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Oecologia

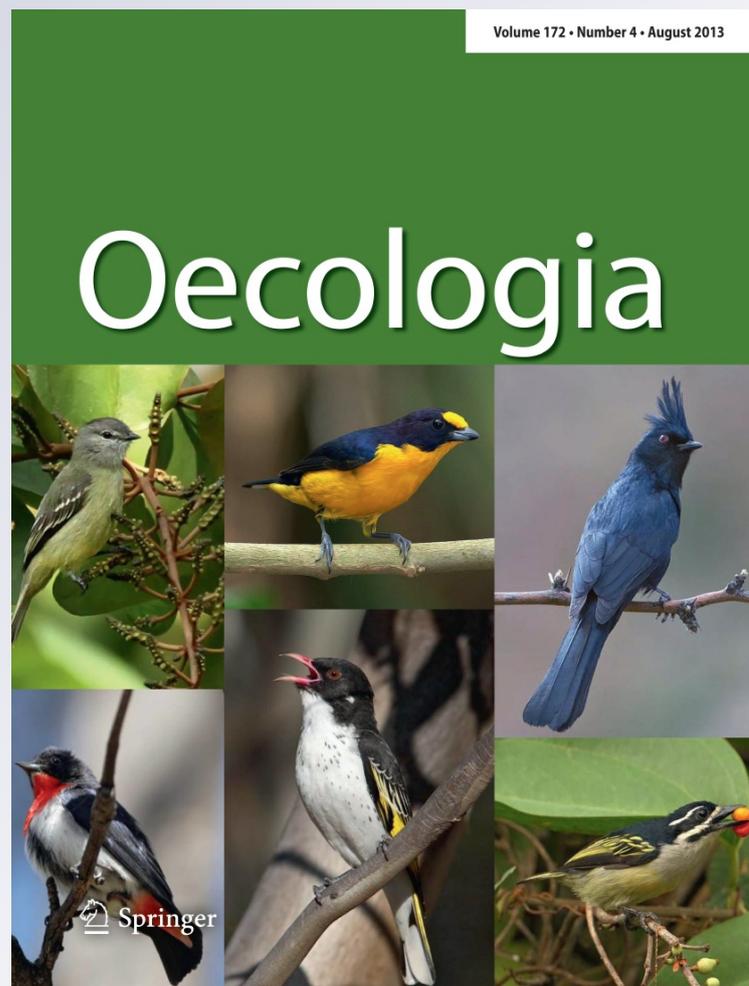
ISSN 0029-8549

Volume 172

Number 4

Oecologia (2013) 172:925-932

DOI 10.1007/s00442-013-2693-9



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Mistletoe specialist frugivores: latterday ‘Johnny Appleseeds’ or self-serving market gardeners?

David M. Watson · John Rawsthorne

Received: 6 March 2013 / Accepted: 21 May 2013 / Published online: 25 June 2013
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Abstract Many plants use birds to disperse their propagules, but mistletoes are especially reliant on their services. As aerial parasites, mistletoe seeds need to be deposited upon branches of suitable hosts, and mistletoe specialist frugivores (from eight different avian families) have long been regarded as their coevolved dispersers. Like the pioneer Johnny ‘Appleseed’ Chapman who established nurseries that helped open up land for settlement, these birds are considered benevolent dispersers of this keystone resource and often invoked as illustrative examples of mutualistic interactions. We have compared recent research on these specialists with studies of other birds with broader diets (generalists) which also disperse mistletoe seed. Rather than mutualists, we suggest that mistletoe specialist frugivores are better considered exploitative, with multiple lineages evolving independently to capitalize on this reliable, nutritious resource. Although mistletoe specialist frugivores are quantitatively important seed dispersers in some regions, their specialized diet restricts them to areas with high mistletoe densities, resulting in contagious dispersal patterns. By intensifying existing infections, mistletoe specialist frugivores increase their own medium-term food security—akin to market gardeners profiting from intensive cultivation. Exploring the ecological and evolutionary implications of this proposition, we evaluate the

consequences of different dispersal patterns on mistletoe fitness and highlight the neglected role of dietary generalists in the stabilization of plant–animal interactions.

Keywords Seed dispersal · Mutualism · Endozoochory · Loranthaceae · Viscaceae

Introduction

As aerial hemiparasites, mistletoes have among the most narrowly defined range of safe sites for recruitment of any plants (Sargent 1994; Aukema and Martínez del Río 2002a), and most rely on frugivorous birds to consume their fleshy fruits and ‘plant’ their seeds upon host branches via defecation or regurgitation (Restrepo et al. 2002). A wide range of birds is known to act as seed dispersers, including mistletoe specialist frugivores—a suite of approximately 100 species that subsist almost exclusively upon mistletoe fruit (Reid 1991; Watson 2004). This specificity—both in dispersal requirements of the plant and dietary breadth of its dispersers—is more pronounced than in most seed dispersal systems, and interactions between mistletoes and their attendant birds are regularly invoked as exemplars of tightly coevolved mutualisms (Howe and Estabrook 1977; Carlo et al. 2003; Montaña-Centellas 2013).

Here, we evaluate this set of interactions from the mistletoe’s perspective, synthesizing recent empirical research and challenging the widely held contention that the presence and repeated evolution of mistletoe specialists is necessarily beneficial for mistletoes. We summarize global occurrence patterns of mistletoe specialists, revealing that they occupy a fraction of the distributional extent of mistletoes. Having considered the components of dispersal success for mistletoes, we synthesize findings from two

Communicated by Carlos L. Ballare.

D. M. Watson (✉) · J. Rawsthorne
Institute for Land, Water and Society, Charles Sturt University,
PO Box 789, Albury, NSW 2640, Australia
e-mail: dwatson@csu.edu.au

J. Rawsthorne
Research Institute for Environment and Livelihoods, Charles
Darwin University, Darwin, NT 0909, Australia

well-studied systems, refuting the presumption that specialists provide superior dispersal services. Mistletoe specialist frugivores might be better considered conditional parasites (Thomson 2003), their morphological adaptations and foraging behaviors enabling them to exploit this high-quality food source and inhabit habitats and regions otherwise devoid of fleshy fruit. Having challenged the prevailing view of mistletoe dispersal, we emphasize the need for dedicated studies of seed dispersal effectiveness, post-dispersal seed fate and the demographic consequences of continual reinfection for both mistletoe and host populations. We conclude by considering the role of specialists more generally, noting the growing appreciation of mutualisms as reciprocally exploitative and highlighting the neglected role of generalist species in the evolution and maintenance of plant–animal interactions.

Mistletoe specialist frugivores

Mistletoe specialists have evolved independently in eight avian families, with representatives in the Lybiidae, Cotinidae, Tityridae, Tyrannidae, Meliphagidae, Ptilonotidae, Nectariniidae (Dicaeinae) and Fringillidae (Euphoniinae) (Reid 1991; Restrepo et al. 2002; Watson 2004; Fig. 1). That this extreme dietary specialization has evolved in non-passerines and repeatedly in sub-oscine and oscine passerines suggests that there are particular characteristics of aerial mistletoes that encourage this extreme specialization. These traits include difficulty-to-process sticky fruits (Reid 1991) of high nutritional quality (Restrepo 1987); complementary phenology, with peak fruit availability often coinciding with periods of regional fruit scarcity (Reid 1986; Watson 2001), and extended phenology, with fruit available for several seasons, occasionally year-round (Restrepo 1987; Barea and Watson 2007). Likewise, these birds tend to exhibit convergent behavioral and morphological adaptations, including large gapes (relative to body size), greatly simplified gastrointestinal tracts and rapid gut-passage rates (Walsberg 1975; Richardson and Wooller 1988; Murphy et al. 1993). Mistletoe fruit specialization by birds results in some of the most narrow dietary niches observed amongst vertebrates (Rawsthorne et al. 2012), with the fruits of one or two mistletoe species comprising up to 90 % of some species' diets (Walsberg 1975; Reid 1989; Sargent 1994). The high lipid and protein content of mistletoe fruits relative to other fruits allows birds to subsist entirely on these fruits, and such is the quality and completeness of this diet that mistletoe specialist birds characteristically feed mistletoe fruits to their nestlings (Walsberg 1977; Snow 1981).

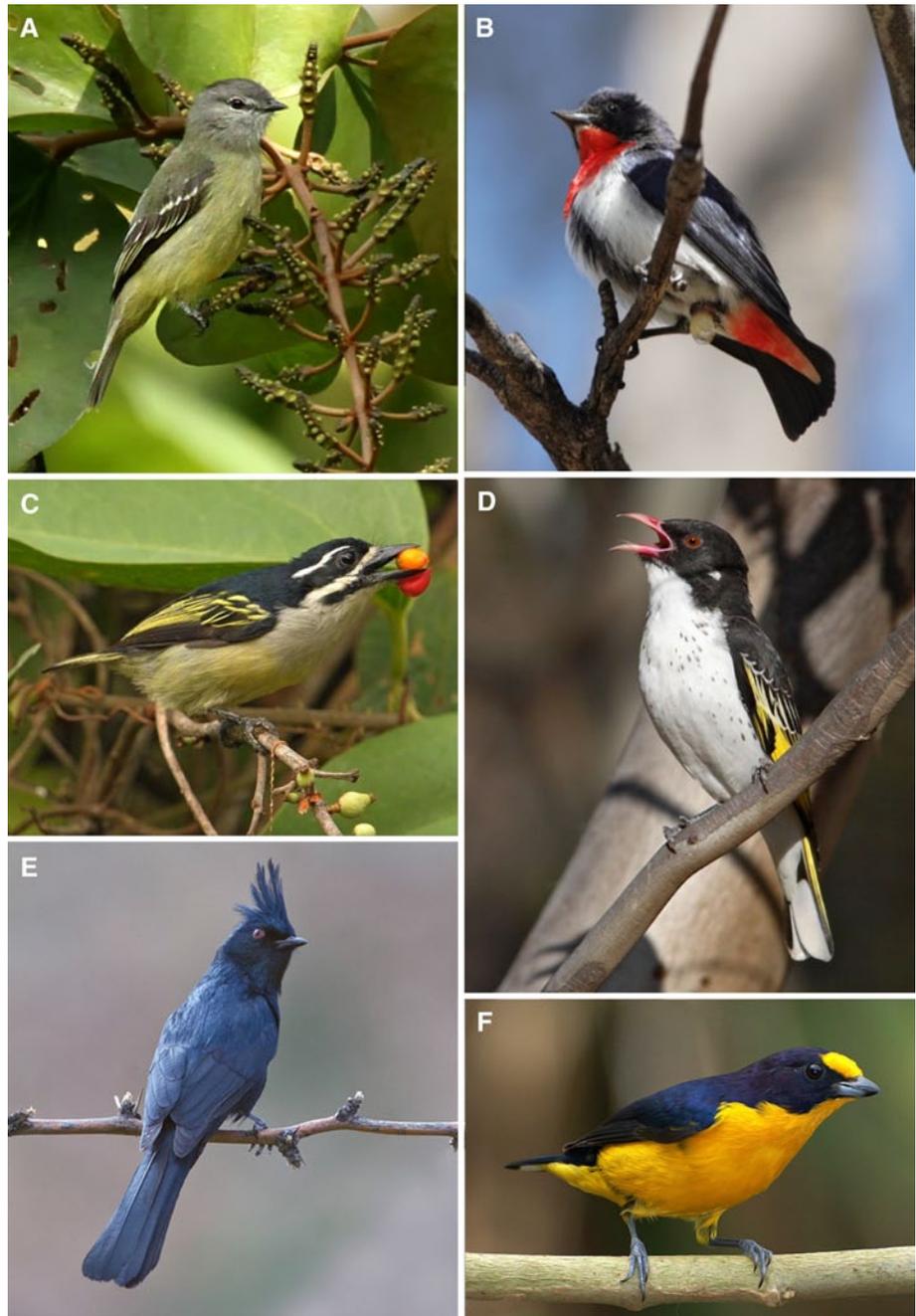
Although mistletoe specialists occur throughout mainland Australia (*Dicaeum hirundinaceum*, *Grantiella picta*) and South America (*Euphonia* spp, *Zimmerius* spp.,

Tyrannulus elatus, *Phylomyias fasciatus*, *Zaratornis stresemanni*, *Phibalura flavirostris*), their occurrence elsewhere is less uniform, and the combined global distribution of these birds is far more restricted than their food plants, especially in the Northern Hemisphere (Fig. 1). Except for several euphonias and two tyrannids in Mesoamerica (restricted primarily to tropical forests), the only specialist in North America (*Phainopepla nitens*) is restricted to the semi-arid woodlands in southwest USA and northern Mexico. In Asia, the sole group of mistletoe specialist frugivores (flowerpeckers in the genera *Dicaeum* and *Prionichilus*) is restricted to tropical forests in southern Asia, and the only African specialists (*Pogoniulus* spp.) are restricted to forests and woodlands in central and southern Africa. Thus, for all of Europe, northern and central Asia, northern Africa and the Middle East, New Zealand, Madagascar and many oceanic islands (home to hundreds of mistletoe species), mistletoes rely exclusively on non-specialist birds for seed dispersal (Fig. 2). Although other bird species (including *Philepitta castanea*, *Mimus thenca*, *Turdus viscivorus*, *Sylvia atricapilla* and *Ptilonotus caudatus*) and one marsupial (*Dromiciops gliroides*) may defend fruiting mistletoe plants and rely on mistletoe fruit seasonally, their diets are more catholic, and we do not consider them to be mistletoe specialists.

Dispersal quality: from the mistletoe's perspective

Having established that mistletoe plants do not require specialist dispersers, in those areas where mistletoe specialist frugivores occur, how do the dispersal services they offer compare with those provided by other, more generalist species? Schupp (1993) distinguished four components of seed disperser effectiveness: frequency of visitation, number of seeds dispersed per visit, quality of seed treatment and quality of seed deposition. While these considerations apply to all animal-dispersed plants, the parasitic habit of mistletoes adds an extra dimension to measures of success. In parasitological parlance, there is a clear distinction between reinfection and transmission (Lewis et al. 2002), a distinction just as applicable and relevant to parasitic plant recruitment. From a strict parasitological perspective, if the seed is not transported beyond the infected host, the mistletoe has not successfully dispersed. Unlike nematodes and other parasitic animals which may preferentially select already infected hosts (to maximize the likelihood of finding a mate; Lewis et al. 2002), parasitic plants (and some plant viruses; Ingwell et al. 2012) often show the reverse pattern. Those plants hosting few or no existing infections are considered to be optimal (Martínez del Rio et al. 1996; Watson 2009)—maximizing the likelihood of recruitment and subsequent transmission by minimizing

Fig. 1 Representatives from six of the eight lineages considered to be mistletoe specialist frugivores. **a** *Tyrannulus elatus*, Tyrannidae (Roger Ahlman), **b** *Dicaeum hirundinaceum*, Nectariniidae (Peter Menkhorst), **c** *Pogoniulus bilineatus*, Lybiidae (Krzysztof Blachowiak), **d** *Grantiella picta*, Meliphagidae (Chris Tzaros), **e** *Phainopepla nitens*, Ptilonotidae (Elaine R Wilson), **f** *Euphonia violacea*, Fringillidae (Dario Sanches). All photographs are used with permission



density-dependent competition with existing mistletoes. Thus, in evaluating the effectiveness of mistletoe dispersers, we consider moving seeds to a suitable host lacking mistletoe to be more effective than seeds being dispersed from one infected host to another (Sargent 1994), effecting greater changes to prevalence, range size and, ultimately, population viability.

Applying these concepts of dispersal success to mistletoes, we distinguish four patterns: (1) contagious dispersal, where most seeds are deposited very close to adult mistletoes (yielding ‘infection centers’ in original hosts or

adjacent conspecifics); (2) directed dispersal, where seeds are preferentially deposited in favorable micro-sites for seedling establishment and recruitment (i.e., in suitable but uninfected hosts); (3) heterogeneous dispersal, where seeds are dispersed through the landscape independently of host quality (sensu Watson 2009) or the presence of existing mistletoes; (4) long-distance dispersal, where propagules are transported beyond the population enabling establishment of new populations or expansion of range boundaries.

Reviewing empirical studies of mistletoe specialists to determine which of these four patterns is more common,

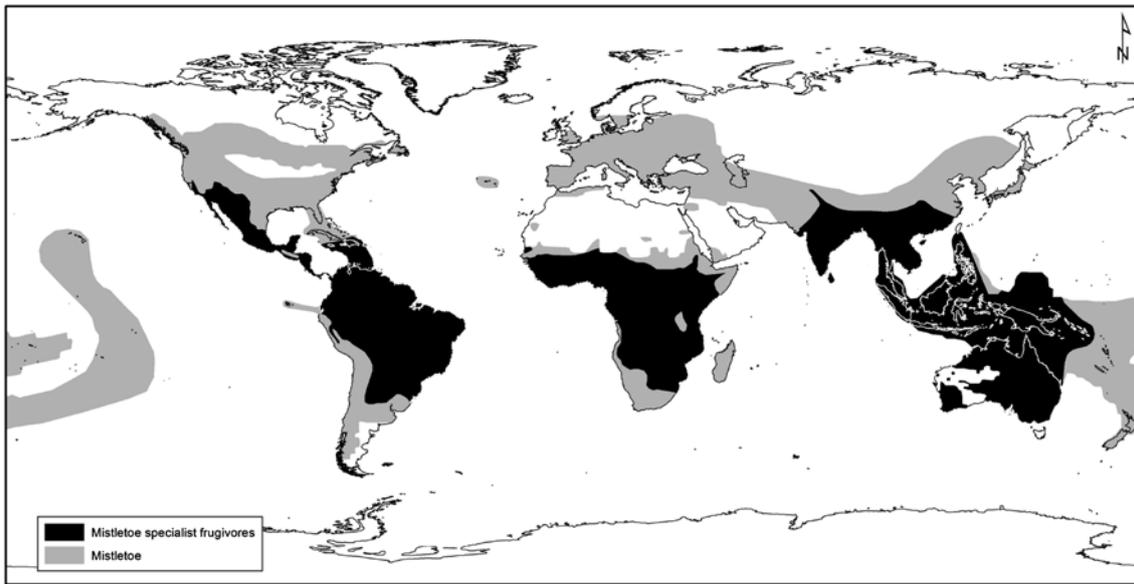


Fig. 2 Map of the global distribution of mistletoes (Loranthaceae and Viscaceae) in *gray*, overlain by the combined distributional extent of mistletoe specialist frugivores in *black*. While the two groups broadly overlap in continental landmasses of the Southern Hemi-

sphere, few specialists occur on islands or in the Northern Hemisphere continents, where most mistletoes rely exclusively on dietary generalists for seed dispersal (after Reid 1991; Watson 2004)

we found conflicting interpretations of what constitutes successful dispersal. Numerous researchers maintain that contagious dispersal represents ‘high-quality’ dispersal (e.g., Aukema 2003; Montaña-Centellas 2013), yet parallel research has demonstrated lower growth rates and decreased survivorship (of both individual mistletoes and host plants) with increased mistletoe densities (Reid et al. 1994; Bowie and Ward 2004; Shaw et al. 2004). Furthermore, directed dispersal is suggested to occur in mistletoes when birds are forced, by the presence of the sticky viscid coating of mistletoe seeds, to wipe those seeds against their perch, typically a slender branch suitable for mistletoe establishment (Reid 1991). Yet, as these purported safe sites are typically concentrated within the canopies of already infected hosts (Martínez del Rio et al. 1996; Aukema 2003), these seeds have actually undergone contagious dispersal, increasing the parasite load of a small number of hosts (Aukema and Martínez del Rio 2002b). Long-distance dispersal is rarely reported and generally evidenced only by extra-limital individual plants (Kuijt 1964; Watson 2011), with no direct way of establishing vector identity.

Case study 1: semi-arid woodlands of southern Australia

As part of our research program in temperate Australian mistletoe systems, we have undertaken dedicated studies on both mistletoe specialist frugivores (*Dicaeum*

hirundinaceum and *Grantiella picta*; Fig. 1) and one widespread generalist forager that regularly consumes mistletoe fruit as part of a broader diet (*Acanthagenys rufogularis*). In the first study of its kind, Rawsthorne et al. (2012) determined that *D. hirundinaceum* disperses most mistletoe seeds to stands of hosts which are already infected. By quantifying bird presence (using vocalizations) and actual seed dispersal (via locating defecated mistletoe seeds), we demonstrated that mistletoebirds foraged exclusively within infected areas. We found no evidence for birds visiting or dispersing seeds to areas lacking mistletoe and, using likelihood analysis, demonstrated that the probability of transmission to uninfected sites was less than 5%. In a matching study, the movements of adult *A. rufogularis* individuals were quantified using radio-telemetry and their habitat use compared with mistletoe occurrence. While these birds were regularly consuming mistletoe fruit and using infected stands as breeding territories, non-breeding individuals that consumed mistletoe fruits also foraged on nectar and insects well beyond the boundaries of the mistletoe infection (Rawsthorne et al. 2011). By combining gut passage rate data with recorded movements, we predicted that some individual birds transported more than 25% of ingested seeds at least 500 m from the source and away from existing mistletoe infections, compared with 3.3% for *D. hirundinaceum* (Ward and Paton 2007). Finally, Barea and Watson (2007) evaluated the reproductive ecology and habitat use of Australia’s other mistletoe specialist, *G. picta*. In addition to timing egg-laying so that

the nestling and fledging period coincided with peak fruit availability, individual pairs selected those areas of woodland with maximum mistletoe densities for breeding territories (Barea 2008). Although breeding birds undertook regular movements when provisioning nestlings, all foraging occurred within stands of high mistletoe density. Combining movement data from radio-tracked individuals with seed retention times (mean of 24 min), a highly skewed dispersal curve resulted—67 % of seeds were dispersed within 100 m of the origin and 5.6 % beyond 500 m (Barea 2008).

Integrating these findings, we find clear evidence that generalists and specialists provide different dispersal services for mistletoes. By restricting their movements to infected areas and not venturing into uninfected areas while fruit was available (and seeds were viable), both specialists effected contagious dispersal. In contrast, the larger-bodied generalist routinely foraged within and beyond infected areas which, coupled with its longer seed retention time (mean of 35 min but with more than one-third of seeds retained for ≥ 45 min compared with a mean of 14 min for *D. hirundinaceum*; Murphy et al. 1993), increased the likelihood of depositing seeds beyond infected stands—i.e. heterogeneous dispersal. Although these spatial differences may be offset by different perching preferences and seed treatment (Murphy et al. 1993), Reid (1989) found that the generalist *A. rufogularis* deposited seeds by haphazard defecation to a set of smaller branch sizes than those accessed by the specialist *D. hirundinaceum* and that the full range of branch sizes suitable for mistletoe establishment was only reached via complementary dispersal by both species.

Case study 2: tropical rainforests of Mesoamerica

The closed-canopy tropical forests of Mesoamerica represent a completely different environment than that described above, with less pronounced seasonality and abundant fleshy-fruited plants supporting diverse assemblages of resident frugivores. The two groups of mistletoe specialist frugivores occurring in this system depend on different groups of mistletoe, with *Euphonia* spp. favoring Viscaceae species (especially *Phoradendron* spp.; Carlo et al. 2003), whereas *Zimmerius vilissimus* and *Tyrannulus elatus* (both Tyrannidae) depend almost exclusively on Loranthaceous mistletoes (Restrepo 1987; Watson 2013). Rather than focusing on individual species, research in these forests has encompassed the full assemblage of species visiting fruiting mistletoe plants, enabling the relative contributions of generalists and specialists to be readily compared. In Sargent's (1994) comprehensive study of a montane forest in Costa Rica, 60 % of visits to *Struthanthus oerstedii* and 71 % of visits to *Orycanthus spicatus* were by the specialist *Z. vilissimus*, while Watson's (2013) work in lowland

forest in Panama found 73 % of *O. occidentalis* fruits was removed by the two specialist flycatchers. The remaining 27–40 % was taken by generalist frugivores and opportunistic visits by dietary generalists that consume both insects and fruit.

The dense canopy of these forests precludes the spatial approach applied in case study 1, but components of dispersal quality can be inferred from dietary breadth and post-consumption behavior relative to mistletoe density. Whereas mistletoe fruit (Loranthaceae) accounted for 77 % of the recorded diet of *Z. vilissimus*, more than 75 % of the dietary records for two generalists visiting the same plants (*Vireo* spp.) related to non-mistletoe resources, of which 45 % comprised insects gleaned from the canopy (Sargent 1994). More detailed research on viscaceous mistletoes revealed the specialist *E. elegantissima* (81 % of feeding records comprised mistletoe fruit) spent more time foraging in heavily infected hosts and stands, perching primarily in mistletoe plants. While most seeds retained in the canopy were deposited in mistletoe clumps, 50 % of defecated seeds fell to the ground. The co-occurring *Chlophonia callophrys* accounted for 37 % of visits to fruiting plants, but mistletoe represented only 38 % of their diet. This dietary breadth coupled with the longer gut passage rate of this species resulted in an estimated 50 % of seeds being dispersed beyond heavily infected stands, rising to 90 % in areas with lower mistletoe density.

Specialists versus generalists as agents of successful mistletoe dispersal

The parallels between these two systems are striking, especially since they involve distinct assemblages of mistletoes and birds within completely different biomes. In both systems, mistletoe specialist frugivores represent the principal consumers of mistletoe seeds, but data on all five species suggest that contagious dispersal is the typical outcome.

Consistent findings have been reported from other systems in which generalists and mistletoe specialists co-occur, with characteristically superior seed dispersal services provided by generalists. Carlo and Aukema (2005) reported high-quality dispersal services provided by two generalist frugivores (Thraupinae) in Puerto Rico which defecated seeds on branches of comparable thickness to those used by co-occurring specialist euphonias. Moreover, since these tanagers also consumed fruits of one of the principal mistletoe hosts, they regularly transported mistletoe seeds to uninfected hosts (i.e., directed dispersal). In southwest China, Luo et al. (under review) found specialist *Dicaeum concolor* preferentially visited trees infected with *Dendrophthoe pentandra* (Loranthaceae), achieving dispersal distances of <150 m, while the generalist *Pycnonotus*

jocosus consistently flew further than 200 m and was recorded more frequently in uninfected trees. In semi-arid woodlands in Arizona, generalist solitaires (*Myadestes townsendi*) visited both infected and uninfected junipers (van Ommeren and Whitham 2002), making directed dispersal far more likely than for the specialist (*Phainopepla nitens*; Fig. 1) which effects contagious dispersal by defending heavily infected hosts (Aukema and Martínez del Río 2002b, but see also Larson 1996).

Although comparatively understudied and, we posit, overlooked, generalist frugivores and insectivores which regularly consume mistletoe fruit consistently provide high-quality seed dispersal, both in regions where they are the sole mistletoe dispersal agents, but also where they co-occur with mistletoe specialists. Dietary generalists often take a significant proportion of all mistletoe fruits (Reid 1989; Larson 1996; Montaña-Centellas 2013) and, even during peak mistletoe fruiting, these birds often forage on other food sources (Jordano et al. 2007; Carlo and Aukema 2005; Watson 2013), thereby regularly transporting mistletoe seeds beyond existing infections (Green et al. 2009, Rawsthorne et al. 2011). Rather than being necessarily deleterious, the longer seed retention times of generalists can yield improved germination and establishment of mistletoe seeds (Soto-Gamboa and Bozinovic 2002). As first contended 30 years ago by Godschalk (1983), it is this combination of varied diet and longer seed retention time of the generalist that entrains heterogeneous dispersal to uninfected hosts and stands.

‘Johnny Appleseed’ reconsidered

While mistletoe frugivory has long exemplified mutually beneficial coevolution (e.g., Howe and Estabrook 1977), Reid (1991), in his review of current understanding of mistletoe specialists, was more cautious in this categorization. Since then, our knowledge of these birds has expanded greatly, and the overall field of coevolution has matured and diversified. Hence, rather than the stereotypically harmonious ideal, an emerging view of coevolution is that of ‘reciprocally exploitative’ interactions, with both parties engaged in an antagonistic struggle comparable to host–parasite dynamics (Thomson 2003). Certainly, mistletoe specialist birds are dependent on mistletoes, and these specialists typically have evolved various morphological traits, such as modified gastrointestinal tracts and large gapes relative to bill size, which make them efficient and effective seed disseminators (Walsberg 1975; Richardson and Wooller 1988; Murphy et al. 1993). But, we have demonstrated that while mistletoes clearly depend on small-bodied aerial dispersers, they are not exclusively

dependent on specialists. Put simply, mistletoe specialists need mistletoe, but mistletoes do not need mistletoe specialists.

We suggest that those mistletoe traits (viscin-coated seeds, complementary and extended phonologies, inter alia) which tend to foster specialization need not have evolved in response to specialists but, rather, evolved as a necessary part of their parasitic habit prior to exploitation by specialists. A parallel example involves another group of plants that rely on birds to disperse their seeds—strangler figs. Distributed throughout tropical forests, a wide range of birds and arboreal mammals consume the fleshy fruits, but only one species can be considered a specialist—Pesquet’s parrot *Psittichas fulgidus*, endemic to New Guinea (Mack and Wright 1998). Rather than a specialized disperser being the necessary precursor to the hemi-epiphytic growth habit, by ‘strangling’ canopy emergent trees, these figs have evolved a key innovation allowing them to become competitively dominant in closed-canopy forests. With its powerful beak and muscular gizzard, *P. fulgidus* is far less likely to effect successful dispersal than co-occurring species—they exploit figs as a resource but do not necessarily ensure their continued supply.

Rather than being destructively exploitative or mutually beneficial, we suggest that mistletoe specialist frugivores inhabit a middle ground, maintaining reliable supplies of their favored food plants through the process of ‘habitat shaping’ (sensu Herrera 1985). In western Europe, extensive stands of fruiting trees occur along migratory routes of frugivorous birds, and these ‘bird orchards’ are considered to have existed for millennia, planted, visited and maintained by generations of birds during seasonal migration (Snow and Snow 1988, see also Jordano et al. 2007). Given the parasitic habit of mistletoe, however, more is not necessarily better, with reduced growth rates and survivorship of host plants associated with increased mistletoe numbers. Effects on host populations will vary with host specificity of mistletoes, relative abundance of hosts and abundance of natural enemies of mistletoe, but predominantly contagious dispersal is likely to have deleterious effects on populations of hosts and, thereby, mistletoe, in many systems. So, rather than the ‘Johnny Appleseed’ analogy in which mistletoe-specialist frugivores are benevolent pioneers spreading mistletoe and providing new opportunities for others, we suggest a more appropriate analogy is that of a market gardener. By consuming most of the fruit and staying close to home, these specialized consumers are exploiting this nutritious and reliable food source, concentrating available fruit resources into more defensible resources for their own direct benefit (Snow and Snow 1988).

Unanswered questions and prospect

The effect of differences in dispersal quality for mistletoes and their hosts have not been comprehensively quantified, leaving many questions about the role of specialist and generalist dispersers unanswered. While several studies have estimated where specialist consumers disperse seeds, only one study has asked the opposite question (Rawsthorne et al. 2012), and determining where seeds are NOT taken is critical to understanding the medium and longer term significance of different seed shadows. Given the status of mistletoe as a keystone resource in many terrestrial ecosystems (Watson and Herring 2012), occurrence patterns of mistletoe are likely to affect a wide range of species and ecological processes, extending well beyond frugivores and host plants (Watson 2001). Mistletoe specialist frugivores and generalists exhibit complementary distributions in some island pairs in the Philippines and Greater Antilles, and these archipelagos represent ideal systems to compare the effectiveness of specialist and generalist dispersers using Schupp's (1993) explicit criteria. In addition to distinguishing the effects of disperser identity on mistletoe and host populations, these comparisons would reveal any interactions between seed disperser identity and host range in mistletoes (Aukema and Martínez del Río 2002b; Shaw et al. 2004). While we have emphasized the importance of dispersal to uninfected but otherwise suitable hosts, we recognize that farther is not necessarily better. Several studies (see Rödl and Ward 2002) have documented declining establishment success of mistletoes with increasing distance from the parent plant, whereby mistletoe seeds will only infect hosts growing within 30–50 km. Inoculation experiments would enable spatial determinants of establishment success to be uncoupled from site-specific components of host quality, revealing whether differential establishment can compensate for initial differences in seed dispersal. Finally, while birds have been implicated in the diversification of mistletoes (Restrepo et al. 2002), the origin and diversification of mistletoe specialist frugivores has not been considered. With five of the eight avian lineages, as well as a relictual marsupial that acts as the sole disperser of a montane mistletoe (Amico and Aizen 2000), the forests of South America represent the obvious starting place.

Rather than a unique set of interactions associated with an idiosyncratic group of parasitic plants, we suggest that the exploitative nature of specialists (and the overlooked influence of co-occurring generalists) is more widespread, with many other 'text-book' examples of plant–animal partnerships awaiting critical scrutiny. The story of the night-flowering cactus and long-nosed bat is now known to be more complicated, with the discovery that a co-occurring insectivorous bat also visits the flowers and acts as a more

effective pollinator (Frick et al. 2013). Whether in the pollination or seed dispersal literature, specialists have attracted disproportionate attention, while the identity, let alone the ecological role, of generalists is typically unknown. We suggest that as well as conferring greater versatility, the breadth of resources used by generalists may help maintain many ecological interactions (see Bascompte and Jordano 2007), moderating the escalating 'arms-race' dynamic that can destabilize pair-wise interactions if left unchecked.

Acknowledgments We are grateful to Tomás Carlo and Patrick Kavanagh for their insightful comments on an earlier version of this manuscript, and we thank Laurence Barea and Karolina Petrovic for their contributions to initial discussions. DMW received support from the Australian Research Council (DP0449417) and Charles Sturt University.

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