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Mistletoe, friend and foe: synthesizing ecosystem implications of mistletoe infection

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Abstract

Biotic disturbances are affecting a wide range of tree species in all climates, and their occurrence is contributing to increasing rates of tree mortality globally. Mistletoe is a widespread group of parasitic plants that establishes long-lasting relationships with a diverse range of host tree species. With climate change, ecophysiological stress is increasing, potentially making trees more susceptible to mistletoe infection, which in turn leads to higher forest mortality rates.

The perception of mistletoe presence in individual trees and forest stands is divided within the scientific community, leading to an ongoing debate regarding its impacts. Forest managers concerned about stand health and carbon sequestration may view mistletoe as a foe that leads to reduced productivity. In contrast, ecologists may see mistletoe as a friend, in light of the wildlife habitat, biodiversity and nutrient cycling it promotes. However, individual studies typically focus on isolated effects of mistletoe presence within their respective research area and lack a balanced, interdisciplinary perspective of mistletoe disturbance.

With this conceptual paper we aim to bring together the positive and negative impacts of mistletoe presence on tree physiology, soil nutrient cycling as well as stand health and stand dynamics. We focus on the role of mistletoe-induced tree mortality in ecosystem succession and biodiversity. In addition, we present potential modifications of mistletoe presence on the energy budget and on forest vulnerability to climate change, which could feed back into stand dynamics and disturbance patterns. Lastly, we will identify the most pressing remaining knowledge gaps and highlight priorities for future research on this widespread agent of biotic disturbance.

1. Introduction

1.1. Disturbance impacts on forest ecosystems

Forest ecosystems contain 80% of aboveground carbon and 40% of belowground carbon stocks globally (Watson et al 2000) along with the capacity of storing carbon over centuries. Disturbances have the potential to alter ecosystem processes and functioning, yet they are part of the natural cycle of any ecosystem (Kulakowski et al 2017). Climate induced disturbances, such as heatwaves and droughts, can significantly lower carbon sequestration rates in forests (Reichstein et al 2013, Yi et al 2015, Yuan et al 2016) and cause wide-ranging tree mortality (McDowell et al 2011, Kara et al 2017). Similarly detrimental effects were reported from excessive wind-throw following storms and cyclones and increasing wildfires as the climate changes (Hutley et al 2013, Schoennagel et al 2017). Furthermore, such climate induced disturbances can weaken ecosystem resilience and alter the occurrence and life-cycle of biotic disturbances (Dukes et al 2009, Johnson et al 2010, Allen et al 2010, Scott and Mathiasen 2012), such as the recent bark beetle outbreaks that affected vast areas across western North America (Edburg et al 2012). Beetle-induced stand mortality can compromise atmospheric carbon sequestration rates (Brown et al 2010), but this has not been found in all cases (Reed et al 2014), indicating uncertainty in effects of biotic disturbance on carbon cycling.

While insect outbreaks and abiotic disturbances like drought, storm and fire often cause wide-spread stand mortality, the presence of parasitic plants is more...
subtle in modifying ecosystem processes and stand dynamics. Unlike cyclones and wildfires, which are not necessarily a threat in every climate region, parasitic plants are globally distributed and an integral component of most ecosystems (Mathiasen et al. 2008).

The relationship between the parasite and the host may reflect mutualism, e.g. vascular epiphytes rely on the structural support of a host plant and in return enhance nutrient cycling by fertilizing the soil with nutrient-enriched litter (March and Watson 2010, Bartels and Chen 2012). The largest group of aerial parasitic plants are mistletoes, which are widespread sap-feeding hemiparasites (i.e. capable of photosynthesis) that portray epiphytic behavior and belong to the order Santalales (Bell and Adams 2011). Over 1600 species of mistletoes world-wide have developed a remarkable range of adaptations for mimicking various morphological traits specific to their local hosts; at least 20 species are listed as endangered. Because mistletoes are long lived (exceeding 30 years) it can take decades to notice their damaging effect on the host (figure 1). The potential positive effects of mistletoe infection arise at the ecosystem scale, such as their ability to boost biodiversity, which has sparked a debate about the role of mistletoes as keystone species and ecosystem engineers (Press and Phoenix 2005, Hatcher et al. 2012, Watson and Herring 2012).

1.2. Mistletoe amplifies tree mortality

Mistletoe abundance has been increasing within existing distributions (Dobbertin and Rigling 2006, Bowen et al. 2009, Turner and Smith 2016), and exacerbation of climatic stress in the form of prolonged droughts has amplified tree mortality rates in mistletoe infected forests (Mathiasen et al. 1990, Dobbertin and Rigling 2006, Way 2011, Sangüesa-Barreda et al. 2012, Kolb et al. 2016, Mutlu et al. 2016). Future climate change is projected to increase the likelihood, frequency and duration of droughts in many ecosystems (Collins et al. 2013), so we must understand the physiological causes, the amplifying role of biotic agents on ecosystem processes and the resulting consequences of this trend (McDowell et al. 2011). This is increasingly complex as parasitic infection on its own is rarely lethal; rather, a combination of multiple stress factors exaggerates stand mortality rates.

Tree mortality after extreme droughts typically indicates that cavitation is the predominant process causing mortality, but native trees in hot and arid climates (such as Australia) are more adapted to drought so that carbon starvation following stomatal regulation might contribute to tree death during prolonged droughts. This is a long-standing debate (McDowell et al. 2008, Sala et al. 2010, Sevanto et al. 2014), and the parasitic and unregulated water use of mistletoes will likely contribute to both processes at its host: exaggerating vessel cavitation might ultimately result in failure of the hydraulic transport system, as well as induce carbon starvation by limiting carbon availability (see section 2). Carbon limitation can be provoked on multiple pathways, such as (i) the acquisition of heterotrophic carbon from the host, (ii) the restriction of photosynthetic carbon gain through inducing increased stomatal regulation and (iii) through failures in the hydraulic system which might impair carbon transport from storage reserves. However, process-based research focused predominantly on the functional understanding of parasite infection on the leaf-level scale (e.g. Mathiasen et al. 2008, Bell and Adams 2011), and we are increasingly recognizing the multifunctional role of mistletoe in communities and ecosystems (e.g. Watson 2001, Press and Phoenix 2005, Hatcher et al. 2012). A holistic view on mistletoe infection is often missing, as we are still limited in our ability of scaling
functional relationships to the ecosystem level and in understanding how changes in functional relationships are regulating biodiversity. Thus, the role of mistletoe as a friend or foe depends on the respective research focus, so we consider it necessary to reconcile mistletoe infection in a holistic approach to assess ecosystem and biodiversity consequences under a changing climate.

2. Process modification through mistletoe infection

Mistletoes have been studied across a large range of ecosystems (see e.g. Mathiasen et al 2008, Bell and Adams 2011), and the process of host infection is similar for all mistletoe species: the mistletoe attaches to a branch, forming a haustorium, and taps into the xylem of the host tree. When mistletoes are well established they can significantly modify the functional processes of the host tree; the links between the carbon, nutrient, water and energy cycles are conceptualized in figure 2.

2.1. Carbon and nutrient cycling

Among the most obvious effects on mistletoe infected stands are reductions in stand basal area and stand volume, which are the result of retarded growth rates of infected trees (Reid et al 1994, Carnegie et al 2009, Sangüesa-Barreda et al 2012). While mistletoe leaves are capable of photosynthesizing and producing basic sugars, they typically have lower photosynthesis rates than their hosts, and many mistletoe species acquire large amounts of heterotrophic carbon from the host phloem sap to allow expansion of the mistletoe leaf area (Lamont 1983, Marshall et al 1994, Matsubara et al 2002, Mathiasen et al 2008). This reduces carbon availability for the host tree, which leads to reduced growth rates and reductions in host leaf biomass (Meinzer et al 2004, Rigling et al 2010, Agne et al 2014, Raftoyannis et al 2015). Such degradations of the host canopy will further reduce carbon assimilation rates and deplete the non-structural carbohydrate reserves of the host tree (Rigling et al 2010, Yan et al 2016).

Because of their fast growth rates and short leaf lifespan (Reid and Stafford Smith 2000, March and Watson 2007), mistletoes also deprive the host of its nutrients which accumulate in the parasite leaves (March and Watson 2010, Galiano et al 2011). However, an increase in nutrient-rich mistletoe litter deposition has a fertilization effect on the soil by enhancing decomposition rates through high-quality substrate provision that increases microbial activity and microbial community size (March and Watson 2007, Mellado et al 2016). This, in combination with increased light penetration, increases soil carbon and nutrient cycling and may boost ecosystem productivity by increasing understory diversity (March and Watson 2007, Watson 2009). We speculate that mistletoe infection may enhance microbial carbon use efficiency and lead to increases in soil respiration through either increased light penetration (host) or increased microbial activity (parasite; figure 2).

2.2. Water and energy cycling

In order to acquire carbon, water and nutrients from the host, mistletoe leaves generally maintain lower xylem water potentials than host leaves (Ehleringer et al 1985, Pate 2001, Strong and Bannister 2002). To achieve this mistletoes increase their stomatal conductance and maintain higher transpiration rates than
the host leaves (Davidson et al 1989, Marshall et al 1994, Canyon and Hill 1997, Cernusak et al 2004). Continuous sap-flow measurements in Pinus sylvestris trees revealed that the host trees compensate for the additional water loss by reducing host transpiration rates via stomatal regulation (Zweifel et al 2012). Thus, along with reduced photosynthetic rates of the parasite, this results in a markedly decreased water use efficiency (WUE) of mistletoes compared to their hosts (Davidson and Pate 1992, Küppers et al 1992, Miller et al 2003, Sangüesa-Barreda et al 2013). Changes in transpiration rates will likely outweigh changes in soil evaporation rates, which may accelerate with increasing light penetration, or decrease with the built up of mistletoe leaf litter. Thus, evapotranspiration is expected to increase with mistletoe infection but to decrease from the host tree perspective (figure 2).

Furthermore, modifications in the water cycle with parasite infection will ultimately alter the energy balance, since reductions in latent heat flux (LE) are counteracted by increases in sensible heat flux (H). Thus, we anticipate that increases in LE with mistletoe infection will decrease the Bowen ratio (BR = H/LE) due to the inherent and above-mentioned parasitic traits, and to increase it through modification of the functional processes of the host tree.

3. Temporal modifications of ecosystem processes through mistletoe infection

Mistletoe infection is a dynamic process that continuously modifies stand dynamics over time with progressively increasing infection rates, potentially leading to increases in tree mortality. The process changes during the parasitic life cycle and their impacts from branch to stand dynamics are summarized in figure 3.

At first the effects of parasite establishment are limited to individual branches, where germination and early growth of the mistletoe seedling increases branch leaf volume through the addition of mistletoe leaves. The mistletoe leaves increase the host’s branch conductivity and lower their water potential to maintain high transpiration rates and to accumulate water, carbon and nutrients from the host. The increase in branch transpiration results in a marginal increase in latent heat flux, along with a marginal decrease in sensible heat flux through increased shading from the mistletoe leaf area.

The parasitic life cycle is optimized for longevity. The mistletoe broom is well established and flowering about a year after infection, while diameters can exceed a meter within the first couple of years (Reid and Stafford Smith 2000, Carnegie et al 2009). Mistletoe dispersers (typically birds, see biodiversity section) will distribute the seeds within the tree and to neighboring trees (Ward and Paton 2007, MacRaid et al 2010). Increasing the mistletoe load on individual trees will start to show notable effects on the host tree after a few years, as described in figure 2. These can be detrimental for young trees, which due to their small canopy volume seem especially vulnerable to mistletoe infection (Carnegie et al 2009). At this early infection stage initial impacts on biodiversity can be noted, as the mistletoe brooms provide favorable nesting sites and food resources for woodland dependent species (Watson 2002, Cooney and Watson 2005, Barea 2008, Napier et al 2014).
Within the next decade, seed dispersers spread the infection from highly infected individuals across the stand (Ward and Paton 2007). At this time step highly infected trees lose vigor, as the canopies increasingly show signs of degradation (Meinzer et al 2004, Raftoyannis et al 2015). The reduction in live canopy area leads to a reduction in stand transpiration rates and an increase in soil evaporation through increased light penetration. Likewise, partitioning of available energy transitions from latent heat flux towards sensible heat flux. The increase in nutrient cycling and light availabil-
ity enhances floral biodiversity, while faunal diversity is enhanced through the increased availability of mistletoe fruits and shelter (Cooney and Watson 2005, Bowen et al 2009, Watson 2009).

On time scales of ten years or more, stands lose resilience and infection rates within localized pockets can reach high enough levels to increase individual tree and stand mortality rates if the unregulated water use during adverse climate conditions cause excessive water stress on the host tree (Dobbertin and Rigling 2006, Carnegie et al 2009, Scott and Mathiasen 2012, Zweifel et al 2012). Multiple tree deaths can potentially modify the water and energy balance to a point that successional and stand dynamics are affected. Mistletoes are predominantly present on dominant and codomi-

nants trees (Worrall et al 2005, Agne et al 2014), which initiates highly localized gaps after affected trees die. However, these small gaps can decrease tree competition through natural thinning in the long term (Millar et al 2007). In addition, an increase in gap distribution typically has positive impacts on biodiversity, and in recent years the role of parasitic plants as ecosystem engineers is increasingly being acknowledged (Hatcher et al 2012).

4. Mistletoe increases biodiversity

Although representing a minor canopy constituent in terms of abundance and biomass, mistletoe contributes disproportionately to species richness, community composition and overall ecosystem function. These effects arise from augmented resource provision (nectar, fruit and foliage), increased structural complexity (associated with the growth habit of the mistletoe itself and/or changes to morphology of infected hosts and canopy architecture at tree and stand scales), and subsidies to food webs from increased rate of enriched litterfall and altered litter inputs from infected hosts at the stand scale. Having synthesized recent work documenting these three classes of direct effects, we review additional research quantifying interactive and indirect effects of mistletoe on biodiversity emphasizing how the influence of mistletoe may intersect with climate change.

As semi-succulent plants with few structural and chemical defenses reliant on animal pollinators and seed dispersers, mistletoes are an important food source for many animals (Watson 2001, Mathiasen et al 2008). Like other parasitic plants, mistletoe tissues characteristically contain higher nitrogen, phosphorus and potassium concentrations than their hosts (March and Watson 2010, Mellado et al 2016), and are preferentially browsed by many herbivores (Canyon and Hill 1997, Shaw et al 2004). Browsing herbivores may constrain mistletoe abundance, especially in arid ecosystems with standing water. As well as a reliable source of water (Walsberg 1977), especially in arid areas where water is unavailable seasonally. Although most research has focused on vertebrates, a large number of arthropod groups have been found associated with mistletoe (Anderson and Braby 2009, Burns et al 2015), both as pollinators and specialist herbivores, with one recent study (Fadini et al 2014) documenting a three way interaction of selective predation of mistletoe seeds on one of several potential host species, resulting in a post-dispersal containment of the parasite.

Most mistletoe lineages have a densely-branched growth habit (known as witches’ brooms), representing distinct structural elements in forest canopies that are used by many animals for shelter, roosting, nesting, hibernating or hiding from predators. This increased structural heterogeneity coupled with the high water content of mistletoe tissues generates a distinct microclimate, and Cooney (2004) (see also Cooney and Watson 2005, Ndagurwa et al 2016) demonstrated within various locations of a woodland canopy that mistletoes were consistently more humid and cooler than comparable sites within Eucalypt foliage, differences in both temperature and humidity becoming greater as ambient temperatures increased. As safe places to raise young, nocturnal animals with lower tolerances to high temperatures seek out mistletoes and mistletoe infected trees for nesting (e.g. Rockweit et al 2012) and shelter during hot weather (figure 1). Even dead mistletoes represent important structural elements for forest and woodland animals, with branch mortality and eventual loss an important mechanism for hollow development. In some systems where mistletoe-induced host mortality drives successional change in even-age stands (Shaw et al 2004, Mellado et al 2016), ‘mistletoes constitute a disrupting force of the frequently assumed equilibrium dominating late stages of ecological succession, where the parasite follows a different successional trajectory from that of the non-parasitized matrix, increasing landscape heterogeneity in space and time’ (Mellado and Zamora, in press).
As with other parasitic plants, mistletoe generate large amounts of nutrient-enriched litter, precipitating a cascading series of facilitative interactions beneath infected hosts. Convergent findings in Australian eucalypt woodlands, African acacia savannah and European pine forests suggest a generalized role of mistletoes as facilitators (reviewed by Watson 2016). In addition to re-allocating nutrients from infected hosts and shedding litter over a longer duration, the addition of mistletoe litter accelerates decomposition of recalcitrant host litter, thereby boosting nutrient availability. These effects have been noted in epigeic arthropods (Ndagurwa et al 2014), understorey plants (March and Watson 2010), seedling growth (Mellado and Zamora, in press), and fungal diversity (Mueller and Gehring 2006).

While these above- and belowground interactions are often studied in parallel, they interact at multiple scales to catalyze successional change and increase the quality of forested habitats for a wide range of biota. The most clear-cut example of these effects is a patch-scale removal experiment that compared eucalypt woodlands before and after all mistletoes were removed relative to a set of otherwise comparable woodlands with either no mistletoe or representative mistletoe abundances (Watson and Herring 2012). Three years after mistletoes were removed from woodland canopies, the richness and incidence of birds decreased by up to 36%, with treatment effects most pronounced for ground-foraging insectivores (Watson 2015). While some of these losses arose from local extirpations post removal, most of the experimental effect was due to interactions with a severe drought that coincided with the removal phase of the experiment. Once drought conditions ameliorated, those control woodlands (with mistletoe) rebounded, receiving more than twice the proportion of woodland-dependent species and ground foraging insectivores than treatment woodlands (with no mistletoe; Watson 2015). This complex interaction between mistletoe occurrence and climatic variation provides direct support for Watson’s (2001) hypothesis that mistletoe buffers the effects of drought and other stochastic events on biodiversity via provision of a suite of limiting resources, thereby increasing community resilience.

5. Priorities for future research

We synthesized how mistletoe infection typically modifies the functional processes of its host tree and how mistletoe infection affects stand dynamics, species occurrence and animal behavior with time. We highlighted recently established links between an increase in tree mortality rates following mistletoe infection and prolonged drought, which is anticipated to worsen in many ecosystems under the predicted changes in climate. Nonetheless, parasite induced tree mortality rarely damages the entire stand, but rather initiates localized gaps that have positive effects for floral and faunal biodiversity, leading to a positive perception of mistletoe parasites as ecosystem engineers. Next, we highlight the most promising approaches to monitor and manage infected stands and conclude with suggestions for future research that examines the link between mistletoe infection and tree mortality.

5.1. Promising monitoring and management approaches

Monitoring of mistletoe populations remains tedious and labor intensive, as it predominantly relies on manual inventories (Carnegie et al 2009, MacRaid et al 2010, Turner and Smith 2016). Remote sensing techniques such as combining hyperspectral imaging spectrometry with LiDAR or airborne surveys might allow mapping of distributions on the landscape level, if mistletoe leaves differ notably in their properties from host leaves (Ancic et al 2013, Barbosa et al 2016, figure 1). However, these landscape-scale assessments of mistletoe abundance are still in development, and although these approaches are promising, they still require testing across a larger range of ecosystems. Another approach might be the use of targeted models that either predict the host range and distribution of mistletoe colonies or the distribution patterns of seed dispersers. The prediction of future population dynamics might then allow for planning and implementing of targeted and timely management strategies to control the distribution of the mistletoe population (Watson et al 2017).

The contrasting perception of mistletoe as either friend or foe is also reflected in highly contrasting management approaches. Selective removal of mistletoe clumps is still practiced in heavily infested stands, where a once-off removal can benefit stand productivity for over a decade (Maffei et al 2016). Fungi can act as a successful biological control agent for mistletoe (Reid and Shamoun 2009, Varga et al 2012), and prescribed burning or wildfires in Australia have been demonstrated to reduce mistletoe abundance (Shaw et al 2004, Start 2011, 2013, 2015). However, the importance of mistletoe as a keystone resource for wildlife is widely acknowledged (Watson 2016 and references therein), with land managers increasingly retaining mistletoe to improve habitat quality for threatened species or to enhance ecosystem function (Norton and Reid 1997, Mellado et al 2016). Whether the goal is to suppress or promote mistletoe infection, attacking the causes of over-proportional mistletoe distribution might allow for longer-term solutions. This could be achieved through implementing environmental planning strategies that reduce land degradation and thus increase wildlife and natural enemies, or to identify and plant infection-resistant host species in order to contain the spatial distribution through seed dispersers (Norton and Reid 1997, MacRaid et al 2010).
5.2. Remaining knowledge gaps

The general link between parasitic infection and increased tree mortality rates is well established and the modifications of host processes following mistletoe infection are increasingly well understood. However, we are still limited in identifying the critical mechanisms that link parasite infection and tree mortality. This remains complex due to the combination of multiple stress factors, since climate change and mistletoe infection can exaggerate stand mortality rates individually and in combination. Within recent years, a number of studies demonstrated a clear link between parasite infection and prolonged drought on increasing tree mortality rates, but it remains unresolved whether hydraulic failure, carbon starvation or a combination of both processes are amplifying mortality rates. In addition, mistletoe interacts with other biotic disturbances (such as insects, pathogens and herbivore browsing), which apart from potentially increasing biodiversity also leads to increased tree mortality. Hence, it will be essential to design targeted studies that focus on deciphering and quantifying these processes and to identify critical thresholds that cause trees to die as projections of increasing climatic stress on most ecosystems will likely increase mortality rates of infected stands. Finally, it will be critical to improve our capabilities of automated spatial mapping and ongoing monitoring of stand health dynamics to enable targeted management strategies and to identify the onset of potential large-scale mortality events as early as possible.

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