles. Nest trees found in urban and suburban areas, and mowed urban parkland (excluding urban natural plant communities) accounted for 49.7% of all nests. A chi-square test of independence for whether woodpecker nest tree types differed from the urban forest community as a whole was highly significant in favor of palms ( $\chi^2$  (2,  $N = 55,565$ ) = 230.6,  $p < 0.001$ ). Woodpeckers avoided excavating the most common hardwood trees, while frequently excavating most of the common palms (Fig. 3). We recorded 26 different species of palms in total, and four additional nest trees were unidentified palm snags. Nests were most common in the most abundant palms species: royal palm (*Roystonea regia*), coconut palm (*Cocos nucifera*), and cabbage palm (*Sabal palmetto*). However, we also recorded nests in rare, exotic palm snags in botanical gardens, such as the critically endangered Haitian endemic carossier palm (*Attalea crassispatha*).

**Table 1** Top 13 habitats sorted by declining density of nests per km searched and number of nest trees in each tree category. We defined each habitat by their key characteristics, described in Appendix 1. Other habitats consist of environments with less than 50 km of search distance. These consist of freshwater slough, cypress strand, melaleuca prairie, melaleuca forest, pine scrub, pine-cypress forest, and salt marsh

Habitat type	Tree categories (number of nest trees found)				Search distance (km)	Nests per km
	Hardwood	Palm	Pine	Utility Pole		
Pine rockland			81		212.3	0.38
Hardwood hammock	34	34	3	2	213.3	0.34
Park	25	72	2	5	313.7	0.33
Botanical garden	8	40			157.2	0.31
Mangrove	34	7			150.0	0.27
Coastal prairie	3	29			138.1	0.23
Campus		8	2		62.9	0.16
Suburban	34	278		14	2083.9	0.16
Beach	2	5			57.2	0.12
Cypress prairie				8	68.2	0.12
Prairie	3	2	5	33	369.8	0.12
Rural	5	73		1	732.1	0.11
Urban		43			412.8	0.10
Other habitats	24	14	17		182.1	0.30

**Fig. 2** Representative images of habitats and the two most common nest trees. **a** Royal palm nest tree in a suburban area. **b** Royal palm nest tree in an urban area. **c** Royal palm nest tree in a hardwood hammock forest. **d** Slash pine nest tree in a pine rockland forest



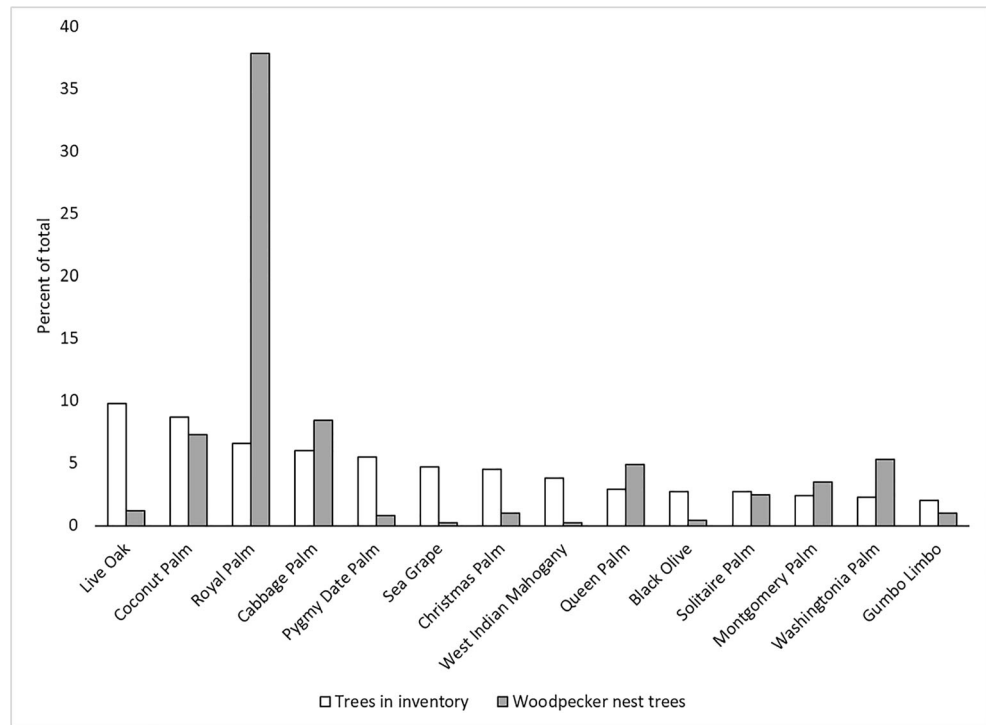
Royal palm plays an important role as a substrate for woodpeckers in the region (Table 2) and they were the most commonly excavated species in urban areas, suburban areas, rural areas, developed parkland, and surprisingly, tropical hardwood hammocks (Fig. 2). Royal palms are uncommon in hammocks, found primarily at edges and in gaps, and we estimated they usually represent <1% of arborescent stems in these forests. In developed areas, they represented 37.1% of all excavated trees. Within the urban tree inventories, they were the third most common tree species, but represented only 6.6% of the total trees (Fig. 3). One quarter of all nest trees found in hardwood hammocks were royal palms, but many hardwood hammocks contained no royal palms, or any other palm species. We found several hammocks with no royal palms that contained few to no nest trees.

The four categories of tree differed significantly in their height, DBH, decay class, and nest height ratio (all  $p < 0.001$ , Table 3). Palm trees were shorter than the other categories of trees except for pines. Pine trees had the thinnest diameter, and often the excavated snags had already lost their bark and sapwood, with only a thin, decayed heartwood spear remaining. Hardwood trees had the largest diameter, with a

mean DBH double that of most other trees. Palm trees were the least decayed category of tree. Cavities in hardwood trees were proportionally lower in height than in other trees. Between hardwoods, palms, and pines, the proportion of nests made in snags versus live trees differed significantly ( $\chi^2(2, N = 780) = 106.5, p < 0.001$ ). Less than two thirds of hardwood nest trees were snags (65 of 105), compared to over 90% of those in palms (528 of 565) and pines (108 of 110). We most often found woodpecker cavities in live hardwood trees in dead limbs or limb stubs below canopy height. All four categories of trees supported an average of about two nest holes per tree, and an ANOVA indicated no differences between tree categories ( $p = 0.866$ ). Likewise, the number of nest holes per tree did not differ among the 20 most abundant species excavated ( $p = 0.219$ ). Seven of these 20 species are exotic invasive trees (Florida Exotic Pest Plant Council 2017).

The coastal habitats, i.e., mangrove forests and coastal prairies, featured moderately high numbers of woodpecker nests, 0.27 and 0.23 per km, respectively. Mangrove forests were the only habitat in which a majority of woodpecker nests were found in broadleaved trees, many in the exotic invasive hardwood Australian Pine (*Casuarina equisetifolia*) which are

**Fig. 3** The 15 most common trees in the inventory listed in descending order of abundance. Woodpeckers seldom excavate the five most common hardwood trees (live oak, sea grape, West Indian mahogany, black olive, and gumbo limbo). Two miniature-sized arborescent palms, the pygmy date palm and Christmas palm, are infrequently used. Cumulatively, these 15 species account for 64.6% of all trees in the inventory, and 74.5% of woodpecker nest trees in developed areas. Pines are <1% of trees in the inventory



emergent above the mangrove canopy. Coastal prairie nests were primarily in palm trees. We found a moderate number of nest trees in suburban areas and campuses; both were 0.16 per km. Nests we found in both environments were primarily in palms. Beaches, cypress prairie, prairie, rural, and urban

environments all had woodpecker nest trees in relatively low numbers ( $\leq 0.12$  per km). The environments in which nest trees were less common also had relatively few trees. Rural areas were variable, some had high concentrations of trees, but others were treeless agricultural lands. Telephone poles were

**Table 2** The top 20 species used by woodpeckers for nesting. The ranked list of nest tree species follows a rank abundance curve,  $p < 0.001$ ,  $R^2 = 0.91$ . This pattern is frequently observed in measurements of species diversity. Status of exotic trees in Florida follows the Florida Exotic Pest Plant Council, where category I

invasive trees are displacing native species, while category II invasive trees have recruited naturally outside of cultivation but not altered plant communities to the extent of category I plants. (Florida Exotic Pest Plant Council 2017)

Species name	Tree category	Status in Florida	Count of nest trees	Mean nest holes
Royal palm ( <i>Roystonea regia</i> )	Palm	Native	271	1.9 ± 1.3
Slash pine ( <i>Pinus elliottii</i> var. <i>densa</i> )	Pine	Native	100	1.9 ± 1.6
Coconut palm ( <i>Cocos nucifera</i> )	Palm	Exotic invasive Cat II	80	2.0 ± 1.7
Cabbage palm ( <i>Sabal palmetto</i> )	Palm	Native	71	1.9 ± 1.4
Utility pole (Treated <i>Pinus</i> spp.)	Utility pole	N/A	64	1.8 ± 1.2
Foxtail palm ( <i>Wodyetia bifurcata</i> )	Palm	Exotic	39	1.9 ± 1.6
Australian pine ( <i>Casuarina equisetifolia</i> )	Hardwood	Exotic invasive Cat I	33	2.9 ± 3.5
Montgomery palm ( <i>Veitchia arecina</i> )	Palm	Exotic	31	2.2 ± 1.7
Washingtonia palm ( <i>Washingtonia robusta</i> )	Palm	Exotic invasive Cat II	30	2.4 ± 1.4
Queen palm ( <i>Syagrus romanzoffiana</i> )	Palm	Exotic invasive Cat II	25	2.2 ± 1.7
Gumbo limbo ( <i>Bursera simaruba</i> )	Hardwood	Native	14	2.6 ± 2.7
Live oak ( <i>Quercus virginiana</i> )	Hardwood	Native	13	2.0 ± 1.7
Solitaire palm ( <i>Ptychosperma elegans</i> )	Palm	Exotic invasive Cat II	13	2.4 ± 1.9
Red mangrove ( <i>Rhizophora mangale</i> )	Hardwood	Native	11	1.7 ± 1.5
Black mangrove ( <i>Avicennia germinans</i> )	Hardwood	Native	10	1.5 ± 0.8
Longleaf pine ( <i>Pinus palustris</i> )	Pine	Native	10	3.3 ± 2.2
MacArthur palm ( <i>Ptychosperma macarthurii</i> )	Palm	Exotic	10	1.5 ± 0.8
Melaleuca ( <i>Melaleuca quinquenervia</i> )	Hardwood	Exotic invasive Cat I	10	2.2 ± 2.1
Strangler fig ( <i>Ficus aurea</i> )	Hardwood	Native	9	1.2 ± 0.4
Javanese bishopwood ( <i>Bischofia javanica</i> )	Hardwood	Exotic invasive Cat I	7	2.4 ± 1.4

**Table 3** Attributes of four categories of nest trees excavated by woodpeckers,  $n = 780$  trees and  $n = 65$  poles with complete data. Letters indicate homogenous subsets

Tree category	Mean height (m)	Mean DBH (cm)	Holes per tree	Decay class (snags only)	Nest height ratio	Proportion of nests in snags
Hardwood $n = 105$	10.6 ± 4.5, b, c	51 ± 41.5, c	2.1 ± 2.1	4.7 ± 2.1, c	0.66 ± 0.25, a	61.9%, a
Palm $n = 565$	8.7 ± 4.0, a	28.5 ± 9.9, b	1.9 ± 1.4	3.4 ± 1.9, a	0.80 ± 0.27, b	93.5%, b
Pine $n = 110$	9.8 ± 4.1, a, b	21.4 ± 9.2, a	2.0 ± 1.7	4.2 ± 2.3, b	0.84 ± 0.15, b	98.2%, b
Utility Pole $n = 65$	11.5 ± 2.1, c	26.5 ± 4.1, a, b	1.8 ± 1.2	N/A	0.82 ± 0.16, b	N/A
$p$ value	$p < 0.001$	$p < 0.001$	$p = 0.866$	$p < 0.001$	$p < 0.001$	$p < 0.001$

important nest sites for woodpeckers in prairie and cypress prairie environments, but palms were the main nest substrate in beaches, rural areas and urban environments.

Four woodpecker species were responsible for the creation of nest cavities. Of the 1864 cavities we recorded, 78.1% were excavated by Red-bellied Woodpeckers (*Melanerpes carolinus*), 16.0% were by Pileated Woodpeckers (*Dryocopus pileatus*), 3.7% by Northern Flickers (*Colaptes auratus*), and 2.3% by Downy Woodpeckers (*Picoides pubescens*). Downy Woodpeckers were the only species to largely avoid palm trees, favoring pines and hardwoods for excavation. Only 16.7% of Downy Woodpecker nest trees were palms. They were also the rarest of the woodpecker species recorded here. The other three species used palms for over half of their cavities. Pileated woodpeckers were the primary user of telephone poles, particularly in the treeless prairie and dwarf cypress prairie. Telephone poles excavated in suburban landscapes were exclusively the work of Red-bellied Woodpeckers.

The four woodpecker species differed significantly in their nest tree height, DBH, and entrance hole diameter (all  $p < 0.001$ , Table 4). Downy and Red-bellied Woodpeckers used shorter trees (9.7 ± 3.3 and 9.1 ± 3.9 m) than Northern Flickers (11.7 ± 4.0 m) and Pileated Woodpeckers (12.7 ± 3.9 m). There was no difference in the nest height ratio ( $p = 0.835$ ). All

woodpecker species placed nests at approximately 80% the height of the tree, although Red-bellied Woodpeckers were more variable in their height selection, and at least one created a nest only a few decimeters above the ground (Diamond 2018). Red-bellied Woodpecker nest trees did not differ in DBH from other species (30.2 ± 18 cm). Downy Woodpecker nest trees were smaller in diameter (23.4 ± 11.7 cm) than either Northern Flicker (32.1 ± 13.1 cm) or Pileated Woodpecker (36.8 ± 24.9 cm) nest trees. All woodpecker species created different diameter entrance holes, with sizes roughly proportional to their body size. Downy Woodpecker holes were the smallest (3.3 ± 0.6 cm), followed by Red-bellied Woodpeckers (6.4 ± 0.9 cm), Northern Flickers (7.9 ± 1.1 cm), and Pileated Woodpeckers (11.6 ± 2.9 cm).

## Discussion

Palm trees are disproportionately important for woodpeckers in our study area; seven of the top ten excavated tree species were palms. Palms were the most excavated trees across all habitat types and woodpeckers even used them more in developed than in areas that are more rural. Palms were also the least decayed category of tree. Woodpeckers prefer softer wood, indicating that palms require less decay than many

**Table 4** Nest tree characteristics and categories excavated by four woodpecker species,  $n = 967$  nest trees and  $n = 1864$  nest cavities

Woodpecker species	Nest tree characteristics				Tree category			
	Tree height (m)	DBH (cm)	Nest height ratio	Nest diameter (cm)	Hardwood	Palm	Pine	Telephone Pole
Downy Woodpecker $n = 42$	9.7 ± 3.3, a	23.4 ± 11.7, a	0.81 ± 0.16	3.3 ± 0.6, a	16, 38.1%	7, 16.7%	19, 45.2%	0, 0%
Northern Flicker $n = 69$	11.7 ± 4.0, b	32.1 ± 13.1, b	0.80 ± 0.17	7.9 ± 1.1, c	2, 2.9%	40, 58.0%	27, 39.1%	0, 0%
Pileated Woodpecker $n = 298$	12.7 ± 3.9, b	36.8 ± 24.9, b	0.78 ± 0.18	11.6 ± 2.9, d	37, 12.4%	177, 59.4%	13, 4.4%	71, 23.8%
Red-bellied Woodpecker $n = 1455$	9.1 ± 3.9, a	30.2 ± 18.0, a, b	0.78 ± 0.27	6.4 ± 0.9, b	257, 17.7%	1006, 69.1%	173, 11.9%	19, 1.3%
$p$ value	$p < 0.001$	$p < 0.001$	$p = 0.835$	$p < 0.001$				



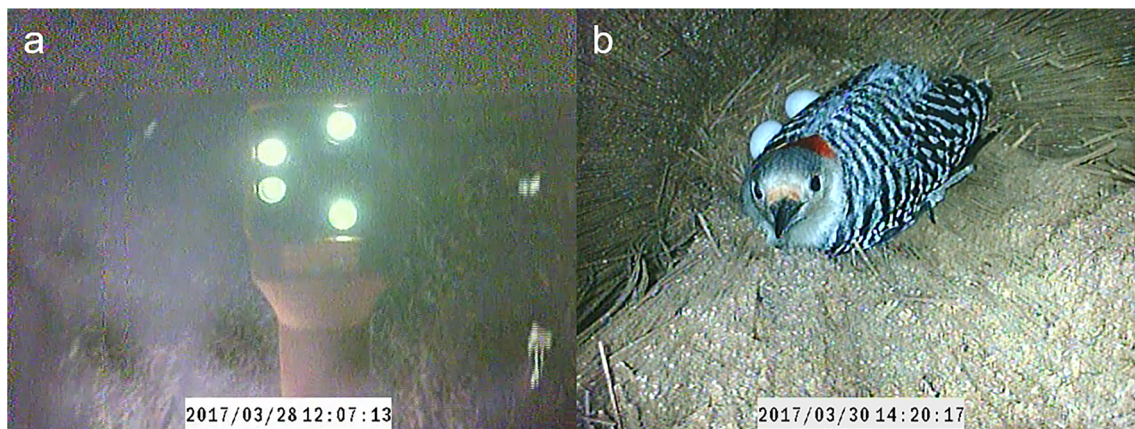
other trees to reach optimal hardness (Schepps et al. 1999; Lorenz et al. 2015; Gutzat and Dormann 2018). The structure of a palm trunk, with a tough exterior and soft, pithy core, may expedite cavity formation processes and thus make them more appealing to woodpeckers (Boyle et al. 2008). Palms have relatively soft wood: in a study of wood density across 2456 neotropical tree species, palms had a mean wood density of 0.488 g/cm<sup>3</sup> compared to a 0.645 g/cm<sup>3</sup> for all species (Chave et al. 2006).

Woodpecker nests in palm snags may also persist longer in the environment because less-decayed snags are more resistant to disturbances (Russell et al. 2006). In contrast to Boyle et al. (2008), who found holes in palms exclusively in snags, we found a small number of cavities in living palm trees. These were primarily old, large royal palms, which had dead portions of their main bole. Still, 93.5% of woodpecker holes in palms were in dead snags. We inserted a pole-mounted nest inspection camera into cavities in live palms, but the holes were usually too shallow or poorly drained to support nests. Cavities in palm snags never contained standing water. We inspected 750 cavities in various tree and snag types starting before the rainy season began. Three cavities in live palm trees contained standing water deep enough to cover the entire cavity floor. We never observed flooded cavities in palm snags, or other substrate types (Fig. 4). Woodpeckers may avoid live palms because of poor drainage, even if portions of the bole are decayed.

The two native upland forest habitats, pine rockland and hardwood hammock, contained the highest density of nests per km searched but not all native environments supported large numbers of woodpecker nests. For example, various prairie types had few and/or dwarf-sized trees. Some prairies had nest substrates only in utility poles. Mowed parkland and botanical gardens contained a greater density of nests than lowland forests and grasslands. Woodlots in urban and suburban areas are

thought to retain a greater density of snags than rural areas because of a lower intensity of harvest (Mörtberg and Wallentinus 2000). This pattern may not be true in developing countries, where concentrated poverty in urban environments can drive the complete exploitation of small woodlots (Makonese and Mushamba 2004). In the absence of extractive harvest, woodpecker nesting peaks at intermediate levels of urban disturbance, a pattern frequently observed among birds (Blair 1996; Alberti 2008; Evans 2010).

The Red-bellied Woodpecker is present in nearly every terrestrial environment in South Florida and, in a study of native and exotic birds in urban Miami-Dade County, they were located at near-constant rates across a large gradient of development (Abdelrahman 2000). Pileated Woodpecker nests were common in parks near the urban core that contained hardwood hammocks, especially near the coastline. Historically, they were thought of as birds of undisturbed, mature forest (Hoyt 1957), but similar to what we observed, Pileated Woodpecker in Seattle, Washington, were found nesting in urban parks and other green spaces where snags were retained (Tomasevic and Marzluff 2018). We found Pileated Woodpecker cavities in palms along the coastal prairies of Everglades National Park as well as in telephone poles in the treeless prairies of the East-central Everglades. We found Northern Flicker nests most often in the rural fringes of our study area, near the border with Everglades National Park, as well as inside the national park. Northern Flickers forage for ants on the ground, potentially leaving them vulnerable to feral cats, which are a common problem in Miami-Dade (Clarke and Pacin 2002; Elchuk and Wiebe 2002; Florida Fish and Wildlife Conservation Commission 2003; Diamond and Ross 2018). Flickers excavated 58% ( $n = 40$ ) of their cavities in palm wood. This observation is important as it suggests other ecological factors excluded Flickers from the urban environment, rather than insufficient nest substrate.



**Fig. 4** Woodpeckers rarely excavated holes in live palms; they excavated 93.5% of palm cavities in snags. Woodpecker cavities in live palms were often too shallow, and poorly drained even in the dry season. Standing water is visible during the dry season, **a** reflecting the light of the nest

inspection camera. Snags were used more for active nesting attempts; **b** a female Red-bellied Woodpecker incubates eggs in a palm snag 2 days after **a** and less than two km away

The results of our study indicate that palms may be an overlooked critical resource for the nesting of woodpeckers in urbanized tropical regions. In subtropical central Florida, Leonard and Stout (2006) were surprised by how frequently woodpeckers nested in cabbage palms; they had expected to find a nesting relationship with oaks (*Quercus* spp.). Consequentially, woodpecker-excavated palms should also be a critical resource to other cavity-nesting birds. Woodpecker nests were critical for secondary users here, unlike portions of South America and Eurasia where natural cavities are plentiful (Cockle et al. 2011b). Most of these cavities are in palm snags, suggesting they are an important link in the cavity nest web. We recorded only 38 natural cavities in our study area; we did not observe active bird nest attempts in them. We once observed an Eastern Screech Owl (*Megascops asio*) roosting in a natural cavity and bees constructed a hive in another. Cabbage palms, which are native to south Florida, were the fourth most common species excavated by woodpeckers in our study. Our results indicate that the retention of palm snags, especially within urban regions, may be important for the conservation of cavity-nesting birds. Local government policies could avoid cutting of snags, especially palms, on public lands where they are not a risk of falling on roads or buildings. Conservation education may convince some private landowners to do the same.

In addition to woodpeckers in tropical Florida, palms appear to be critically important for at least two imperiled woodpeckers in the Caribbean: Fernandina's Flicker (*Colaptes fernandinae*) and the Guadeloupe Woodpecker (*Melanerpes herminieri*). The vulnerable Fernandina's Flicker is endemic to Cuba. One study found nests of this species exclusively in palm snags (Mitchell et al. 2000). The Guadeloupe Woodpecker is endemic to the two main islands of Guadeloupe and is listed as near-threatened and declining; a study of the species' ecology found coconut palm snags were their primary nest tree (Villard and Rousteau 1998). A strategy suggested for providing nest substrate to Guadeloupe Woodpeckers in urban areas was attaching 1 m sections of coconut palm trunks to the upper section of utility poles (Villard et al. 2010). Other woodpeckers of the New World tropics, particularly *Melanerpes* spp., use palm-dominated habitats like coconut palm plantations, and we expect them to preferentially nest in these trees (Gorman 2014). In addition to the rare woodpeckers that require conservation efforts, protecting the more common woodpecker species in urban areas will provide nest cavities to many secondary-cavity nesters. The endemic Hispaniolan Woodpecker (*Melanerpes striatus*) has been documented nesting from undeveloped coastlines to the urban center of Santo Domingo, preferring palms snags over all other trees (Short 1974) and the near-threatened Hispaniolan Trogon (*Priotelus roseigaster*) has been documented breeding in former Hispaniolan Woodpecker nests (Bond 1928). In Cuba, the West Indian

Woodpecker (*Melanerpes superciliaris*) and Cuban Green Woodpecker (*Xiphidiopicus percussus*) excavate nests in palms, which are used by the near-threatened Cuban Parrot (*Amazona leucocephala*) (Acosta et al. 2004).

Protecting palm snags alone will not be enough to conserve woodpeckers in urban regions. Not all woodpecker species prefer palm snags, as our data shows. Downy Woodpeckers, for example, used but did not prefer palm snags. This is a widely distributed temperate species and our study area is the extreme southern and tropical edge of its geographic range. Palms are tropical trees, and woodpecker species richness is greatest in the tropics and declines rapidly in temperate latitudes (Bjorholm et al. 2005). We expect the use of palms as nest substrates to decline greatly in temperate versus tropical bird communities for similar guilds. When specific plant-animal associations can be identified between woodpeckers and nest trees, conservation efforts should be made to maintain them (e.g. Kratter 1998). Our study shows that palm snags are critical resources for woodpeckers in one urbanized tropical area, and are likely to be important for the conservation of cavity-nesting birds elsewhere in the tropics, as evidenced by the few studies done so far in the Caribbean. We strongly encourage more such studies.

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