

Functional Roles of Parasitic Plants in a Warming World

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Abstract

We consider the mechanistic basis and functional significance of the pervasive influence of parasitic plants on productivity and diversity, synthesizing recent findings on their responses to drought, heat waves, and fire. Although parasites represent just 1% of all angiosperms, the ecophysiological traits associated with parasitism confer pronounced impacts on their hosts and disproportionate influence upon community structure, composition, and broader ecosystem function. New insights into the roles of their pollinators, seed dispersers, and litter-dependent detritivores have advanced our understanding of how parasitic plants modulate animal communities via their extended and complementary phenology. Direct and indirect impacts of climate change on parasitic plants and their ecological roles are already apparent. Trade-offs between maximizing efficiency at obtaining water from hosts and sensitivity to water stress underlie range shifts and host switching of parasitic plants and increased reliance on these plants by animal communities for food and shelter.

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INTRODUCTION

Parasitic plants are contradictions in terms, defying conventional definitions and necessitating the coining of new words to describe their growth habits, life histories, and ecological interdependencies (Krasnylenko et al. 2021). Both virulent parasites and beneficial facilitators (Griebel et al. 2017, Watson 2016), variously compromising food security (Rubiales 2020) and boosting diversity (Pennings & Callaway 1996), they yield some of the world's most valuable forest products (McLellan et al. 2021) yet include some of the most invasive agricultural weeds (Masteling et al. 2019). As model systems for ecological research, these paradoxical plants defy established paradigms (Watson 2009) and catalyze new ways of thinking about autecological drivers of climate change resilience (Fontúrbel 2020). In the past decade, studies of parasitic plants have discovered *inter alia* chemical signaling among three kingdoms (Lanfranco et al. 2018), the only known loss of respiratory complex 1 in a multicellular eukaryote (MacLean et al. 2018, Petersen et al. 2015), the complete loss of the chloroplast genome (Molina et al. 2014), and the horizontal transfer of hundreds of genes between hosts and parasites (Yang et al. 2019). The ecological insights from parasitic plant research have been similarly profound, catalyzed by a synthesis of mistletoe–animal interactions and the development of the hypothesis that these plants represent ecological keystones, exerting disproportionate influence on diversity and community structure in forests and woodlands worldwide (Watson 2001). In the twenty years since that review, many knowledge gaps regarding mistletoe ecology have been filled, and the keystone hypothesis has been strongly supported and extended to parasitic plants generally.

Here, we draw on recent findings about parasitic plants across the disciplines of forestry, ecology, systematics, plant science, and agronomy to summarize our current understanding of how these plants affect resource availability, community structure, and ecosystem health, focusing on functional roles in a warming world and complementing comprehensive reviews on their phylogenetic history (Nickrent 2020), biology (Těšitel 2016), germination (Bouwmeester et al. 2021), management (Watson et al. 2020), and molecular evolution (Bromham et al. 2013). Just as they have helped our understanding of basic biology progress, we demonstrate that parasitic plants are also at the forefront of advances in ecology and climate change impacts, revealing the hitherto unrecognized role of ecological generalists in maintaining community structure, the influence of small-scale nutrient subsidies on promoting diversity, the mechanistic role of plant phenology underlying community sensitivity to drought (Fontúrbel et al. 2021), and the significance of plant growth habit for promoting microclimatic diversity and ameliorating the impacts of extreme weather events and global climate change. While integrating work on the breadth of parasitic plants, we focus on the two most diverse lineages that account for the bulk of ecological research: mistletoes in the Viscaceae and Loranthaceae (Santalales) and broomrapes and allies in the Orobanchaceae (Lamiales), building on existing reviews of the two groups (Fisher et al. 2013, Fontúrbel 2020, Griebel et al. 2017, Phoenix & Press 2005). In addition to synthesizing these advances, we note those open questions where established conceptual frameworks, resolved phylogenies, and the logistical ease of comparing and experimentally manipulating host–parasite interactions make parasitic plants ideal models for future discoveries.

PARASITIC PLANTS: DIVERSITY AND EVOLUTIONARY DYNAMICS

Of the more than 374,000 described flowering plants (Christenhusz & Byng 2016), approximately 4,750 have a parasitic growth habit (Kuijt 1969, Nickrent 2020, Těšitel 2016). Like carnivorous plants and mangroves, parasitic plants are a functional group unified by their growth habit rather than shared ancestry, defined by their ability to derive nutrients and water directly from their hosts (Kuijt 1969, Press 1989). While most are capable of photosynthesizing carbohydrates



Figure 1

Parasitic plants exhibit a variety of growth forms, illustrated by representatives of the three most diverse lineages. (a) Leafless root holoparasite (*Orobanche*, Orobanchaceae, Australia). (b) Woody aerial hemiparasite (*Desmaria*, Loranthaceae, Chile). (c) Herbaceous root hemiparasite (*Castilleja*, Orobanchaceae, United States). (d) Herbaceous twining aerial hemiparasite (*Cuscuta*, Convolvulaceae, Australia).

autotrophically but are dependent on host plants for structural support, water, and nutrients (hemiparasitic) (Kuijt 1969, Press & Graves 1995), approximately 10% of described species are wholly parasitic (holoparasitic), with no capacity to photosynthesize (Těšitel 2016).

Parasitic flowering plants occur as a wide range of plant forms, including herbs, vines, shrubs, and trees (Atsatt & Strong 1970, Těšitel 2016) (**Figure 1**), but intriguingly, there are none in aquatic systems. Parasitic plants attach themselves to host plants via highly specialized absorptive organs called haustoria (Kuijt 1969), which enable parasitic plants to penetrate the tissue of host plants' branches and stems aboveground (aerial parasites) or roots belowground (root parasites) to access vascular tissues and their contents of water and dissolved nutrients (Phoenix & Press 2005, Press & Graves 1995). Approximately 40% of parasites are aerial, and 60% are root parasites (Press 1989, Press & Graves 1995). Although detailed life history data are unknown for some genera (especially in the Olacaceae and Aptandraceae), available information suggests that once a lineage acquires the parasitic habit, reversion to full autotrophy does not occur, consistent with Dollo's law of irreversibility. A separate group of plants attach to mycorrhizal fungi, acquiring carbohydrates, water, and dissolved nutrients from other plants indirectly via shared mycelial networks. Known as mycoheterotrophs, these plants lack haustoria and have mixotrophic (a combination of

photosynthesis and heterotrophic feeding) and nonphotosynthetic (holoparasitic) representatives. Although technically parasitic on other plants via fungal intermediaries, these poorly known plants are beyond the scope of our review, and our emerging understanding of their biology, evolution, life history, and physiology is reviewed elsewhere (Selosse & Cameron 2010).

Acquiring a parasitic habit does not necessarily promote diversification; all but three parasitic plant lineages across 12 divisions are represented by one to three genera and fewer than 40 species, and six of those lineages are represented by 12 or fewer species (Nickrent 2020). As Těšitel (2016) noted, these six depauperate groups are all highly specialized holoparasites which, along with most holoparasitic genera in the Orobanchaceae and both holoparasitic families within the Santalales (Balanophoraceae, Mystropetalaceae), are restricted in abundance, distribution, and host range (Heide-Jørgensen 2008, Nickrent 2020). Over time, reliance on their host for all nutritional needs has driven iterative matching of physiologies, an increasingly specialized trajectory that is apparently incompatible with the acquisition of a more generalized mode of parasitism essential for establishing in new areas and infecting new host species. This begs the question of whether these 12 independent acquisitions of parasitism in extant plants are a subset of a larger number of historic lineages—are there extinct groups of parasitic plants, and are they necessarily specialized holoparasites? As most extant groups have little or no macrofossil record, this intriguing possibility cannot be definitively tested; suffice to conclude that, with three notable exceptions, parasitism in plants is better regarded as an evolutionary constraint than a key innovation. This is in stark contrast to animals, parasitism being both labile and frequently associated with adaptive radiations (Poulin 2011, Siddall et al. 1993).

One of the three exceptions is *Cuscuta*, the sole parasitic genus in the Convolvulaceae, with approximately 200 species found worldwide. Known as dodders, these annual plants exhibit highly reduced leaves and a unique haustorial structure—direct phloem contact via cells with labyrinthine walls—enabling efficient phloem-to-phloem nutrient transfer. Although they retain some photosynthetic function, most are functionally holoparasitic, with many species characteristically yellow in color. Their most characteristic feature, shared with the genus *Cassytha*, sole parasitic member of the Lauraceae and a remarkable case of convergence, is their twining habit; growing rapidly during favorable conditions, individual plants are capable of attaining a combined length exceeding a kilometer (Heide-Jørgensen 2008). This rapid growth rate, coupled with their ability to parasitize multiple hosts simultaneously, allows individual plants to move through the canopy, using directed growth and airborne volatiles to locate and exploit favored hosts (Runyon et al. 2006).

The two remaining groups account for most parasitic plant species and share the hallmarks of adaptive radiations. At 2,428 described species and 179 genera, the Santalales is the most diverse group in terms of both taxonomy and morphology, ranging from canopy-emergent forest trees to miniature endophytes that live entirely within their hosts. Within this division, five of the 20 lineages currently recognized as families independently switched from root to stem parasitism; these comprise the functional group collectively termed mistletoes (Nickrent 2020). Two of these lineages account for most species: Viscaceae (450 species in 11 genera) and Loranthaceae (over 1,000 species in 76 genera). The transition from root-parasitic shrub to stem-parasitic mistletoe predates the origin of the birds acting as contemporary seed dispersers (Liu et al. 2018, Restrepo et al. 2002), with ancient mammals hypothesized to have catalyzed the transition in growth habit (Watson 2020). Of the other parasitic plant lineages, only one approaches this diversity: the broomrapes and allies (Orobanchaceae, Lamiales), with over 2,100 root-parasitic species in 101 genera. Patterns of evolution within this group are complex, with three lamiid families acquiring the parasitic habit (along with dodders in the Convolvulaceae and Lennoaceae) and five independent transitions from hemiparasitism to holoparasitism within the Orobanchaceae. These herbaceous root-parasitic plants include both annual and perennial species, with some departing from the usual

growth habit, including the shrubby *Brandisia* (Fischer 2004, Nickrent 2020) and a recently described species of *Pedicularis* that infects epiphyte roots and grows within the canopy of Himalayan fir forests (Heide-Jorgensen 2008). Twenty-five genera are economically significant agricultural weeds, including *Striga* and *Alectra* species; their dust seeds are produced in very large numbers and lie dormant in the soil for ten years or longer, with germination triggered by strigolactones produced by host roots.

Rather than parasitism necessarily conferring adaptive advantages, it is a generalist habit afforded by particular combinations of specific life history traits (twining annual with direct phloem contact, aerial parasite dispersed by birds, and root-parasite with host-induced germination) that can be considered key innovations driving diversity (in the cosmopolitan dodders, mistletoes, and broomrapes, respectively). Freed from the limitations imposed by available nutrients and soil moisture, these lineages spread from their mesic origins across a broad range of terrestrial vegetation types, including forests, woodlands, grasslands, and deserts (Kuijt 1969).

FUNCTIONAL ROLES

The idea of parasitic plants as ecological keystones stimulated research into ecological interactions involving parasitic plants, above- and belowground. More recently, research on the influence of parasitic plants on microclimate is emerging, driven by their dense structure and high transpiration rates. With many parasitic plants favoring dominant species as hosts, their role in promoting coexistence via altered competitive dynamics is apparent in many vegetation communities. Although the collective influence of these roles tends to boost productivity in undisturbed ecosystems, these effects can be disruptive in agricultural settings and other heavily modified systems, with both native and introduced parasitic plants intensifying infections in the dense monocultures that characterize intensive crop production systems.

Resource Provision

Parasitic plants necessarily depend on other plants in order to survive (Těšitel 2016) and, as with all parasites, maximizing the likelihood of spreading to uninfected hosts is critical to maintaining a viable population. Some groups achieve this by producing high volumes of seeds (e.g., *Striga* and *Orobanch*e species, which can produce hundreds of thousands of seeds per plant). Others invest in a small number of larger seeds, often investing further in fruit to attract animal dispersers. The relationship between mistletoes and birds is a textbook example of plant–animal mutualism, with specialist birds relying on the nutritious fruits and the plants reliant on the directed dispersal services the birds provide. However, recent work has added more complexity to this story. Mistletoes are not dependent on specialist frugivores; rather, both field-based observations and global distributional patterns have demonstrated that generalist frugivores are far more important (Watson & Rawsthorne 2013). Unlike specialists, which travel from one mistletoe-infected stand to another, intensifying infections and undermining populations of hosts and parasites (Rawsthorne et al. 2011), the broader diet of generalists leads to a more diffuse seed rain (Medel et al. 2004), initiating new infections and effecting long distance seed dispersal and, over time, diversification (Watson & Rawsthorne 2013). Some mistletoes take this one step further, mimicking the foliage of their principal hosts and preventing frugivorous birds from forming a mistletoe-specific search image. By hiding within their hosts, mistletoes effectively force their dispersers to search the canopies of preferred hosts systematically to find ripe fruit, in so doing, dispersing seeds from previous meals, increasing the likelihood of reaching both preferred host species and uninfected individuals (Cook et al. 2020). Rather than solely affecting mistletoes, changing occurrence patterns of frugivores drive distributional changes in other fleshy fruited species. For example,

mistletoe occurrence was found to be a strong predictor of understory shrub communities in Spanish pine forests (Mellado & Zamora 2017). Mistletoes' parasitic habit enables the production of more abundant high-quality fruit than those from nonparasitic plants, influencing community-scale diversity (Napier et al. 2014), seed dispersal services, and successional dynamics (Monteiro et al. 2020).

Although many parasitic plants are capable of self-pollinating, most rely on animal vectors, with insects (especially bees) and birds the two principal groups. Most pollinators are generalists. Ollerton et al. (2007) noted that the root parasitic *Orobancha elatior* shared the same species of bumblebee pollinator as its preferred host, *Centaurea scabiosa*, with observations and floral experiments demonstrating a low frequency of switching from one plant to the other. The combined display likely increases pollination services for both. The community-wide influence of parasitic plants on pollination services is exemplified by *Tristerix corymbosus* in southern South American temperate rainforests (Aizen 2003). This mistletoe has a long flowering period and represents the sole winter nectar source for the generalist nectarivore *Sephanoides sephaniodes*, the southern-most hummingbird, which is responsible for pollinating ~20% of the woody flora in this system (Fontúrbel 2020). The extended phenology and high floral density of the mistletoe allowed hummingbirds to switch from seasonal migrants to year-round residents, increasing pollination and seed set in co-occurring plants and ameliorating effects of both seasonal and interannual variability in rainfall.

Beyond pollination and seed dispersal, parasitic plants are visited by a wide range of animals that source food from fruit, foliage, nectar, flowers, stems, bark, and litter. Indeed, several studies have demonstrated that selective feeding by herbivores likely limits parasitic plant populations. This relates to both specialist insects (especially butterflies) that lay their eggs exclusively on certain parasitic plant lineages and large mammals that seek out parasitic plants as preferred browse (Watson 2001). In turn, invertebrates attract insectivores, with root-parasitic plants supporting greater invertebrate abundances and insectivore activity than their hosts (Watson et al. 2011) and mistletoe supporting distinct assemblages of spiders within host canopies (Anderson & Braby 2009, Burns et al. 2011, Burns & Watson 2013).

Litterfall and Effects on Nutrient Availability

Four aspects of parasitic plants are noteworthy with respect to litterfall. First, parasitic plants concentrate nutrients within their aboveground tissues, with concentrations of many cations greatly exceeding concentrations in host tissues. Second, they do not withdraw nutrients from their leaves prior to abscission, leading to enriched litterfall. Third, parasitic plants replace their leaves more frequently than their hosts (Hatcher et al. 2012, Press 1989), leading to high volumes of litterfall dropped over most months of the growing season (year-round in temperate systems) (March & Watson 2007). Finally, parasitic plants exhibit characteristically patchy occurrence patterns (Watson 2009), even within continuous populations of preferred hosts (Cameron et al. 2009). The combined effect of these factors is greatly increased heterogeneity of nutrient returns: Areas with high numbers of parasitic plants are associated with far greater productivity and more rapid decomposition. Although most of these nutrients are reallocated from long-lived hosts, visiting animals contribute additional cations from elsewhere, small-scale nutrient subsidies accentuating the heterogeneity of nutrient inputs and minimizing net losses from infected hosts. In addition to enhanced nitrogen availability and cycling (Ameloot et al. 2008; Ndagurwa et al. 2013, 2014; Press 1989), litter of parasitic plants also boosts return rates of other nutrients such as carbon, phosphorus, and potassium (Bardgett et al. 2006, Ndagurwa et al. 2016, Qusted 2008). The consequences of these changes to nutrient inputs are manifested in marked changes to soil microbial communities (Li et al. 2014, Spasojevic & Suding 2011), decomposition (Bardgett et al.

2006; Quested et al. 2002, 2003b), understory plant composition and growth (Mellado & Zamora 2017, Ndagurwa et al. 2016), and occurrence patterns of ground-foraging animals (Ndagurwa et al. 2014, Watson 2015).

Microclimate and Habitat Structure

Plants, especially trees, form distinct microclimates within and beneath their canopies, due to their leaves and branches intercepting solar radiation (Nadkarni et al. 2001, Vetaas 1992). This phenomenon in turn leads to microclimatic niches within plant structures and plant communities that provide critically important microrefuges capable of determining species assemblages or the biotic composition of communities and ecosystems (Halaj et al. 2000, Reside et al. 2019, Woods et al. 2015).

Mistletoes have a densely branched characteristic structure which, together with their consistently high transpiration rate, increases both the structural complexity and microclimatic heterogeneity within host canopies (Griebel et al. 2017, Sala et al. 2001). Increases in leaf transpiration rates are known to cool leaves' surfaces, with leaf surface temperatures varying from surrounding temperatures by several degrees (Pincebourde & Casas 2019). This microclimatic effect is particularly important in hotter, drier conditions (Phoenix & Press 2005) when higher transpiration rates recalibrate leaves' energy budgets, generating markedly cooler microclimates (Griebel et al. 2017, Press 1989). This was noted by Mitchell & Wilcox (1988, p. 455) regarding *Santalum spicatum*: "Sandalwood is parasitic on the roots of other plants. On the hottest days the leaves of sandalwood will be cool to the touch." Other studies have highlighted the fact that many parasitic plants can increase their host's transpiration rates, which can influence the water dynamics of parasite–host relationships (Phoenix & Press 2005) and create microclimatic effects such as lowering leaf temperatures via evaporative cooling (Press 1989). For root parasites, influences on host transpiration rates and microclimate are relatively subtle, but Griebel et al. (2022a) note significant whole-of-tree influences by mistletoes. With mistletoe water potentials consistently 30% lower than those of their hosts, sap flow rates of stems and branches on infected trees remained unregulated during hot, dry conditions, leading to a fourfold increase in transpiration (Griebel et al. 2022b). In addition to effects on overall water use and the likelihood of xylem cavitation, transferring water from the soil to within the canopy during hot, dry conditions leads to noticeable changes in tree-scale evaporative cooling (Griebel et al. 2017).

Some parasitic plants are preferentially selected as habitat, and a variety of species have been observed providing a place for animals to nest, shelter, hibernate, roost, or seek refuge from daytime heat during hot summer days (Griebel et al. 2017). A wide range of birds (including species from at least 60 families) have been recorded nesting in mistletoes, both within the clump and upon the enlarged host branch and haustorial attachment (Cooney et al. 2006, Watson 2001). While some of these instances may be opportunistic or accidental, there is emerging evidence that mistletoes and other parasitic plants are actively selected by animals for nesting and roosting substrates. Focusing on woodlands in New South Wales, Cooney & Watson (2005) demonstrated that diamond fire-tails (*Stagonopleura guttata*) preferentially nested in two mistletoe species (*Amyema*, Loranthaceae). Although mistletoe was conservatively estimated to account for 2.3% of the woodland canopy volume, a third of all nests were located within mistletoe clumps, with every large mistletoe in the study area occupied. Subsequent experimental work estimated predation rates, finding consistently lower rates of predation for artificial nests located within mistletoe clumps than within host foliage (Cooney & Watson 2008). Several studies have noted disproportionate use of root-parasitic plants for nesting and roosting. Watson et al. (2011) summarized empirical research on *Exocarpos strictus*, a root parasitic understory shrub in open eucalypt forests, noting that every nest of the

vulnerable Gilbert's Whistler (*Pachycephala inornata*) was located within the parasitic plant, rather than the far more abundant acacias and young eucalypts in the forest understory.

Dwarf mistletoes (*Arceuthobium*, Viscaceae) differ from other parasitic plants, effecting fundamental changes in the architecture of infected host plants. As obligate parasites of coniferous trees, they transform usually open and homogenous monospecific stands into drastically different forests with complex canopies containing standing dead trees, clearings, and increased coarse woody debris (Shaw et al. 2004, Watson 2001). Many dwarf mistletoes induce the formation of structures known as witches' brooms in infected trees: large dense branches with increased resin and retained dead branchlets (Shaw et al. 2004). As well as favored sites for nesting, many birds and mammals use these structures as shelter, from winter hibernaculae and cool denning sites during summer to communal roosts during migration (Watson 2001). Arthropods also inhabit these brooms; experimental trials suggest they are responding to increased host branch density rather than the mistletoe itself (Halaj et al. 2000).

The most definitive study quantifying microclimatic effects of parasitic plants on wildlife habitat use consisted of a manipulative experiment in a desert shrubland in which mistletoes were removed from selected trees in a desert system, and kangaroo activity was assessed around treatment trees compared with control trees and procedural control trees from which host foliage comparable in volume to mistletoes was removed (Chu et al. 2021). Kangaroo activity (resting during the heat of the day) was consistently lower beneath treatment trees, with kangaroos preferentially seeking shade beneath trees with mistletoe. These differences aligned with measured temperature differences beneath these groups; trees with mistletoes left in the canopy were consistently 2°C cooler during the heat of the day. This study was conducted in winter, and preferences for mistletoe-infected hosts are predicted to be even greater during summer, when ambient temperatures regularly exceed 45°C.

Evaluating how parasitic plants compare to autotrophic plants regarding shade provision, temperature amelioration, and increased humidity is hampered by the lack of contemporaneous comparable data. Although studies of thermal tolerances of animals and determinants of microclimate underpin burgeoning research on climate change impacts and physiological ecology (Rabaiotti & Woodroffe 2019, Scheffers et al. 2014), microclimatic profiles of individual plant species, let alone comparisons between functional groups, are lacking (Chmura et al. 2018, Vetaas 1992). Martin et al. (2015) present a notable exception, comparing substrates selected by four bird species for foraging with the shade density of the main plant species. In addition to showing a significant preference for the shadier tree species during days exceeding 35°C, two bird species exhibited a pronounced switch in substrate selection, avoiding the shadier trees on days below 35°C but spending more time in the shadier species on hot days. We suggest their finding is likely indicative of a widespread preference by animals to rest, nest, and feed within those plants that offer a more benign microclimate. Parasitic plants likely represent cool spots in many landscapes, especially during heat waves and droughts, when thermal tolerances of both animals and autotrophic plants become increasingly compromised.

EFFECTS ON DIVERSITY

Rather than operating independently, the effects of parasitic plants on resource provision, nutrient availability, habitat structure, and microclimate are additive and interacting; their combined influence on ecological communities is best quantified by controlled comparisons of species composition and diversity (Lafferty et al. 2006, Watson 2016). An increasing number of these comparative studies are available, unified by findings of strong positive influences of parasitic plant occurrence on the species richness of both plants and animals (Ameloot et al. 2005; Cooney et al. 2006; Davies

et al. 1997; Grewell 2008; Mellado et al. 2019; Mellado & Zamora 2017; Pennings & Callaway 1996; Press & Phoenix 2005; Shaw et al. 2004; Watson 2001, 2002, 2011, 2015, 2016; Watson & Herring 2012). A smaller number of studies find a broader range of responses in soil microbial communities (Bardgett et al. 2006, Spasojevic & Suding 2011). Two systems are sufficiently well studied that the mechanisms driving this pervasive influence can be determined: broomrapes and allies in grasslands and mistletoe in woodlands and forests.

Research on *Rhinanthus* and other members of the Orobanchaceae family first led to the idea that parasitic plants affect diversity, with studies from multiple systems consistently demonstrating major influences on plant diversity via direct and indirect effects. *Rhinanthus minor* characteristically parasitizes a subset of grassland plants, especially legumes and grasses (Gibson & Watkinson 1992), reducing their biomass and suppressing their competitive dominance (Wagner et al. 2011), thereby creating space for a wide range of typically rare species to establish (Hellström et al. 2011), boosting species richness (Gibson & Watkinson 1992) and stabilizing temporal dynamics in plant communities (Cameron et al. 2009). These effects are magnified by nutrient reallocation via high rates of litterfall, with enriched litter effectively taking nitrogen and other limiting resources from dominant species (Ameloot et al. 2008), thereby reducing their hosts' standing crop and increasing overall sward productivity (Ameloot et al. 2005). Rather than a uniform pattern, the annual *R. minor* grows in characteristically dense patches (Wagner et al. 2011), depleting resources from their favored hosts till their density decreases (Joshi et al. 2000), creating gaps in summer. The next cohort grows in areas with higher densities of grasses and legumes, with this continuous sequence of selective growth, nutrient transfer, and gap formation driving a small-scale shifting mosaic that moves across the grassland (Cameron et al. 2009), boosting plant species richness by imposing heterogeneity and also affecting both abundance and species richness of grassland-dwelling animals including arthropods and snails (Chaudron et al. 2021). Indeed, the use of *R. minor* as a restoration tool is widespread in Europe (Westbury et al. 2006); their seed is added to wildflower mixtures to transform species-poor old fields to herb-rich grasslands (Davies et al. 1997), leading to their alternate name: meadow maker.

Other groups within the Orobanchaceae have been found to play comparable roles. *Bartsia alpina* has significantly higher nitrogen and phosphorus concentrations in their leaves than in those of the dominant shrubs in its sub-Arctic heath community of northern Scandinavia (Quested et al. 2002, 2003a). By reallocating limiting nutrients from these long-lived shrubs and increasing their availability via litterfall, the hemiparasite mobilizes nutrients that would have been retained for a longer period. Although most are reabsorbed by hosts, patches of enriched litter allow other species to colonize and grow (Ameloot et al. 2008), an effect magnified by the accelerated rate of decomposition of recalcitrant host litter with increased nitrogen availability (Quested et al. 2003a, 2005). In tidal wetlands in northern California, the presence of two root hemiparasites (*Cordylanthus maritimus* and *Cordylanthus mollis*) increased heterogeneity, allowing species with divergent site preferences to coexist and increasing overall species richness (Grewell 2008). Wood betony (*Pedicularis canadensis*) and bastard toadflax (*Comandra umbellata*) increase floristic quality and species richness in tallgrass prairie communities in the United States (DiGiovanni et al. 2017). In addition to increasing plant diversity, these hemiparasites can also affect higher trophic levels; for example, *Castilleja wightii* growing on leguminous hosts promotes aphid abundance (Marvier 1998).

The idea of parasitic plants having a disproportionate influence on animal diversity was catalyzed by research on mistletoes, and a series of experimental studies in southern Australia (Watson & Herring 2012, Mellado et al. 2019) provides the strongest direct evidence for both the magnitude of these effects and the main mechanistic determinants. All mistletoes were removed from twenty woodlands, and quarterly bird surveys in subsequent years compared species richness

between this treatment group and otherwise comparable woodlands where mistletoes were left in the canopy. For those control sites with mistletoe, procedural controls were conducted, removing equivalent volumes of host (*Eucalyptus* spp.) foliage but avoiding all mistletoes. Three years after treatment, the species richness of birds in treatment sites dropped by a mean of 26.55% of pretreatment numbers; this proportional loss rose to 34.8% when just considering woodland resident species (Watson & Herring 2012). Relative to the proportional biomass of mistletoe in this woodland, this response equates to a keystone index of 132.5 for all birds (including waterbirds, raptors, and aerial foragers) and 174 for woodland residents (after Mills et al. 1993). Rather than fruit- or nectar-dependent species or those birds known to nest in mistletoe, this community-wide response was driven by insectivores. Indeed, when insectivores were analyzed separately, the remainder of the bird assemblage exhibited no change between treatment and control woodlands; the response was further isolated to ground-foraging insectivores (Watson 2015). This assemblage is the same suite of species referred to collectively as declining woodland birds that exhibits range-wide declines in distribution, abundance, and reproductive success (Watson 2011).

Paradoxically, although distinct arthropod communities are associated with mistletoes (Burns et al. 2011, Zamora et al. 2020), this assemblage of birds spends little time in the canopy and is not known to interact with mistletoe plants, suggesting the causative mechanism may relate to litterfall. Subsequent comparisons between the invertebrate community beneath infected and uninfected eucalypts revealed a consistent difference, equating to more than 1,000 more insects per square meter (Mellado et al. 2019), including significant increases in those arthropod groups known to be preferred prey for the affected birds (Razeng & Watson 2012). When this estimate is extrapolated to field densities of mistletoes in this habitat type, the addition of mistletoes to woodland canopies causes an increase of 2.5 million preferred prey per hectare each year, an especially noteworthy finding given prior work that demonstrated occurrence patterns in these birds is constrained by invertebrate availability (Zanette et al. 2000). In addition to affecting higher trophic levels, many of the invertebrate groups found in greater numbers in areas with more mistletoe litter are important decomposers, contributing to increased nutrient inputs via accelerated decomposition and bioturbation (Mellado et al. 2019). Influences on microbial activity and function have not been assessed in this system, but these positive effects were found to extend to understory plants; a close association was found between mistletoe occurrence and understory plant biomass (March & Watson 2007).

Rather than an idiosyncratic finding, studies of mistletoe in other systems have found consistently strong influences on diversity patterns. The dwarf mistletoe *Arceuthobium vaginatum* has a close positive correlation with bird abundance and species richness (as well as deer and elk populations) in pine forests in Colorado (Bennetts et al. 1996), and in a Western Australian desert community, Napier et al. (2014) found a positive correlation between the presence of mistletoes and the abundance of both nectarivores and frugivores. Ndagurwa et al. (2014), in a study of three hemiparasitic plants (*Erianthemum ngamicum*, *Plicosepalus kalachariensis*, and *Viscum verrucosum*) in the savannas of southwest Zimbabwe, found a positive correlation between mistletoe occurrence and the presence, diversity, and abundance of litter-dwelling arthropods. As well as providing a nurse function for animals, mistletoes have been documented providing similar facilitation for other plants, including their principal hosts (Candia et al. 2014, Carlo & Aukema 2005). Mistletoes are considered pests in some agricultural contexts (Watson et al. 2020), and water and nutrient uptake can reduce host growth and eventually increase their mortality (Henríquez-Velásquez et al. 2012). However, the positive effects of mistletoes outweigh the negative ones (Fontúrbel 2020, Těšitel et al. 2021), and their local extinction can trigger cascading effects across the community, disrupting mutualistic interactions and limiting the recruitment of many plant species (Rodríguez-Cabal et al. 2013). This emerging understanding is already being applied to restoration initiatives; various

species of mistletoe have been reintroduced to parts of their former range to boost biodiversity and maintain ecosystem function (Duquesnel et al. 2017, Norton et al. 2018). Most research on mistletoe interactions is focused on direct interactions, and our knowledge of their indirect interactions remains quite limited. Considering that indirect interactions increase exponentially with species diversity within a community (Estes et al. 2013), the study of indirect mistletoe interactions is encouraged.

Data from other groups of parasitic plants are limited but consistent with findings from mistletoes and broomrapes. Density of pale-fruit ballart (*Exocarpos strictus*), a root-parasitic shrub, was the most significant determinant of richness patterns of bird communities in a floodplain forest. This plant has a much denser structure than other understory species and a higher abundance of arthropods, and its shrubby growth habit has a positive correlation with increased arthropod abundance and bird species diversity in southeast Australia (Watson et al. 2011). In a study of salt marsh communities in California, Pennings & Callaway (1996) found a close association between Marsh Dodder (*Cuscuta salina*) occurrence and plant diversity within the community, due to direct suppression of the dominant species (*Salicornia virginica*) that allowed the emergence of other plants. These congruent findings across a wide range of ecosystems are strong evidence for the generalized role of parasitic plants as disproportionately influential determinants of community structure, with some evidence this influence extends beyond stand-scale composition and alters successional trajectories of entire ecosystems (Casadesús & Munné-Bosch 2021, Mellado & Zamora 2017).

Previous researchers have described this role with a variety of terms, including keystone species, keystone resource, keystone structure, ecosystem engineer, physical ecosystem engineer, nurse species, facilitator, dryad, Robin Hood, and driver. Compared to most other processes, species, and structures that share these names, the influence of parasitic plants hinges on their complex trophic status: simultaneously taking from their hosts without completely consuming them; providing a variety of nutritional, structural, and microclimatic resources; making a variable fraction of their own food via photosynthesis; and altering the spatial and temporal distribution of nutrient inputs from other organisms (Hatcher et al. 2012, Watson 2009). For a nonscientific audience, we prefer the term keystone, because its scientific ambiguity allows the full range of influences to be included and allows informal comparison with the functional role of other groups (Allaby 2010). Parasitic plants are characteristically minor components of their respective communities, in terms of species richness, abundance, and biomass, yet their functional influence extends well beyond their footprint. For ecologists, however, and life scientists more generally, we favor the term facilitator to emphasize their indirect positive roles. Rather than forming a sharp dichotomy, these terms are complementary; in addition to being intended for different audiences, they also emphasize different aspects of their role, with facilitator describing the process and keystone describing the outcome.

CLIMATE CHANGE IMPACTS

Parasitic plants have characteristically high transpiration rates, with many groups exhibiting limited stomatal control. During regular conditions, these elevated water demands are advantageous, effecting more negative water potentials than their hosts and enabling constant passive uptake of water (Griebel et al. 2022b) and uninterrupted growth. During periods of water scarcity, however, this becomes a problem, with their unregulated demand leading to acute water stress in both parasite and host (Henríquez-Velásquez et al. 2012, Nabity et al. 2021, Sala et al. 2001). Previous work on water relations of host–parasite pairs has demonstrated that prolonged water stress can be fatal for both, with sublethal effects also manifesting in reduced production of flowers and fruit. Although several parasitic groups contain species adapted to xeric conditions, many parasitic

plants are constrained by water availability, characteristically occupying the more temperate portion of their preferred hosts' distributional range (Watson et al. 2016).

Anthropogenic climate change is altering rainfall patterns and water availability, with extreme climatic events increasing in frequency and magnitude (Walther et al. 2002). Warmer temperatures have rearranged air circulation patterns, resulting in an unprecedented streak of drought events around the world. Severe and prolonged drought events cause water stress in all plants but, considering the high water demands of parasitic plants, both hosts and parasites are predicted to be especially sensitive to soil drying (Phoenix & Press 2005). Several studies have already documented mistletoe mortality events associated with drought, heat waves, and other climatic perturbations. In summer 2009, a prolonged heatwave in Melbourne, Australia, that included the hottest day ever recorded ($46.4^{\circ}\text{C} = 115.5^{\circ}\text{F}$) led to the death of 210 out of 237 mistletoes (*Amyema miquelii* and *Amyema pendula*) being monitored growing on 46 *Eucalyptus camaldulensis* (Moore & Lefoe 2020). No host mortality was reported, and two years following this event, high growth rates led to increased canopy density. A larger-scale mortality event was reported in eucalypt woodlands and forests across south-eastern Australia (Crates et al. 2022). Mistletoe counts at 2,111 sites across a 350,000 km² area noted associations between the proportion of dead plants and both summer temperatures and summer rainfall totals. A third study found similar patterns in the temperate forests of southern South America, with the most severe drought in 50 years leading to a doubling in the mortality of both mistletoes (*Tristerix corymbosus*) and principal hosts (*Aristotelia chilensis*); experimental trials demonstrated this was driven by acute water stress (Gonzalez-Villagra et al. 2018).

In addition to mortality, all three studies noted profound effects of drought on other aspects of mistletoes and their ecological associates. Five years after the Melbourne mortality event, nine new mistletoes had established, exclusively on the largest trees being monitored (Moore & Lefoe 2020). In the larger-scale study, live mistletoe abundance was a strong predictor of bird diversity, consistent with prior work noting the importance of mistletoe as a reliable source of both nectar and invertebrate prey, despite it being a minor woodland component (Crates et al. 2022). Following the mortality event, bird abundances and species richness both fell dramatically, with reductions in breeding activity for small-bodied residents and insectivores. Additionally, in the South American temperate forests, mistletoe flower and fruit production was reduced by half (Fontúrbel et al. 2018), with similar drops in visitation rates by both the hummingbird pollinator and marsupial seed disperser (Fontúrbel et al. 2021). In this system, both animal associates visit a wide range of other plants for which they are the principal pollen and seed vectors; hence, reduced mistletoe numbers are predicted to trigger a community-wide extinction vortex driven by reduced recruitment.

While the effects of droughts are relatively well studied, there are other extreme climatic events that can potentially affect parasitic plants (Walther et al. 2002). Climate change does not mean only warmer and drier climates but implies a wider climatic variance that can involve flooding or freezing temperatures. Many groups within the Orobanchaceae require cold stratification for germination (Ter Borg 2005); warmer winters therefore potentially diminish the realized distribution of *Rhinanthus* and other large-seeded taxa. Facing multiple stressors at once can either collapse the functional role of parasitic plants and their interactions if they fail to adapt or trigger rapid evolutionary responses involving a rearrangement of their interactions (Kinnison et al. 2007). Such rearrangement is expected to lead to simpler and less-resilient communities via a cascade of events (Figure 2). In summary, as novel climatic conditions become dominant, we expect species diversity and functional diversity to change, ending in a collapse once a resilience threshold is surpassed (Figure 3).

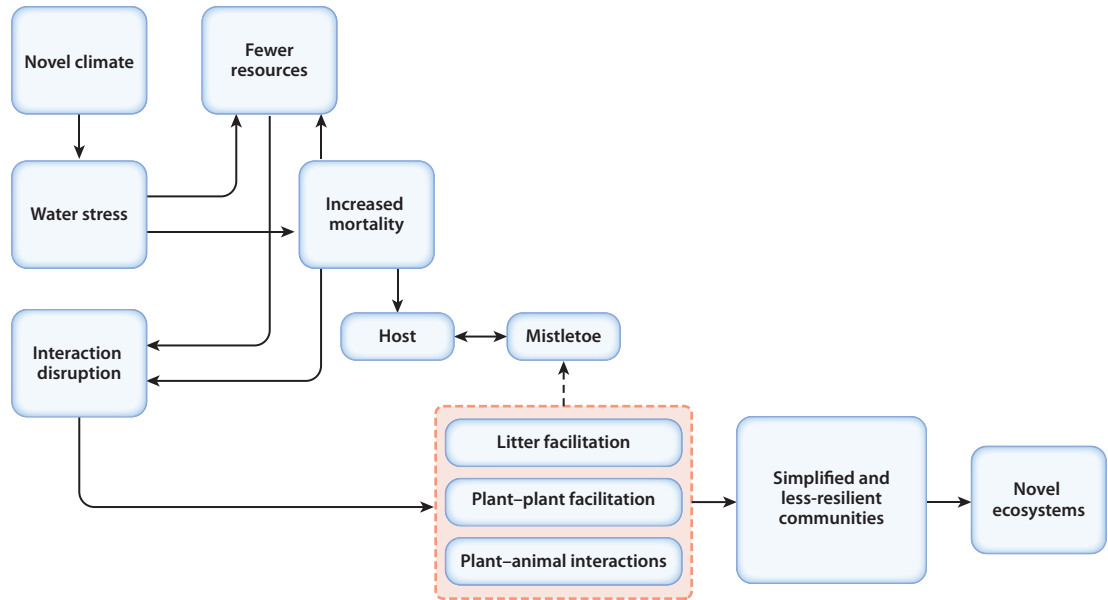


Figure 2

From novel climates to novel ecosystems: causal relationships of drought effects on mistletoes through their interactions with host plants and mutualists. Solid lines represent direct relationships, and the dashed line represents an indirect relationship. The dashed box represents the positive effects that mistletoes have on the environment through facilitation and mutualistic interactions.

Many climate-related impacts on parasitic plants are host mediated, with switches to novel hosts and associated range shifts already being observed. *Loranthus tanakae* is a mistletoe restricted to broad-leaved forests in Japan and the Korean peninsula that was recently observed switching to a novel host (*Ulmus davidiana*) in Hokkaido further north than previously recorded (Yamazaki

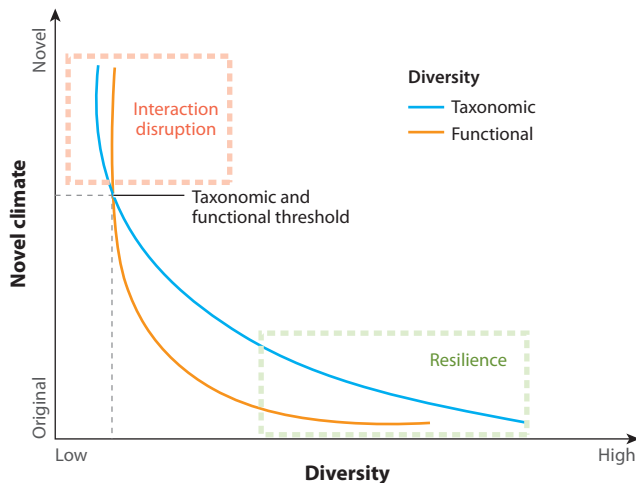


Figure 3

Taxonomic and functional thresholds of parasitic plant-driven interactions in the community as a result of novel climates. These relationships show how taxonomic and functional diversity is modified by climate change, with a tipping point (threshold) indicating that the loss of taxonomic diversity beyond that point causes cascading functional diversity loss.

et al. 2020). Comparisons of the two subspecies of *Viscum album* in Europe revealed subtle differences in freezing tolerance (Tikkanen et al. 2021). Coupled with host-mediated differences in growth rate and reproductive output, these differences are already apparent in montane forests in Spain, where distributional changes in *V. album* subsp. *austriacum* are associated with switching hosts and growing at increasingly higher elevations (Zamora & Mellado 2019). Parallel work in the center of diversity for the genus *Pinus* has noted climate-mediated changes in two species of dwarf mistletoe, with severe infections on the range-restricted *Pinus hartwegii* driving overall declines in tree health (Sáenz-Romero et al. 2020).

Given the facts presented in the last section, it is inevitable to ask: How long can mistletoes, their host plants, and their mutualists endure such severe climatic conditions? Sustained reduction in parasitic plant recruitment and survival would cause their functional extinction (Valiente-Banuet et al. 2015). If populations fall below a minimum threshold, the facilitation effects that these plants bring to the community will be disrupted. A similar situation is expected for flower and fruit production; if resource availability falls below a minimum threshold, mutualists will reconfigure their interactions and shift to different resources, move elsewhere, or die out. Parasitic plants with narrow host ranges are more likely to suffer direct effects of climate change (Reid & Lange 1988), with range-restricted taxa more sensitive to indirect effects like altered fire regimes (Start 2011); trait-based approaches are recommended to quantify the extinction threat (after Cizauskas et al. 2017).

The importance of one particular ecosystem function—the provision of microclimatic refuges that provide shelter from hot conditions—is likely to become increasingly important for ecosystems predicted to experience warmer and dryer climates (Reside et al. 2019, Scheffers et al. 2014). Parasitic plants may have a particular significance in this context due to their structure and associated attributes outlined in the section titled Microclimate and Habitat Structure. Crates et al. (2022), for example, found that mistletoes had a buffering effect on the degree to which drought impacted associated biodiversity. This is especially important in arid and semiarid landscapes that are predicted to become progressively more arid in the future. In addition, given the recent finding that climatic variables rather than photoperiod influence the phenology of some parasitic plants (Qaglia et al. 2020), early impacts might be expected for both pollinators and seed dispersers, affecting community-wide plant recruitment and cascading up through food webs to dependent biota (Figure 2).

FUTURE DIRECTIONS

Having synthesized research on the functional roles of parasitic plants, we are well placed to identify future research priorities—both knowledge gaps regarding the ecology and evolution of parasitic plants but also those larger open questions in the life sciences where parasitic plants would make model subjects. In terms of ecology, the number of interactions involving parasitic plants makes them ideal candidates for sensitive indicators of a wide range of ecosystem-scale stressors. Lacking storage organs, they are highly sensitive to fire, drought, heat waves, and frost. Therefore, fixed protocols for parasitic plant surveys to generate baseline metrics and repeat surveys at fixed sites or large-scale citizen-science initiatives would yield regular system-wide indices of a variety of impacts. Given the reliance of many nectarivore communities on parasitic plants, especially during periods of community-wide scarcity, we suggest they are a priority for targeted research on the recently discovered role of plant microbiome dynamics. Bacteria and yeasts have been recently discovered living within plant nectaries (Vannette & Fukami 2018) and modifying the volatiles used by pollinators to locate flowers (Klaps et al. 2020). Are those plants visited by a greater subset of a community's pollinators repositories of microbial diversity, and how do

changes in parasitic plant populations affect other plants with shared pollinators? How does the microbiome within flowers affect developing fruit, in terms of both attractiveness to dispersers and viability, and can this question yield new tools for controlling invasive species (after Masteling et al. 2019) or boosting declining populations? More broadly, do bacteria from animals visiting parasitic plants contribute to soil microbial diversity and function, further boosting their roles as facilitators?

Mistletoes, in particular, represent model parasites for further research, due in part to their tremendous variation in ecological traits displayed and in part to logistical simplicity. Just as it is possible to remove all mistletoes from entire woodlands (Watson & Herring 2012), target plants can also be experimentally inoculated with these aerial hemiparasites, enabling predictions to be rigorously tested regarding host preferences and disperser behavior (Lemaitre et al. 2012), competition and virulence (Nabity et al. 2021), and the role of climatic factors in constraining distributions (Smith & Wass 1979). Unlike most parasitic animals, mistletoes are readily observed and identified from afar, allowing range-wide studies of host use and detailed estimates of host range (Milner et al. 2020) and combining observed patterns with genetic data to study host switching and subsequent gene flow among host races (Yule et al. 2016). Recent revelations regarding genomic reductions in mistletoe (Lanfranco et al. 2018, MacLean et al. 2018, Petersen et al. 2015) also await broader comparative treatment to unveil genomic patterns associated with parasitism and specialization. With representative species across the spectrum from host generalists to specialists and with both holoparasitic and hemiparasitic representatives, the genera *Viscum* and *Tristerix* are ideal candidates for further work.

Now that robust phylogenies are available for all parasitic plants and life history traits are available for most taxa, numerous questions can now be addressed regarding the evolutionary origins of parasitism. Given the lack of reversibility of parasitism in plants, the fact that all five mistletoe families arose from root parasitic ancestors and that all instances of holoparasitism are associated with increasing specialization and reduced propensity to speciate, parasitic plants are ideal models to address questions about evolutionary trade-offs between ecological specialization and diversification and to explore the ecological contexts determining which traits underlie adaptive radiations versus evolutionary dead ends. These results would then inform fascinating contrasts with other taxa, including carnivorous plants where specific traits rather than broad growth habits might explain divergent evolutionary dynamics, parasitism in animals where reversibility is routine (Kilimov & Connor 2013), and the evolution of generalism in parasitoids (Stireman 2005).

Strategic research on parasitic plants can also help address other open questions in the life sciences. Are there generalized trade-offs between efficiency in resource use by constituent species and leakage from inefficient resource use within food webs? Are small-scale nutrient subsidies mediated by reallocation from sessile organisms and active transport by mobile organisms key determinants of diversity patterns across scales? In plants and other clonal organisms, what are the implications of functional individuals being composed of multiple genetic individuals? Are mutualisms better regarded as aberrant symmetrical instances within a dynamic spectrum of reciprocal exploitation? Do the nonconsumptive energetics of parasites make food webs more or less prone to trophic cascades? Whether being studied to answer focused questions about individual interactions or open-ended questions about ecosystems and evolutionary dynamics, parasitic plants are an intriguing group with much to offer inquiring minds.

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