

(RESEARCH ARTICLE)



## Mistletoes and their diversity in the Bwindi Impenetrable National Park, Uganda

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### Abstract

Relatively little is known about the diversity, distribution, and community ecology of parasitic plants in the forests of equatorial Africa. We examined mistletoes in the mountain forests of the Bwindi Impenetrable National Park in Southwestern Uganda. We recorded 1,496 individual mistletoes in 64 0.1-ha plots (6.4 ha total), evenly distributed between open (forest-edge) and closed (forest-interior) locations and spanning an elevation range of 1160 to 2607 m above sea level. These mistletoes included 21 species, seven genera and two families and were recorded on 542 host trees comprising 45 tree species. Overall, mistletoes were more common in open than in closed conditions (356 ha<sup>-1</sup> versus 129 ha<sup>-1</sup>). The most abundant mistletoe species was *Englerina woodfordioides* (Schweinf. ex Engl.) Balle (328 records) followed by *Viscum fischeri* Engl. (316 records). Six mistletoe species were recorded just once. *Harungana madagascariensis* Lam. ex Poir. hosted the greatest diversity of mistletoes with nine species, while *Maesa lanceolata* Voigt hosted eight. Chao's estimator indicates that mistletoe species richness across the whole forest likely exceeds 40 species which would be over ten percent of the mistletoe taxa known from the continent. The overall diversity and density of mistletoes appears high when compared to reported surveys from elsewhere. Mistletoes add significant botanical diversity in this forest and likely make a substantial contribution to its ecology.

**Keywords:** Distribution; Mistletoes; Parasitic-plants; Host; Loranthaceae; Viscaceae; Santalaceae

### 1. Introduction

Parasitic and hemi-parasitic plants occur in most biomes (1, 2). These plants influence the productivity, viability and reproduction of their hosts, impact competition, and provide food resources for other species, and are sometimes viewed as keystone species (1, 3, 4). Estimates suggest that approximately 1% of angiosperm species are parasitic with the majority being found in the wet tropics (5). Globally, an estimated 4,926 species of parasitic plants have been described of which 1647 are mistletoes (6). Mistletoes are woody evergreen hemi parasites which attach to their hosts above ground using a specialized structure called the "haustorium", that not only anchors the plant but penetrates the host facilitating the flow of water and nutrients. Mistletoes depend on their hosts for water and nutrients but also require light for photosynthesis. The mistletoes' need for light combined with their physiological need to maintain a lower water potential than their hosts tends to limit these plants to relatively well-lit environments (7). Phylogenetic analysis groups mistletoes into three families: Loranthaceae (1016 species, widespread and mostly tropical), Santalaceae (623 also widespread and mostly tropical, and until recently often described under the "Viscaceae") and Misodendraceae (8, exclusive to South America) (6).

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The ecology of mistletoes involves interactions with their hosts, pollinators, seed dispersers and herbivores. Many tropical mistletoes possess colorful nectar-rich flowers that attract birds and insects some of which appear specialized for the task of pollination. Various impacts and influences of mistletoe presence have been observed or predicted (8, 9). For example, studies have indicated an impact on the litterfall, productivity and nutrient turnover of forests where mistletoes are sufficiently abundant (10). Other studies show mistletoes influence nutrient availability under the host canopy impacting herbaceous plants, herbivores and associated biota (11).

Mistletoes may influence overall species diversity through multiple mechanisms including the suppression of dominant species, increasing resource heterogeneity and supporting dependent taxa (9). For example, mistletoes may bear flowers and fruit for longer than other plants in their environment, sustaining nectar and fruit eating species when other resources are scarce (12). Parasitized trees also appear to attract and support a greater diversity and abundance of invertebrates than do unparasitized trees (13).

African mistletoes have many interactions with other species. Observations show that their fruits, flowers and leaves are consumed by various vertebrates including hornbills, bulbuls, thrushes and turacos, as well as gorillas, chimpanzees and various other primates (14). The larvae of various species of Lepidoptera in the genus *Mylothris* depend on these plants as food (15). Observations show that many African Loranthaceae depend on birds for pollination and bats and birds for seed dispersal (16) though the links remain incompletely documented (14). Data concerning three species of mistletoe 1400–1600 m above sea level (asl) in Nigeria indicate dependency on sunbirds for effective pollination and suggest that these plants are indicators of a functioning ecosystem (17). Observations of *Tapinanthus dodoneifolius* (DC.) Danser on *Parkia biglobosa* (Jacq.) R. Br. ex G. Don trees (also in Nigeria) suggest, counterintuitively, that these mistletoes may benefit their host trees by attracting and sustaining potential pollinators, seed dispersers, and insectivores (18).

Systematic accounts of African mistletoes remain sparse and incomplete (14). With this study we sought to characterize the distribution, diversity and possible significance of mistletoes in the forests of Uganda's Bwindi Impenetrable National Park filling a clear gap in current knowledge

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## 2. Material and methods

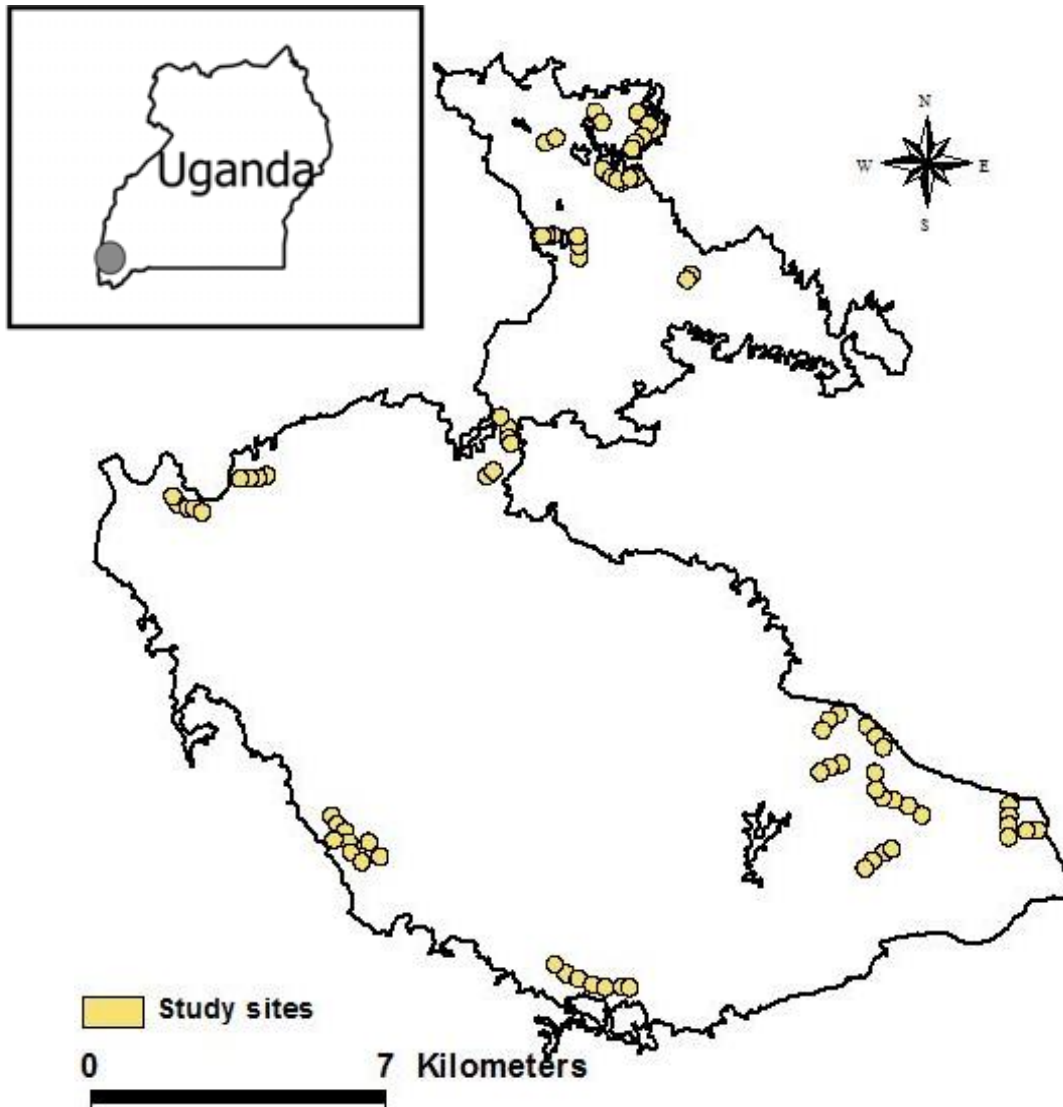
### 2.1. Location

The 331 km<sup>2</sup> forest of the Bwindi Impenetrable National Park ("Bwindi") is a UNESCO World Heritage site in Southwest Uganda (Figure 1). The forest is one of the few protected areas in East Africa which combines lowland and montane vegetation with elevation ranging from 1,200 m to 2,600 asl. It is believed to be a refuge for forest cover through the last glacial, making it among the region's richest forests (19, 20) and it is often considered the most important of Uganda's forests in terms of plant diversity and related conservation values (21). The forest includes disturbed vegetation and secondary regrowth especially around the forest edge (21-24).

Bwindi has a cool wet equatorial climate. It experiences two annual rainfall peaks (March to May and September to November). Long-term annual rainfall ranges from 1,392 mm (elevation 1,890 m) to 1,826 mm (elevation 1,494 m), while the mean annual temperature ranges from 16.4 C (elevation 2,300 m) to 21.7 C (elevation 1,433 m) (Institute of Tropical Forest Conservation (ITFC) <http://www.itfc.org> 9/7/2017).

### 2.2. Field methods

We selected accessible locations in each sector of the park (generally by tracks or forest edges). Paired 0.1-ha plots were established to ensure equal numbers of edge ("open" forest) and interior ("closed") forests in each location along transects from the selected location and (25, 26). A plot comprised searching for mistletoes in an area measured to be 10 m to either side of a 50 m line. Plot number and elevation was noted and when mistletoes were noted we recorded their species, tree location, host tree species, tree DBH, and tree height (m). To ensure consistent naming we collected herbarium specimens of all the mistletoes (species and forms) and host species encountered with additional material collected to cross-check and group as necessary. In total 64 plots were examined (6.4 ha) covering a broad range of elevations (1160 to 2607 m, see Figure 1).



**Figure 1** Location of the Bwindi Impenetrable National Park in Uganda (inset) and the 0.1-ha plots in the forest.

### 2.3. Processing and analyses

All collected botanical materials were matched to material held at the herbaria at the Institute of Tropical Forest Conservation (ITFC) or at Makerere University. When uncertain we consulted with, and took guidance from, professional botanists. In selected cases we sent photographs to an overseas botanist to double check names and groupings. Unfortunately, not all specimens could be matched and named with confidence and have been given numbers as “morpho-species”. Unfortunately, some specimens were combined and became detached from their labels before taxonomic evaluations were completed, this led to some data-gaps, so not all individual plot level designations could be properly confirmed or updated. For this reason, we cannot summarize species numbers by plot, list parasite to host listings for low abundance mistletoe taxa or provide the collection locations for *Tapinanthus bangwensis* and *Tapinanthus erianthus*.

The taxonomy of mistletoes has advanced over the last century meaning that not all reference materials follow the same nomenclature and spelling: we therefore standardized our taxonomy using the International Plant Names Index (2022 <https://www.ipni.org/>).

Our analyses are primarily descriptive and result from simple compilation of records which we performed using MS-Excel. We applied Chao’s estimator to estimate a lower bound on species richness from an incomplete sample (27). Chao’s lower bound estimator for  $\hat{S}$ , estimated species number, is given by:

$$\hat{S} = D + f_1(f_1 - 1) / [2(f_2 + 1)],$$

Where  $D$  is the number of distinct species in the sample and  $f_1$  is the number of species that are represented exactly once and  $f_2$  is the number of species that are represented exactly twice. This simple method is widely used as a simple and robust means of estimating the total number of species in incomplete samples from species rich systems (28) though has recently been subjected to some criticism (29).

### 3. Results and discussion

#### 3.1. Number and density of mistletoes

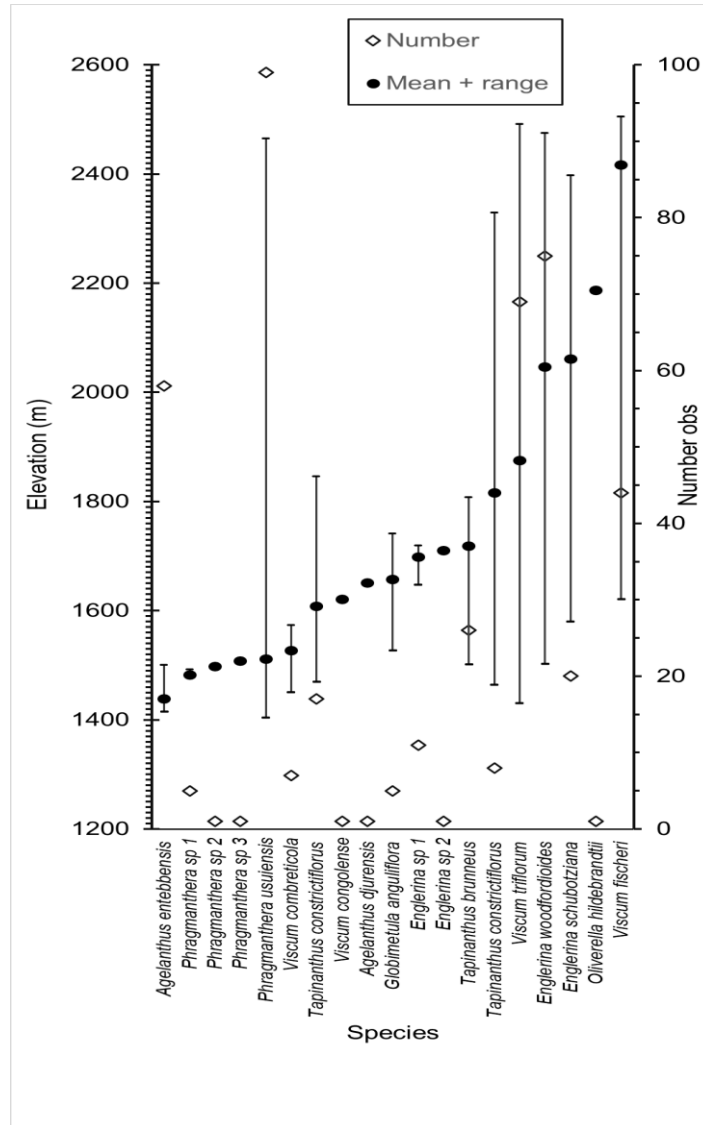
We recorded 1,452 mistletoes comprising 21 taxa (15 species and 6 unnamed morpho-species given numbers in our collection) in seven genera and two families in our 64 0.1-ha plots (Table 1). The Loranthaceae are represented by 993 individuals in 17 taxa assigned to six genera while the Santalaceae are represented by 559 individuals in four taxa in one genus. Of the 21 mistletoe taxa recorded, 10 appeared only in disturbed forests and four only in denser forest while seven occurred in both.

**Table 1** Hemi-parasitic species (full taxonomy) recorded in more and less open conditions ranked by counts.

Hemi-parasitic species	Family	Counts by forest condition		
		Open	Closed	Total
<i>Englerina woodfordioides</i> (Schweinf. ex Engl.) Balle	Loranthaceae	187	141	328
<i>Viscum fischeri</i> Engl.	Santalaceae	306	10	316
<i>Phragmanthera usuiensis</i> (Oliver) M.G.Gilbert	Loranthaceae	184	59	243
<i>Viscum triflorum</i> DC.	Santalaceae	215	12	227
<i>Agelanthus entebbensis</i> (Sprague) Polhill & Wiens	Loranthaceae	107	0	107
<i>Englerina schubotziana</i> (Engl. & K.Krause) Polhill & Wiens	Loranthaceae	56	48	104
<i>Tapinanthus brunneus</i> (Engl.) Danser	Loranthaceae	0	82	82
<i>Tapinanthus constrictiflorus</i> (Engl.) Danser	Loranthaceae	33	8	41
<i>Englerina</i> sp 2	Loranthaceae	0	21	21
<i>Phragmanthera</i> sp	Loranthaceae	18	0	18
<i>Agelanthus djurensis</i> (Engl.) Polhill & Wiens	Loranthaceae	1	15	16
<i>Viscum combreticola</i> Engl.	Santalaceae	15	0	15
<i>Globimetula anguliflora</i> (Engl.) Danser	Loranthaceae	0	10	10
<i>Tapinanthus bangwensis</i> (Engl. & K.Krause) Danser	Loranthaceae	10	0	10
<i>Englerina</i> sp 1	Loranthaceae	0	8	8
<i>Viscum congolense</i> De Wild. & T.Durand	Santalaceae	1	0	1
<i>Tapinanthus erianthus</i> (Sprague) Danser	Loranthaceae	1	0	1
<i>Phragmanthera</i> sp 1	Loranthaceae	1	0	1
<i>Phragmanthera</i> sp 2	Loranthaceae	1	0	1
<i>Phragmanthera</i> sp 3	Loranthaceae	1	0	1
<i>Oliverella hildebrandtii</i> Tiegh.	Loranthaceae	1	0	1

#### 3.2. Elevation

Mistletoes occur at all elevations examined. Most species exhibit limited ranges (Figure 2), though *Phragmanthera usuiensis* and *Viscum triflorum* both span over 1,000 m (1,060 m each) while *Englerina woodfordioides*, *Viscum fischeri* and *Tapinanthus constrictiflorus* also span large ranges (972, 884 and 865 m respectively).



**Figure 2** Highest, lowest and mean elevation in meters (left hand axis and filled circles ●) and number of observations (right hand axis and open diamonds ◇) for each mistletoe taxa recorded.

**3.3. Host trees**

The mistletoes were recorded on 542 individual trees comprising 45 host species (Table 2) in 18 families. Euphorbiaceae, Leguminosae, and Moraceae supported the most.

**Table 2** Host trees (full taxonomy) by forest condition

Species	Family	Counts by forest condition		
		Open	Closed	Total
<i>Macaranga kilimandscharica</i> Pax	Euphorbiaceae	33	137	170
<i>Maesa lanceolata</i> Voigt	Myrsinaceae	19	60	79
<i>Millettia dura</i> Dunn	Leguminosae	66	1	67
<i>Sapium ellipticum</i> (Krauss) Pax.	Euphorbiaceae	35	0	35
<i>Harungana madagascariensis</i> Lam. ex Poir.	Clusiaceae	8	25	33
<i>Macaranga barteri</i> Müll.Arg.	Euphorbiaceae	17	1	18
<i>Neoboutonia</i> sp.	Euphorbiaceae	0	17	17

<i>Alangium chinense</i> Rehder	Alangiaceae	11	2	13
* <i>Pinus taeda</i> Blanco	Pinaceae	1	10	11
<i>Teclea nobilis</i> Delile	Rutaceae	0	8	8
<i>Neoboutonia macrocalyx</i> Pax	Euphorbiaceae	0	7	7
<i>Bridelia micrantha</i> (Hochst.) Baill.	Euphorbiaceae	2	4	6
<i>Ficus</i> sp.	Moraceae	0	6	6
<i>Albizia gummifera</i> C.A.Sm.	Leguminosae	5	0	5
<i>Ficus capensis</i> Hort.Berol. ex Kunth & C.D.Bouché	Moraceae	5	0	5
<i>Maesopsis eminii</i> Engl.	Rhamnaceae	3	2	5
<i>Newtonia buchananii</i> (Baker) G.C.C.Gilbert & Boutique	Leguminosae	5	0	5
<i>Prunus africana</i> (Hook.f.) Kalkman	Rosaceae	0	5	5
<i>Psychotria mahonii</i> C.H.Wright	Rubiaceae	0	4	4
<i>Allophylus abyssinicus</i> (Hochst.) Radlk.	Sapindaceae	1	2	3
<i>Markhamia lutea</i> K.Schum	Bignoniaceae	3	0	3
* <i>Persea americana</i> Mill. "Avocado"	Lauraceae	3	0	3
<i>Carapa grandiflora</i> Sprague	Meliaceae	0	2	2
<i>Faurea saligna</i> Harv.	Proteacea	0	2	2
<i>Ficalhoa laurifolia</i> Hiern	Theaceae	0	2	2
<i>Hagenia abyssinica</i> (Bruce) J.F.Gmel.	Rosaceae	0	2	2
<i>Mystroxydon aethiopicum</i> (Thunb.) Loes.	Celastraceae	0	2	2
<i>Pellaea</i> sp.	Pteridaceae	2	0	2
* <i>Pinus patula</i> Schiede & Deppe ex Schltdl.	Pinaceae	2	0	2
<i>Rapanea melanophloeos</i> Mez	Myrsinaceae	0	2	2
<i>Strombosia scheffleri</i> Engl.	Olacaceae	1	1	2
<i>Trema orientale</i> (L.) Blume	Ulmaceae	2	0	2
<i>Trichilia rubescens</i> Oliv.	Meliaceae	2	0	2
<i>Alchornea hirtella</i> Benth.	Euphorbiaceae	1	0	1
<i>Aningeria altissima</i> (A.Chev.) Aubrév. & Pellegr.	Sapotaceae	0	1	1
* <i>Camellia sinensis</i> (L.) Kuntze "Tea"	Theaceae	0	1	1
<i>Clerodendrum</i> sp.	Lamiaceae	1	0	1
<i>Ficus sur</i> Forssk.	Moraceae	1	0	1
<i>Ilex mitis</i> (L.) Radlk.	Aquifoliaceae	1	0	1
<i>Lindackeria bukobensis</i> Gilg	Flacourtiaceae	0	1	1
<i>Myrianthus holstii</i> Engl.	Cecropiaceae	1	0	1
<i>Nuxia congesta</i> R.Br.	Buddlejaceae	0	1	1
<i>Tabernaemontana orientalis</i> R.Br.	Apocynaceae	1	0	1
<i>Tetrorchidium didymostemon</i> (Baill.) Pax & K.Hoffm.	Euphorbiaceae	1	0	1
<i>Vernonia</i> sp.	Asteraceae	0	1	1

\*Indicates an exotic species (presumed planted)

Mean densities of individual mistletoes in edge habitat were 2.7 times greater than in neighboring interior forest, i.e., 1138 versus 414 mistletoe individuals respectively or 356 ha<sup>-1</sup> versus 129 ha<sup>-1</sup>. Trees often hosted multiple mistletoes.

On average 85 trees over 10 cm dbh in each hectare supported mistletoes. Host species were dominated by fast growing pioneer tree species. Just three species, *Macaranga kilimandscharica*, *Maesa lanceolata* and *Millettia dura* hosted over half of all observations (58 %). Four exotic species (17 stems) were included, two pines, tea and avocado, as several plots were situated near the edge of the forest and included planted boundary trees.

*Harungana madagascariensis* hosted most (nine) mistletoe species, while *Maesa lanceolata* hosted 8. Another 6 species were observed to host three or more mistletoe species, 13 host two and 21 just one. In total, Loranthaceae were recorded on 36 tree species and the Santalaceae on ten.

We did not assess trees without mistletoes, so have not quantified these relationship formally but our observations indicate that the probability that a tree hosts mistletoes increased not only with exposure but with size—as noted elsewhere, larger trees have larger canopies, and tend to be older and better lit thus providing more space and time for the mistletoes to establish (30). Nonetheless the overall pattern is more complex and deserves further characterization, as in most natural forests smaller trees are much more common than larger trees (31, 32) and thus provide a high proportion of the canopy space available to be colonized by mistletoes.

### 3.4. Specificity

Mistletoe species were often found on multiple hosts. *Phragmanthera usuiensis* was found on 18 host species while *Englerina woodfordioides* was found on 12. The most common two-species combinations were *Viscum triflorum* on *Macaranga kilimandscharica* (245 occurrences), *Viscum fischeri* also on *Macaranga kilimandscharica* (179) and *Englerina woodfordioides* on *Harungana madagascariensis* (118). Other common pairings are *Phragmanthera usuiensis* on *Sapium ellipticum* (97), *Agelanthus entebbensis* on *Millettia dura* (82), *Viscum triflorum* on *Macaranga barteri* (77) and *Englerina woodfordioides* on *Maesa lanceolata* (58). Unsurprisingly, mistletoes that were more frequently recorded were also found on more host species (taking only species with at least five records, Pearson's  $r = 0.62$ ,  $n=15$  and assuming a null hypothesis of no correlation,  $p= 0.013$ ).

### 3.5. Diversity

Chao's estimator for the lower-bound of overall richness indicates that the forest-wide species richness of mistletoes is likely double what we observed in this survey (38.5 for the total data, but 44.5 for only the more open vegetation). There is uncertainty around all these numbers. As not all specimens could be named, we remain unclear whether all our morphospecies represent separate taxa. The number of additional species that might be found with additional sampling is in any case an imperfect estimate (29). Nonetheless, our study suggests that Bwindi, a single forest, hosts a substantial fraction of the total mistletoe diversity in Africa (313 species noted in ref. 14).

Is Bwindi unusual in its diversity and abundance of mistletoes? Our general impression is that mistletoes are usually considered a relatively minor element of overall forest diversity accounts from commercial forestry and horticulture show that they can reach sufficient densities to cause concern in these contexts (34). Data, however, are scarce. When looking for comparable assessments of total plant diversity in natural forests at either the plot or the forest level, few studies or compilations include parasitic plants—in part this reflects the sometimes ephemeral visibility of some parasitic taxa, but should not apply to mistletoes (33). Nonetheless, mistletoes can be small, cryptic and easy to overlook and are often hard to access. When “total” plant surveys have been published, mistletoes appear scarce in natural forests. For example, in their documentation of all the plants in 100 m<sup>2</sup> of lowland forest in Costa Rica, Whitmore and colleagues (35) counted 233 vascular taxa but made no mention of mistletoes or other parasites. In some cases such omissions may reflect unclear or inconsistent definitions, such that mistletoes are sometimes counted as “epiphytes” (36). For example, in one study of epiphytes in one hectare of forest in Southwestern Japan two species of mistletoes were noted (37). Even when the definitions appear consistent, parasites appear scarce, such as in an apparently comprehensive botanical assessment of three one hectare forest plots of in Santa Cruz, Central Bolivia, where just one parasite taxa was reported and it occurred on one of the three plots (38). Viewed in a global context, it appears that Bwindi, with its abundance and diversity of mistletoes appears unusual. Further ecological examination of this diversity and its wider implications is justified (8, 14).

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## 4. Conclusion

We provided an initial characterization of mistletoes in the Bwindi Impenetrable National Park. More than twenty mistletoes taxa were recorded and a similar number are predicted to have remained undetected. Densities were typically over one hundred mistletoe plants per hectare across the forest and occurred over the whole elevation range. Mistletoes represent a significant component of the forest's biological diversity and ecology.

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## Compliance with ethical standards

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### *Disclosure of conflict of interest*

The authors declare no conflict of interest.

### *Statement of ethical approval*

All work was conducted with formal approval from the Uganda Wildlife Authority. This work did not involve any research on animals or on human subjects.

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