Mistletoe, Friend and Foe; Synthesis on 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. Over 1300 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. With climate change, ecophysiological stress is increasing, potentially making trees more susceptible to mistletoe infestation, 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 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 will focus on the implications of mistletoe-induced tree mortality on changes in stand succession and implications for biodiversity. In addition, we will 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.

## Keywords

mistletoe, mortality, climate change, biodiversity, disturbance, parasitic plants

## Introduction

### Background on biotic tree mortality

Forests ecosystems have large economical values, as they contain 80% of aboveground carbon and 40% of belowground global carbon stocks (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). Climatic induced disturbances, such as heatwaves and droughts, can significantly lower carbon sequestration rates in forests (Yuan *et al* 2016, Yi *et al* 2015, Reichstein *et al* 2013) and cause wide-ranging tree mortality (Kara *et al* 2017). Similarly detrimental effects were reported from cyclones and an increase in 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 such as pest and insect outbreaks(Dukes *et al* 2009, Johnson *et al* 2010, Allen *et al* 2010, Scott and Mathiasen 2012), the most prominent being the bark beetle outbreaks that affected vast areas across the central and western United States. However, while the latter caused a substantial increase in stand mortality (almost 80%), atmospheric carbon sequestration rates remained unchanged (Reed *et al* 2014), indicating potential for a substantial mis-match between changes in stand dynamics and carbon cycling.

While insect attacks and large-scale disturbances like cyclones and wildfires often cause wide-spread stand mortality, the presence of parasitic plants is typically less obvious as they are slower and more subtle in modifying ecosystem processes and stand dynamics. And unlike cyclones and wildfires, which are concentrating in lower latitudes and 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 is often symbiotic, 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 (Bartels and Chen 2012, March and Watson 2010). The largest group of areal parasitic plants are mistletoes, which are widespread hemiparasites that portrait epiphytic behaviour and belong to the order of Santalales (Bell and Adams 2011). However, mistletoes are long lived (exceeding 30 years) and it can take decades to notice their damaging effect on the host. This resulted in an increasing number of studies examining potential positive effects of mistletoe infestation beyond the parasite-host symbiosis, and their ability to boost biodiversity in e.g. bird and understory species richness 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).

Recent reviews concatenated our current state of knowledge on the the functional relationships between parasitic plants and their hosts (e.g. Bell and Adams 2011, Mathiasen *et al* 2008) and the effect of parasitism on community processes and biodiversity (e.g. Hatcher *et al* 2012, Watson 2001, Press and Phoenix 2005). However, a number of studies reported a recent increase in mistletoe abundance within existing distributions (Dobbertin and Rigling 2006, Bowen *et al* 2009, Turner and Smith 2016), and increasing evidence emerges that exacerbation in climatic stress amplified tree mortality rates in mistletoe infested forests (Way 2011, Dobbertin and Rigling 2006, Kolb *et al* 2016, Mutlu *et al* 2016, Sangüesa-Barreda *et al* 2012, Mathiasen *et al* 1990). Overall, most process-based research focused predominantly on the functional understanding of parasite infestation on the leaf-level scale. This often presents just a snapshot in time, and we are just starting to recognize the dryad role of parasites in biodiversity through the provision nesting sites and food resources for woodland dependent species (Watson 2002, Napier *et al* 2014, Barea 2008, Cooney and Watson 2005). The link between both 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, parasites being friends or foes depends on the respective research focus, so we consider it necessary to reconcile mistletoe infestation in a holistic approach to assesses the winners and losers of parasite infection under a changing climate.

## Modifications of functional processes through mistletoe infestation

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 mistletoes: the mistletoe attaches to a branch and taps into the xylem of the host tree. When mistletoes are well established they can notably modify the functional processes of the host tree, and the links between the carbon, nutrient, water and energy cycle are conceptualized in Figure 1.

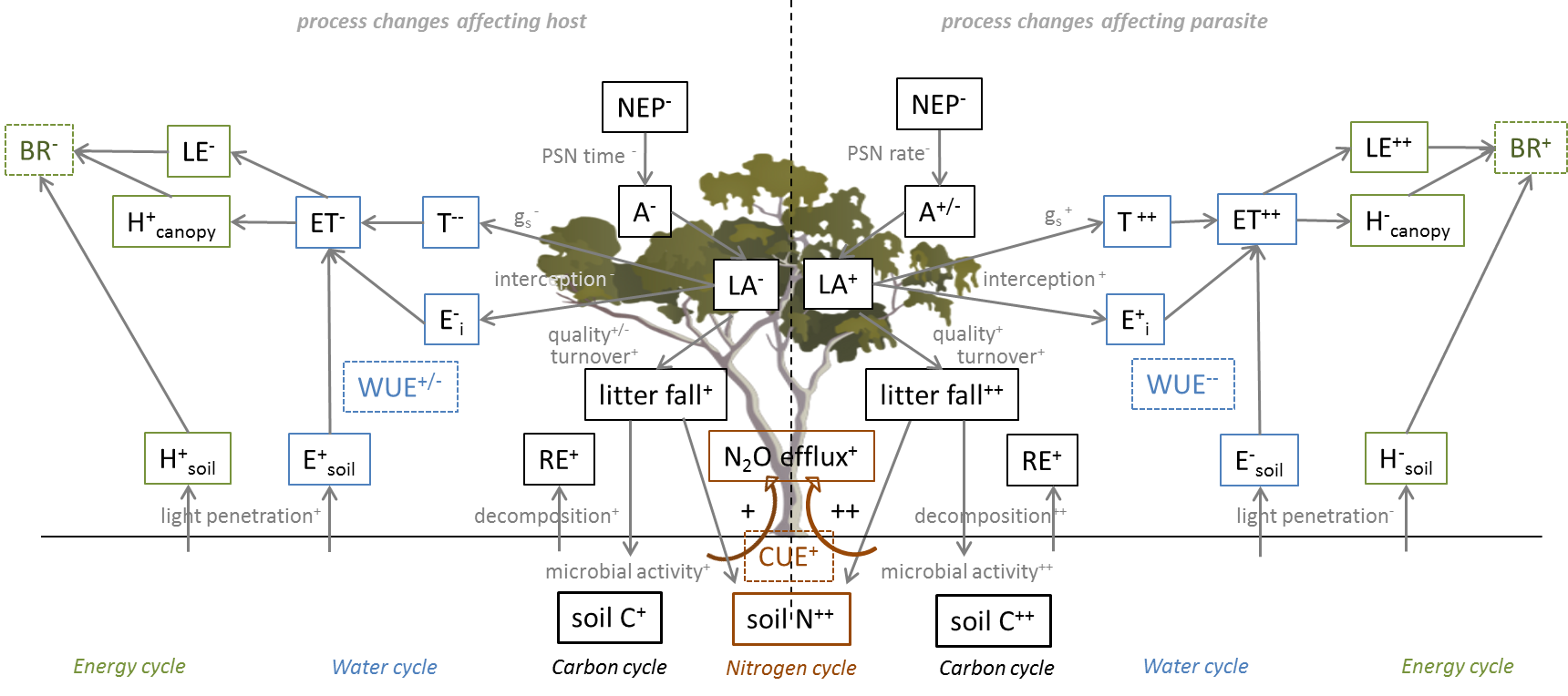


Figure 1. Comparison betweent the modification of functional relationships at the parasite and a eucalypt host and how these affect the nitrogen, carbon, water and energy cycles. Note that this figure is a simplification to conceptualize the process changes at the host (left side) and at the parasite (right side) of a moderatly infested tree with ca. 50% parasite and 50% host foliage remaining, while in reality the mistletoe brooms will be mixed within the host's canopy. Abbreviations are as follows: NEP=Net ecosystem productivity, A=Assimilation, PSN=Photosynthesis, gs=Stomatal conductance, RE=Ecosystem respiration, E=Evaporation, T=Transpiration, Ei=Interception loss, ET=Evapotranspiration, H=Sensible heat flux, LE=Latent heat flux, BR=Bowen ratio, CUE=Carbon use efficiency, WUE=Water use efficiency.

### Carbon and nitrogen 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 (Carnegie *et al* 2009, Reid *et al* 1994, Sangüesa-Barreda *et al* 2012). While mistletoe leaves are capable of photosynthesizing and producing basic sugars, they have typically lower photosynthesis rates than their hosts, and they acquire large amounts of heterotrophic carbon from the host xylem sap to allow expanding the mistletoe leaf area (Lamont 1983, Matsubara *et al* 2002, Marshall *et al* 1994, Mathiasen *et al* 2008). This reduces carbon availability for the host tree, which is typically compensated with reduced growth rates and reductions in host leaf biomass (Raftoyannis *et al* 2015, Meinzer *et al* 2004, Agne *et al* 2014, Rigling *et al* 2010). Such degradations of the host canopy will further reduce carbon assimilation rates, primary productivity and increase the depletion of the nonstructural carbohydrate reserves of the host tree (Yan *et al* 2016, Rigling *et al* 2010).

The carbon and the nutrient cycle are closely coupled, as mistletoes also deprive the host of its nutrients which are then accumulated in the parasite leaves (Galiano *et al* 2011, March and Watson 2010). Mistletoe presence increases the cycling of dead matter through either degrading the canopy of the host or through faster turnover rates of mistletoe leaves, especially in evergreen trees where leaves have a multi-year lifespan. However, an increase in nutrient-rich mistletoe litter turnover has a fertilization effect on the soil by enhancing decomposition rates through 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 nitrogen cycling and boosts productivity by notably increasing understorey species richness (March and Watson 2007, Watson 2009). Hence, mistletoe infestation indicates an increased microbial carbon use efficiency (CUE) albeit likely increases in soil respiration through either increased light penetration (host) or increased microbial activity (parasite).

### 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 (Canyon and Hill 1997, Cernusak *et al* 2004, Marshall *et al* 1994, Davidson *et al* 1989). 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, Sangüesa-Barreda *et al* 2013, Miller *et al* 2003, Küppers *et al* 1992). Changes in transpiration rates will likely outweigh changes in soil evaporation rates, which are partly anticipated to accelerate with increasing light penetration, or to decrease with the built up of mistletoe biomass. Thus, evapotranspiration is expected to increase with mistletoe infestation but to decrease from the host tree perspective.

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

## Temporal modifications of ecosystem processes through mistletoe infestation

In the above paragraph we described the parasite induced functional changes within a snapshot in time when mistletoe occupied about 50% of the canopy. However, mistletoe infection is a dynamic process that continuously modifies stand dynamics over time with progressively increasing infection rates. The process changes during the parasitic life cycle and their impact from branch to stand dynamics are summarized in Figure 2.

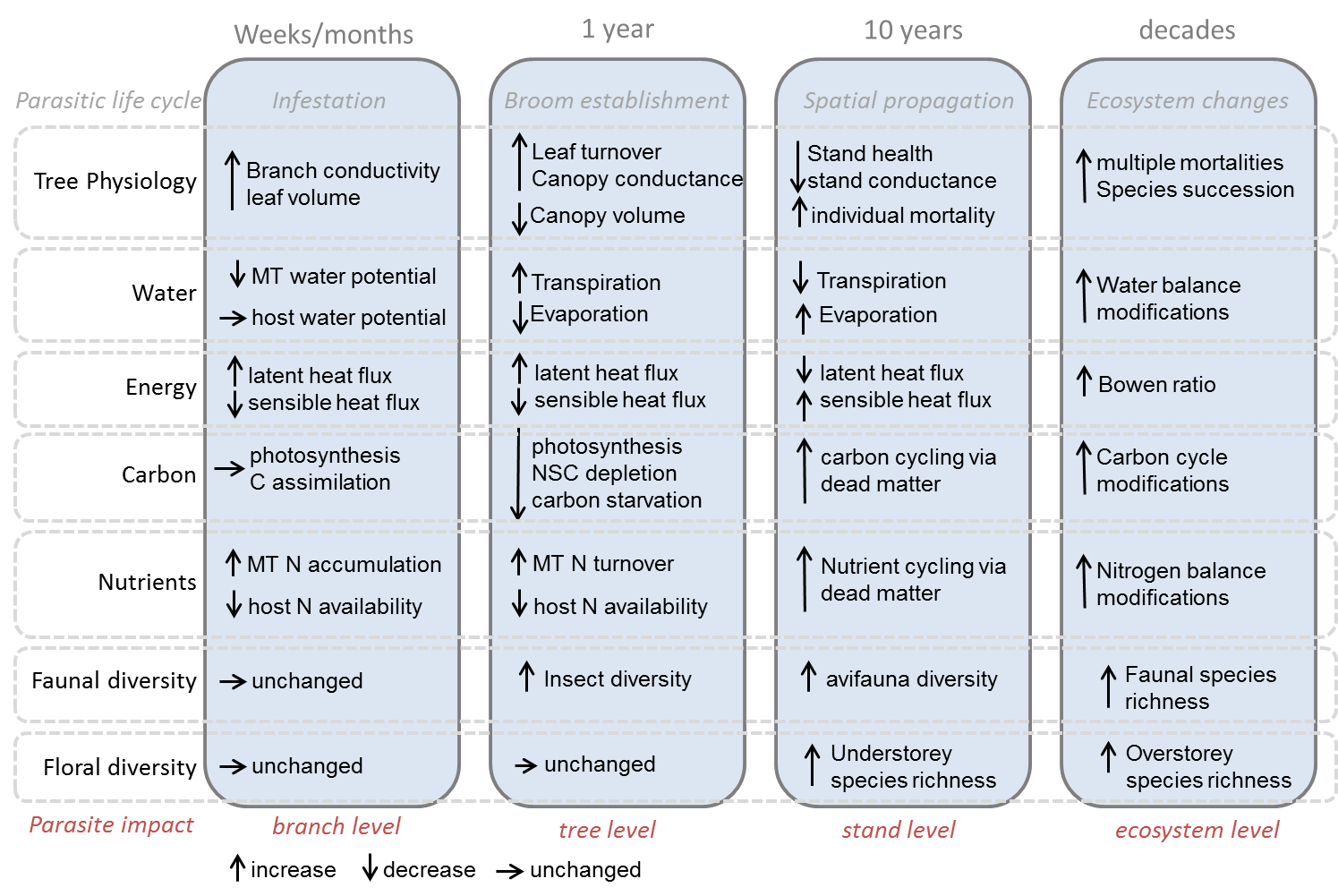


Figure 2. Conceptual figure indicating the temporal dynamics of mistletoe infection from the branch to the ecosystem level with a focus on tree phsysiology, matter and energy fluxes, and floral and faunal diversity.

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 energy 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, where 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 neighbouring trees (Ward and Paton 2007, MacRaild *et al* 2010). Increasing the mistletoe load on individual trees will start to show notable effects on the host tree, as described in Figure 1. These can be already detrimental for young trees, which due to their small canopy volume seem especially vulnerable to mistletoe infection (Carnegie *et al* 2009). At this infection stage initial impacts on biodiversity can be noted, as the mistletoe brooms provide favourable nesting sites and food resources for woodland dependent species (Watson 2002, Napier *et al* 2014, Barea 2008, Cooney and Watson 2005).

Within the next decade, seed dispersers spread the infection from individual highly infested clusters across the stand (Ward and Paton 2007). At this time step highly infected trees are losing vigour, as the canopies are increasingly showing signs of degradation and the carbon and nitrogen cycling transitions towards dead matter cycling (Raftoyannis *et al* 2015, Meinzer *et al* 2004). The reduction in live canopy area follows a reduction in stand transpiration rates and an increase in soil evaporation through increased light penetration. Likewise, latent heat flux transitions towards sensible heat flux. However, the floral biodiversity increases markedly through the alternation in nutrient cycling and light availability, as does the faunal diversity through the increased availability of mistletoe fruits and shelter (Cooney and Watson 2005, Watson 2009, Bowen *et al* 2009).

When a stand is loosing resilience and external events further affect tree health, then infection rates within localized pockets can reach high enough levels to increase individual tree and stand mortality rates (Carnegie *et al* 2009, Dobbertin and Rigling 2006, Scott and Mathiasen 2012). Multiple tree deaths can potentially modify the water and energy balance to a point that species succession dynamics can alter stand dynamics. Mistletoes are predominantly present on dominant and codominant trees (Worrall *et al* 2005, Agne *et al* 2014), which initiates highly localised gaps after affected trees die. However, these small gaps can increase stand resilience 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).

## Mistletoe and biodiversity

David will talk about this.

## 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 with time. We highlighted recently established links between a global increase in tree mortality rates following mistletoe infection and prolongued drought, which is anticipated to worsen in many ecosystems under the predicted changes in climate. Nonetheless, parasite supported tree mortality is rarely damaging the entire stand, but rather initiates localized gaps that have positive effects for floral and faunal biodiversity, leading to an increase 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.

### Promising monitoring and management approaches

Monitoring of mistletoe populations and population dynamics remains tedious and labour intensive, as it predominantly relies on manual inventories (Carnegie *et al* 2009, MacRaild *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 (Barbosa *et al* 2016, Ancic *et al* 2013). However, these landscape-scale assessments of mistletoe mapping are still in development, and although these approaches are promising, they require significantly more 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 widely in heavily infested stands, where a once-off removal can benefit stand productivity for over a decade (Maffei *et al* 2016). Funghi can act as a successful biological control agent for mistletoe (Varga *et al* 2012, Reid and Shamoun (2009)), whereas prescribed burning or wildfires in Australia act as a successful natural control agent (Shaw *et al* 2004, Start 2011, 2013, 2015). However, the role of mistletoe as a keystone species has been increasingly acknowledged (Watson 2016), and mistletoes are now also managed for conservation biodiversity in some regions of the world (Norton and Reid 1997). For both positions, attacking the causes of over-proportional mistletoe distribution might allow for a longer-term solutions. This could either be achieved through implementing environmental planning strategies that either reduce land degradation and thus increases wildlife and natural enemies, or to identify and plant resistant species in order to contain the spatial distribution through seed dispersers (Norton and Reid 1997, MacRaild *et al* 2010).

### Remaining knowledge gaps

The link between parasitic infestation and increased mortality rates is well established and the modifications on host processes following mistletoe infection are increasingly well understood. However, we are still limited in identifying the critical processes that link parasite infection and tree mortality rates. This is increasingly complex as parasitic infection on its own is rarely lethal, and it's often the combination of multiple stress factors that exaggerates stand mortality rates. Within recent years, a number of studies demonstrated a clear link between parasite infection and prolongued drought on increasing tree mortality rates. Tree mortality after extreme droughts might indicate that cavitation is the predominant process causing mortality, while native trees in hot and arid climates (such as Australia) are more adopted to drought and thus carbon starvation following stomatal regulation might become the predominant role for tree death. This is a long-standing debate, but future research needs to focus on deciphering the critical thresholds that causes trees to die as projections of increasing climatic stress on most ecosystems will likely increase mortality rates of infected stands. In addition, 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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