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Review

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Fleshing out facilitation – reframing interaction networks beyond top-down versus bottom-up

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Summary

Rather than direct plant–plant interactions, research on the community-scale influence of mistletoes reveals hitherto unappreciated roles of animals in mediating facilitation. Lacking roots and reliant upon animal vectors, mistletoes represent model systems with which to understand mechanisms underlying interaction networks. In addition to direct effects on nutrient dynamics via enriched litter-fall, mistletoes are visited by pollinators, seed dispersers and natural enemies, complementing increased heterogeneity in nutrient returns reallocated from infected hosts with increased external inputs. These amplified bottom-up effects are coupled with top-down influences of insectivores attracted to infected hosts and stands by increased availability of favoured prey. Simultaneously influencing nutrient dynamics and plant–plant interactions from below and above, visiting animals help explain variation in the context dependence of facilitation.

I. Introduction

Defined as mutually beneficial interactions between organisms, facilitation is emerging as a unifying theme in ecology (Watson & Herring, 2014; Michalet & Pugnaire, 2016; M. S. Thomsen *et al.*, unplublished), providing a common framework within which to explore community function. Originating in plant ecology as a counterpoint to competition (Grime, 1977), facilitation is typically invoked for two classes of interaction – resource enhancement and stress reduction (Callaway, 2007). Building on a foundation of empirical research documenting variation in facilitative relationships across systems (Callaway, 1995; Michalet & Pugnaire, 2016), a current research focus is to identify associated functional traits (Bishop *et al.*, 2013; Butterfield & Callaway, 2013). Although trait-based facilitation is apparent in some biotic interactions (e.g. shrub/nurse plant and protection from herbivory), trait-based predictions presently lack the requisite reliability to enable generalized determinants of facilitation to be compared across systems (Butterfield & Callaway, 2013) and the context dependence of facilitation remains poorly understood.

Whereas marine ecologists consider facilitative relationships as networks involving a range of organisms (including microbial communities, plants, and colonial, sessile and free-swimming animals; Stachowicz, 2001; Bishop *et al.*, 2013; Thomsen & Wernberg, 2014; Watson & Herring, 2014), terrestrial ecologists characteristically study facilitation as pair-wise relationships between plants (Callaway, 1995; Verdú & Valiente-Banuet, 2008; but see van der Putten, 2009). The shrub/nurse plant literature contains numerous examples of plant–animal interactions (e.g. spiky shrubs deterring herbivores from more palatable understorey plants (Rohner & Ward, 1997); shrubs promoting invasion of bird-dispersed plants (Milton *et al.*, 2007)), but these relationships are treated as nested assemblies within plant–plant associations rather than interacting elements (Verdú & Valiente-Banuet, 2008; but see Carlo & Tewksbury, 2014). Having reviewed 53 shrub–plant–animal and shrub–animal–plant facilitations in 79 published studies, Lortie *et al.* (2016) determined that 'None of these studies explored reciprocal plant–animal interactions, used a network approach to the study [sic] facilitation, estimated costs to benefactors nor contrasted interaction strengths'.

Parasitic plants necessarily rely on other plants for their livelihood, with many groups dependent on animal vectors to transport their pollen and seeds. The status of parasitic plants as facilitators has emerged over the past decade (Press & Phoenix, 2005; Quested, 2008; Watson, 2009a), empirical research on multiple groups and biomes yielding convergent results relating to two main processes. First, parasitic plants alter competitive interactions between host and nonhost species, boosting alpha diversity by tipping the balance in favour of nonhosts and steering plant communities away from monodominance (Press & Phoenix, 2005; Mudrák & Lepš, 2010). As well as explaining observed patterns of host preference and distribution patterns of parasites and hosts (Watson, 2009b; and references therein), this mechanism has inspired the use of parasitic plants in restoration (Ameloot *et al.*, 2008). Second, parasitic plants concentrate resources, reallocating nutrients from relatively long-lived hosts and shedding them in discrete patches, increasing heterogeneity of nutrient availability (Fisher *et al.*, 2013), thereby boosting diversity by promoting local coexistence. Much of this research involves root-parasitic plants and, although root-zone effects are probably critical in regulating nutrient availability and community structure (Bardgett *et al.*, 2006), the influence of belowground processes in contributing to aboveground patterns is rarely quantified. Likewise, effects of interactions with animals are rarely considered (Watson, 2009a), despite known roles as pollinators, seed dispersers, herbivores and litter-dependent detritivores (above- and belowground). Mistletoes are a diverse and well-studied group of hemiparasites with a global distribution (Watson, 2001), their rootless habit enabling direct effects (via litter-fall) and indirect effects (mediated via visiting animals) to be uncoupled and quantified, revealing the identity and magnitude of pathways underlying their role as facilitators. Here, I review recent research findings on the role of mistletoe in divergent ecosystems, demonstrating that both bottom-up and top-down roles of visiting animals underlie mistletoe's status as a facilitator. I consider the wider ramifications of this refined understanding, ask whether animals are critical components of facilitation cascades in general, and articulate the research needed to answer this open question.

II. Case study 1 – Mediterranean pine forest

In a series of studies conducted in a Mediterranean pine forest in southeastern Spain, Mellado *et al.* (2016) evaluated the direct and indirect effects of mistletoe infection (after March & Watson, 2007, 2010). In this system, mistletoe *Viscum album austriacum* (Wiesb.) Vollmann (Viscaceae) relies on pines as principal hosts, with seeds dispersed by a range of fruit-eating birds (including residents and seasonal migrants). In addition to mistletoes, these birds consume the fruits of shrub species that dominate the understorey of these extensive forests. In addition to estimating how mistletoe occurrence affects seed dispersal by comparing overall seed rain beneath infected and uninfected pines, the effect of mistletoe on nutrient inputs was quantified (Mellado *et al.*, 2016).

Mistletoe infection affected organic inputs to the soil in three complementary ways. Infected pine trees grew more slowly than uninfected trees, shedding proportionally less litter (mean of 1.33 times less biomass of shed needles than uninfected trees). Given the high turnover of enriched tissues of the mistletoe, however, overall litter-fall of infected hosts increased both in quantity and quality, mistletoe-derived material accounting for more than a third of litter collected. This is reflected in a 1.38-fold increase in total organic carbon in the top 100 mm of soil beneath parasitized trees. Bird excrement was also quantified, with $> 15\times$ greater biomass recovered from litter traps beneath parasitized hosts (Mellado *et al.*, 2016). Although soil moisture, pH and total nitrogen (N) were comparable, phosphorus (P) and potassium (K) availability was significantly greater beneath infected trees, with mean microbial biomass *c.* 1.2 times greater. Finally, seed rain differed dramatically – in addition to receiving an average of 4.5 g m^{-2} of mistletoe seeds, parasitized trees received 2.98 g m^{-2} of understory seeds compared with 0.2 g m^{-2} beneath unparasitized pines.

As the only study to quantify seed rain of co-occurring species and distinguish direct from indirect nutrient inputs, this work demonstrates that the disproportionate influence of these plants extends well beyond pair-wise host–parasite dynamics. Moreover, with effects of mistletoe observable beneath long-dead parasitized pines, the patterns described in this work extend beyond short-term fluxes, driving persistent differences in heterotrophic microbial communities belowground. When these ecosystem-level findings are integrated with spatial and temporal patterns of seed dispersal (Mellado & Zamora, 2014, 2015), mistletoe distribution provides the context explaining broad-based variation in forest composition within this system, shifting successional dynamics to occupy a different stable state.

III. Case study 2 – semi-arid tropical savannah

Working across several sites in southeastern Zimbawe, Ndagurwa and colleagues have undertaken a comprehensive series of studies to evaluate how mistletoe influences ecosystem properties in semi-arid savanna. As with other tropical habitats, this system is characterized by multiple mistletoe species, including representatives of the two most diverse families (Loranthaceae and Viscaceae). Initial research (Ndagurwa *et al.*, 2012) demonstrated that larger individuals of four *Acacia* species were more likely to be parasitized for two of three mistletoes studied, consistent with studies elsewhere demonstrating the link between mistletoe occurrence and perching preferences of seed-dispersing birds (Aukema & Martínez del Rio, 2002; Roxburgh & Nicolson, 2008). The ramifications of this patchy distribution for nutrient dynamics were studied in terms of litter-fall (after March & Watson, 2007, 2010). Although the litter of two mistletoe species was lower in N than that of the host (as a result of both initial differences in foliar N and far greater resorption efficiency in the host), mistletoe infection resulted in 1.4–2.8 times greater litter returns, increasing N returns by a factor of 1.4–2.0 (Ndagurwa *et al.*, 2013). Soil beneath infected trees had consistently higher concentrations of N, P and calcium (Ca) and, although not measured, the authors noted 'numerous bird droppings beneath mistletoe-infected trees were observed' (Ndagurwa *et al.*, 2013). Using litterbags containing litter of one of three mistletoe species and their *Acacia* host, mistletoe litter was found to have a characteristically lower lignin concentration and lower lignin : N ratio, resulting in faster decomposition rates (a mean decay constant of 0.79 yr^{-1} compared with 0.63 yr^{-1} for *Acacia* litter; Ndagurwa *et al.*, 2014a). Rather than this just relating to *Acacia* hosts, parallel research on four other tree species (infected by five mistletoe species) yielded consistent findings (Ndagurwa *et al.*, 2014b), mistletoe infection leading to elevations in soil nutrient concentrations ranging from 2.25× for N, 2.28× for P and 3.78× for magnesium (Mg) up to 8.55× for Ca and 39× for K (Muvengwi *et al.*, 2015). The final element of this work evaluated the effect of these altered nutrient inputs on litter-dwelling arthropods (Ndagurwa *et al.*, 2014c). Despite having significantly drier soils, infected trees consistently supported more diverse arthropod assemblages and, for two of the three mistletoe species, greater abundances. Indeed, seven of the 17 arthropods studied were recorded only beneath infected hosts, this association probably reflecting structural differences in the forest floor, areas beneath infected trees having deeper, more persistent and more structurally complex litter beds with greater cover of understorey vegetation. Different responses were noted with termites, which were more abundant beneath uninfected trees, and this was interpreted to reflect both avoidance of predators favouring deeper litter beds beneath hosts and higher soil moisture beneath uninfected hosts better suited to gallery and nest construction (Ndagurwa *et al.*, 2014c). Given the influence of termites on nutrient dynamics and soil properties, these patterns probably have far-reaching consequences (Schuurman, 2005).

IV. Mistletoes as facilitators – top-down, bottom-up or both?

Despite relating to divergent ecosystems involving completely different sets of host trees, mistletoes and animal associates, the findings from these two sets of studies exhibit remarkable convergence with one another, and with the findings of studies from elsewhere. The original research on the contribution of mistletoe to nutrient dynamics was in temperate woodlands in southern Australia (March & Watson, 2007, 2010). Despite being minor constituents of the woodland in terms of standing biomass, leaf longevity trials demonstrated that the high turnover of leaves contributed large volumes of enriched litter, often exceeding the contribution of host trees. Beneath infected trees, increased availability of all 13 elements measured was recorded, along with deeper, more complex litter beds and increased diversity of understorey plants. Other research in coniferous forests of south-western USA found dwarf mistletoe infection led to profound belowground changes, with infected pinyon (*Pinus edulis*) hosts characterized by increased fungal inoculum, higher levels of ectomycorrhizal colonization and greater seedling densities (Mueller & Gehring, 2006).

The contribution of animals visiting mistletoes was also noted in studies from elsewhere, increased visitation driving a series of top-down influences. Thus, trees infected by mistletoe were more likely to attract frugivores, leading to enhanced fruit removal and seed dispersal for hosts (Van Ommeren & Whitham, 2002; Carlo & Aukema, 2005). Mistletoes are also widely used by nesting birds, denning mammals and ambush predators, the semi-succulent foliage and densely branched structure increasing canopy complexity and ameliorating climatic extremes (Watson, 2001; Cooney *et al.*, 2006). Finally, with their enriched tissues and high water content, mistletoes attract a wide range of herbivores – from specialist insects and canopy-dwelling marsupials to browsing ungulates (Watson, 2001; Mooney & Linhart, 2006; Burns & Watson, 2013).

Rather than mistletoes being either facilitators that augment nutrient inputs from the bottom up or keystone resources that increase animal diversity and exert top-down control over communities, they're both (Fig. 1). The net effect of mistletoes on forest communities was quantified with a patch-level removal experiment (Watson & Herring, 2012). 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 & Herring, 2012). Rather than nectarivores or frugivores, the group of birds exhibiting the greatest response to mistletoe removal was the insectivores – specifically, those insectivores foraging on the forest floor (Watson, 2015). Indeed, once this functional group was removed, mistletoe removal had no significant effects on the remaining bird assemblage. Rather than direct effects, this unprecedented response relates to indirect effects mediated via litter-fall, mistletoe litter increasing the heterogeneity of nutrient inputs (March & Watson, 2010) and boosting the availability of litter-dwelling arthropods, including those preferred by ground-feeding insectivores (Razeng & Watson, 2012). This group includes some of the more abundant bird species in eucalypt woodland which forage for arthropods across multiple substrates, from the forest floor, understorey plants and canopy. Thus, subtle changes in the occurrence of mistletoe in woodland and forest canopies may boost community-wide insectivory and, given that arthropods represent dominant herbivores in this and many other systems (Lowman & Heatwole, 1992), changes to community-level herbivory and plant biomass (Mooney & Linhart, 2006).

V. Beyond parasitic plants – do animals drive facilitation cascades?

Rather than an idiosyncratic attribute of mistletoes, or parasitic plants more generally (Quested, 2008; Watson, 2009a; Spasojevic & Suding, 2011; Watson *et al.*, 2011), might other facilitative effects noted between plants relate to interactions with visiting animals? Bromeliads are a well-studied group of plants, many of which grow as epiphytes in tropical forests. With tight whorls of

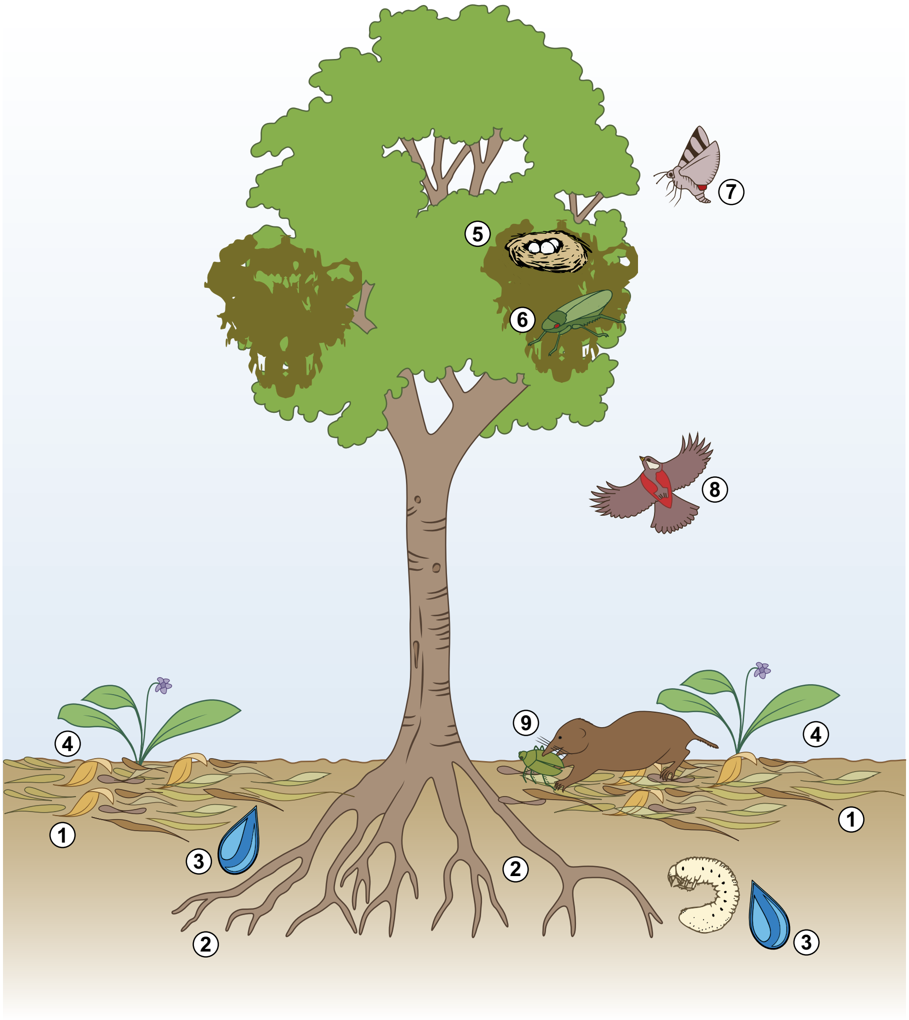

Fig. 1 Schematic representation of direct contributions of mistletoe (left) and indirect contributions mediated via visiting animals (right). Numbers refer to the contributions known to result from mistletoe infection: 1, increased litter-fall; 2, increased microbial biomass and mycorrhizal colonization; 3, decreased soil moisture; 4, changes to understorey plants including increased biomass, species richness and density of host seedlings; 5, increased likelihood of nests located within host canopy; 6, increased richness of herbivores; 7, increased visitation to both host and mistletoe by pollinators; 8, increased visitation by seed dispersers, increased seed dispersal of both mistletoe and host and increased seed deposition of mistletoe and understorey plants; 9, increased abundance and richness of litter-dwelling insects and ground-foraging insectivores. Once the indirect contributions of animals are included, a more complete understanding of the mechanisms underlying the role of mistletoe as a keystone facilitator is revealed. Artwork by Maggie J. Watson.

leaves forming water-holding tanks, bromeliads facilitate the establishment and growth of other vascular epiphytes and attract a wide range of animals. Thus, as well as facilitating adjacent plants via decreased drought stress (Köhler *et al.*, 2007), predatory arthropods and insectivorous birds attracted to bromeliads (Díaz *et al.*, 2012; and references therein) probably enhance growth by constraining herbivory. Another group of plants with well-studied facilitative effects are legumes, rhizobial symbionts boosting N availability for adjacent plants. Legumes are often highly palatable, Nitschke *et al.*'s (2015) microcosm experiments demonstrating complex interactions between a generalist herbivore (grasshoppers), plant diversity and microbial biomass, mediated via frass fall. But what do these findings mean for grasshopper consumers and higher trophic levels, and how do these direct and indirect nutrient inputs affect mycorrhizal symbionts and root-zone regulation of productivity (after Ossler *et al.*, 2015)? To date, these bottom-up and top-down processes have been investigated in parallel, separate strands of research exploring plant–plant interactions and tritrophic dynamics. By reframing the study of facilitation in terms of interaction networks, the significance of these nested interactions with animals can be identified (e.g. Saiz *et al.*, 2014). While necessarily dependent on the facilitator itself (mistletoe, bromeliad or legume), their cascading influence across food webs hinges on a wider set of interactions (van der Putten, 2009).

VI. Conclusions

Hemiparasites necessarily take from their hosts but, when these dynamics are considered beyond the scale of infected individuals, their influence is found to resonate across food webs. As aerial hemiparasites, mistletoes are doubly instructive – their occurrence is determined by a suite of interactions with hosts, pollinators, seed dispersers, seed predators and other natural enemies, and these interactions are sufficiently discernible to be readily studied. The mechanistic understanding of how mistletoes act as keystone facilitators draws on multiple disciplines, just as dependent on animal ecology, geochemistry and ecosystem science as plant ecology. Just as soil microbiota are increasingly acknowledged as key contributors to facilitation (Montesinos-Navarro *et al.*, 2012; Rodríguez-Echeverría *et al.*, 2016), I contend that incorporating interactions with animals is essential to the study of facilitation and facilitation cascades, and have summarized three priorities to guide further research (Box 1). By amplifying or constraining plant–plant

Box 1 Research priorities

Research priorities		
1. Specificity and redundancy	**2. Exclosures**	**3. Above-ground below-ground linkages**
 A persistent challenge in the study of facilitation is the identity of the interactors – are particular roles solely played by individual species or are multiple taxa involved? In addition to examining these patterns within systems through time, looking across spatial scales (both within and among systems) is crucial to understand the maintenance of facilitative relationships and their resistance to perturbation. In addition to species-scale resolution, examining deeper taxonomic levels will elucidate the evolutionary basis of facilitation cascades, determining whether certain groups are predisposed to involvement.	 Although studies of plant–plant interactions often rely on microcosm experiments, manipulative field experiments are essential to quantify the role of visiting animals. One of the simplest and most effective ways to quantify the influence of visiting animals on facilitative interactions is installing exclosures. By customizing the design to the organisms of interest (e.g. fences for ground-dwelling browsers, cages for volant pollinators, trunk collars for arboreal species), the magnitude of their influence can be isolated and quantified (relative to procedural controls).	 Building on current efforts to characterize the identity and function of soil micro-organisms, greater scrutiny on epigeic macro-organisms is a priority. In addition to detritivores, many soil and litter-dwelling organisms burrow, changing the structural properties of soil and enhancing nutrient uptake, litter decomposition and water infiltration. How these biological properties interact with soil chemistry and, therefore microbial and plant function are unknown.

interactions, linking plant–plant interactions with higher trophic levels and transferring nutrient subsidies between systems, visiting animals help explain variation in the occurrence, specificity and strength of facilitation.

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