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The diversity, distribution and conservation status of the tree-cavity-nesting birds of the world

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Abstract

Aim: Globally, many bird species nest in tree cavities that are either excavated or formed through decay or damage processes. We assembled an overview of all tree-cavity nesters (excavators and non-excavators) in the world, analysed their geographic distribution and listed the conservation status of all species.

Location: This is a global analysis of species from every continent except for Antarctica where the lack of trees precludes the occurrence of this group.

Methods: We reviewed the online version of the Handbook of the Birds of the World Alive, http://www.hbw.com/, and primary literature for species known to nest in tree cavities, with tree cavities defined as holes that a bird can enter such that it is not visible from the outside. We classified species by nester type (excavator or non-excavator, and obligate or facultative where possible), conservation threat status and zoogeographic region, and tested for statistical differences in species distributions across realms using chi-square tests.

Results: At least 1878 species (18.1% of all bird species in the world) nest in tree cavities, of which we considered 355 to be primary excavators, 126 facultative excavators and 1357 non-excavators (we were unable to classify nesting type for 40 species). At least 338 species use cavities created by woodpeckers (Picidae), excluding reuse by woodpeckers themselves. About 13% (249 species) of tree-cavity nesters experience major threats (i.e., status of vulnerable, endangered or critically endangered). The highest richness of tree-cavity nesters is found in the Neotropical (678 species) and Oriental (453) regions, and the highest proportion of threatened species in Australasia (17%).

Main conclusion: Maintenance of a continual supply of cavities, a process in which woodpeckers and the processes of decay play critical roles, is a global conservation priority as tree cavities provide important nesting sites for many bird species.

KEYWORDS

hole-breeding birds, keystone excavator species, nestwebs, species interactions, woodpeckers

1 | INTRODUCTION

A wide diversity of bird species nest in tree cavities and may interact with one another through the use of and competition for cavities excavated by birds and those formed through decay (Cockle & Martin, 2015; Cockle, Martin, & Robledo, 2012; Martin & Eadie, 1999; Newton, 1994). In these "nest webs" of interactions, primary excavators usually excavate their own cavities, facultative excavators use existing holes, excavate new holes or enlarge existing cavities, and non-excavators predominantly use cavities excavated by other species, or cavities formed through decay (Gibbons & Lindenmayer, 2002; Martin, Aitken, & Wiebe, 2004). Many non-excavators use cavities excavated by woodpeckers (Picidae), which are therefore often considered keystone "ecosystem engineers," as they provide a critical ecological resource for nesting or roosting (Cockle & Martin, 2015; Daily, Ehrlich, & Haddad, 1993; Floyd & Martin, 2016; Robles & Martin, 2013). Thus, excavators can be useful as indicator species for forest bird diversity and forest health (Mikusiński et al., 2001; Drever, Aitken, Norris, & Martin, 2008). Studies of cavity nesters can help us understand interactions within bird communities and may aid in forest management by means of improved knowledge of species requirements (e.g., retention of trees of a specific species or size; Politi, Hunter, & Rivera, 2009; Ruggera, Schaaf, Vivanco, Politi, & Rivera, 2016). Conservation actions to ensure persistence of tree-cavity-nesting birds, through measures such as nest box addition for non-excavators (Cornelius et al., 2008; Lindenmayer et al., 2009; Pöysä & Pöysä, 2002) or community-based conservation initiatives (Poonswad et al., 2005), are much desired as many of these birds play important ecological roles such as for seed dispersal or pest control (Fayt, Machmer, & Steeger, 2005; Şekercioğlu, Wenny, & Whelan, 2016; Wenny et al., 2011). Tree-cavity-nesting birds are under increasing threat from a host of disturbance factors (Cockle, Martin, & Drever, 2010; Cockle, Martin, & Wesolowski, 2011; Cornelius et al., 2008; Drever & Martin, 2010; Eadie, Sherman, & Semel, 1998; Lammertink, 2014; Olah et al., 2016).

Despite considerable work on tree-cavity nesters (e.g., Cockle et al., 2011; Gibbons & Lindenmayer, 2002; Newton, 2013), reliable life-history data are lacking for many species using tree cavities, especially those taxa found within the tropics (Cockle et al., 2012; Cornelius et al., 2008). We expect to find the highest diversity of tree-cavity nesters in the tropics (e.g., woodpecker diversity is highest in the Asian, South American and African tropics (Mikusiński, 2006; Winkler & Gusenleitner, 2015)), and the most threatened primary excavator species (i.e., the highest numbers of red-listed woodpeckers are found in tropical Asia and Latin America (Lammertink, 2014)). Moreover, nestweb structure could look very different in the tropics compared to more temperate regions, as non-excavators seemingly use cavities created by excavators less often in the tropics, instead relying more often on cavities formed in old trees through processes of decay or environmental damage (see review by Cockle et al., 2011). As tree cavities can be a limiting resource for non-excavators (Aitken & Martin, 2008; Newton, 1994), ensuring the availability of both suitable substrates (i.e., required trees with specific characteristics) and decay-forming processes might be even more critical in the tropics than in the temperate regions of the world.

There are no global or continental lists of tree-cavity-nesting birds available in the primary literature, nor do we have an overview of the distribution of these species or their conservation status, a reflection of the often regional (e.g., Monterrubio-Rico & Escalante-Pliego, 2006) or taxonomically narrow (e.g., woodpeckers, Lammertink, 2014) focus of most cavity-nester studies. We aimed to provide the first global overview of all tree-cavity-nesting birds, to facilitate future studies on cavity nesters, and to aid our understanding of this important, yet potentially vulnerable, group of birds. Our global data summary allows the identification of regions in the world where hotspots of tree-cavity nesters are found and where conservation measures are most urgently needed (i.e., where the most threatened species are found). In addition, our overview can be used as a starting point for future biogeographic and ecological studies on tree-cavity nesters and nestweb interactions. For future studies, our global species list can be cross-checked readily with local, regional or national checklists of cavity-nesting species to facilitate local research initiatives.

2 | METHODS

2.1 | Bird data and creation of the global cavity nester list

We started our compilation of a global list of tree-cavity-nesting birds by searching the entire online edition of the Handbook of the Birds of the World Alive (del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2016; accessed between January and May 2016) for species that had at least one record of a nest placed in a tree hole, hollow, or cavity. We also considered species that place nests inside hollow stumps or tree knotholes, and species that make use of cavities in cacti (Cactaceae) and palms (Arecaceae). We did not include species using nesting holes such as those in river banks, cliffs, nests placed on the tops of tree branches, stumps or similar substrates, or nests in shallow depressions or niches of trees. We defined a tree cavity as one that a bird can enter the cavity and descend or move laterally such that it is not visible from the outside. Finally, several species use holes in non-tree structures such as arboreal termitaria, wasp or ant nests for nesting and roosting. We did not include the species using such non-tree cavities in our global list as the processes that determine the availability of these resources differ from those that produce wood cavities (e.g., the availability of snags and processes of fungal decay; Gibbs, Hunter, & Melvin, 1993). Nevertheless, for completeness and potential future research projects, we did include a few species using arboreal termitaria in a separate list of potential cavity nesters (added as supplementary material), as they are closely related (at the genus or family level) to known tree-cavity nesters. As many of these species are not well-studied, we foresee future discoveries of tree-cavity-nesting behaviour in several of these species.

We complemented records found in del Hoyo et al. (2016) with additional reviews of cavity nesters found in the primary literature following a search for "cavity," "hole" or "hollow" in Google Scholar (we used information from Skutch, 1944, 1959, 1962; Phillips, 1987; Mack, 1994; Sherman, 1995; Walker & Seroji, 2000; Riley & Mole, 2001; Gibbons & Lindenmayer, 2002; Monterrubio-Rico & Escalante-Pliego, 2006; Cockle et al., 2007; Wesołowski, 2007; Sandoval & Barrantes, 2009; Courtney, 2010; Cockle et al., 2012; Johansson et al., 2013; Warakai, Okena, Igag, Opiang, & Mack, 2013; Pasquet et al., 2014; Reuleaux et al., 2014; Ojeda, 2016). Finally, we reviewed the list compiled by Walters—which in turn is based on species records from Harris (1984), Ehrlich, Dobkin, and Wheye (1988), Canevari et al. (1991), Mullarney, Svensson, Zetterström, and Grant (2000), Coates and Bishop (1997), MacKinnon and Phillipps (1993), and Robson

(2000)—on the website CAV-NET (www.cavitynester.org), as well as an unpublished data set compiled for 10 countries on five continents created by one of the authors (KM).

Tree-cavity nesters were reported to be found predominantly in 10 avian orders Anseriformes, Falconiformes, Psittaciformes, Strigiformes, Caprimulgiformes, Apodiformes, Trogoniformes, Coraciiformes, Piciformes and Passeriformes (Newton, 1994), but there are limited data on breeding behaviour for many species in these orders, especially from Africa, and parts of Asia and South America. As we aimed to include all probable tree-cavity nesters belonging to these orders, we carefully read the descriptions of breeding behaviour of each species belonging to the families Anatidae, Psophiidae, Trogonidae, Bucerotidae, Alcedinidae, Capitonidae, Semnornithidae, Megalaimidae, Lybiidae, Ramphastidae, Picidae, Falconidae, Cacatuidae, Psittaculidae, Psittacidae, Sittidae, Paridae and Strigidae, and considered whether we could infer that they could be listed as a potential tree-cavity nester. We provide the evidence that we used to classify each species, by including a column in our final list of species where we indicate for each species whether we could derive its classification as a tree-cavity nester directly from del Hoyo et al. (2016), whether we used an additional primary literature source to classify it, or whether we inferred its classification based on recorded behaviour of other species within the same genus or family.

2.2 | Status assignment, mapping and analyses

We classified each species as a primary cavity excavator (species that nearly always excavates its own nesting cavities), facultative excavator (when known to regularly use existing holes, but also to excavate new holes or enlarge existing cavities), or non-excavators (species that use only existing decay-formed or excavated-tree cavities, and do not or only rarely excavate or renovate). We also classified a few species as "unknown" cavity-nester type when we found almost no data on breeding behaviour for several species, such as the Red-faced Fig-parrot (*Psittaculirostris cervicalis*) and the Yunnan Nuthatch (*Sitta yunnanensis*), and did not find consistency in the classification of species in the same genus or family (see Pasquet et al. (2014) for an assessment of cavity-nesting behaviour in nuthatches following a phylogenetic approach). We inferred these species to be tree-cavity nesters based on the behaviour of their sister species.

We aimed to determine whether a species was known to breed in excavated-tree cavities, in tree holes or hollows formed by the processes of decay or damage, or in holes formed through either process. We also considered whether a species is thought to nearly always breed in tree cavities (obligate) or whether it was also known to use other nest types (facultative; e.g., also uses nesting cavities in rocks, in old stick nests, or in holes in river banks or arboreal termitaria). We classified some facultative cavity users as occasional cavity nesters as they use cavities only rarely, or do so only in small portions of their species range. Although obligate cavity use is relatively straightforward to determine, it is harder to distinguish between facultative and occasional use based on the limited amount of data available for most species. Those species that were known to show only occasional usage of tree cavities (approximately 0–10% of nesting records) were listed as such in a separate column in a supplementary table. Therefore, a few of the species we deemed to be facultative cavity users might in fact do so only on rare occasions, and thus should be classified as occasional users.

As del Hoyo et al. (2016) does not always provide recent data on breeding behaviour, we conducted an additional search in English in both Google and Google Scholar (April 2017) for the breeding behaviour of each species (scientific name and common name) in our list that was classified as "unknown" for type of cavity used or whether they were obligate or facultative cavity nesters. For species in Central and Southern America, we also searched for publications in Spanish. We included citations for references in Table S1 that provided additional information from del Hoyo et al. (2016) allowing us to classify species for one or both traits.

For each species, we adopted assessments of conservation status from del Hoyo et al. (2016), which are based on the IUCN Red List status (BirdLife International, 2016) and considered the status of each species, in increasing order of threat, as "status not assessed" (includes the status of "no data" and "not assessed"), "not globally threatened" (includes the status of "least concern" and "near threatened"), "vulnerable," "endangered" or "critically endangered." Second, we classified each species according to their breeding distribution (breeding visitor or year-round resident) using data provided by del Hoyo et al. (2016), as present in six zoographic regions: Nearctic, Palaearctic, Neotropical, Afrotropical, Oriental and Australasia. Some species have distributions encompassing several zoogeographic regions. To analyse the distribution of tree-cavity nesters, we counted the number of species that have a breeding range within each region and visualized richness patterns in a manner similar to Jenkins, Pimm, and Joppa (2013). To visualize richness patterns, we used the packages "rgdal" (Bivand, Keitt, & Rowlingson, 2014), "raster" (Hijmans, 2014) and "tmap" (Tennekes, Gombin, Jeworutzki, Russell, & Zijdeman, 2017) in R (R Core Team, 2016) to overlay breeding range maps (using only highly probable presence: extant or probably extant) derived from BirdLife International & NatureServe (2015), until we obtained a global grid (projected in Eckert IV equal distance projection) of 10 × 10 km cells with values of species richness.

We provide the numbers and percentages of species within specific nester types (primary excavator, facultative excavator, non-excavator) that experience different levels of conservation threat and that breed in each zoogeographic region. We used chi-square tests to calculate whether the different cavity-nester types differed in the percentages of threatened species, and whether any region has significantly more species of a specific type or threat category than other regions, the latter indicating that conservation measures are more urgent in these regions.

3 | RESULTS

When we accessed the Handbook of the Birds of the World Alive online (del Hoyo et al., 2016), it had records for 10,394 bird species.

We determined that at least 1878 (18.1%) of these species nest in tree cavities (Table 1, Table 2, Table S1). Tree-cavity nesters were found in 16 avian orders, with many tree-cavity-nesters found among the Passeriformes (586 species), Piciformes (404), Psittaciformes (371) and Strigiformes (219) (Table 2). The behaviour of tree-cavity-nesting occurs in 72 families in these 16 avian orders, but is especially common among 22 families, where over 75% of all species in the family are known to use tree cavities for nesting: the Aegothelidae, Psophiidae, Tytonidae, Strigidae, Phoeniculidae, Bucerotidae, Lybiidae, Megalaimidae, Capitonidae, Ramphastidae, Semnornithidae, Picidae, Cacatuidae, Psittacidae, Dendrocolaptidae, Climacteridae, Paridae, Sittidae, Certhiidae, Pardalotidae, Buphagidae and Sturnidae.

We classified 355 species (19% of the total number of tree-cavity nesters) as primary excavators, 126 species (7%) as facultative excavators and 1357 species (73%) as non-excavators (Tables 1, S1). Considering both primary and facultative excavators, we estimate that at least 481 species (26%) have the capacity to excavate cavities (excavators). We classified 40 species as being of "unknown" nester type, as due to limited data we were unable to infer whether they can excavate their own cavities or use only existing cavities.

We were able to determine the type of cavity used (excavated by woodpecker or other, decay-formed) for less than half of the species, and therefore, numbers in Table 1 should be considered as "minimum numbers" of species. At least 338 cavity nesters (that are not woodpeckers) utilize cavities created by woodpeckers, but this is likely to be an underestimate. For example, there are few observations of breeding behaviour published for owls of the genus *Otus*, but many of the species for which we do have records (at least seven out of 53 species in this genus) use woodpecker-excavated cavities. Very likely, some of the other 46 species also use woodpecker cavities to some extent. Despite these lack of data, we estimated that at least 792 species (42% of all tree-cavity nesters) use excavated cavities to some extent, including all primary and facultative excavators and some non-excavators that use excavated-tree cavities at least occasionally (Table S1). Furthermore, a cautious first estimate suggests that at least 49% (914 species) of tree-cavity nesters could be considered obligate tree-cavity nesters (i.e., they do not regularly utilize other nest types such as cavities in earth banks or termitaria, stick nests, etc.), but this number might change considerably when new information on little-studied species becomes available (Table S1). At least 69 species in Table S1 are known to use tree cavities only rarely, or only in specific geographic regions. We considered these species, as "occasional" tree-cavity-nesters and thus are unlikely to be dependent on the availability of tree cavities for their nesting sites (Table S1).

A total of 249 tree-cavity-nesters (13.2% of all tree-cavity nesters) are officially considered to be globally threatened (vulnerable, endangered, critically endangered; Table 3), with 41 (2.2%) of all tree-cavity-nesters considered critically endangered. Of the five critically endangered primary excavator species, at least two are considered extinct (the Ivory-billed Woodpecker (*Campephilus principalis*) and Imperial Woodpecker (*Campephilus imperialis*)). Eighteen species lacked the information to evaluate an accurate risk status (e.g., Przewalski's Nuthatch, *Sitta przewalskii*). Excluding the 40 species of "unknown" nester type, the percentage of threatened species varied among primary excavators, facultative excavators and non-excavators ($\chi^2 = 25.4$, $df = 2$, $P < .001$), with threatened species being most common among the non-excavators (15% of all non-excavators) and less so among primary (6%) and facultative (6%) excavators). This pattern holds if we consider only two groups, excavators (pooling primary and facultative excavators) versus non-excavators, with more threatened species among non-excavators ($\chi^2 = 25.7$, $df = 1$, $P < .001$).

We expected the largest numbers of tree-cavity-nesting species to be found in the Neotropical zoogeographic region, given the high overall species richness in this region. Indeed, total species richness of tree-cavity-nesters is highest in the Neotropical (678 species) and Oriental (453) regions (Table 4; the total species number is greater than 1878 as some species occur in two or more realms). However, correcting for the total number of species (following numbers provided by del Hoyo et al. (2016)) shows that the proportion of tree-cavity-nesting species in the avifauna varies across regions from 10.9% to 19.5%, being most common in the Oriental region, with 19.5% of all bird species in this region showing use of tree cavities for nesting, followed by Australasia (17.2%). Visualization through richness maps showed that richness is especially high in parts of the Amazon basin and along the Eastern Andean slope of several countries of the Neotropical region, as well as in south-eastern China and the Asian countries of Laos, Myanmar, Vietnam, Thailand, Cambodia, Malaysia and Indonesia, with

TABLE 1 Overview of all bird species that nest in tree cavities

Nester type	Number of species[a]	Species reusing cavities excavated by Picidae (*n*)	Species reusing cavities excavated by barbets[b] (*n*)	Species reusing cavities excavated by species other than Picidae and barbets[c] (*n*)
Primary excavator[d]	355 (19%)	0	0	0
Facultative excavator	126 (7%)	49	3	2
Non-excavator	1357 (73%)	289	50	9
Unknown	40 (2%)	0	0	0
Total	1878	338	53	11

[a]Number in parentheses is the percentage of the total number of tree-cavity-nesting species.
[b]Capitonidae, Semnornithidae, Megalaimidae and Lybiidae.
[c]Species such as trogons (Trogonidae), nuthatches (Paridae) or tits (Sittidae).
[d]We did not count primary excavators using cavities created by other primary excavators (e.g., woodpeckers using holes made by other woodpeckers, although this behaviour does occur regularly).

TABLE 2 Estimated number of tree-cavity nesters (confirmed and inferred) per order and family. Taxonomy and species numbers per family follow del Hoyo et al. (2016)

OrderFamily	# of all species in family	# of tree-cavity-nesting species in order/family	% of tree-cavity-nesting species in the family
Galliformes		1	
Phasianidae (Pheasants, Grouse and Allies)	187	1	<1
Anseriformes		46	
Anatidae (Ducks, Geese and Waterfowl)	165	46	28
Phaethontiformes		1	
Phaethontidae (Tropicbirds)	3	1	33
Columbiformes		4	
Columbidae (Pigeons and Doves)	351	4	1
Caprimulgiformes		30	
Aegothelidae (Owlet-nightjars)	10	10	100
Nyctibiidae (Potoos)	7	2	29
Apodidae (Swifts)	96	18	19
Cuculiformes		1	
Cuculidae (Cuckoos)	149	1	<1
Gruiformes		8	
Psophiidae (Trumpeters)	6	6	100
Rallidae (Rails, Gallinules, Coots)	143	2	1
Strigiformes		219	
Tytonidae (Barn-Owls)	16	15	94
Strigidae (Owls)	222	204	92
Cathartiformes		5	
Cathartidae (New World Vultures)	7	5	71
Trogoniformes		40	
Trogonidae (Trogons)	43	40	93
Bucerotiformes		70	
Phoeniculidae (Woodhoopoes and Scimitar-bills)	8	8	100
Bucerotidae (Hornbills)	62	61	98
Upupidae (Hoopoes)	2	1	50
Coraciiformes		57	
Alcedinidae (Kingfishers)	120	45	38
Coraciidae (Rollers)	13	12	92
Piciformes		404	
Bucconidae (Puffbirds)	38	4	11
Lybiidae (African Barbets)	52	49	94
Megalaimidae (Asian Barbets)	35	28	80
Capitonidae (New World Barbets)	18	18	100
Ramphastidae (Toucans)	50	50	100
Semnornithidae (Toucan-Barbets)	2	2	100
Picidae (Woodpeckers)	254	253	100[a]
Falconiformes		35	
Falconidae (Falcons and Caracaras)	64	35	55
Psittaciformes		371	
Strigopidae (New Zealand Parrots)	3	1	33
Cacatuidae (Cockatoos)	21	21	100

(Continues)

TABLE 2 (Continued)

OrderFamily	# of all species in family	# of tree-cavity-nesting species in order/family	% of tree-cavity-nesting species in the family
Psittacidae (Parrots)	374	349	93
Passeriformes		586	
Furnariidae (Ovenbirds)	241	23	10
Dendrocolaptidae (Woodcreepers)	52	52	100
Thamnophilidae (Typical Antbirds)	213	6	3
Formicariidae (Ground-antbirds)	65	8	12
Rhinocryptidae (Tapaculos)	62	4	6
Tyrannidae (Tyrant Flycatchers)	432	53	12
Acanthisittidae (New Zealand Wrens)	3	1	33
Hirundinidae (Swallows)	83	27	33
Pycnonotidae (Bulbuls)	158	1	<1
Motacillidae (Wagtails and Pipits)	65	1	2
Troglodytidae (Wrens)	87	12	14
Prunellidae (Accentors)	13	1	8
Turdidae (Thrushes and Allies)	339	30	9
Muscicapidae (Old World Flycatchers)	117	78	67
Sylviidae (Old World Warblers)	273	10	4
Timaliidae (Babblers)	54	1	2
Pachycephalidae (Whistlers)	56	3	5
Petroicidae (Australasian Robins)	46	10	22
Maluridae (Fairy-wrens)	27	1	4
Acanthizidae (Thornbills and Allies)	63	4	6
Climacteridae (Australasian Treecreepers)	7	7	100
Paridae (Tits, Chickadees, and Titmice)	56	54	96
Remizidae (Penduline-Tits)	13	1	8
Sittidae (Nuthatches)	27	26	96
Certhiidae (Treecreepers)	10	8	80
Pardalotidae (Pardalotes)	4	3	75
Meliphagidae (Honeyeaters)	175	1	1
Cinclosomatidae (Quail-thrushes and Jewel babblers)	11	1	9
Artamidae (Woodswallows)	11	6	55
Corvidae (Crows, Jays and Magpies)	123	5	4
Paradisaeidae (Birds-of-Paradise)	42	1	2
Callaeidae (Wattlebirds)	3	1	33
Notiomystidae (Stitchbird)	1	1	100
Buphagidae (Oxpeckers)	2	2	100
Sturnidae (Starlings)	112	87	78
Passeridae (Old World Sparrows)	40	18	45
Estrildidae (Waxbills and Allies)	134	11	8
Fringillidae (Finches, Euphonias and Allies)	144	3	2
Parulidae (New World Warblers)	116	4	3
Thraupidae (Tanagers and Allies)	283	10	4
Emberizidae (Buntings and New World Sparrows)	326	3	<1

(Continues)

TABLE 2 (Continued)

OrderFamily	# of all species in family	# of tree-cavity-nesting species in order/family	% of tree-cavity-nesting species in the family
Icteridae (Troupials and Allies)	111	7	6
Grand Total		1878	

[a]Rounded up from 99.6%. Not all (100.0%) of Picidae use tree cavities as the Ground Woodpecker (*Geocolaptes olivaceus*) uses only burrows and other ground cavities for breeding.

TABLE 3 Numbers of tree-cavity nesters assigned different IUCN Red List threat categories

Nester type	Not assessed	Not globally threatened	Vulnerable	Endangered	Critically endangered	Total[a]
Primary excavator	0	332	14	4	5	355 (19)
Facultative excavator	0	118	5	3	0	126 (7)
Non-excavator	17	1130	108	67	35	1357 (73)
Unknown	1	31	6	1	1	40 (2)
Total[a]	18 (1)	1611 (86)	133 (7)	75 (4)	41 (2)	1878

[a]Number in parentheses is the percentage of the total number of species (1878).

TABLE 4 Tree-cavity nester richness in six zoogeographic regions and the number of species assigned IUCN Red List threat status (vulnerable, endangered and critically endangered). Note that totals do not equal 1878 as some species occur in multiple regions

	Primary excavator	Facultative excavator	Non-excavator	Unknown	Total[a]	Threatened species[b]
Nearctic	25	19	93	0	137 (7%)	6 (4%)
Palaearctic	35	22	168	3	228 (12%)	11 (5%)
Neotropical	137	51	481	9	678 (36%)	96 (14%)
Afrotropical	70	9	232	0	311 (17%)	28 (9%)
Oriental	103	37	312	1	453 (24%)	61 (13%)
Australasia	13	4	258	28	303 (16%)	52 (17%)

[a]Total number of cavity nester species in zoogeographic region (del Hoyo et al., 2016), percentage of all species in zoogeographic region, in parentheses.
[b]Vulnerable, endangered and critically endangered. Percentage of total number of species in parentheses.

regional richness occasionally reaching over 100 species (Figure 1). In contrast, the number of species at given locations in the other realms generally ranged from 40 to 60 species.

The regions differed significantly in the percentages of species classified as primary excavators, facultative excavators or non-excavators (χ^2 = 204.2, *df* = 10, *P* < .001; Figure 2), and between those classified as excavators (both primary and facultative excavators) versus non-excavators (χ^2 = 66.9, *df* = 5, *P* < .001). Excavators (primary and facultative excavators pooled) are the least common in the Australasian region (~ 6% of all tree-cavity users in this region), primarily due to the absence of woodpeckers and barbets, are most common in the Nearctic region (32%), and range from 25% to 31% for the other regions. An estimate of the proportion of non-excavators using excavated cavities versus non-excavated cavities indicates that use of excavated holes by non-excavators is particularly rare in the Australasian region (three species; ~1% of 258 non-excavators with data available for this region), and most common in the Nearctic (49 species; 53% of non-excavators in this

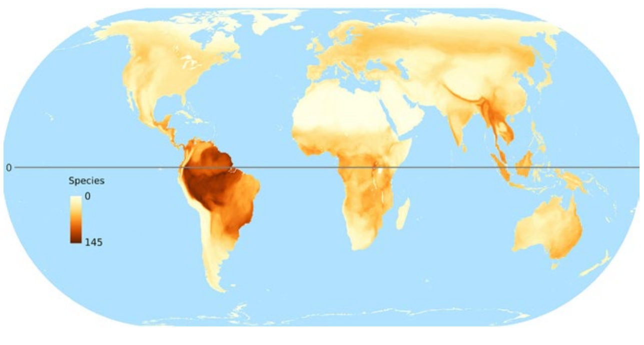

FIGURE 1 Global map of richness of all bird species estimated to nest in tree cavities regularly or occasionally derived from an overlay of breeding range maps (in Eckert IV projection). Distribution is given for 1856 species, 22 species fewer than listed in Table S1 due to differences in taxonomic classification between del Hoyo et al. (2016), from which our global list of species was compiled, and BirdLife International & NatureServe (2015), from which we derived shapefiles of species breeding range maps. [Colour figure can be viewed at wileyonlinelibrary.com]

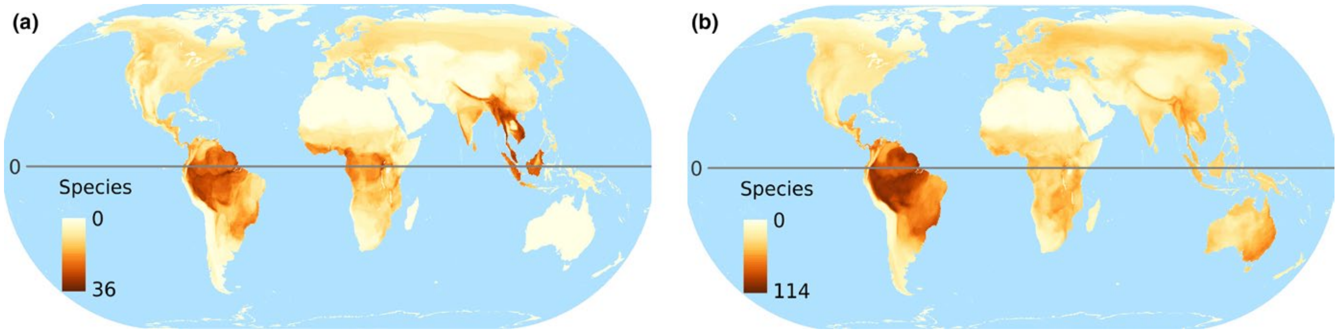

FIGURE 2 Global maps of richness of all tree-cavity-nesting-bird species classified as either primary or facultative excavators (a) or non-excavators (b) in Eckert IV projection. [Colour figure can be viewed at wileyonlinelibrary.com]

region; NB: we were unable to determine the type of cavities used for 125 non-excavators, Table S1).

We found that the percentage of threatened tree-cavity-nesting species differed between the regions (χ^2 = 37.0, df = 5, P < .001), with apparent hotspots of tree-cavity-nesting species considered globally threatened (vulnerable, endangered or critically endangered) found in the Neotropical and Oriental, and Australasian regions (Table 4, Figures 3, 4). In Australasia, up to 17% of tree-cavity nesters are classified as globally threatened, compared to only 4% of species in the Nearctic region.

Finally, we found that most species for which we lacked sufficient knowledge to classify them as primary or facultative tree-cavity nesters (323 species), or as users of excavated, decay-formed or both types of tree cavities (155 species), can be found in the tropics (Figure 5a,b).

4 | DISCUSSION

We estimate that at least 18.1% of global avifauna makes at least occasional use of tree cavities for nesting, of which at least 49% are obligate tree-cavity nesters. All species in our list, even species that nest only occasionally in tree cavities, are consumers of tree-cavity resources, resources that could otherwise be used by other members in the tree-cavity-nesting community, potentially impacting cavity availability for obligate users. Woodpeckers are globally important in providing tree cavities, with at least 338 (18%) species using woodpecker-excavated cavities for nesting. Retention of old trees seems equally important (e.g., in ways outlined in Wesołowski, 2007; Drever & Martin, 2010; Bunnell, 2013; Lindenmayer et al., 2014), as cavities formed by decay or mechanical damage, usually found in older, larger, trees, are used by many tree-cavity nesters.

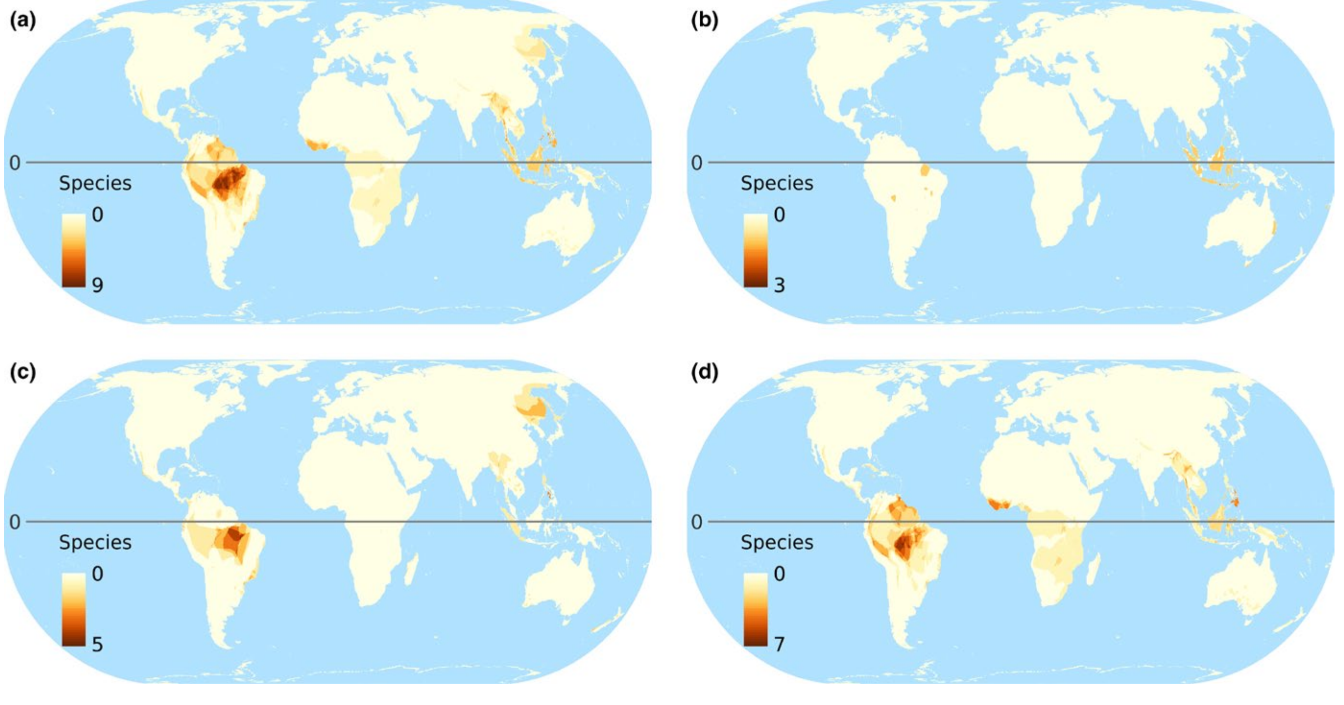

FIGURE 3 Global maps of species richness of all extant tree-cavity-nesting birds (a) that are considered threatened (critically endangered, endangered or vulnerable) by the IUCN (BirdLife International, 2016). Panels (b), (c) and (d) show the distribution of critically endangered, endangered and vulnerable species, respectively, in Eckert IV projection. [Colour figure can be viewed at wileyonlinelibrary.com]

Even in areas where there is a sufficient supply of excavated cavities, non-excavators may tend to utilize cavities formed by decay. For example, in Europe, decay-formed cavities may be preferred due to the fact that certain woodpeckers prey on nests or adults of non-excavators (Paclík, Misík, & Weidinger, 2009; Wesołowski & Martin, in press).

Approximately 13% of tree-cavity-nesting species are recognized as vulnerable, endangered or critically endangered by the IUCN, similar to the percentage of all threatened bird species in the world (BirdLife International, 2016). Although many of the facultative cavity users in Table S1 (at least 69 species) use tree cavities only rarely, and are unlikely to depend on them for survival, availability of cavities can be an important limiting factor for many other tree-cavity-nesting species or populations (see e.g., Cockle et al., 2011; Cornelius et al., 2008; Pöysä & Pöysä, 2002; Wiebe, 2011). The elimination of trees with cavities through processes such as logging or forest clearing for agriculture or urbanization may lead to population declines that can endanger the persistence of intact tree-cavity-nesting communities (Politi et al., 2009; Politi, Hunter, & Rivera, 2010; Cockle et al., 2010; Wesołowski & Martin, in press).

Patterns of global distribution and species richness of tree-cavity-nesting species are largely similar to those of Picidae (Winkler & Gusenleitner, 2015), and avifauna in general (Pimm et al., 2014), with the tropics being especially species rich. Given the requirement for trees as nest substrates, this distribution roughly follows the same pattern as that of world's forests (Pan, Birdsey, Phillips, & Jackson, 2013), with near absence of tree-cavity-nesting birds in the major deserts of the world (e.g., Sahara, Gobi, Great Victoria Desert). As pointed out in a review by Cockle et al. (2011), use of excavated cavities by non-excavators seems most common in the Nearctic (North America) and is least common in the Southern Hemisphere—partially due to the absence of excavators in the Australasian region, but likely also due to lower persistence of excavated cavities than decay-formed cavities in these regions. Regarding the distribution of threatened species, the highest absolute numbers of threatened species are found in the Neotropics (especially

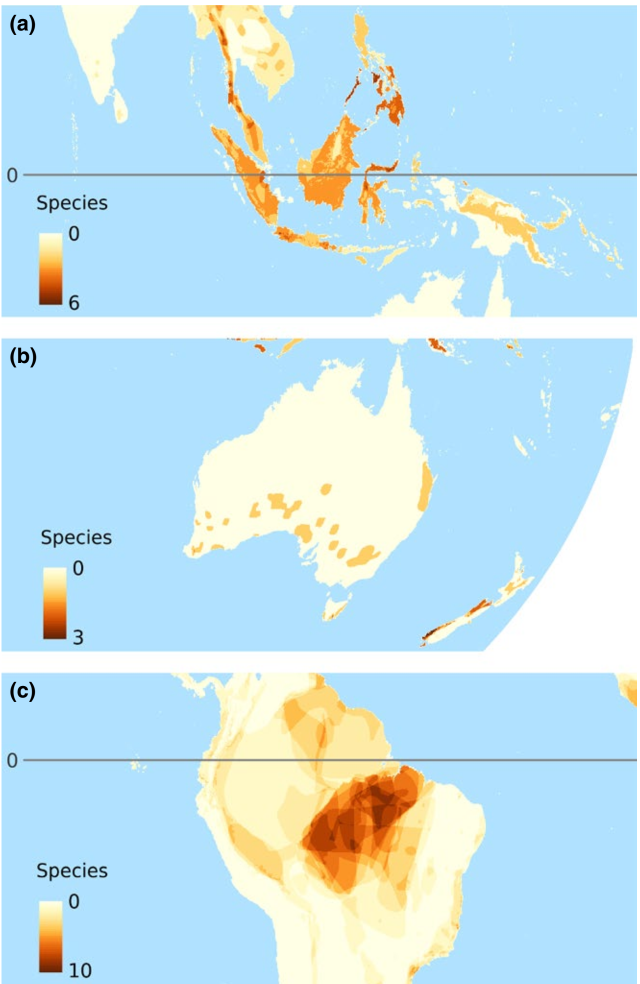

FIGURE 4 Examples of hot spots of globally threatened (critically endangered, endangered or vulnerable) tree-cavity nesters, in Southeast Asia (a), Australia (b) and Central South America (c) in Eckert IV projection. [Colour figure can be viewed at wileyonlinelibrary.com]

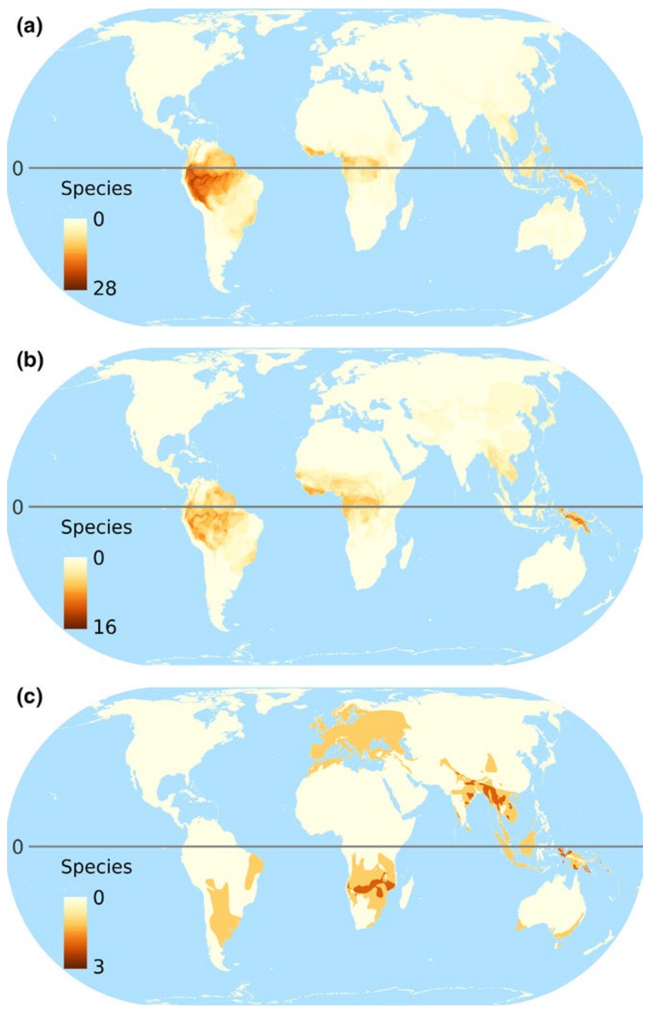

FIGURE 5 Distribution of species for which we lacked sufficient knowledge to classify them as obligate or facultative tree-cavity nesters (a), as users of specific cavity formation types (i.e., excavated, decay-formed or both types of tree cavities), (b), and by their global conservation status (c) in Eckert IV projection. [Colour figure can be viewed at wileyonlinelibrary.com]

central Brazil), but the highest relative numbers of threatened species are found in Australasia. Although these regions might have the highest percentages of threatened cavity nesters in general, threatened woodpeckers are found predominantly in Asia (the Oriental region), some of which require urgent conservation measures (Lammertink, 2014). Of greater conservation concern, these tropical and subtropical regions, with high numbers of threatened species, are also the regions for which data are lacking on many tree-cavity-nesting birds.

We are aware that our study is by necessity incomplete, given that limited or no data exist for some species, and we expect that future observations will update our knowledge of the types of cavities that some species use (excavated or decay-formed). Thus, when we list a species as using excavated cavities, we do not exclude the possibility that it might also use decay-formed cavities, or vice versa. Similarly, some species are currently considered obligate tree-cavity nesters, but future records may show the use of other nest types. Finally, it is difficult to classify some species in discrete classes based on their propensity to excavate tree cavities, as this characteristic may follow a gradient of tree-cavity resource use from "always excavating everywhere" to "almost never excavating". On the extreme ends, we are confident in classifying most primary excavators and most non-excavators as such, but the amount of excavation done by facultative excavators varies substantially both spatially and temporally. In addition, some non-excavators might occasionally renovate or enlarge cavities, for example in rotten palm stumps or very soft wood, and could thus be classified as facultative excavators. In that regard, Parrots (Psittacidae) and Kingfishers (Alcedinidae) were especially difficult to classify as we had limited information on breeding behaviour of several species, and there is little consistency in the propensity to excavate among sister species. Some species that we listed as non-excavator might have the capacity to excavate in rotten or soft wood, or to enlarge or renovate cavities. In fact, recent breeding behaviour observations of the relatively well-studied and critically endangered, Swift Parrot (*Lathamus discolor*) show that this species can substantially enlarge existing cavities in Tasmania, making it in fact a weak facultative excavator (Stojanovic et al., 2016; we listed this parrot as non-excavator with an asterisk in Table S1, indicating that there were two records of excavation for this species).

Local and regional field guides and additional natural history notes on nesting might offer additional useful details not currently incorporated in our list of tree-cavity nesters. Moreover, new research findings will indicate that additional species are also tree-cavity nesters. For example, at the time of writing, new evidence emerged that the Buff-winged Cinclodes (*Cinclodes fuscus)* also uses tree cavities for nesting, where it was previously considered to be a ground-nesting ovenbird associated with open habitat (Ojeda, 2016). We thus urge researchers to use our list, but also to adapt it for local situations and questions, update it with additional literature and data, and fill in the gaps for regions or species of interest. We also recognize that the total number of species provided in our overview might change if we were to adopt another taxonomic classification (e.g., the one provided by Gill and Donsker (2016)), as some classifications recognize additional species ("splitting") or fewer species ("lumping"). In fact, the richness maps we created were based on the classification adopted by BirdLife International & NatureServe (2015), which differed slightly from the classification of del Hoyo et al. (2016), which we used for all other analyses. Thus, the maps are based on ranges of 1856 species instead of the 1878 species we listed as "tree-cavity nesters." Nevertheless, the broader patterns of distribution, abundance and status shown here are likely robust, regardless of minor differences resulting from different taxonomic classifications used.

We show, like Pimm et al. (2014) and Kissling, Şekercioğlu, and Jetz (2012), that species richness mapping can be extended beyond the mapping of mere taxonomic groups (e.g., mapping of global richness of Picidae by Winkler and Gusenleitner (2015)). Mapping richness of species that are grouped by life-history traits (e.g., Xiao et al. (2017)), ecological functions, or other factors, can improve our understanding of biogeographic patterns in more complicated ecological dynamics, such as those that include species interactions related to nesting or feeding habits (e.g., between cavity excavators and non-excavators, a future research direction we intend to explore). Effective conservation measures for the global avifauna require us to fill in our knowledge gaps of tree-cavity nesters, for example by focusing on interactions among tree-cavity nesters (i.e., understand nest webs, sensu Martin & Eadie, 1999) and how these interactions might change in the future. Many tree-cavity nesters play important ecological roles, such that of seed disperser or ecosystem engineer (Floyd & Martin, 2016; Robles & Martin, 2013). We encourage the development of both future research projects and conservation or management policies focused on this species group. The future of at least 18% of global avifauna might depend on it.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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