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. 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.

# Temporal dynamics of mistletoe infestation

## Life cycle and traits of a mistletoe plant

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. The parasitic life cycle is optimized for longevity, where the mistletoe broom is well established and flowering about a year after infection (Figure 1; Reid and Stafford Smith (2000)). In the subsequent years the mistletoe dispersers (typically birds, see section 3) will distribute the seeds at a landscape scale (Ward and Paton 2007, MacRaild *et al* 2010), where infection rates can reach high enough levels to decrease stand health and increase stand mortality rates (Carnegie *et al* 2009, Dobbertin and Rigling 2006, Scott and Mathiasen 2012). The seedlings are already capable of photosynthesizing and producing basic sugars (Lamont 1983), but mistletoes generally maintain lower xlem water potentials to additionally absorb water and nutrients from the host (Ehleringer *et al* 1985, Pate 2001, Strong and Bannister 2002). This typically leads to higher moisture contents and higher transpiration rates of individual mistletoe leaves (Canyon and Hill 1997, Cernusak *et al* 2004, Marshall *et al* 1994, Davidson *et al* 1989), translating to an increase of transpiration rates with mistletoe broom establishement on an ecosystem scale. However, reductions in overall leaf biomass were observed in severely infected trees (Raftoyannis *et al* 2015, Meinzer *et al* 2004, Agne *et al* 2014, Rigling *et al* 2010), and thus stand-level transpiration rates may decrease again in the later stages of mistletoe infestation. Albeit higher transpiration rates, mistletoes have typically lower photosynthesis rates and they acquire up to 15% of heterotrophic carbon from the host xlem sap (Marshall *et al* 1994). In Pinus sylvestris stands it was demonstrated that the host trees compensate for the additional water loss by closing their stomates (Zweifel *et al* 2012) and that mistletoe infection resulted in canopy degradation, which was followed by a reduction in primary productivity and a depletion of the non structural carbohydrate reserves of the host tree (Yan *et al* 2016, Rigling *et al* 2010). Thus, ecosystem carbon sequestration rates may also be reduced after broom establishment, while the cycling of dead matter may increase progressively with mistletoe establishment. The carbon and the nutrient cycle are closely coupled, and increasing infection rates continuously deprive the host of nutrients as they accumulate in the leaves of the parasite(Galiano *et al* 2011). However, an increase in nutrient-rich mistletoe litter turnover enhanced decomposition rates and had a fertilization effect on the soil (March and Watson 2010, Mellado *et al* 2016). This boosted productivity and lead to an increase in understorey species richness(March and Watson 2007, Watson 2009). Likewise, mistletoe establishment was linked to have a significant positive effect on woodland-dependent species richness by providing nesting sites and food resources (Watson 2002, Napier *et al* 2014, Barea 2008, Cooney and Watson 2005).

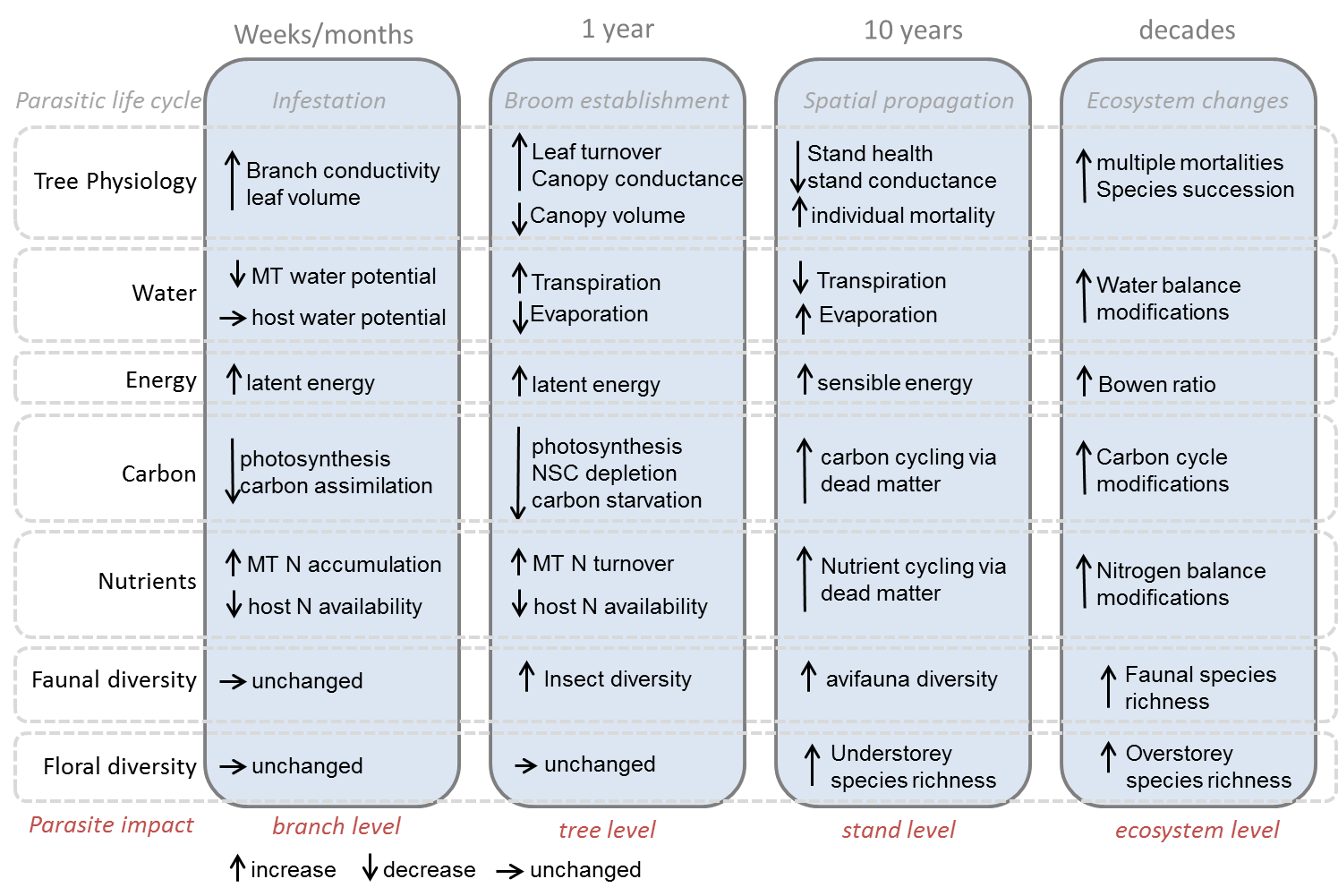


Figure 1. Conceptual figure indicating the temporal dynamics of mistletoe infection from the branch to the ecosystem level with a focus on tree phsysiology, matter and energy fluxes, and floral and faunal diversity.

# Mistletoe and biodiversity

David will talk about this.

# Mistletoe infestation modifies ecosystem processes

This less regulated water use increases the water stress on the host (Miller *et al* 2003), which results in stomatel regulation of the host's leaves to minimise water loss in addition to the parasite (Zweifel *et al* 2012). Thus, severe infection can significantly reduce carbon accumulation in the host tree, which in return results in reductions in leaf biomass which ultimately cause decreasing tree-level transpiration rates in the later stages of mistletoe infestation (Raftoyannis *et al* 2015, Meinzer *et al* 2004). Likewise, increased transpiration will first decrease the Bowen ration in the early stages of infestation, before increasing again with a decrease in canopy biomass. carbon starvation?

resulting in lower water use efficiency (Davidson and Pate 1992, Küppers *et al* 1992).

and the volume of mistletoe infection has clearly been associated with a decrease in tree growth and tree survival rates in Australia (Reid *et al* 1994, Reid *et al* (1992)), which was especially detrimental in young trees (Carnegie *et al* 2009). This overall increase in autotrophic water use on the ecosystem scale will decrease again once the tree

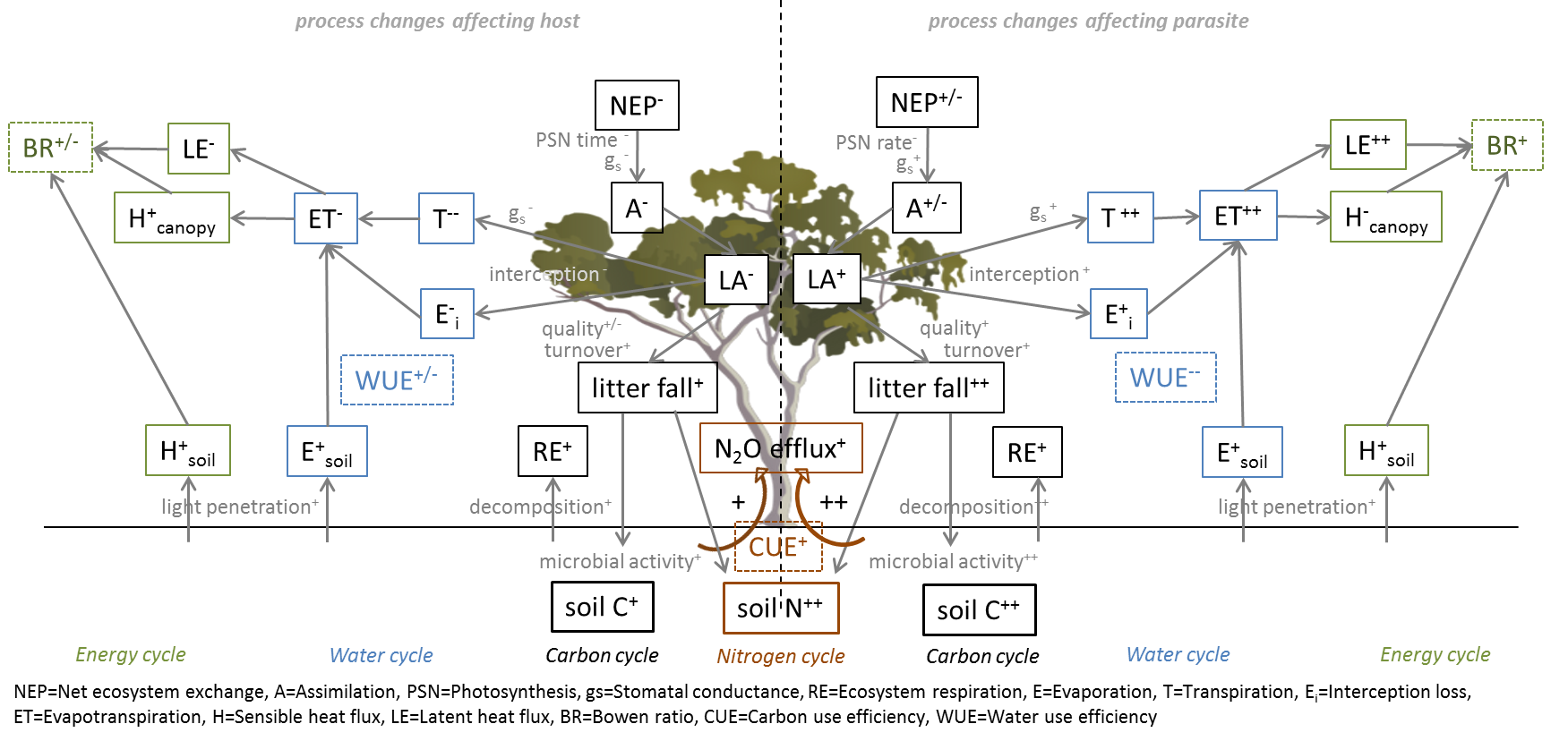


Figure 2. Comparison betweent the modification of functional relationships at the parasite and the host and how these affect the nitrogen, carbon, water and energy cycles.

## Priorities for future research

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

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