

On tropical mistletoes: tractable models for evolutionary ecology, ecosystem function, and phytochemistry¹

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Abstract: In 2001, I synthesised published information on mistletoe–animal interactions, demonstrating the pervasive influence these hemiparasites have on community composition and proposing that mistletoes represent keystone resources. Although the review was global in scope, I noted “Tropical regions, in particular, are under-represented in the mistletoe literature, and it is unclear if mistletoe is as important in structuring these highly diverse ecosystems as in less diverse temperate areas”. Since then, research on tropical mistletoes has burgeoned, as a growing number of researchers use these forest and woodland hemiparasites to address a wide range of ecological and evolutionary questions. In this commentary, I highlight some recent findings, revisit and refine some emergent inferences, and suggest that tropical mistletoes offer many opportunities for further research, representing tractable models to address many unanswered questions in the life sciences. As well as reinforcing the role of mistletoes as facilitators for plant communities and keystone resources for animal assemblages, research on mistletoe pollination, seed dispersal, and host-range, challenge the established views about the ecological maintenance and evolutionary trajectory of specialization.

Key words: hemiparasite, keystone resource, facilitation, seed dispersal, long distance dispersal, model system, specialization.

Résumé : En 2001, l’auteur a réalisé une synthèse de l’information publiée sur les interactions gui–animal, démontrant l’influence généralisée qu’ont ces hémiparasites sur la composition de la communauté et proposant que le gui représente une ressource clé. Même si cette synthèse était globale dans ses objectifs, il avait noté que « les régions tropicales en particulier sont sous-représentées dans la littérature portant sur le gui, et on ignore si le gui est aussi important dans la structuration de ces écosystèmes hautement diversifiés que dans les zones tempérées moins diversifiées ». Depuis lors, la recherche sur le gui tropical a pris son essor comme le nombre croissant de chercheurs qui utilisent ces hémiparasites des forêts et des régions boisées pour répondre à un vaste spectre de questions liées à l’écologie et à l’évolution. Dans ce commentaire, l’auteur met l’accent sur certaines découvertes récentes, revisite et raffine quelques conclusions nouvelles et suggère que le gui tropical offre plusieurs opportunités de recherche avancée, représentant un modèle malléable pour répondre à plusieurs questions encore sans réponses en sciences de la vie. Tout en renforçant le rôle du gui comme facilitateur des communautés végétales et ressource clé pour les assemblages animaux, la recherche sur la pollinisation du gui, la dispersion des graines et la gamme des plantes hôtes a remis en question les points de vue établis sur la gestion écologique et la trajectoire évolutive de la spécialisation. [Traduit par la Rédaction]

Mots-clés : hémiparasite, ressource clé, facilitation, dispersion des graines, dispersion sur de longues distances, système modèle, spécialisation.

Introduction

Mistletoes are an enigmatic group of plants, their parasitic habit, co-evolved partnerships, and cultural prominence inspiring observers of nature for centuries. Pliny the Elder, Linnaeus, and Darwin were fascinated by European mistletoe *Viscum album*, noting its dependence on trees for nutrition and birds for seed dispersal (Watson 2001). As explorers and naturalists returned from far-

flung lands with specimens and anecdotes, it became clear that mistletoe was not an aberrant European plant but a diverse group of hemiparasites with a global distribution. For tropical biologists, mistletoes have emerged from obscurity (Fig. 1), with recent evolutionary and ecological research shining a light on their diversification and ecological partnerships. As well as ecology and evolutionary biology, botany, and zoology, this research

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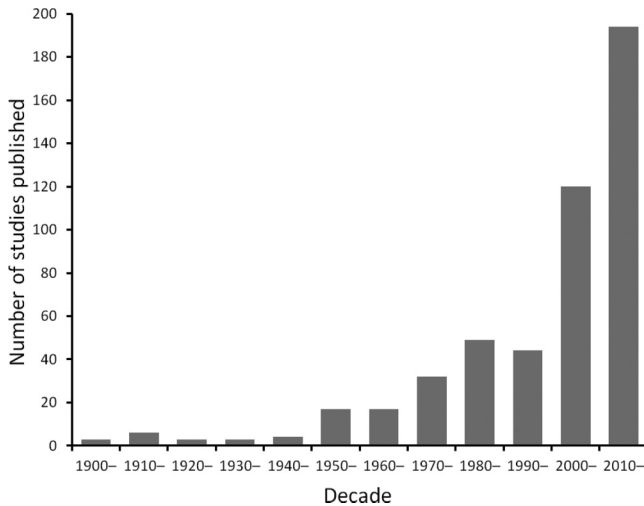
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Fig. 1. Number of peer-reviewed studies from 1900 to present involving tropical mistletoes, derived from a systematic survey (Google Scholar, search terms “tropical” and “mistletoe”) conducted in August 2016.

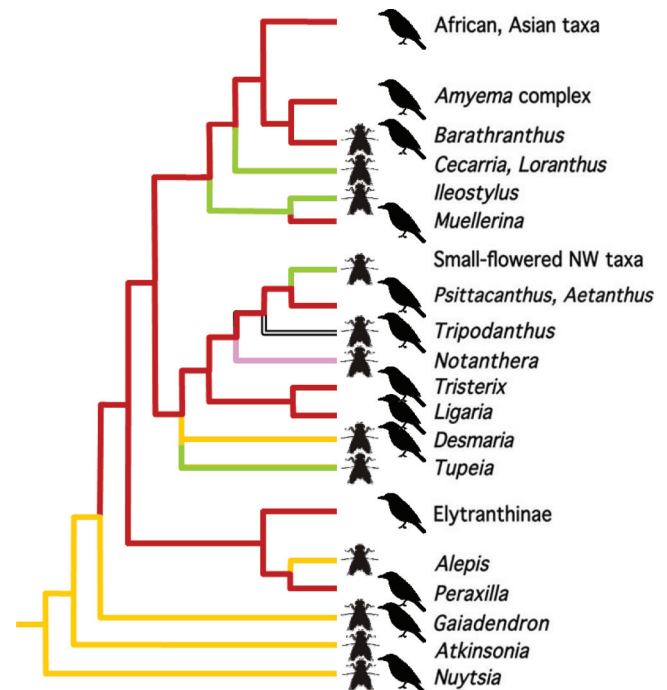


relates to biogeography, chemistry, ethnobotany, forestry, forest pathology, parasitology, pharmacology, and remote-sensing, making it especially challenging for researchers in any one discipline to remain abreast of recent discoveries about these plants. Here, I highlight some recent findings and suggest that mistletoes offer many opportunities for further tropical research, representing tractable models to address many unanswered questions in the life sciences.

Mistletoe origins and early diversification

Rather than a monophyletic group, the aerial parasitic habit is considered to have evolved independently in five lineages of root parasites within the Santalales (Vidal-Russell and Nickrent 2008 and references therein); those mistletoe groups relying on birds to disperse their seeds and (or) pollen co-diversifying and spreading to new habitats and biomes (Watson 2004). While previous work has noted reciprocal diversification in fruit-eating birds and bird-dispersed mistletoes (Restrepo et al. 2002), nectarivorous birds may likewise have been key to mistletoes' ascent to forest canopies. The three basal lineages within the Loranthaceae are root-parasitic with yellow, perfumed flowers pollinated by insects (Fig. 2). This contrasts with the most diverse genera (including the Neotropical *Psittacanthus* and *Struthanthus*, Australasian *Amyema*, Asian *Dendrophthoe*, and African *Agelanthus* and *Tapinanthus*), which typically have orange/red scentless flowers born in compound inflorescences high in the canopy (Fig. 3A). Indeed, when flower colour is mapped onto the genus-level phylogeny of the Loranthaceae, at least five lineages are characterized by red flowers, consistent with the hypothesis that bird-pollinated red flowers represents the basal condition for stem-parasitic loranthaceous mistletoes, coinciding with their switch from root-parasitic insect-pollinated ancestors (Fig. 2). Whether the evolution of red flowers rep-

Fig. 2. Hypothesized phylogeny of the Loranthaceae depicting predominant flower colour of lineage (double line where colour is white) redrawn after Vidal-Russell and Nickrent (2008), with permission. Symbols depict principal pollinators for each lineage (insects or birds).



resents a key innovation that catalysed the expansion and early diversification of the Loranthaceae has not been considered previously, exemplifying the value of a well-resolved phylogeny to inspire novel insights and frame novel evolutionarily-explicit comparisons.

Recovering evolutionary radiations

Having resolved the deep phylogenetic structure across families, attention has shifted to within-lineage patterns, with noteworthy insights emerging from two tropical genera. The neotropical genus *Tristerix* (Loranthaceae) is familiar to anyone visiting the Andes, their distinctive tubular flowers apparent in many habitats (Fig. 3A). A phylogeny of the genus by Guillermo Amico and collaborators (Amico et al. 2007) found evidence for recent diversification in the high elevation species, consistent with colonization of these geologically recent habitats as predicted by Simpson (1975). The phylogeny also revealed the imprint of long-standing partnerships with pollinators and seed dispersers. Unlike many South American mistletoe groups that rely on insect pollinators and flower in the warmer months, the red-flowered mistletoes *Tristerix* and *Ligaria* flower in the winter; cold-season flowering is hypothesized to have coevolved with homeothermous birds (Amico et al. 2007). This may be especially advantageous in the Andes, where two bird lineages with divergent foraging strategies act as pollinators. Hummingbirds (Trochilidae) of various shapes and sizes are important pollinators, hovering beneath the hanging flowers to

Fig. 3. (A) *Tristerix corymbosus* exemplifying the contrasting coloration and fused corolla tube that typifies the bird-pollinated flowers that characterize many lineages within the Loranthaceae (Nahuelbuta National Park, Chile; photo by G. Glatzel). (B) *Korthalsella complanata*, one of the Hawaiian representatives of this pantropical genus, here parasitizing an *Acacia koa* (Oahu; photo by G. Glatzel). (C) Fruiting *Lysiana exocarpia* showing the contrasting coloration of ripe fruits which attract a variety of seed-dispersing birds (Sturt National Park, Australia; photo by D.M. Watson). (D) Growth habit of *Psittacanthus schiedeana* in the upper canopy of host *Drimys granadensis*, a keystone resource in the cloud forests of Mesoamerica (Volcán Poás, Costa Rica; photo by F. Xaver). [Colour online.]



extract nectar. Flowerpiercers (*Diglossa* spp., Thraupidae) take a different approach, perching upon inflorescences and using their distinctively hooked bill-tip to pierce the corolla to access nectar directly. These competing strategies have driven floral evolution down multiple paths.

For two cloud-forest mistletoes, corollas have lengthened to deter nectar-robbers, with the spectacular flowers of *T. grandiflorus* growing up to 160 mm in length, pollinated by the equally impressive sword-billed hummingbird *Ensifera ensifera*. At lower elevations, flowers

are characteristically banded, with red bases and tips separated by a yellow band. Maturing flower buds of several species exhibit a “fenestration phase” with petals separating midway along the corolla tube forming a series of vents, coinciding with the yellow band. The distribution of these banded mistletoes overlaps with various *Diglossa* species, Amico et al. (2007) suggesting the colour change guides flowerpiercers to open the flower at the fenestrated area, prolonging floral longevity and likely enhancing self-pollination by dislodging pollen grains (after Navarro et al. 2008). Although other mistletoes exhibit these traits (maturing *Amyema* flower buds have the characteristic “Chinese lantern” phase: *Amylothea* flowers are characteristically banded), it is only these mid-elevation *Tristerix* species that combine them, these mistletoes the only plants for which nectar-robbing flower-piercers may represent genuine pollinators (Graves 1982; Maloof and Inouye 2000). Having established evolutionary relationships between extant groups, variation in floral morphology across the family and within particular genera can be related to historic shifts in pollinators, these patterns also evident in current population structure within individual species mediated via directional gene flow (Amico et al. 2014).

Another genus to have received a recent phylogenetic treatment is *Korthalsella*, a group of diminutive jointed plants in the Viscaceae known from east Africa, Madagascar, Asia, Australasia, and isolated islands throughout the Pacific Ocean (Fig. 3B). These cryptic plants have long defied botanists and ecologists — even the number of species is contested, variously considered to include ~30 range-restricted species or ~8 morphologically variable species. For his Ph.D. work, Amir Sultan gathered molecular sequence data from previously-studied species together with 16 additional species and found strong support for biogeographically defined taxa, hypothesized relationships suggesting parallel evolution of remarkably similar morphotypes (Sultan 2014). Species were found to group into four clades, each representing a separate radiation across thousands of kilometres. While the Asian and Australian endemics result from multiple radiations, most other groups of endemics cluster together within a single lineage. Thus, the 5–7 *Korthalsella* “species” endemic to the Hawaiian archipelago were found to result from a single colonization by an ancestral species, sister to the mistletoe which colonized the South Pacific. Just as “happy face” spider and anole relationships have far more to do with which island they inhabit than their morphology or behaviour (Gillespie and Clague 2009), so these *Korthal* mistletoes have undergone occasional over-water dispersal events followed by rapid morphological change and in-situ speciation, often associated with switching to new families of host plants. Once this work is fully published, taxonomy revised, and unsampled taxa incorporated to recover ancestral relationships, a highly-resolved map of putative long-distance dispersal

events will become available, enabling tropical biologists to explore how long-distance dispersal, host–parasite dynamics, and phenotypic plasticity evolve and interact.

Mistletoe dispersal

One of the best-studied aspects of mistletoe ecology is dispersal — particularly how fruit-eating birds contribute to mistletoe occurrence. Given their aerial parasitic habit, mistletoes are more reliant on directed dispersal than other plants, with most groups using fleshy fruits to attract and reward birds and the occasional mammal (Mathiasen et al. 2008; Fig. 3C). Inspired by pioneering work in England by the Snows (Snow and Snow 1988), ecologists searched for similar patterns elsewhere (Davidar 1983; Godschalk 1985; Reid 1986), their work reinforcing the view that mistletoes and mistletoe-fruit specialists are mutually interdependent. Carla Restrepo (1987) and Sarah Sargent (1994, 1995) conducted monographic studies in Colombia and Costa Rica, revealing the diversity of birds visiting fruiting mistletoes and potentially dispersing their seeds. With new data from Australia (Rawsthorne et al. 2011, 2012) and Panama (Watson 2012), I revisited these earlier studies and found that the supposedly reciprocally beneficial interaction was decidedly one-sided — while mistletoe-specialists necessarily need mistletoes, mistletoes do not need mistletoe-specialists (Watson and Rawsthorne 2013). In many regions, mistletoes are dispersed exclusively by dietary generalists and, even where mistletoe-specialist frugivores occur, their role is more exploitative than mutualistic, intensifying infections into defendable, dependable resources (Luo et al. 2015). This new interpretation opens up many questions regarding mistletoe dispersal, with the lesser Antilles and the Philippines — both tropical archipelagos where loranthaceous and viscaeous mistletoes are dispersed by generalists and (or) specialists — representing ideal arenas to test these ideas and explore how disperser ecology affects mistletoe populations (Watson and Rawsthorne 2013). With representatives of all eight families of mistletoe-specialist frugivores, tropical forests are presumably where this extreme dietary specialization evolved, with elevational shifts (historic and recent) indicative of the dynamic nature of these partnerships. More generally this research illustrates that, while plant–animal interactions may promote specialization, many may rely on unsung generalists for their longevity (Bascompte and Jordano 2007; Frick et al. 2013), suggesting ecologists may need to revisit our favourite mutualisms and reassure ourselves that we really do have the story straight!

In addition to determining distributions and, over time, diversification, dispersal is inextricably tied to many other life history traits, exemplified by research on *Psittacanthus schiedeanus* in the cloud forests of eastern Mexico (Fig. 3D). Peak availability of lipid-rich ripe fruits was found to coincide with a period of regional fruit scarcity in winter (López de Buen and Ornelas 2001), maximising visitation by generalist frugivores, including Cedar Waxwings and

other overwintering neotropical migrants. Germination experiments found higher germination rates for seeds defecated by Cedar Waxwings than either seeds manually extracted from their exocarp or seeds defecated by resident Grey Silky Flycatchers, presumed to be related to their longer gut passage rates (Ramírez and Ornelas 2009). Hence, the parasitic habit that necessitates directed dispersal also affords mistletoes greater flexibility in phenology by buffering seasonal constraints on productivity. As with most other Loranthaceous mistletoe, this species also relies on birds as pollen vectors, those plants pollinated by hummingbirds yielding proportionally greater seed set than self-pollinated caged plants (Ramírez and Ornelas 2010). The abundant, sugar-rich nectar represents an important food resource for several months in summer, and infected trees are visited by hummingbirds, parrots, flowerpiercers, butterflies, and bees. As well as underpinning plant demography and population viability, these ecological partnerships also play key roles in shaping distributional ranges. By comparing present-day phylogeographic patterns of *P. schiedeana* with estimated distributions during the last glacial maximum and last interglacial period (20 000 and 130 000 years ago, respectively), Ornelas et al. 2016 found the imprint of history to be far less pronounced than for co-occurring plants with wind or gravity dispersed seeds. Rather than echoing variation in their principal host or retaining the genetic structure from prior range contractions, the phylogeographic patterns of *P. schiedeana* lineages were found to align more closely with habitat type. Indeed, the north-south migratory route of Cedar Waxwings may have erased past phylogeographic patterns, divergent levels of variation in nuclear versus plastid genes suggesting gene flow mediated by pollinators may also be involved. By comparing distributions and phylogeographic patterns of mistletoes along the spectrum of specialist to generalist (the genus *Psittacanthus* with ~120 species is an ideal candidate), trade-offs associated with host specificity can be identified (Lara et al. 2009). In addition to improving our understanding of trait-mediated life history evolution, this research would also define those interactions, habitats and taxa most threatened by accelerating rates of climate change.

Mistletoe medicine

One of the most active areas of current mistletoe research (contributing to the spike in research during the past decade, Fig. 1) is natural products medicine, specifically phytochemistry. *Viscum album* has a long history of medicinal and therapeutic use in Europe, with clinical trials confirming anticancer activity for several compounds isolated from its leaves (Lev et al. 2011 and references therein). Mistletoe-derived compounds are widely-used as complementary therapy for several forms of cancer (Marvibaigi et al. 2014), with consistent differences noted for extracts derived from mistletoes infecting different hosts (e.g., Bar-Sela 2011). It is only in the last two decades

that other species of mistletoe have been screened for potential activity (against many kinds of cancer and other diseases like diabetes and hypertension), with pioneering work by Patience Osadebe on African mistletoes (both Viscaceae and Loranthaceae; Osadebe and Ukwueze 2004). More recently, exploratory research has investigated Asian mistletoes, informed by traditional ethnobotanical knowledge (Dashora et al. 2011; Zhao et al. 2012), extending to potential applications of antimicrobial and antiviral compounds for livestock production (Kim et al. 2007) and aquaculture (Park and Choi 2012). Research on the medicinal properties of neotropical mistletoes is in the early stages (Fernández et al. 2003). In addition to high diversities (over 245 mistletoe species are known from Brazil alone; Arruda et al. 2012), many new species are still being discovered, as exemplified by Job Kuijt's (2009) much anticipated monograph on the genus *Psittacanthus* in which 51 new species are described. This exploratory research has the potential to discover a great many novel compounds with therapeutic properties, and will be facilitated by greater collaboration with ethnobotanists and tropical ecologists alike (Coley et al. 2003). Whether advising on those tissues more likely to contain defensive compounds (e.g., growing tips, partly chewed leaves) or which regions to prioritize (e.g., range boundaries of host, mistletoe or both), tropical ecologists have given more thought to determinants of secondary metabolite occurrence than pharmacologists.

Mistletoes as facilitators

The final set of opportunities for research on tropical mistletoes transcends individual interactions and explores the overall influence of these plants on diversity and ecosystem function. Through a series of studies in temperate Australian woodlands, the effects of mistletoe on diversity have been quantified, unravelling the mechanisms underlying their role as ecological keystones (Watson and Herring 2014). Compared with otherwise similar control woodlands, those from which mistletoe was experimentally removed lost more than a third of their woodland resident bird species (Watson and Herring 2012), the community-wide response driven by ground-foraging insectivores (Watson 2015). Rather than direct effects, community structure was influenced by litter-fall, with mistletoe litter increasing the heterogeneity of nutrient inputs (March and Watson 2010) and boosting the availability of litter-dwelling arthropods, including those preferred by ground-feeding insectivores (Razeng and Watson 2012). Many elements of this work have been replicated in other systems, with studies in semi-arid savannah in Zimbabwe finding more litter (Ndagurwa et al. 2013), greater nutrient inputs (Ndagurwa et al. 2014), and more arthropods (Ndagurwa et al. 2015) beneath mistletoe-infected trees. Facilitative effects of mistletoe (and other hemiparasites) are more likely in low productivity systems (e.g., subtropical savannah, tropical dry forests and subalpine zones) where slight increases in

litter quantity and quality can have dramatic effects on bottom-up processes (Watson 2009). In more mesic habitats, these effects are likely to be more subtle, but the research from Australia and Zimbabwe highlight the interactive effects of animal communities on nutrient inputs (Watson 2016), with slight changes in litter-fall potentially mediating changes to animal occurrence and behaviour, setting up positive feedbacks that boost availability of limiting nutrients in forest soils (Janzen 1976; Vitousek 2004) and insectivore diets (Razeng and Watson 2015).

Prospect

In 2001, I noted “Tropical regions, in particular, are underrepresented in the mistletoe literature” but, between now and then, research involving tropical mistletoes has flourished (Fig. 1). By continuing to build on this foundation and occasionally pausing to check whether conceptual frameworks need adjusting or overhauling, tropical mistletoes will continue to inform many aspects of ecological thought and evolutionary theory.

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