








REVIEW

Consuming and consumed: Biotic interactions of African mistletoes across different trophic levels

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Abstract

Mistletoes, as perennial hemiparasitic angiosperms that parasitize woody plants, are an important component of the highly diverse, endemically rich and mosaic African flora, which is attributed to the Holarctic, Paleotropical, and Cape Floristic kingdoms. The richness of African mistletoes from the Loranthaceae and Viscaceae, along with many aspects of their biology and ecology, was covered in the comprehensive monograph of Polhill and Wiens (1998, *Mistletoes of Africa*, Royal Botanic Gardens). The present review is devoted to the taxonomic and functional diversity of symbionts associated with mistletoes in Africa and adjacent islands that contribute to the major biological functions of mistletoes, such as establishment and growth, nutrition and fitness, resistance to external stresses, as well as pollination and dispersal. These functions are favored by more or less distinct sets of associated bionts, including host plants, animal herbivores, frugivorous birds, nectar- and pollen-feeding insects, and endophytic microorganisms. A separate section is devoted to mistletoe epiparasitism as a special case of host selection. All these organisms, which are components of the mistletoe-associated community and multitrophic network, define the role of mistletoes as keystone species. Some aspects of the symbiont communities are compared here with patterns reported for mistletoes from other continents, particularly to identify potential relationships that remain to be explored for the African species. In addition, properties of endophytic mistletoe associates that contribute to the plant's communication with coexisting organisms are considered. We also highlight the important gaps of knowledge of the functioning of mistletoe-associated communities in Africa and indicate some applied issues that need future attention.

Abstract in French is available with online material.

KEYWORDS

dispersers, frugivores, hemiparasites, host plant, host preference, microbiome, pollinators, vectors

1 | INTRODUCTION

The term “mistletoe” refers to a functionally well-defined yet polyphyletic group of aerial plant hemiparasites that share common life history traits, such as rootless habit, a specific type of biotic interactions with the host plants, host-dependence, cryptic mimicry of host plants, and the presence of a specialized organ, the haustorium, for gaining water and nutrients from the host (Kuijt & Hansen, 2015; Okubamichael et al., 2016). Mistletoes occur on all continents except Antarctica and represent several families in the order Santalales, especially Lorantheaceae (ca. 900 species) and Viscaceae (ca. 500 species), but also some Santalaceae, Amphorogynaceae, and Misodendraceae (Nickrent et al., 2010).

The African flora is dominated by tropical and subtropical elements belonging to different biomes (e.g., savanna, fynbos, desert, Nama, Succulent Karoo, deciduous, and evergreen forests) that have evolved in isolation and includes numerous biodiversity hotspots (such as the Cape Floristic Region) with remarkable occurrences of endemics (Klopper et al., 2006). African mistletoes (including those on adjacent islands) are represented by Lorantheaceae (258 species from 23 genera) and Viscaceae (81 species from 3 genera) (see Table S1), both of which have a presumed Gondwanan origin but apparently different dispersal histories. The Lorantheaceae presumably spread from Asia across the Northern Hemisphere to mainland Africa in the Eocene (Grímsson et al., 2018; Liu et al., 2018), whereas the major African genus of Viscaceae, *Viscum*, probably originated in Africa in the Eocene, followed by dispersal to other continents and a later colonization of northern Saharan Africa from continental Asia (Maul et al., 2019). Mistletoes on islands neighboring Africa (i.e., Madagascar and Western Indian Ocean islands) may have arrived at their present location by dispersal from the continent, as has been hypothesized for *Socratina* and *Viscum* species (Maul et al., 2019; Vidal-Russell & Nickrent, 2008). In addition, *Bakerella* (currently found on Madagascar, Mascarenes, and Seychelles) and *Korthalsella* (with patchy distribution across South-Eastern Asia to Australia, Pacific and Indian oceans, and Eastern Africa) could hypothetically have spread from South or South-Eastern Asia via a southern hemisphere route, for example, by vicariance during the breakup of Gondwana or by steppingstone and long-distance dispersal pathways (Molvray et al., 1999; Polhill & Wiens, 1998).

Based on the haustorial anatomy and development in African mistletoes, 14 haustorium types are known that are divided into 4 basal types with at least 3 subtypes: woodroses, epicortical roots, clasping unions, and bark strands (Calvin & Wilson, 1998). Woodrose-forming mistletoes include some representatives of *Erianthemum*, *Moquiniella*, *Pedistylis*, *Tapinanthus* (Lorantheaceae), and *Viscum* (Viscaceae) (Calvin & Wilson, 1998; Dzerefos et al., 1998, 2003). In turn, epicortical roots occur in the mistletoe genera *Bakerella*, *Helixanthera*, *Plicosepalus*, *Taxillus*, and *Vanwykia* (Calvin & Wilson, 2006), whereas clasping unions characterize *Actinanthella*, *Emelianthe*, *Englerina*, *Globimetula*, *Oedina*, *Oliverella*, *Oncella*, *Phragmanthera*, *Septulina*, *Spragueanella*, and *Oncocalyx* section *Oncocalyx* (Calvin & Wilson, 1998, 2006). According to Teixeira-Costa et al. (2020),

Helixanthera and all Viscaceae develop bark strands, similarly to some members of the genera *Oncocalyx* (sections *Longicalyculati* and *Oncocalyx*), *Agelanthus* (sections *Erectilobi* and *Purpleiflori*), *Oedina*, and *Spragueanella* (Calvin & Wilson, 1998; Kuijt & Hansen, 2015). In general, the external haustorium morphology may vary in the same mistletoe species depending on the host plant, whereas the developmental process is more conserved, allowing for a more precise differentiation of haustorium types (L. Teixeira-Costa, pers. comm.). No information is currently available as to haustorium structure in *Berhautia* and *Socratina* (Lorantheaceae).

Populations of some African mistletoes are reportedly declining (Polhill & Wiens, 1998). For instance, of the 11 occurrences of epiparasitic mistletoes reported by Soyer-Poskin and Schmitz (1962) from a locality in the Democratic Republic of the Congo, no epiparasite and few likely habitats remained by 2015 (Wilson & Calvin, 2017). Habitat transformation and overharvesting by humans have been reported as major drivers of decline of some mistletoe species in the Mascarene Islands and Seychelles, while the near-extinction of *Bakerella hoyifolia* subsp. *bojeri* on Reunion was attributed to the loss of its hypothetically main dispersers (flying foxes, doves, and parrots) since human colonization of the island (Albert et al., 2017). Many species of African mistletoes are being studied by ethnobotanists due to their traditional use in spiritual practices as well as increasing exploitation in officinal medicine and by herbalists as “all-healing,” “bone-setting,” and “fertility-boosting” drugs (Koffi et al., 2020; Oriola et al., 2020). At the same time, due to their broad host range and tendency to spread rapidly, many mistletoe species have gained a reputation as notorious pests that cause significant losses in tree crops (Dibong et al., 2008).

Nevertheless, mistletoes play a crucial role in ecosystems as secondary foundation species, providing key resources such as substrate and microhabitat for microorganisms and arthropods (Peršoh, 2013; Zamora et al., 2020), a food source for herbivores (Těšitel et al., 2021; Watson & Herring, 2012), and a nesting site for birds (Cooney et al., 2006; Ndagurwa et al., 2016; Těšitel et al., 2021; Watson & Herring, 2012). Consequently, mistletoes contribute to the symbiotic communities of their hosts by increasing the total load of microbial associates, inquilines, herbivores, pollinators, and dispersers, bringing an array of other associated guilds including predators, parasites, and parasitoids (Zamora et al., 2020). Studies in the northern temperate regions have empirically demonstrated mistletoes promoting the diversities of endophytic fungi (Peršoh, 2013; Peršoh et al., 2010), arthropods (Lázaro-González et al., 2017, 2020; Zamora et al., 2020), and frugivorous birds (Mellado & Zamora, 2016) in the host-tree canopies. In addition to the direct mistletoes' input to biodiversity, modifications in the host plant metabolome in response to permanent mistletoe parasitism impose selective pressure on associated communities (Lázaro-González et al., 2021), triggering cascading responses in ecosystems. Mistletoes can therefore exert an ambivalent effect on host plants by facilitating their reproduction through the attraction and permanent support of shared generalist pollinators and vectors (Těšitel et al., 2021), but

at the same time reducing the physiological fitness of the hosts by depletion of their water and nutrient supplies and increasing susceptibility to pathogens and herbivores (Griebel et al., 2017). Furthermore, community-level impacts of mistletoes are seen beyond their hosts through the production of nutrient-rich litter that enhances host litter decomposition and contributes to carbon and nutrient fluxes in ecosystems (Ndagurwa et al., 2020), as well as attraction of seed dispersers that bring in and deposit (as excreta) the seeds of other plants, promoting increased plant diversity in forests (Těšitel et al., 2021). These effects, when combined, facilitate changes in the composition of soil microbiota, vegetation, and associated herbivore fauna beneath parasitized trees, leading to long-term vegetation shifts and habitat restructuring (Hódar et al., 2018; Mellado et al., 2016; Mellado & Zamora, 2017; Ndagurwa et al., 2014; Watson & Herring, 2012). Current understanding of the top-down and bottom-up effects of mistletoes within symbiotic networks is still at an early stage, and more empirical data at finer levels (individuals and populations) both in the spatial and temporal contexts are required to make broad-scale inferences.

Presently, little is known about the composition and function of the organisms associated with mistletoes in Africa (Figure 1). In this review, we summarize existing knowledge on this topic, highlight major gaps to be filled, and identify challenges for future research. Due to the complicated biogeography of some African mistletoe taxa, the geographic scope of this review includes mainland Africa with its neighboring islands to the west (in the Gulf of Guinea) and east (Madagascar, Comoros, Mascarenes, and Seychelles). We organize our review by discussing symbiont guilds with different trophic positions relative to mistletoes, and in regard to their roles in mistletoe function. First, through an analysis of published and herbarium data, we address patterns of host preference in mistletoes that contribute to their growth, distribution, and speciation. The following sections are devoted to mistletoe consumers and such reproduction-associated symbionts as pollinators and dispersers. We then discuss the diversity and composition of endophytic mistletoe associates, emphasizing their contribution to the role of mistletoes as interaction “hubs” in ecological networks. Finally, we touch upon some applied aspects of symbiotic interactions in mistletoes that require more attention in the future.

2 | HOSTS OF AFRICAN MISTLETOES: DIVERSITY AND ASSOCIATION PATTERNS

Following the last comprehensive assessment of host associations in African mistletoes by Polhill and Wiens (1998, 1999a, 1999b) and a number of regional studies (see Table S1 for the reference list), Grímsson et al. (2018) have recently compiled the continent-wide published host species records for the African Loranthaceae. In contrast, the island mistletoe taxa (from the Madagascar and neighboring islands) have remained virtually unaddressed in terms of host

associations since Balle (1964a, 1964b) and Philcox (1982), except for occasional studies dealing with individual mistletoe taxa (Albert et al., 2017). Here, we discuss host diversity and patterns of host use in the African mainland and island mistletoes based on historical and recently published data supplemented with herbarium specimen records retrieved from various online databases and digitized herbarium specimens. Our data set (Table S1) includes over 1000 host plant species from 553 genera, 119 families, and 40 orders recorded for 313 mistletoe species (plus 25 infraspecific taxa) from 26 genera. Host species data are still lacking for 39 mistletoe taxa (26 species and 13 infraspecific taxa), requiring further studies.

Host preferences in mistletoes are reputedly dynamic and attributed to several factors such as host morphology defining the compatibility with a mistletoe's haustorium, physiological fitness and nitrogen content determining the host's “quality,” as well as host abundance and stability in an ecosystem crucial for the duration of mistletoe-host contact (Gairola et al., 2013; Norton & Carpenter, 1998; Polhill & Wiens, 1998; Teixeira-Costa et al., 2020). In Africa, most mistletoe's host plants belong to the core eudicotyledons, with the greatest mistletoe diversity confined to host families such as Fabaceae, Malvaceae, Euphorbiaceae, Rubiaceae, and Combretaceae that are central to the African flora and contain numerous woody species with diverse habitat requirements (Figure 2). Gymnosperms, Magnoliids, and monocots are occasionally parasitized by promiscuous mistletoe species, with the exception of *Pinus* and *Juniperus*, which host some specialized taxa from the Viscaceae (Table S1). On the genus level, *Combretum* and *Ficus* host the greatest mistletoe diversity, with 72 and 62 mistletoe species, respectively (Figure S1), whereas nearly 35% of the host genera are associated with only one mistletoe species. Fossil pollen evidence indicates that many of the host families of extant mistletoes (including some of those listed above) were available as potential hosts for African mistletoes in the early Miocene (Grímsson et al., 2018), suggesting long-term relationships between present-day mistletoe species and these host families. Patterns of host use by mistletoes, such as the relative number of specific host taxa within the overall host range and the host overlap, vary across mistletoe genera. The high proportion of specific host taxa (e.g., families and genera) may reflect significant niche differentiation and geographic isolation of mistletoes (this may apply to the genera occurring on islands: *Bakerrela*, *Korthalsella*, and *Viscum*) or the presence of highly indiscriminate species that act as opportunists (e.g., in *Erianthemum* and *Tapinanthus*) (Figures 2 and S2). Such opportunistic species seem to be also the main contributors to the considerable host overlap between *Agelanthus*, *Erianthemum*, *Globimetula*, *Phragmanthera*, and *Tapinanthus*, and between these and the other mistletoe genera (Figure S3). In *Viscum*, the increased host overlap with other mistletoes likely stems from the high richness and ecological/geographic differentiation of species. *Arceuthobium* and *Taxillus* appear segregated from the other African mistletoe genera due to the lack of shared host species (Figure S3). These two genera, along with *Korthalsella*, have their main distribution ranges outside Africa (Polhill & Wiens, 1998) and thus may be distantly related to other African mistletoes. Liu et al. (2018), however, speculated that

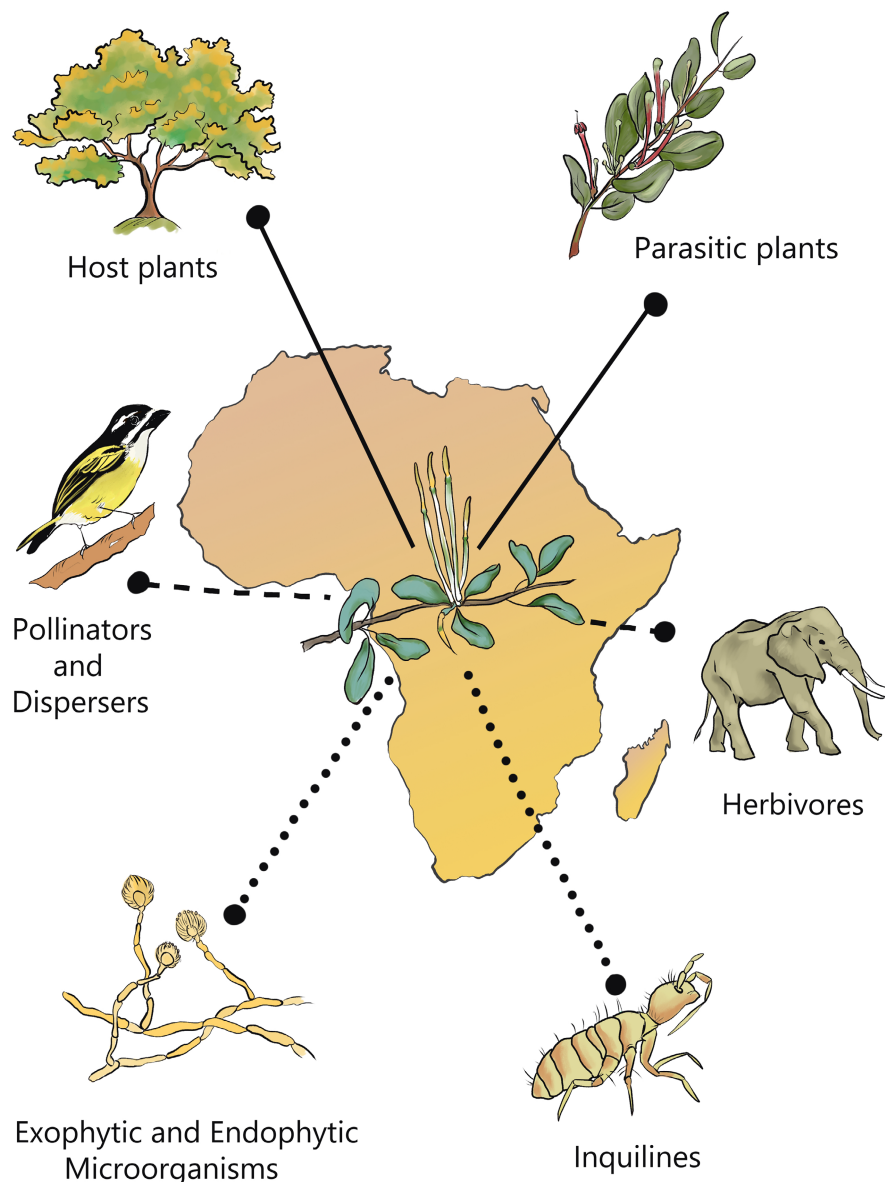


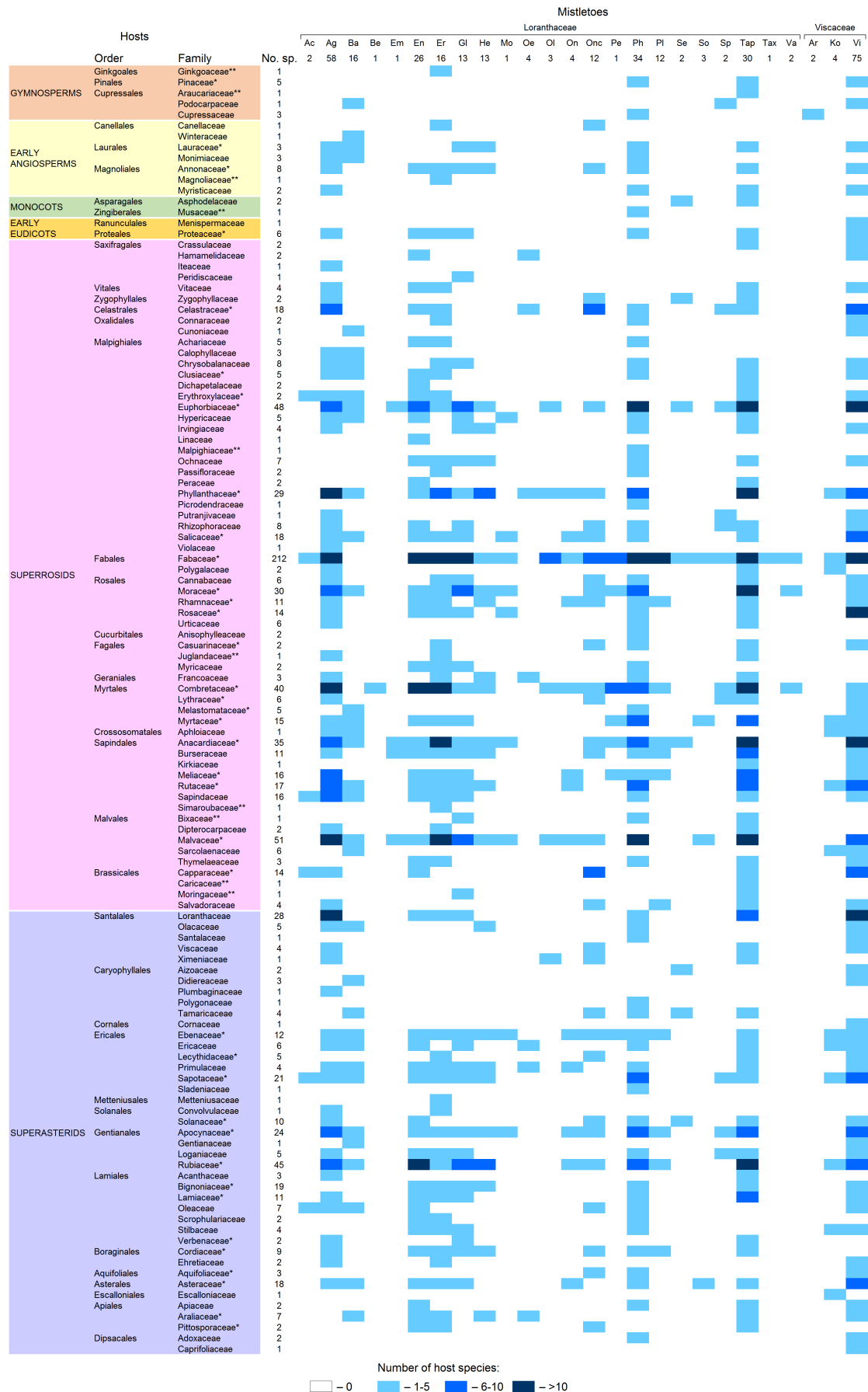
FIGURE 1 Diversity of biotic associations of African mistletoes. Indications: straight lines—well-studied; dashed lines—scarcely studied; dotted lines—still unstudied. Graphical drawing by Natalia Pendiur

the only African species of *Taxillus*, *T. wiensii*, has derived from a local lineage rather than from the rest of *Taxillus* residing in Asia.

Much of the available host records are at the genus and family ranks (Table S1), making it difficult to accurately assess host preferences in mistletoes. This is especially true when assessing

species-level host specificity trends and host overlap among mistletoes, geographic patterns (as many African plant genera contain both narrow- and broad-ranged species whose distributions overlap), and recently revised taxa that have undergone changes to established names. As arguably the most striking example of the latter,

FIGURE 2 Host associations of mistletoes in Africa at the family level, based on data in Table S1. Host plant classification follows Stevens (2001 onwards), The Angiosperm Phylogeny Group (2016), and Ran et al. (2018), and the coloring of major plant clades follows Byng et al. (2018). Classification of the Santalales (including hosts and mistletoes) follows Kuijt and Hansen (2015). No. sp. indicates (horizontally) the number of African mistletoe species in each genus and (vertically) total number of host-plant species in each family (including hybrids but excluding infraspecific taxa such as subspecies and varieties) recorded for these mistletoes in Africa and adjacent islands. In all calculations, familial and generic host records (those with "sp." in Table S1) were omitted when identified subordinate plant taxa (genus or species, respectively), were additionally present among hosts for a given mistletoe taxon; otherwise, all "sp." records of a family or genus were counted as one "species." Host families with some records of taxa introduced to Africa are marked with "*", and those containing introduced host records only are marked with "***". Mistletoe genera are listed alphabetically and by family as follows: *Ac Actinanthella*, *Ag Agelanthus*, *Ba Bakerella*, *Be Berhautia*, *Em Emelianthe*, *En Englerina*, *Er Erianthemum*, *Gl Globimetula*, *He Helixanthera*, *Mo Moquiniella*, *Oe Oedina*, *Ol Oliverella*, *On Oncella*, *Onc Oncocalyx*, *Pe Pedistylis*, *Ph Phragmanthera*, *Pl Plicosepalus*, *Se Septulina*, *So Socratina*, *Sp Spragueanella*, *Tap Tapinanthus*, *Tax Taxillus*, *Va Vanwykia*, *Ar Arceuthobium*, *Ko Korthalsella*, *Vi Viscum*



Acacia serves as key host for numerous African mistletoe species but is treated *sensu lato* in many host records due to only recent reclassification of the genus, which placed all the African taxa into *Senegalia* and *Vachellia* (Kyalangalilwa et al., 2013). Extraction of species records of *Acacia* s.str. (most of which have been introduced into the area covered in this review) shows that these plants are common hosts for *Globimetula*, *Phragmanthera*, and *Tapinanthus* mistletoes, whereas the two above-mentioned indigenous genera are apparently preferred by *Plicosepalus*, *Tapinanthus*, and some *Viscum* species (Table S1).

Generalist mistletoes (i.e., with broad host specificity and no clear preference; associated with three and more host families) account for most of the total host diversity recorded, although relatively few of them (some *Agelanthus*, *Erianthemum*, *Globimetula*, *Phragmanthera*, and *Tapinanthus*) have a very broad host range of more than 50 plant species (up to 181 in *Tapinanthus globiferus*; Table S1). About 42% of all mistletoe taxa with host records appear to be specialists, assigned here to several categories: (1) mistletoes that occur on multiple host species of two families with unclear preference and regarded as potential specialists (35.5% of all specialists); (2) family specialists that are associated with one to several host families but clearly prefer hosts of one family or genus (16.3%); and (3) strict specialists that have only one to several records on plants of a single genus (48.2%). Among the major mistletoe genera, the proportion of specialists is highest in *Plicosepalus* (primarily specialized on fabaceous hosts), followed by *Helixanthera*, *Bakerella*, *Viscum*, *Erianthemum*, and *Agelanthus*, whereas the prevailing majority of *Oncocalyx*, *Tapinanthus*, and *Phragmanthera* species are generalists (Figure S2). Although these patterns are predominantly consistent with those reported by Polhill and Wiens (1998), they may be somewhat compromised by limited data from poorly studied species and the lack of frequency data for each mistletoe-host pair. In addition, generalist mistletoes may exhibit regional host specialization, a phenomenon often attributed to the occurrence of intraspecific races in mistletoes, as has been documented for some species of *Agelanthus*, *Erianthemum*, *Phragmanthera*, *Tapinanthus*, and *Viscum* in Africa (Gairola et al., 2013; Okubamichael et al., 2014; Okubamichael, Griffiths, & Ward, 2011; Polhill & Wiens, 1998). Furthermore, mistletoe occurrence on a particular host may depend on factors other than host preference, such as microclimatic conditions (which are critical for mistletoe germination and establishment), dispersal constraints (feeding habits of dispersers, lack of suitable vectors, or low fruit palatability), or mistletoe consumption by herbivores. Finally, the remarkable ability of some generalist mistletoes to mimic their preferred hosts in leaf shape, texture, and color (e.g., as a concealing strategy to avoid consumption by herbivores; Polhill & Wiens, 1998; Dibong et al., 2008) may contribute to observation bias (i.e., over-looking by humans).

Island mistletoe taxa (from Madagascar and the western Indian Ocean islands) show higher overall host specificity compared to mainland ones (Figure S2). However, this trend may be confounded by the unresolved phylogenetic and phylogeographic relationships of the mistletoe genera discussed here, some of which (e.g.,

Helixanthera and *Korthalsella*) presumably include components with distinct dispersal histories and of independent, relatively recent South Asian origin (Grímsson et al., 2018; Liu et al., 2018; Molvray et al., 1999; Polhill & Wiens, 1998). Overall, our compiled records (Table S1) do not indicate a consistent preference trend for island versus mainland mistletoes, with significant overlap in their general host ranges at the genus level. Island mistletoes apparently avoid some host families that are widely distributed and usually preferred by mainland mistletoe species, such as Combretaceae and Fabaceae. Conversely, in families associated exclusively with island mistletoes (Cunoniaceae, Escalloniaceae, Menispermaceae, Sarcolaenaceae, and Winteraceae), most of the records pertain to host taxa that are endemic to the islands but parasitized by generalist mistletoes. The exception is Sarcolaenaceae, where half of the host records are of specialists. Furthermore, island endemics appear to also prevail among all host species recorded exclusively for island mistletoes (ca. 60 species from 34 families that constitute half of the island host records, the rest being mostly at the genus level and from genera that occur both on the island and on mainland Africa, such as *Erica*, *Eugenia*, and *Symphonia*). However, whether the specialist mistletoes target local endemics or more widespread congeneric species as hosts remains unclear, as many of these mistletoes' host records are at the genus level. Nevertheless, the above evidence suggests that island mistletoes favor local narrowly restricted host lineages over widespread species that extend to mainland Africa. The widespread species (e.g., *Cerriops tagal* and *Aphloia theiformis*) and the introduced crops are usually shared as hosts by the generalist island mistletoes with their mainland relatives.

In *Viscum*, the differentiation in host preference between mainland and island is most apparent: almost twice as many strict specialists are present among island taxa (about 37% of all *Viscum* taxa with host records; Table S1) as among their mainland relatives, although the proportion of all specialists is nearly equal in the two groups. Furthermore, of all host genera associated with *Viscum*, ca. 16% (32 genera) are recorded only for island mistletoes, and only 9.4% are common to both island and mainland *Viscum*. However, about half of the former genera are not endemic to the islands but include species that are either parasitized by mainland non-*Viscum* mistletoes (such as *Acalypha*, *Dalbergia*, *Vernonia*, and *Uapaca*) or do not have mistletoe associations on the mainland (e.g., *Bruguiera*, *Cerbera*, *Cryptocarya*, and *Hirtella*). Most of the records of specialist island *Viscum* refer either to endemic host genera (e.g., *Oncostemum*, *Xerochlamys*), endemic species of more widespread genera (such as *Brachylaena merana* and *Neocussonia bojeri* from Madagascar), or widespread genera known to contain species endemic to the islands (*Croton* and *Erica*). Following Maul et al. (2019), the above patterns suggest that geographic isolation is the main driver of host preference shifts in African mistletoes, with novel lineages likely deriving from generalist species through niche shifting promoted by both migrant and local dispersers.

Approximately 13.5% of all host taxa recorded for African mistletoes are introduced species from other continents (Table S1). Most of these are from families that also comprise many native host plants,

such as Fabaceae (25 introduced host species), Euphorbiaceae (10), and Malvaceae (8) (Figure 2), implying an increased predisposition of mistletoes to these plant families. Mistletoe diversity is particularly high in species grown either as large trees or in dense plantations (e.g., *Hevea brasiliensis*, *Persea americana*, *Psidium guajava*, *Theobroma cacao*, species of *Citrus* and *Prunus*), probably due to the frequent visits by certain guilds of birds (such as woodland species, habitat generalists, and migrants; Bennett et al., 2021) and other mistletoe vectors. Generalist species of *Agelanthus*, *Erianthemum*, *Globimetula*, *Phragmanthera*, and *Tapinanthus* are the main users of introduced plants, both in terms of numbers of mistletoe and host species involved in these interactions (Figure S4). Nevertheless, these mistletoe genera differ greatly as to their propensity to form novel host associations (expressed here as an “opportunism” index, based on the proportion of species within each mistletoe genus that parasitize introduced hosts), which is the highest in *Tapinanthus* and *Globimetula* and lowest in *Helixanthera* and *Plicosepalus* (Figure S4). The share of generalist mistletoe species in each genus, however, only partly explains the above trend, given that some mistletoes regarded as potential or family specialists (e.g., *Agelanthus flammeus*, *Bakerella gonoclada*, and *Erianthemum melanocarpum*) also employ introduced species as hosts while many generalist mistletoes apparently avoid them (Table S1). In this respect, of particular interest are species recorded primarily or exclusively on introduced hosts (e.g., *Agelanthus guineensis* on *Citrus* sp. and *Viscum ceibarum* on *Ceiba pentandra*), suggesting that they may have broader yet undocumented host ranges or have specialized on local archaeophytes as hosts. In addition, numerous species widely cultivated in Africa have their natural range in some parts of the continent or adjacent islands (all treated here as “native”), and many of these (indigenous acacias as well as *Coffea*, *Ficus*, *Nerium*, *Syzygium*) serve as important hosts for some generalist and specialist mistletoe species (Table S1). The introduction and artificial expansion of the range of plant species suitable as hosts for mistletoes may therefore facilitate the spread of mistletoes into new areas and habitats, where they can establish novel symbiotic interactions that impact local ecosystems.

3 | EPIPARASITISM AS A PATTERN OF HOST CHOICE IN MISTLETOES

Epiparasitism as a type of plant hyperparasitism in which an aerial parasite (such as a mistletoe, love vine, or dodder) uses other parasitic plant as a host (Krasylenko et al., 2021), has been observed in various parts of the world, most commonly in Oceania, but relatively few cases are known from Africa (Wilson & Calvin, 2017). Records of 42 African mistletoe species from 10 genera acting as epiparasites show that this phenomenon is most common in *Agelanthus*, *Tapinanthus*, and especially *Viscum* (Figure 3; Table S1). The latter genus accounts for almost half of all epiparasite records on mistletoe hosts in Africa and, together with *Tapinanthus*, harbors the greatest diversity of epiparasites. Among mistletoes, the most common “epiparasite—parasitic host” combinations are Viscaceae epiparasitic

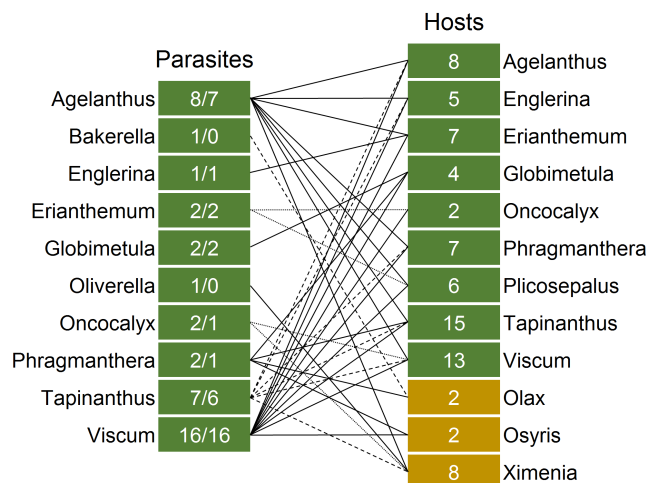


FIGURE 3 Occurrence of mistletoe epiparasitism on other mistletoes (green blocks) and root-parasitic plants (light-brown blocks) in Africa. Numbers under “parasites” indicate the total number of species in each genus recorded to act as epiparasites and the subtotal of species parasitizing other mistletoes, and those under “hosts” indicate the number of epiparasitic mistletoe species hosted by members of each host genus. Different line patterns are given for clarity. Mistletoe genera not involved in epiparasitic interactions are not shown

on Loranthaceae and Loranthaceae epiparasitic on Loranthaceae, both in Africa (Figures 2 and 3) and globally (Wilson & Calvin, 2017). The majority of African species are facultatively epiparasitic generalists (Table S1), which is also true at the global level (Krasylenko et al., 2021; Wilson & Calvin, 2017). Obligate epiparasitism occurs in two African *Viscum* species—*V. goetzei*, parasitizing solely an *Englerina* host, and *V. loranthicola*, associated with a number of Loranthaceae host genera—and has also been suspected for *Agelanthus dichrous* being highly selective towards Loranthaceae hosts (Wilson & Calvin, 2017; see also Table S1). In addition, the lack of host evidence may mask epiparasitic potential of other African mistletoes, such as *Agelanthus kraussianus* (detected on only two hosts; Table S1) and probably some *Viscum* species (Wilson & Calvin, 2017).

Records of mistletoe autoparasitism in Africa, a peculiar type of interaction in which a hyperparasite uses individuals of its own species as hosts (Krasylenko et al., 2021), are found for only two species—*Globimetula braunii* and *G. cupulata* (Table S1). Interestingly, these species apparently do not interact parasitically with any other mistletoe, neither as epiparasites nor as hosts, suggesting their inter-specific incompatibility. Of the other mistletoes occurring in Africa, *Viscum album* is perhaps the one most known for its autoparasitic potential (Krasylenko et al., 2021), although the documented records come from that part of the species' range that lies outside Africa. As it is difficult to distinguish autoparasitic individuals from their conspecific hosts, this interaction may be more common among mistletoes than reported (Krasylenko et al., 2021; Wilson & Calvin, 2017). Importantly, autoparasitism should not be confused with the self-parasitism (i.e., attachment of haustoria to different parts of the same individual plant), which is common in the mistletoes that form

epicortical roots and is sometimes referred to as epiparasitism, but is a completely different phenomenon (Krasylenko et al., 2021; Wilson & Calvin, 2017).

In addition, root hemiparasites (such as some Santalaceae) reportedly serve as common hosts for mistletoes in Asia and Australia (Wilson & Calvin, 2017), whereas the occurrence of this association in Africa has been greatly overlooked. African records associate epiparasitic mistletoes with three santalalean root-parasitic host genera: *Olex* (Olacaceae), *Osyris* (Santalaceae), and *Ximenia* (Ximeniaceae), which appear to be almost exclusively parasitized by Loranthaceae (Figure 3). *Ximenia* seems to be the most susceptible host, although this pattern may be biased by the relatively frequent occurrence of *Ximenia* in habitats where the respective mistletoe species occur, such as open woodlands and dry dense and gallery forests dominated by Combretaceae and Fabaceae species (Lompo et al., 2021). Other Santalales have also been recorded as mistletoe hosts in Africa, such as *Diogoa*, *Heisteria*, and *Strombosia* (Olacaceae) (Table S1). Although the species of these genera are considered autotrophic (Kuijt & Hansen, 2015), a more detailed study of their nutrient acquisition mechanisms may shed light on the functional aspects of associated mistletoe parasitism.

Physiological ecology, evolutionary advantages, and ecosystem outcomes of epiparasitism in plants are poorly studied (reviewed by Krasylenko et al., 2021), not to mention the remarkable cases of tripartite associations such as the occurrence of *Viscum verrucosum* on *Tapinanthus quequensis* on *Agelanthus natalitius* growing upon *Combretum apiculatum* (Combretaceae) in South Africa (Nickrent, 2002). Limited evidence suggests that epiparasites tend to sustain lower water potentials and higher concentrations of mineral nutrients compared to parasitic and nonparasitic (primary) hosts, likely leading to selection on associated herbivores (Krasylenko et al., 2021). In addition, the tendency of epiparasites to have smaller fruits and seeds compared with their parasitic hosts, as reported for some Viscaceae and Loranthaceae species from North America and Africa (Calvin & Wilson, 2009), may affect the dispersal of epiparasites by selecting for frugivores with certain dietary preferences.

4 | RECIPROCAL BENEFITS: MISTLETOE FEEDERS AND POLLINATORS

In several biomes in Africa, including neighboring islands, mistletoes are visited by mammals, birds, and insects for regular/concomitant feeding. This type of feeding is most important in dry savannas and montane tropical forests, as these areas have high rates of mistletoe endemism and/or specialized intraspecific interaction between mistletoes, their consumers, and hosts. Among mammals, nutrient-rich mistletoe foliage is often preferred by ruminants in African drylands, for example, in savannah (Ehleringer et al., 1986; Marshall et al., 1994). Large ungulates such as the Common Eland (*Taurotragus oryx*) and Greater Kudu (*Tragelaphus strepsiceros*) feed on mistletoe leaves in the dry season (Roxburgh & Nicolson, 2008). In addition, various species of Bovidae (antelopes, cattle, gazelles, goats, and sheep)

feed on *Helixanthera mannii* in tropical regions (EOL, 2021). In South Africa, elephants consume clumps of *Moquiniella rubra*, *Viscum com-breticola*, *V. crassulae*, and *V. rotundifolium*, despite these mistletoes usually reside on high branches (Midgley & Joubert, 1991). In turn, Thick-tailed Bushbaby (*Otolemur crassicaudatus*) was found consuming berries of *Viscum songimveloensis* (Oosthuizen & Balkwill, 2018).

African mistletoes attract also other mammals such as Bushveld Elephant-shrew (*Elephantulus intufi*), Multimammate Mouse (*Mastomys coucha*), Natal Multimammate Mouse (*M. natalensis*), and Namaqua Rock Mouse (*Aethomys namaquensis*), which feed on mistletoe fruits, especially during the winter season, when other nutritional sources are scarce, and use habitats formed by mistletoe-infected shrubs as shelter (Amutenya, 2017). Furthermore, the evergreen mistletoe *Tapinanthus bangwensis* has been suggested as a promising safe forage plant that does not cause digestive disorders in ruminants and local poultry in Nigeria (Egbewande et al., 2011), and Ndagurwa and Dube (2013) reported that mistletoes are consumed as highly nutritious supplements for goats.

Observations in the forests of Rwanda, the Democratic Republic of the Congo and other areas of West Africa have shown that the leaves, fruits, and flowers of several mistletoe species (*Agelanthus brunneus*, *Englerina woodfordioides*) are consumed by primates, such as the Doggett's Blue Monkey (*Cercopithecus mitis* ssp. *doggetti*), the Tantalus Monkey (*Cercopithecus aethiops*), the Eastern Chimpanzee (*Pan troglodytes schweinfurthii*), and mountain gorillas (Basabose, 2002; Kaplin et al., 1998; Weston, 2009). In Madagascar, the endemic *Bakerella* mistletoes serve as an important nutritional source for lemurs during the dry season (Irwin, 2008; Powzyk & Mowry, 2003). The sifakas (*Propithecus diadema* and *P. edwardsi*) rely on foliage, flowers, buds, and fruits of *Bakerella clavata*, especially in fragmented forests due to the extended phenology of this mistletoe and its availability during the lean season, and despite its relatively low protein content (Irwin et al., 2015; McGee & Vaughn, 2017). The same was assumed for cheirogaleid lemurs (*Cheirogaleus* and *Microcebus*) in disturbed habitats (Atsalis, 2008; Crowley et al., 2013). Similarly to *Bakerella*, *Viscum* ssp. may be a major food source for *Microcebus* lemurs due to the high lipid content in fruits compared to the loranth (Atsalis, 2008). Moreover, *Bakerella* ssp. provide food resources for three birds and one bat species (Bollen et al., 2004; Bollen & Van Elsacker, 2002).

The coevolution of mistletoes and birds has resulted in the evergreen clumps of semi-succulent foliage and attractive nutritious fruits being a valuable food source for many birds (Martínez del Rio et al., 1996). Raji et al. (2021) indicated 9 bird species that regularly forage on the fruits of *Agelanthus dodoneifolius* parasitizing *Parkia biglobosa* and 71 species just visiting both the host trees and their associated mistletoes in central Nigeria. The Stripe-cheeked Greenbul (*Arizelocichla milanensis*) was observed feeding on *Viscum shirens*, *Agelanthus subulatus*, and *Englerina inaequilatera* fruits, while the Black-bellied Starling (*Notopholia corrusca*)—on *Erianthemum* ssp. (EOL, 2021). Moreover, Long-tailed Glossy Starling (*Lamprolornis caudatus*), Blue-spotted Wood Dove (*Turtur afer*), and Speckled Pigeon (*Columba guinea*) are considered as opportunistic mistletoe

feeders, but not their vectors (Boussim et al., 1993). Seven species of Nectariniidae observed on *Phragmanthera dschallensis* have been identified as major nectar-feeders in East Africa (Gill & Wolf, 1975). Besides their trophic importance, mistletoes are known as important nesting and roosting sites for birds (Zuria et al., 2014). For instance, the Gray Go-away-bird (*Corythaixoides concolor*, Musophagidae) nests in *Plicosepalus kalachariensis* and *Viscum verrucosum* in a semi-arid savannah of southwest Zimbabwe (Ndagurwa et al., 2016).

A variety of invertebrates interact with mistletoes during their life cycle, using these plants as food and/or for reproduction in different parts of the world (Burns et al., 2011; Zamora et al., 2020), although the relevant data from Africa are incredibly scarce and incoherent. The one and most detailed community-level study in Africa was that by Room (1971, 1972a, 1972b, 1973) on *Tapinanthus bangwensis* parasitizing cocoa (*Theobroma cacao*) in Ghanaian horticulture, which demonstrated the role of multipartite interaction networks (such as “plant host – parasite – insect herbivore – predator”) in enhancing the impact of mistletoes on their host plants. More recently, the effect of mistletoes on the arthropod abundance and diversity in the litter layer in a semi-arid savanna in southwest Zimbabwe has been assessed (Ndagurwa et al., 2014), and several other studies addressed the diversity of Formicinae and Myrmicinae ants associated with *Phragmanthera capitata* and *P. nigriflora* in Cameroon (Noutcheu et al., 2013; Ondoua et al., 2016). Numerous African mistletoe species from different genera were recorded as hosts of caterpillars of species of the Pieridae (*Mylothris* sp.) (Braby, 2005) and Lycaenidae (*Iolais* sp. and *Stugeta carpenteri*) (Congdon et al., 2017). Boussim et al. (1993) reported a small creamy-white butterfly foraging the flower tufts of *Tapinanthus* in Burkina Faso. The two above-mentioned lepidopteran families, both of which have a cosmopolitan distribution, are known to contain many species whose larvae feed exclusively on mistletoes (Watson et al., 2020).

The pollination of mistletoes occurs through abiotic (wind and thermogenesis) and biotic components of ecosystems (Kuijt, 1969; Mathiasen et al., 2008). Many tropical mistletoes have colorful flowers producing large amounts of sugar-rich nectar that attract birds and insects as pollinators (Mathiasen et al., 2008; Vidal-Russell & Nickrent, 2008). Although many mistletoes that are bird-pollinated are visited by a wide range of bird species, none of the latter can be considered mistletoe specialists (Watson, 2001). In West Africa, mistletoe flowers are mainly pollinated by sunbirds (Nectariniidae), whose tapered and curved beaks with long mobile tongues are well-adapted to the morphology of the tubular flowers of the Loranthaceae, allowing for greater efficiency of flower visits. Species such as Western olive (*Cyanomitra obscura*), Green-headed (*C. verticalis*), Scarlet-chested (*Chalcomitra senegalensis*), Northern double-collared (*Cinnyris reichenowi*), Variable (*C. venustus*), and Beautiful (*C. pulchella*) sunbirds are the most active in West Africa (Boussim et al., 1993; Raji et al., 2021; Weston et al., 2012). Olive-bellied (*Cinnyris chloropygius*) and Collared (*Hedydipna collaris*) sunbirds have been specified as potential pollinators of *Tapinanthus bangwensis* in Ghana (Room, 1972b), while Copper Sunbird (*Cinnyris cupreus*) – of *Agelanthus dodoneifolius* in Nigeria (Raji et al., 2021).

Apart from the Nectariniidae, some passerine birds such as the White-eyes (Zosteropidae) are regarded as secondary pollinators, since they can open simpler flowers and forage nectar (Polhill, 1989). Two species of White-eyes (*Zosterops borbonicus* and *Z. chloronothos*) endemic to Reunion and Mauritius, respectively, have been observed visiting the flowers of local *Bakerella* mistletoe species (Albert et al., 2017; Gill, 1971). Of other birds endemic to Madagascar, the Forest Fody (*Foudia omissa*, Ploceidae) and Velvet Asity (*Philepitta castanea*, Philepittidae) have also been observed as nectar feeders on *Bakerella*, and two species of *Neodrepanis* are known to suck nectar from the elongated flowers with their curved long beak (Craig, 2014; Raheirilalao & Goodman, 2011; Rakotomanana & Rene de Roland, 2004). Feehan (1985), in his study on pollination mechanisms in African Loranthaceae, reported that nectar-feeding birds are crucial for the pollination of *Erianthemum* mistletoes and that both size and shape of the pollinator's beak and its behavioral patterns during flower visits define the pollination mechanism in *Tapinanthus* and *Plicosepalus*. In Cameroon, weavers (Ploceidae) with short thick beaks consume nectar of *Tapinanthus* flowers by piercing the corolla tube without pollination, hence being nicknamed “nectar-robbers” (Kirkup, 1984; Weston, 2009).

Apart from birds, some insects are known to be key pollinators of some Viscaceae and Loranthaceae species (Godfree et al., 2003; Kuijt, 1969), although the records of such associations in Africa are extremely rare. The genus *Helixanthera*, regarded as the most primitive of the African Loranthaceae, might be the only one having flowers adapted to insect pollination (Dibong et al., 2008; Polhill & Wiens, 1998). The honeybee (*Apis mellifera*) and a small social wasp from the Vespinae visited the flowers of *Agelanthus brunneus* and *A. djurensis* in Nigeria, robbing nectar by making perforations in the bases of corollas (Weston, 2009; Weston et al., 2012).

5 | AERIAL AND TERRESTRIAL VECTORS OF MISTLETOES

Birds as crucial mistletoe dispersers, being either generalists or specialists with or without exclusive mistletoe feeding, are an important component of the coevolving bird-mistletoe mutualistic system (Reid, 1991). Specialization of birds on mistletoe frugivory and dispersal has been well documented for Australia, South America, and tropical Asia as compared with Africa (Davidar, 1983; Martínez del Rio et al., 1996; Reid, 1989; Watson & Rawsthorne, 2013). At the same time, apart from their important contribution to long-distance mistletoe dispersal and establishment of new patches (Watson & Rawsthorne, 2013), the ecological role of mistletoe generalists remains unclear (Mellado & Zamora, 2014). This makes distinguishing between generalist dispersers and fruit predators challenging, given the great diversity of frugivorous birds that feed on mistletoes (Mathiasen et al., 2008; Raji et al., 2021).

The African Loranthaceae and Viscaceae produce brightly colored fruits, whose seeds are usually coated with sticky viscin (also called “birds' glue”) to attach firmly to a potential vector

(e.g., bird's feathers, beak, or legs) and to the host plant to ensure establishment of the haustorium. Among the key aspects of mistletoe dispersal is the ability of the vector to remove the fruit exocarp, being a precondition for breaking seed dormancy and germination (Okubamichael, Rasheed, et al., 2011). Therefore, the role of vectors should only be assigned to those birds that have been observed depositing mistletoe seeds on potential host trees, either in an aviary or in the wild (for an overview of avian vectors of African mistletoes, see Table S2). However, the related species (e.g., hornbills, turacos, mousebirds, and thrushes) that feed on *Viscum* and Loranthaceae fruits, but for which there are no documented records of seed deposition (Bosque et al., 2017; Brosset & Erard, 1986; Sun & Moermond, 1997) may also play a vector role, so, this list is still incomplete.

Based on the way birds peel off the exocarp of mistletoe fruit as a primary factor of vector efficiency, there are three approaches of bird's feeding on mistletoe fruits: regurgitation, defecation, and bill wiping (Godschalk, 1985; Roxburgh, 2007). In an aviary experiment with three bird species (Cape White-eye (*Zosterops virens*), Speckled Mousebirds (*Colius striatus*), and Red-winged Starling (*Onychognathus morio*) feeding on the fruits of *Agelanthus natalitius*, Okubamichael, Rasheed, et al. (2011) revealed that regurgitation provides the highest germination success, corroborating the findings of Roxburgh (2007) for *Phragmanthera dschallensis*.

The distance of potential dispersal and type of avian vector feeding, related to the time of gut passage or regurgitation of mistletoe seeds, are poorly studied. Some birds in the southern parts of Africa (e.g., Zambia and South Africa) contribute as short-distance dispersers of mistletoe seeds between the same host species within the existing mistletoe patches (Godschalk, 1985; Roxburgh & Nicolson, 2005).

The main African mistletoe vectors are resident or mostly resident tinkerbirds (*Pogoniulus*). Thus, the breeding areas of Mustached (*P. leucomystax*) and Yellow-rumped (*P. bilineatus*) Tinkerbirds in Malawi forests are correlated with the presence of 4–6 mistletoe species (Dowsett-Lemaire, 1988; Polhill, 1989). A more widespread Yellow-fronted Tinkerbird (*P. chrysoconus*) visits mistletoe patches in its breeding territory and often infects the same host trees or the trees within individual patches due to regurgitating seeds soon after their swallowing (Godschalk, 1985; Roxburgh & Nicolson, 2005, 2008). This behavior potentially limits the likelihood that the bird will colonize new mistletoe patches and disperse the seeds at long distances. A similar behavioral pattern has been observed in birds with specialized digestive systems for rapid seed passage through the gut—mistletoe birds (*Dicaeum hirundinacum*) in Australia and Phainopepla (*Phainopepla nitens*) in the New World (Reid, 1990; Walsberg, 1975).

However, data on the potential long-distance dispersal of mistletoe seeds are missing. Using a theoretical vector-based model, Mokotjomela et al. (2013) estimated the potential seed dispersal distance for South African species—Cape White-eye (*Zosterops capensis*), Cape Bulbul (*Pycnonotus capensis*), and Speckled Mousebird (*Colius striatus*)—to be much greater than 8 km. These species were

recognized as mistletoe vectors and defecated the seeds, favoring a much longer retention time in the birds' digestive tract and, hence, a much longer distance of dispersal (Godschalk, 1983c, 1985; Okubamichael, Rasheed, et al., 2011). Moreover, mousebirds (Coliidae) and bulbuls (*Pycnonotus*) are considered long-distance dispersers because of their considerably long post-feeding flights and great mobility during feeding (Godschalk, 1985; Green et al., 2009). The morphology of mistletoe fruits determines the range of avian vectors, as seen in *Viscum*: the fruits with thick exocarps are dispersed by tinkerbirds and barbets, while those with thin exocarps—additionally by Knysna Turaco (*Tauraco corythaix*), bulbuls, and weavers (Godschalk, 1983a, 1983b).

It might be assumed that a highly specialized coevolutionary plant-frugivore system, such as those involving mistletoe birds in Australia and flowerpeckers in Indo-Malaya, did not have enough time to have evolved in Africa, given a relatively recent (i.e., late Oligocene) origin of African Loranthaceae, forming the youngest clade within the family (Liu et al., 2018). Tinkerbirds (*Pogoniulus*), regarded as specialists among avian vectors in the forests and woodlands of central and southern Africa (Watson & Rawsthorne, 2013), regurgitate the seeds as opposed to the Australian and Asian mistletoe specialists which disperse the seeds via defecation (Polhill, 1989). The retention time of seed regurgitation in an aviary was reported to be 10–15 min in the Red-winged Starling (*Onychognathus morio*) (Okubamichael, Rasheed, et al., 2011) and ca. 20–24 min in the Black-collared Barbet (*Lybius torquatus*). The general speed of fruit removal is also very rapid in the Yellow-fronted Tinkerbird (*P. chrysoconus*) (Godschalk, 1985). This pattern of seed consumption and other behavioral features of tinkerbirds therefore restrict the long-distance dispersal of African loranthids despite their efficiency as vectors.

At the same time, the spread of Viscaceae seeds might also be related to generalist avian feeders, for example, intra-African and Palearctic long-distance migrants. In their breeding areas in Europe, some of them (e.g., *Sylvia* and *Turdus*) are recognized as frugivore vectors for many plants including mistletoes (Costa et al., 2014; Mellado & Zamora, 2014). They may play an important role in the long-distance dispersal of African mistletoes and the colonization of the new territories by patches, particularly in regions across the Sahara, where mistletoes infect large numbers of hosts including introduced and native ornamental crops (Dibong et al., 2008; Tizhe et al., 2016).

The close mutualistic relationships between the Madagascan endemic *Bakerella* and its seed disperser, the Brown mouse Lemur (*Microcebus rufus*), are of particular interest. *Bakerella* seeds have been ingested and subsequently observed intact and sticky in the feces of lemurs on tree trunks (Atsalis, 2008). Due to the absence of frugivorous birds on the island, small mammals such as some cheirogaleid lemurs may act as mistletoe short-distance vectors (Atsalis, 2008; Lahann, 2007). In addition, the Madagascar Flying Fox (*Pteropus rufus*), also known to consume *Bakerella* fruits, is reputedly among the key long-distance seed dispersers on the island, especially in the isolated parts of fragmented forests (Bollen et al., 2004).

6 | UNSEEN DIVERSITY: ENDOPHYTIC ASSOCIATES OF MISTLETOES AND THEIR ROLE IN ECOSYSTEMS

The plant microbiome is an integrated functional unit comprising the exo- and endo-phytic microbiota (including bacteria, archaea, fungi, and protists) with their “theatre of activity,” whose roles in host plant life range from mutualism (e.g., promotion of plant growth and resistance to various stresses) to neutral coexistence and to detrimental impacts on plant fitness and survival (Berg et al., 2020; Kalaiselvi & Panneerselvam, 2021). The presence of a haustorium—the interface between a mistletoe and its host plant—and the proximity of both associates within the same canopy make the mistletoe-host plant system an appropriate model for studying host preferences and specificity in bacterial and fungal endophytes. Nevertheless, the mistletoe microbiome is just an emerging research topic, which is why the available information is scarce and pertains to few mistletoe species analyzed to date.

The microbiota of African mistletoes remains barely investigated, with only a few studies known to address the use of bioactive compounds from a limited number of mistletoe-inhabiting ubiquitous fungi, such as *Aspergillus*, *Penicillium*, and *Nigrospora* (Abba et al., 2016; Ebada et al., 2016; Ladoh-Yemeda et al., 2015). In addition, several older studies report a number of ascomycetes (*Asterinella*, *Clypeolina*, *Meliola loranthi*, and a probable mycophile *Septonema loranthi*) and basidiomycetes (*Aecidium cookeanum* and *Septobasidium*) associated with some mainland African Loranthaceae and *Viscum* species (Balle, 1964a; Hansford, 1937, 1943; Hughes, 2007). Balle (1964a) also reported *A. cookeanum* to infect *Socratina keraudreniana* in Madagascar. In the temperate ecosystems of Europe and North America, where this issue has gained more attention, mistletoes reportedly harbor taxonomically and functionally diverse endophytic communities dominated by ecologically pliable saprotrophic hyphomycetes (Capnodiales, Eurotiales, Hypocreales, Pleosporales), which are known to be common plant endophytes and litter decomposers (Hampel et al., 2016; Peršoh, 2013; Peršoh et al., 2010). Lower occurrence was reported for wood-decaying and corticioid fungi (e.g., some Coniochaetales and Xylariales) and yeasts (Saccharomycetales and Tremellales from Europe), with sporadic occurrences of ectomycorrhizal (in Europe) and mycophilous taxa. Many of these fungi are known opportunistic plant pathogens (e.g., *Alternaria*, *Colletotrichum*), and several mistletoe-specific species have also been recorded (Baranyay, 1966; Karadžić & Lazarov, 2005; Kotan et al., 2013; Shamoun et al., 2003; Wicker & Shaw, 1968). Reports from tropical South America indicate—as major differences from the above patterns—the apparent rarity of taxa that are otherwise common plant endophytes in the tropics (e.g., some Botryosphaerales, Glomerellaceae, and Xylariaceae), and the high frequency of the ubiquitous Diaporthaceae (such as *Phomopsis*), which have not been recorded as associates of temperate mistletoes. This is coupled with the lack of records of the guilds that occur as incidental symbionts in temperate mistletoes, such as yeasts and mycorrhizal fungi (Abreu et al., 2010; Guimarães et al., 2013). Such

a disparity among endophytic assemblages in mistletoes suggests non-random selection even among widespread fungal taxa without host specificity. Though, this may also stem from undersampling (Abreu et al., 2010) or the use of different techniques (cultivation-based and cultivation-independent) to assess endophytic community patterns (Peršoh, 2013). Given that many associated saprotrophic and wood-inhabiting taxa often dominate endophytic mycobiomes in African non-parasitic woody plants that are known as mistletoe hosts (Begoude et al., 2010; Jami et al., 2015; Jordaan et al., 2006; Linnakoski et al., 2012; Toghueo et al., 2017), detailed comparative studies of endophytic assemblages in African mistletoes are needed to elucidate the patterns of their variation across the globe.

The composition of mycobiomes in the surrounding environment and the host preferences of the fungi are thought to be the main factors determining the diversity and distribution patterns of mistletoe endophytes (Peršoh, 2013). As suggested by studies both in temperate and tropical ecosystems (Abreu et al., 2010; Guimarães et al., 2013; Hampel et al., 2016; Peršoh, 2013; Peršoh et al., 2010), a mistletoe and its host plant would always exhibit an overlap in the composition of their endophytic communities, although the degree of this overlap is highly dependent on the geographic location and season. In addition, variation in plant organ selectivity and/or mode of transmission among endophytic fungi is also an important factor, as shown by the significant differences between mycobiomes associated with different mistletoe organs (i.e., young vs. old leaves vs. stems) (Abreu et al., 2010; Hampel et al., 2016; Peršoh, 2013). In view of the above evidence, mistletoes may play a role as a “bank” of latent decomposers, pathogens, and other fungal guilds that are selected in mistletoe tissues (either by competition or differential compatibility with the host) and then contribute to litter decomposition and soil community function (Peršoh, 2013).

Beneficial effects of endophytic fungi, including those of mistletoes, are also exhibited through the production of bioactive secondary metabolites, such as plant hormones, adenine ribosides, flavonoid glycosides, as well as defense-related and aromatic compounds (Ebada et al., 2016; Pirttilä et al., 2004; Qian et al., 2014; Tanaka et al., 2005; Tudzynski, 1997). Thus, endophytes are involved in processes related to important plant functional traits, including the resistance to pathogenic organisms and synthesis of plant volatiles. For instance, the ability to suppress plant pathogens has been demonstrated for some American and African mistletoe endophytes (Abba et al., 2016; Martin et al., 2012; Ribeiro et al., 2018), whereas an endophytic ascomycete *Lasiodiplodia* produced essential floral oil components in *Viscum coloratum* from East Asia (Qian et al., 2014). Plant volatiles provide cues to next-level consumers such as insect herbivores, parasitoids, and pollinators (Ponzio et al., 2013; Schiestl, 2015). The latter, in turn, play a role in the transfer of bacteria and microfungi between and within plants, contributing to the spatiotemporal turnover of the microbiotas between plant vegetative organs, floral parts, nectar and pollen, and seeds, which then transfer these microbes (along with those acquired internally) to the next plant generation (Álvarez-Pérez & Herrera, 2013; Goelen et al., 2020; Prado

et al., 2020). Mistletoes raise the complexity of these multitrophic interactions, involving plant endophytes, to a new level by blending (both internally and externally) into the symbiotic communities of their host plants to form shared symbiotic networks with additional trophic links.

7 | CONCLUSIONS AND FUTURE PERSPECTIVES

Mistletoes, as important components of the African flora, attract great interest from researchers all over the world due to their peculiar evolution, extensive network of biotic interactions, and unique pollination and seed dispersal strategies. Nevertheless, there are significant knowledge gaps in many aspects of African mistletoe ecology, highlighting the need for multidisciplinary and field-based studies that address both fundamental (e.g., evolutionary and biogeographic reconstructions, taxonomic updating, physiology and ecology of multitrophic interactions, and ecosystem impacts) and applied aspects at pan-African and local levels. Among the latter, the use of mistletoes for the production of bioactive compounds with multiple applications (e.g., in biocontrol of agricultural pests) is a promising challenge that deserves attention. In addition, more attention should be given to issues related to the conservation of declining mistletoe species, which play a key role in wildlife communities.

Disentangling the interactions within symbiotic communities associated with mistletoes is key to understanding the role of these plants in ecosystems. Many aspects of such interactions, including those between organisms of different phyla and with contrasting life histories, have so far been studied in non-parasitic plants and without considering the possible bottom-up effects (such as nutrient and metabolite exchange, cross-talks with co-existing organismic communities). Little-studied associations that are particularly interesting when applied to the mistletoe-host plant system include the reciprocal relationships between plant visitation by different insect guilds and the composition of phyllosphere-associated microbial communities (Bitar et al., 2021; Goelen et al., 2020), or the effects of nectar microbiota on plant pollination success (Rering et al., 2020). The perennial above-ground growth habit and easily traced physical contact with the host in mistletoes (in contrast to the root-hemiparasites) make them a perfect model for studying functional links within and between different trophic levels to reveal interlevel nutrient and energy flux pathways, patterns of horizontal gene transfer, and large-scale trends in ecosystem functioning.

It is widely acknowledged that mistletoes can make detrimental impacts on parasitized woody crops, affecting the fitness, yield, and longevity of host plants (Dibong et al., 2008). Of particular concern is the fact that many economically important plant species, including both native and introduced ones, are susceptible hosts for numerous mistletoe species in Africa. Planted across the continent and serving as a reservoir for mistletoe germplasm, these crops provide a living

route for the unwanted intrusion of mistletoes into new areas and natural habitats where they may spread in an uncontrollable manner due to the lack of specific consumers or other limiting factors. Crops planted in large quantities and visited by generalist pollinators and frugivores (Bennett et al., 2021) may therefore facilitate the spread of mistletoes across the continent. It is thus essential to unravel the feeding habits, population dynamics, migration routes, and mistletoe dispersal efficiency of frugivores recorded as potential or recognized mistletoe vectors. This would provide a rich source of information to improve our knowledge on mistletoe biogeography and current distribution patterns in Africa, as well as guide crop industries and environmental planning programmes in managing their plant resources to restrain the spatial distribution of mistletoes by seed dispersers (Griebel et al., 2017).

In addition, the use of plant pathogens (such as fungi and bacteria) in biological control of pest mistletoes is increasingly gaining attention as an environmentally beneficial method applicable to agroecosystems (Shamoun et al., 2003). Given the potential success and major challenges of this method as outlined by the recent efforts of its implementation against *Viscum album* in Europe (Kotan et al., 2013; Pocza et al., 2015; Varga et al., 2014), designing targeted studies on the identification and use of specific mistletoe pathogens in Africa would be crucial for controlling mistletoes in areas where they threaten crop production.

AUTHOR CONTRIBUTIONS

YK involved in conceptualization, data curation, funding acquisition, investigation, methodology, supervision, validation, visualization, and writing—original draft, review and editing. TRK involved in conceptualization, funding acquisition, investigation, and writing—original draft, review and editing. YS involved in conceptualization, data curation, formal analysis, investigation, validation, visualization, and writing—original draft, review and editing. NA involved in conceptualization, data curation, investigation, validation, visualization, and writing—original draft, review and editing. KHT involved in conceptualization, investigation, and writing—original draft, review and editing. OH and GR involved in investigation and writing—review and editing.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Open Science Framework repository ([10.17605/OSF.IO/KVZYM](https://doi.org/10.17605/OSF.IO/KVZYM)), as well as in the Supporting Information.

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