Mistletoe, Friend and 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, biodiversity, mortality, climate change, ecosystem processes

# 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 and Climate Change. 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 sublte 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 itegral component of most ecosystems. The relationship between the parasite and the host is often symbiotic, e.g. vasucluar epiphytes rely on the structural support of a host plant and in return enhance nutrient cycling by fertilizing nutrient-enriched litter to the soil (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 longlived (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).

Increasing evidence emerges that these climatic dynamics, in addition to parasitic infestation, further increase host stress and exacerbate 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). On the other hand, mistletoe induced mortality is selecting typically dominant/codominant trees(Worrall *et al* 2005, Agne *et al* 2014), which initiates highly localised and comparably small gaps that in return can modify biodiversity dynamics and increase stand resilience through natural thinning in the long term (Millar *et al* 2007). 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, current research focussed predominantly on a process-based understanding of parasate infestation on the leaf-level scale that typically presents a snapshot in time, and we are just starting to reckognize the dryad role of parasites in biodiversity throught 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 and 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.

We will focus on mistletoe infestation in Australia as an example for parasite infection, since mistletoe is widespread throughout Australian ecosystems with a recent increase in mistletoe abundance within existing distributions in Australia (Bowen *et al* 2009, Turner and Smith 2016). In addition, the harsh Australian climate is already imposing regular heat and drought stress on many ecosystems that is expected to further increase in the coming decades, making this an ideal example of potential increases in tree mortality due to parasitic infestation 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 can be considered similar for all mistletoes: the mistletoe attaches to a branch and taps into the xlem 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 conceptualised in Figure 1.

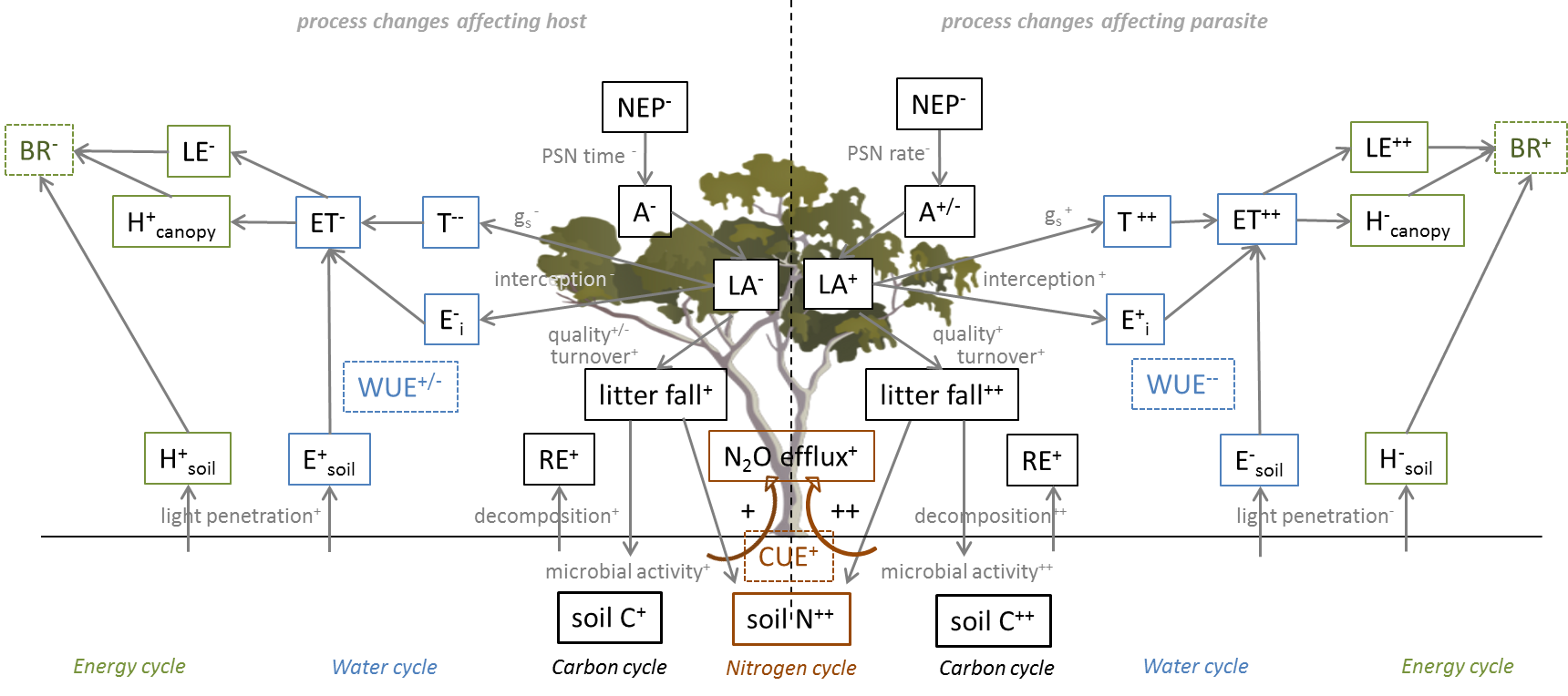


Figure 1. Comparison betweent the modification of functional relationships at the parasite and a eucalypt host and how these affect the nitrogen, carbon, water and energy cycles. Note that this figure is a simplification to conceptualize the process changes at the host (left side) and at the parasite (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 exchange, 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

Most obvious effects on 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). Mistletoe leaves are capable of photosynthesizing and producing basic sugars, however mistletoes have typically lower photosynthesis rates than their hosts and they acquire large amounts of heterotrophic carbon from the host xlem 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 availablity 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 further reduce carbon assimilation rates, primary productivity and lead to the depletion of the non structural 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 mistletoe 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, which boosted in productivity and lead to notable increases in understorey species richness (March and Watson 2007, Watson 2009). Hence, mistletoe infestation indicates towards an increase in 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 aquire carbon, water and nutrients from the host, mistletoe leaves generally maintain lower xlem 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). Along with reduced photosythetic rates, this results in a markedly decreased water use efficiecy (WUE) compared to its host (Davidson and Pate 1992, Sangüesa-Barreda *et al* 2013, Miller *et al* 2003, Küppers *et al* 1992). 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). Changes in transpiration rates will likely outweigh changes in soil evaporation rates, which are anticpated to accelerate with increasing light penetration and 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 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.

At first the effects 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 to maintain high transpiration rates and lower their water potential 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 and 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 section 3) 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 already be 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 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 availablity of mistletoe fruits and shelter (Cooney and Watson 2005, Watson 2009, Bowen *et al* 2009). If a stand is loosing resilience and if external events adversly 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. 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).

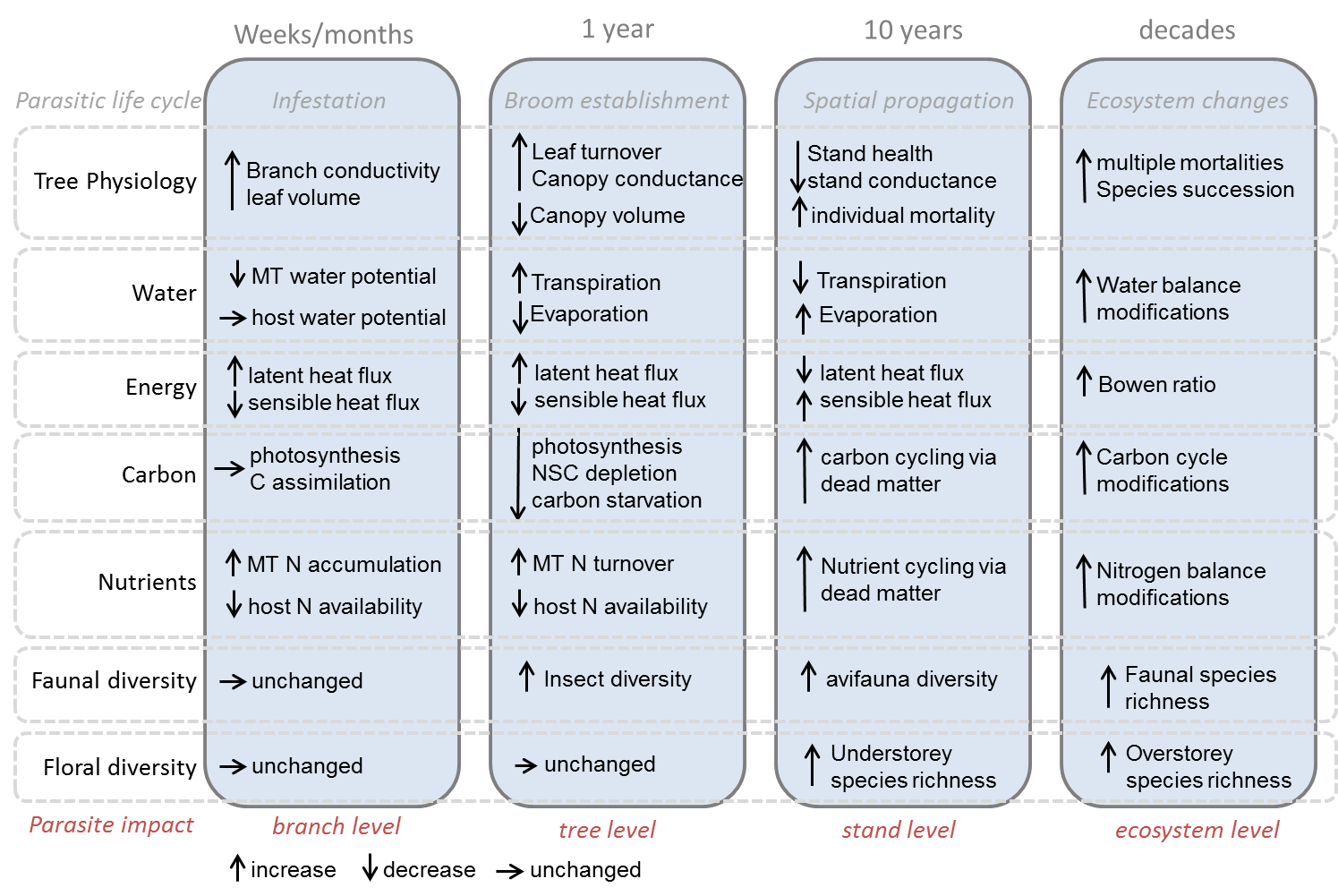


Figure 2. Conceptual figure indicating the temporal dynamics of mistletoe infection from the branch to the ecosystem level with a focus on tree phsysiology, matter and energy fluxes, and floral and faunal diversity.

# Mistletoe and biodiversity

David will talk about this.

## Priorities for future research

Fungal control of mistletoe successful biological control agaent for european mistletoe (Varga *et al* 2012)

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