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SPECIAL FEATURE

FACILITATION IN PLANT COMMUNITIES

Parasitic plants as facilitators: more Dryad than Dracula?

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Summary

1. Despite being components of most vegetation types, the community-level effects of parasitic plants are often ignored. The few studies adopting a broader view have revealed that these plants mediate a series of direct and indirect competitive and facilitative effects on community structure and ecosystem processes.

2. I summarize findings from the two best-studied systems: a set of experimental and manipulative studies from northern Sweden and an integrated research programme in southern Australia, both focusing on the most abundant hemiparasite in the region – *Bartsia alpina* (Orobanchaceae; Lamiales) and *Amyema miquelii* (Loranthaceae; Santalales), respectively.

3. Despite broad-based differences between these regions, their vegetation types and biotic constituents, rates of litter-fall, litter decomposition, nutrient return and plant growth all increased near the hemiparasites in both cases. This leads to changes in the abundance of other plants and the increased species richness and total biomass reflects an indirect form of facilitation.

4. In addition to reallocation of nutrients from host tissues, some of the additional nutrients may be excreted by other organisms, such as visiting pollinators, seed dispersers, herbivores and members of below-ground decomposer communities. Small-scale heterogeneity in nutrient availability could provide a mechanistic process underlying the role of parasitic plants as keystone resources.

5. Parasitic plants can be regarded as either malevolent predators (Dracula) or charitable benefactors(Robin Hood), but may be better described as Dryads (Greek deities associated with specific trees, which, in addition to being reliant on their host for their wellbeing, affect nearby trees and visiting animals, rendering the surrounding stand a sacred grove).

6. *Synthesis*. The Dryad role may be applicable to a wide range of facilitators, whereby indirect interactions with other organisms affect both hosts and adjacent plants, augmenting direct plant–plant interactions. However, while consistent with both case studies and information from studies of other parasitic plants, this role may be most apparent in low productivity systems. Addition, removal and animal exclosure experiments are highlighted as useful approaches to quantify the community-level influence of parasitic plants, in addition to dedicated work on the below-ground influences of parasitic plants.

Key-words: Amyema, *Bartsia*, facilitation, hemiparasite, keystone, mistletoe, productivity

Introduction

Parasitic plants are components of all terrestrial vegetation types, from mangal, rainforest and savanna through to desert, saltmarsh and tundra (Kuijt 1969; Heide-Jørgensen 2008). This functional group consists of over 4,500 species from twelve orders – each representing an independent evolutionary origin of parasitism (APG 2003; Barkman *et al*. 2007; Der & Nickrent 2008) – and contains plants ranging from diminutive annual herbs to long-lived canopy-emergent trees. There has been considerable anatomical, physiological, systematic and autecological research into the parasitic habit in general, and haustorial structure in particular, but there have been far fewer community-level studies (see Pennings & Callaway 2002; Press & Phoenix 2005), limiting our understanding of the broader role of parasitic plants in natural communities.

As they are neither herbivores nor predators, falling somewhere between primary producers and secondary consumers,

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the parasitic habit that defines these plants makes them difficult for ecologists to categorize. Similar difficulties exist for animal parasites and these challenges are still being surmounted, with food web theory only recently adjusted to incorporate parasitism explicitly (Sukhdeo & Hernandez 2005 and references therein). This is remarkable when one recalls that parasitism is the most common dietary mode (Combes 2005). While these difficulties have been largely procedural – how can non-destructive consumption be depicted and quantified in simple linear diagrams? – they have constrained our ability to understand the roles that parasites play within their communities. Revised food webs, including parasites have been found to behave very differently and parasites are now regarded as key regulators of energy flow and trophic dynamics (Lafferty, Dobson & Kuris 2006).

Previous work on interactions between parasitic plants and other plants has largely been restricted to quantifying direct effects on hosts. Species that depend on hosts for all metabolic needs (holoparasites) exert a range of direct, deleterious effects on their hosts, both in natural communities and in croplands and other agricultural settings. In addition to impacts on growth and mortality, they may also affect reproductive output of hosts, and holoparasitic plants therefore comprise some of the most destructive agricultural pests for cereal producers in many regions (Parker & Riches 1993; Kroschel 2002). Most parasitic plants, however, photosynthesize their own carbohydrates (Press & Graves 1995) and rely on their host primarily for water and dissolved nutrients (hemiparasitism). High hemiparasite loads can also lead to premature host death but, as this outcome is rare in undisturbed systems, parasitic plants are generally considered to have negative, but sublethal effects on hosts (Reid, Yan & Fittler 1994; Smith 2000; Pennings & Callaway 2002; Cameron *et al.* 2005; Press & Phoenix 2005). However, these sublethal effects on hosts, in combination with host preferences, can appear to produce positive responses, i.e. strong indirect facilitative effects on species that are infected less (Pennings & Callaway 1996; Cameron *et al.* 2005).

Some research has moved beyond pair-wise host–parasite interactions, evaluating the impact of parasitic plants at the community level, and quantifying competitive and facilitative effects on neighbouring plants, animal associates and ecosystem processes. Interactions with other plants (non-hosts) have been found to entrain a series of effects, mediated by changes to competitive dynamics and nutrient inputs (Quested 2008). An increasing proportion of recent parasitic plant research has focused on interactions with animals; especially those that disperse their propagules, consume their tissues and use their structures for shelter (Watson 2001; Mathiason *et al.* 2008). This expanded view has found that direct costs of infection can be offset by indirect benefits, including improved rates of seed dispersal for parasitized hosts, as more potential dispersers are attracted by the additional fruit resources (Van Ommeren & Whitham 2002; Carlo & Aukema 2005). These findings culminated in the formal proposal that mistletoes (Watson 2001) and parasitic plants generally (Press & Phoenix 2005) be considered keystone resources, boosting species richness at local and regional scales and having a disproportionate influence on community composition and ecosystem processes.

These divergent roles were contrasted by Press (1998), when he asked whether parasitic plants were better represented by Count Dracula or Robin Hood. From the perspective of the host, parasitic plants can be regarded as villains that rob their hosts of precious resources. Yet, at a community level, they can be considered benefactors that redistribute resources for the common good. In the decade following this publication, numerous studies have quantified interactions involving parasitic plants, using a range of descriptive and manipulative approaches in a wide range of vegetation types, allowing a re-evaluation of this dichotomy.

The objective of this contribution is to synthesize recent research findings to evaluate whether the direct effects of parasitic plants lead to net losses (competition) or net gains (facilitation) for ecosystem functions and for other species in their communities. I introduce two well-studied systems – a root-parasitic herb in a sub-Arctic heathland and a stem-parasitic woody perennial in a warm-temperate forest – and compare effects on hosts, non-hosts, community composition and ecological processes to determine if these parasitic plants act as facilitators. Building on the Count Dracula vs. Robin Hood analogy, I suggest an alternative mythological character to personify facilitation (both direct and indirect), articulating a series of priorities to guide further work on the effects of parasitic plants on their communities.

Case study 1: *Bartsia alpina*

The open forests and heathlands of sub-Arctic Fennoscandia would seem an unlikely place for parasitic plants to thrive. With a mean annual temperature of −1.1 °C and deep snow cover for more than half the year, plant growth rates are slow and restricted to the 4-month growing season (when soil temperature rises to 9.0 °C average; Quested *et al.* 2002). Plant growth in this mesic system is limited primarily by nutrient availability, leading to a range of strategies to acquire nutrients, including fixing atmospheric nitrogen, mycorrhizal associations and carnivory (Berendse & Jonasson 1992). An additional strategy is parasitism, exhibited by a range of genera within the Orobanchaceae (ex-Scrophulariaceae) (Lewejohann & Lorenzen 1983). These herbs – both annuals and long-lived perennials – are root parasites, with dense adventitious roots forming multiple haustoria where they contact roots of neighbouring plants.

Bartsia alpina is the largest and most abundant hemiparasite in this community (up to 92 stems per m^2, mean density of 11 stems per m^2; Quested, Press & Callaghan 2003a). This perennial species is bee-pollinated and one of the earliest-flowering species in the region (Molau 1993), maximizing the likelihood of successful pollination (Bennett 1968; Kwak & Bergman 1996). As with other sympatric hemiparasites, *B. alpina* is highly palatable and preferentially browsed by many ungulates, both wild and domestic (Staaland *et al.* 1995; Hülber *et al.* 2005), and is also highly favoured by herbivorous arthropods and molluscs (Taylor & Rumsey 2003; S. Barlow, unpublished data). Although this species is broadly distributed throughout the Holarctic, it generally occurs in low to very low densities (Taylor & Rumsey 2003), hence the research findings summarized here should not be applied throughout the species' range.

Quested *et al.* found that *B. alpina* accounted for 3–4% of above-ground biomass in the study area but was patchily distributed, with most plants occurring in dense aggregations (Quested, Press & Callaghan 2003a). The plants yielded an average litter-fall of 37 g m^{-2} $year^{-1}$, representing *c.* 17% of annual litter-fall in areas immediately adjacent to *B. alpina* stems (equating to 0.15 g per stem; Quested *et al.* 2005). Microcosm studies found that N and P content of fresh and shed leaves were enriched in hemiparasite leaf litter relative to other species, because of high initial concentrations and low resorbtion rates prior to abscission compared with the dwarf shrubs they parasitize (Quested *et al.* 2002). *Bartsia alpina* litter also released a greater proportion of N, yielding 5.4–10.8 times more N than the four shrub species studied. Based on mean site densities of 43 plants per m^2, *B. alpina* leaf litter delivered an estimated 53% increase in N input (Quested, Press & Callaghan 2003a). The addition of *B. alpina* litter also accelerated overall rates of decomposition, measured in terms of mass loss (5.0–12.0% increase) and CO_2 efflux (7.7–29.1% increase; Quested *et al.* 2002). In a litterbed study, *B. alpina* litter decomposed more quickly than litter of host species and, when rates are combined with initial differences in N content, this equates to an 18-fold difference in N release to the soil.

The implications of these differences in decomposition for facilitative effects on other species were evaluated using phytoassay trials, growing two species (*Betula nana* and *Poa alpina*) in pots with various mixtures of host and hemiparasite litter (Quested *et al.* 2003b). After one growing season, harvested *B. nana* seedlings were 51% greater in mass when grown in *B. alpina* litter (at field concentrations) compared with host litter (in this case, *Vaccinium uliginosum*), with significantly more biomass allocated to leaves. Moreover, the seedlings grown with parasite litter had almost double the concentration of N and P. Results from the grass trial were similar: plants grown in *B. alpina* litter attained 23–46% greater biomass than those grown in the litter of three dwarf shrubs (Quested *et al.* 2003b).

In summary, hemiparasitic herbs in general (and *B. alpina* specifically) were found to modify nutrient inputs in these sub-Arctic heathlands, mediated via enriched and abundant leaf litter shed early in the growing season and, through these processes, indirectly facilitated other species (Quested *et al.* 2005). Although the host plants are necessarily the proximate source of the elements enriching the parasite's litter, the ultimate source of these nutrients is not known, nor is the effect of interactions with other species (plant and animal) in modifying availability of these nutrients.

Case study 2: *Amyema miquelii*

The setting for this integrated research programme is the eucalypt forests of inland south-eastern Australia; warm-temperate open forests with a grassy understorey and scattered shrubs. The dominant canopy trees are eucalypts (Myrtaceae), long-lived sclerophyllous trees that act as principal hosts for eight mistletoe species (Santalales: Loranthaceae; Shaw, Watson & Mathiason 2004). Of these, box mistletoe (*Amyema miquelii*) is the most abundant and widespread, and although occasionally occurring in densities exceeding 500 plants ha^{-1}, 7–10 plants ha^{-1} is more typical of undisturbed forest (Turner 1991; Watson 2002). This aerial hemiparasite forms large (to 3 × 5 m) woody clumps in the crown of host trees, with pendulous leaves highly mimetic of host foliage (Reid, Yan & Fittler 1994). Although short-lived relative to their host, individual plants can live for several decades.

Effects of *A. miquelii* on hosts are comparable with findings for other mistletoe species: infected hosts typically have slower growth rates but do not experience elevated mortality rates (Reid, Yan & Fittler 1994; see also Bowie & Ward 2004 and references therein). High parasite loads can be associated with premature host death, but the interaction may not be causative: tree-scale mistletoe removal experiments found no difference in subsequent mortality of treated vs. untreated eucalypt trees (Reid, Yan & Fittler 1994). The same attributes that make particular trees more suitable hosts (in this region, higher available nutrients, especially phosphorus) may increase mortality because these sclerophyllous species are sensitive to elevated nutrient levels (McLaughlin 1996). The combined effects of nutrient overload and increased water-stress mediated by mistletoe infection are especially severe in open woodlands used for grazing, where soil compaction by livestock exacerbates stress on infected trees (leading to widespread death of mature trees known as 'dieback', Adams 1996). Even though mistletoe is not the direct agent of this degradation, the hemiparasite is widely regarded as a pest and actively removed from habitats throughout its native range (Coleman 1949; Reid, Yan & Fittler 1994).

Most ecological research on *A. miquelii* has concentrated on interactions with vertebrate associates: pollinators, seed dispersers, herbivores and other natural enemies. As with congeners and loranthaceous mistletoes generally, *A. miquelii* relies on animals to disperse both pollen (primarily generalist nectarivorous birds) and seeds (primarily specialist frugivorous birds). Flowers and fruit are available year-round (March 2007; fig. 2.16) and constitute an important resource for a variety of consumers (Reid 1986). The foliage is also widely consumed by arthropods and arboreal marsupials: the nutrient rich, semi-succulent leaves are favoured over the heavily defended host foliage (Canyon & Hill 1997). Indeed, selective herbivory is considered to have led to the remarkable host mimicry displayed by this species and other Australian mistletoes (Barlow & Wiens 1977), with large plants often difficult to discern within the canopy. The dense clumps formed by these plants are commonly used as nesting substrates by mammals and birds (Cooney, Watson & Young 2006), with several bird species exhibiting preference for mistletoe as a nest site (Cooney & Watson 2005; see also Barea & Watson 2007).

The combined effect of these interactions was evaluated in a community-level study by Watson (2002), comparing two adjacent eucalypt forests similar in all respects except mistletoe occurrence: all mistletoe plants (both *A. miquelii* and the congeneric *A. pendula*) had been removed from one forest. Comprehensive bird surveys quantified broad-based differences in the avifauna of these two forests: the control site supported nine more bird species, of which eight were woodland dependent (21% more than the removal site). Of those 44 woodland bird species occurring at differing frequencies in the two forests, 30 were more frequently recorded in the control site. Rather than nectarivores and frugivores, most of these species were ground-feeding insectivores. Percent coverage of bare ground, grass and leaf litter were not found to differ between sites, but litter depth was noticeably greater in the control site, and mistletoe litter was suggested to provide an important resource in this system (Watson 2002).

March (2007) conducted a series of studies on the contribution of *A. miquelii* to nutrient dynamics in eucalypt forests: the first dedicated research on ecosystem effects of mistletoe mediated by litter-fall. Contrary to expectation, infection status had little effect on host litter-fall, with no significant difference in the amount of litter shed over a 12-month period (infected trees, $n = 20$, 252 ± 18 g m^{-2} year^{-1}; uninfected trees, $n = 15$, 233 ± 18 g m^{-2} year^{-1} $P > 0.05$; March 2007). But infected trees had an average of an additional 156 g m^{-2} year^{-1} of mistletoe litter – with a linear relationship between the biomass of mistletoe in the canopy and litter-fall – increasing total litter-fall per tree by up to 189%. These tree-scale data were comparable to quantities estimated at the mistletoe and stand scale and, overall, the amount of litter produced at all three scales ranged from 123 to 162 g leaf litter per m^3 of mistletoe in the canopy; equivalent to 544–648 g of leaf litter per mistletoe plant falling in a 12-month period (March & Watson 2007). Rather than being uniform or reflecting patterns of eucalypt litter, mistletoe litter-fall displayed a distinct temporal signature. Leaf litter from uninfected trees exhibited a pronounced peak during the Austral summer, mean values exceeding 0.4 g m^{-2} day^{-1} for the months of January and February (March & Watson 2007, fig. 2). Eucalypt litter for infected trees showed the same pattern, but the addition of mistletoe litter expanded this peak considerably, with mean total litter estimates for infected trees exceeding 0.4 g m^{-2} day^{-1} from October to May (> 0.7 from November to March).

Two factors were found to explain observed patterns of mistletoe litter-fall: between-plant differences in timing of leaf fall and more rapid rates of leaf turnover than hosts. While eucalypts are not deciduous, individuals exhibit congruent patterns of leaf fall, with most litter produced during the hot-dry summers. By contrast, mistletoe plants exhibited high inter-plant variation (March 2007). Hence, the between-month differences in mistletoe litter-fall noted at the tree and stand scales were not apparent at the individual mistletoe scale, with little synchronicity in the timing of maximum and minimum litter-fall. This finding is similar to well-described patterns of phenology in mistletoes, whereby complementary peaks in flowering and fruiting in individual plants expand the overall reproductive period into seasons when few other nectar or fruit resources are available (Watson 2001). The other mechanism underlying the pattern of mistletoe litter-fall was the rate of leaf turnover, quantified by marking mistletoe and eucalypt leaves and measuring how frequently leaves were shed (March 2007; March & Watson 2007). Mean mistletoe leaf life span was estimated at 1.50 years, compared with 4.47 years for eucalypt leaves from infected trees and 3.97 years for uninfected trees (the minor difference further demonstrating the negligible effect of mistletoe infection on host ecology).

Unlike most autotrophic plants that withdraw nutrients from leaves prior to abscission, mistletoes and other parasitic plants shed their leaves as is, with the composition of fresh and abscised leaves comparable (Pate, True & Kuo 1991; Quested *et al.* 2002). The same samples that were sorted and dried to calculate biomass were used for elemental analysis of both mistletoe and eucalypt litter, quantifying total carbon, total nitrogen, P, Ca, K, Mg, Na, S, Al, B, Cu, Fe and Zn (concentrations expressed as % of dry wt or mg kg^{-1}; see March & Watson (in press), for details). Eight elements had significantly enriched concentrations in mistletoe litter relative to host litter; K, Cu, Na, P, Zn, Mg, B and S, in descending order of concentration difference between mistletoe and host. In contrast, Al, Fe, C and N had significantly lower concentrations in the mistletoe leaf litter than host litter. There was no detectable effect of parasite load (measured as biomass) on host element concentration for all 13 elements in host leaves, again demonstrating the negligible effect of mistletoe parasitism on host condition (March & Watson, in press).

So, mistletoe leaves are replaced more frequently, leading to elevated volumes of litter enriched in most nutrients. Litterbag experiments were conducted in the field (as compared to the controlled environment used in the *Bartsia* work) to measure decomposition rates of host and parasite litter and discern any interactions between them. Litterbags of eucalypt litter, mistletoe litter and mixed litter (50 : 50) lost mass at the same rate for the first 88 days and then began diverging, with mistletoe litter (and the eucalypt litter associated with mistletoe litter) losing more mass than pure eucalypt litter: after 1 year, percentage mass loss was 63% for eucalypt litter, 46% for mixed eucalypt litter and 46% for mistletoe litter. Mistletoe leaf litter had greater nutrient retention than the pure eucalypt leaf litter and slowed the nutrient release from the mixed eucalypt litter for 9 of 13 elements measured (March 2007). This effect was also apparent in the understorey – the slowly decomposing litter resulted in a thick layer of litter beneath infected trees with no clear separation between litter and soil (i.e. mull form), compared with a more sparse coverage of litter beneath uninfected hosts forming a distinct layer atop the soil (i.e. mor form, March 2007).

To evaluate potential facilitative effects of these altered rates of litterfall and nutrient return on the forest understorey, above-ground plant biomass was harvested beneath 20 hosts with variable numbers of mistletoe in their canopy. A close relationship emerged between mistletoe leaf biomass in the canopy and above-ground dry biomass of understorey plants growing beneath the crown, with a doubling of mistletoe biomass leading to a doubling of understorey plant biomass, strong evidence for an indirect facilitative effect of the mistletoe (March & Watson 2007). Rather than affecting all plant groups equally, this increase was because of the changes in annuals. Moreover, the number of exotic species increased and natives decreased with mistletoe infection, and there were five species found only beneath trees with high mistletoe densities (March 2007). Mistletoe infection was associated with higher concentrations of many soil nutrients (N, P, K, Mg and Na), and changes in soil N and P were most closely related to observed changes in plant productivity and composition.

Phytoassay trials using *Lolium perenne* were conducted after 2 and 9 months decomposition time. The only significant difference after 2 months was between control pots (no litter) and all treatments (mistletoe litter, mixed litter and eucalypt litter), but after 9 months there was significantly greater plant biomass from mistletoe litter pots than mixed litter. Specifically, the control and mistletoe litter treatment were both significantly greater than the mixed litter treatment (March 2007). This was despite finding greater P concentrations in mixed pots and suggests that growth may have been limited by N, consistent with previous decomposition experiments demonstrating that net N was still being mobilized 519 days after eucalypt litter addition (Attiwill, Guthrie & Leuning 1978). Longer-term phytoassay trials using both annuals and perennials are needed to clarify the effect of mistletoe litter on plant growth, in particular to establish the effect of differing proportions on decomposition rate and nutrient availability.

Other work

The congruence in the indirect facilitative effects from these two sets of studies is remarkable when one considers the differences between study systems. One is a sub-Arctic heathland, the other a warm-temperate forest; the parasitic plants are from different orders and exhibit different modes of parasitism – one an aerial hemiparasite relying exclusively on a single host, the other a root-parasite tapping multiple hosts simultaneously. While these case studies were chosen because they represent the two best-studied systems, it is unclear whether the *Bartsia* and *Amyema* examples are exceptional or representative of the generalized influence of parasitic plants on their communities.

Several other parasitic plants have been studied with respect to the facilitative effect they have on adjacent plants and on the nutrient status of the soil, and many of these display patterns consistent with the case studies described above (Hobbs & Atkins 1991; Pennings & Callaway 1996; Smith 2000; Cameron *et al*. 2005; Cameron & Seel 2007; Grewell 2008; Yu *et al*. 2009). The influence of various *Rhinanthus* species (Orobanchaceae) has been studied in natural and managed grasslands using a range of descriptive and manipulative approaches (Bardgett *et al*. 2006; and references therein). A recent study by Ameloot *et al*. (2008) evaluated how these hemiparasitic annuals affect N availability in the soil in 11 restored grasslands sown with two *Rhinanthus* species. Grass from infected plots had an average of 30% more N than control plots, yet the net effect of parasitism at the community level was a decreased removal of N driven by a marked reduction in grass biomass (37% of control plots). A tracer experiment using ^{15}N confirmed that the hemiparasites increased the overall pool of available N in the soil, mediated by enriched and easily decomposed litter shed early in the season. In a parallel study, Bardgett *et al*. (2006) found that *Rhinanthus minor* lowered overall productivity in a sown grassland model community, thereby facilitating coexistence of grasses and forbs leading to an increase in species diversity. They also reported changes consistent with a shift in the soil microbial community, with a slightly lower fungal-to-bacterial ratio in the presence of the hemiparasite. These findings support the widely used restoration technique of sowing *Rhinanthus* to alter dominance patterns in favour of herbs (Ameloot *et al*. 2008), thereby increasing species richness in grasslands and meadows.

These community-level field studies are underpinned by extensive experimental and anatomical studies of *Rhinanthus minor* grown under controlled conditions (Cameron & Seel 2007; Rümer *et al*. 2007 and references therein). This work has revealed the costs associated with parasitism, both to infected hosts (through a range of direct and indirect pathways) and hosts that do not become infected, but devote resources to structural and chemical defense (Cameron *et al*. 2005). Hence, some forbs actively prevented access to their xylem through encapsulation of haustoria with lignin, whereas various grass species did not exhibit any defense responses to infection (Rümer *et al*. 2007). These findings suggest that differential susceptibility to parasitism may account for some of the patterns noted in the field, with *R. minor* generally reducing the dominance of grasses while favouring legumes and forbs (Cameron *et al*. 2005, Table 2).

Where do these additional nutrients come from?

Experimental and observational data from multiple systems demonstrate effects of parasitic plants that are consistent with facilitation (see Callaway 2007), and are comparable to the influence of nitrogen fixing plants for N (May & Attiwell 2003), with even more pronounced effects with other elements. Are these simply short-term effects due to reallocation of nutrients bound up in the host, enriching parasite tissues which are then shed (the Robin Hood model), or are other sources involved?

If the host is the principal source for these nutrient inputs, clear differences would be expected in the nutrient status and vigour of infected and uninfected hosts. However, in most systems – for both aerial and root parasites, holoparasites and hemiparasites – this is not the case, with slight to no measurable effects of parasitism on a range of elements (Lamont & Southall 1982; Press & Graves 1995). Note, however, that hosts and non-hosts may be intrinsically different, whereby those potential host plants with higher nutrient status or water content are more likely to support parasitic plants to maturity (the host quality hypothesis; Watson 2009). Moreover, once infected, host plants can grow differently, exemplified by the broom-forming dwarf mistletoes (Viscaceae; *Arceuthobium spp.*) where infected coniferous hosts become more densely branched and irregular in shape (Hawksworth & Wiens 1996; Shaw, Watson & Mathiason 2004; Watson 2004; fig. 10–5). There has been a suggestion that infected hosts may invest more into root growth and allocate more nutrients below-ground, but evidence from empirical studies is conflicting (Quested 2008), with the only positive results noted for N. So, given that nutrients in parasitic plants necessarily come from their host, why are the differences between hosts and non-hosts not clearer, and where else might these dramatic increases in nutrients mediated by parasitic plants come from?

As mentioned, many parasitic plants are pollinated by animals, and most rely on animal vectors to transport their seeds to new hosts, but parasitic plants also provide structure used by other animals. Kangaroos frequently rest in the shade provided by the dense semi-succulent foliage of *Exocarpus strictus* (Santalaceae), in otherwise open eucalypt forests with sparse canopies (McGregor 2007). Monitor lizards (*Varanus* spp) have been reported using mistletoe clumps (Loranthaceae) as ambushes to hunt birds (Rose 1962). Some mistletoes are preferentially used as nesting sites and hibernaculae (Cooney, Watson & Young 2006 and references therein), with data from several studies demonstrating high visitation rates to infected hosts (Bennetts *et al.* 1996). Many small to medium-sized mammals in coniferous forests of North America use the witches' brooms resulting from dwarf mistletoe infection as resting areas, with several using them to overwinter (Parks, Bull & Tinnin 1999). While these interactions led to the proposal that mistletoes, and parasitic plants in general, function as ecological keystones (Watson 2001, 2004), could these interactions also represent sources for these additional nutrients? These fragmentary observations suggest that infected hosts attract greater numbers of animals, which would lead to elevated concentrations of animal-derived nutrients from their excreta and unfinished meals.

In addition to frugivores, nectarivores, opportunistic predators and species seeking shade or shelter, many herbivores also visit parasitic plants (Sessions & Kelley 2001; Watson 2004). In addition to enriched tissues with higher water content than their hosts, these plants have few structural and chemical defenses. Mistletoe has been noted as a popular browse for many mammals (Hawksworth & Wiens 1996; Watson 2001), and serves as host plant for many arthropod herbivores (Braby & Nishida 2007; Burns 2009 and references therein). With increasing rates of herbivory, the amount of grass and exudates increases and, while some of these nutrients compensate for the losses associated with parasitism, the remainder represent supplementary nutrients from elsewhere. Given that many of these animal associates are from wide-ranging groups like mammals, birds and insects, the potential catchment for these nutrients is great.

Similar patterns have been noted for other structures: with marked patterns of nutrient enrichment recorded beneath hollow-bearing trees in neotropical rainforests (Janzen 1976), large trees in open savanna of southern Africa (Dean, Milton & Jeltsch 1999) and rocky outcrops in high Arctic tundra (Derry, Kevan & Rowley 1999). By offering a vantage point or shelter, increased visitation rates of animals lead to boosted input of nutrients and seeds, providing additional resources that, in turn, lead to further increases in visitation rates. In addition to elevated N inputs, animals also concentrate and excrete P, Mg and several other metals as cations (Derry, Kevan & Rowley 1999; Vitousek 2004), consistent with the patterns documented beneath mistletoe plants (March 2007; March & Watson, in press). This positive feedback loop has been used in restoration efforts, adding artificial perches to accelerate plant growth rates and colonization of understorey species (Zanini & Ganade 2005), and provides a testable explanation for the effects of parasitic plants on nutrient inputs.

So, how does the proposal that *parasitic plants facilitate growth of neighbouring plants* relate to the existing hypothesis that *parasitic plants are keystone resources*? Rather than being separate ideas involving independent ecological pathways, I suggest that both emanate from the same network of interactions: the former being the outcome, the latter one of the underlying processes. With enriched tissues and animal-mediated dispersal systems, parasitic plants attract sufficient numbers of animal visitors to alter overall nutrient inputs in their immediate vicinity, modifying the growth and competitive dynamics of adjacent plants, changing the composition and structure of plant assemblages and increasing local species richness.

Rather than Robin Hood or Dracula, I suggest an alternative mythological analogy consistent with the role of a heterotrophic, host-dependent parasite that can facilitate growth of nearby plants. Dryads (specifically, hamadryades) or tree nymphs are deities in Greek mythology that are attached to a particular tree, protecting it throughout their shared life, yet wholly dependent on it. First proposed by Knott (1908) in specific reference to *Viscum album* (and independently invoked in forest 'ethology' by Van Steenis (1956)), the dryad analogy can be applied to parasitic plants generally and incorporated into our current consideration of patterns of facilitation and other forms of co-dependence in plant communities. In addition to being reliant on their 'host' for their wellbeing, these nymphs also affect nearby plants and associated animals, elevating the surrounding stand to the status of a sacred grove (Graves 1960). Unlike Dracula or Robin Hood, the focus is on the neighbourhood rather than the individual, and fits closely with our emerging understanding of how nurse plants, nitrogen fixers and other facilitators can influence community structure in their immediate environment as described in other papers in this special feature.

Prospect

By taking a broader view of parasitic plants and considering the full breadth of their biotic associates, their role as facilitators becomes clear. Through selective patterns of infection, some hosts exhibit diminished competitive ability, while other non-host species increase in dominance, leading to changes in the community composition and successional dynamics. Rather than relating to all parasitic plants in all settings, most of the supportive evidence comes from inherently low productivity systems, where their role may be more obvious (Press 1998; but see Pennings & Callaway 1996). Whether parasitic plants also increase nutrient returns and affect plant occurrence in more productive systems (especially in tropical regions) is unclear, and represents a key priority for further work. Likewise, the effects of altered nutrient inputs on soil biota and below-ground processes requires dedicated research and may elucidate the facilitative effects of parasitic plants on other species (see van der Putten 2009).

As well as increasing small-scale heterogeneity and promoting greater coexistence of species, parasitic plants can alter successional dynamics (Shaw, Watson & Mathiason 2004; Ameloot *et al.* 2008) and control the spread of exotic species (Yu *et al.* 2009), suggesting that they could be used more widely to improve restoration of their respective communities. In addition to their influences on plants (hosts and non-hosts), could their network of interactions with pollinators, dispersers, herbivores and other associates be used to fast-track habitat rehabilitation? Given their ability to accumulate cations (Stewart & Press 1990), inherently high transpiration rates and rapid leaf turnover, do parasitic plants have a role in bioremediation, removing metals, salts and other contaminants from the soil and potentially playing a role in combating salinization and abating the effects of acid sulphate soils?

To evaluate these and other questions, manipulative experiments will be an especially useful approach. For some species, including those root-parasitic species with wide-host ranges and high seed-set (*e.g. Rhinanthus* spp.), addition experiments enable the effect of parasitic plant presence and density to be measured directly (both above- and below-ground). For other groups, especially woody species and those parasitic plants with narrow host ranges, removal experiments are more tractable, with targeted stand and patch-removals allowing direct and indirect effects of parasitic plants to be discerned. Finally, for those systems where neither addition nor removal is practical or possible, exclosures will allow the effect of animals to be quantified, distinguishing those effects mediated by the parasitic plants themselves from those effects due to pollinators, seed dispersers, herbivores and other visitors. This work is essential to discern the mechanisms underlying the documented influence of parasitic plants at the community-level, and distinguish the relative importance of direct and indirect competitive and facilitative effects of parasitic plants on their hosts vs. their effects on adjacent plants through altering nutrient availability and modifying competitive dynamics. Once a clearer view of the role of parasitic plants on their communities emerges, detailed comparisons with other kinds of parasites are needed. The idea of parasites having negligible, or even positive, effects on their hosts and thus boosting community productivity and species richness is not new, and students of both animal parasites and parasitic plants may benefit from considered cross-kingdom contrasts.

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