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. 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 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 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 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). 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), such as the recent bark beetle outbreaks that affected vast areas across western North America. 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 attacks and large-scale disturbances like cyclones and wildfires 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 (Bartels and Chen 2012, March and Watson 2010). The largest group of areal parasitic plants are mistletoes, which are widespread hemiparasites that portray epiphytic behaviour and belong to the order of Santalales (Bell and Adams 2011). Because mistletoes are long lived (exceeding 30 years) it can take decades to notice their damaging effect on the host. The potential positive effect of mistletoe infestation are 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).

### 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 in climatic stress in the form of prolounged droughts has amplified tree mortality rates in mistletoe infected forests (Way 2011, Dobbertin and Rigling 2006, Kolb *et al* 2016, Mutlu *et al* 2016, Sangüesa-Barreda *et al* 2012, Mathiasen *et al* 1990). Future climate change is projected to increase the likelyhood, frequency and duration of droughts in many ecosystems, so we must understand the physiological causes and ecosystem consequences of this trend (Collins *et al* 2013). Most process-based research focused predominantly on the functional understanding of parasite infection on the leaf-level scale (e.g. Bell and Adams 2011, Mathiasen *et al* 2008), and we are just starting to recognize the multifunctional role of mistletoe in biodiversity (e.g. Hatcher *et al* 2012, Watson 2001, Press and Phoenix 2005). 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 infestation in a holistic approach to assesses ecosystem and biodiversity cosequences under a changing climate.

## Modifications of leaf-to-ecosystem functioning 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 significantly modify the functional processes of the host tree; the links between the carbon, nutrient, water and energy cycles are conceptualized in Figure 1.

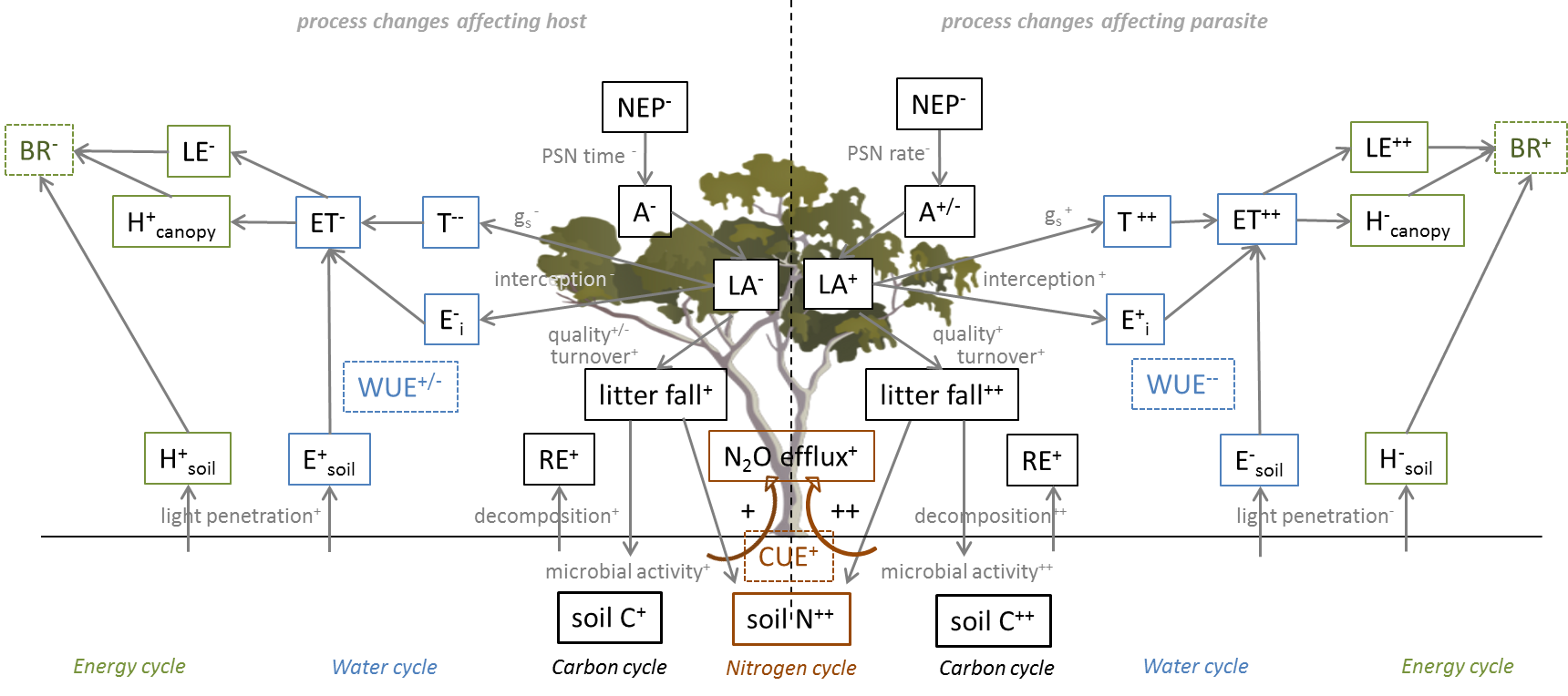


Figure 1. Comparison between the modification of functional relationships of the parasite and a eucalypt host and how these affect the nitrogen, carbon, water and energy cycles. Note that this figure is a simplification to conceptualize the process changes at the host (left side) and at the parasite (right side) of a moderately 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 many 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 and deplete the non-structural carbohydrate reserves of the host tree (Yan *et al* 2016, Rigling *et al* 2010).

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 are then accumulated in the parasite leaves (Galiano *et al* 2011, March and Watson 2010). 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 nitrogen cycling and may boost productivity by increasing understory species richness (March and Watson 2007, Watson 2009). We speculate that mistletoe infection may enhance microbial carbon use efficiency (CUE) and lead to increases in soil respiration through either increased light penetration (host) or increased microbial activity (parasite; Figure 1).

### 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 may accelerate with increasing light penetration, or decrease with the built up of mistletoe leaf litter. Thus, evapotranspiration is expected to increase with mistletoe infestation but to decrease from the host tree perspective (Figure 1).

Furthermore, modifications in the water cycle with parasite infection will ultimately alter the energy balance, 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

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 2.

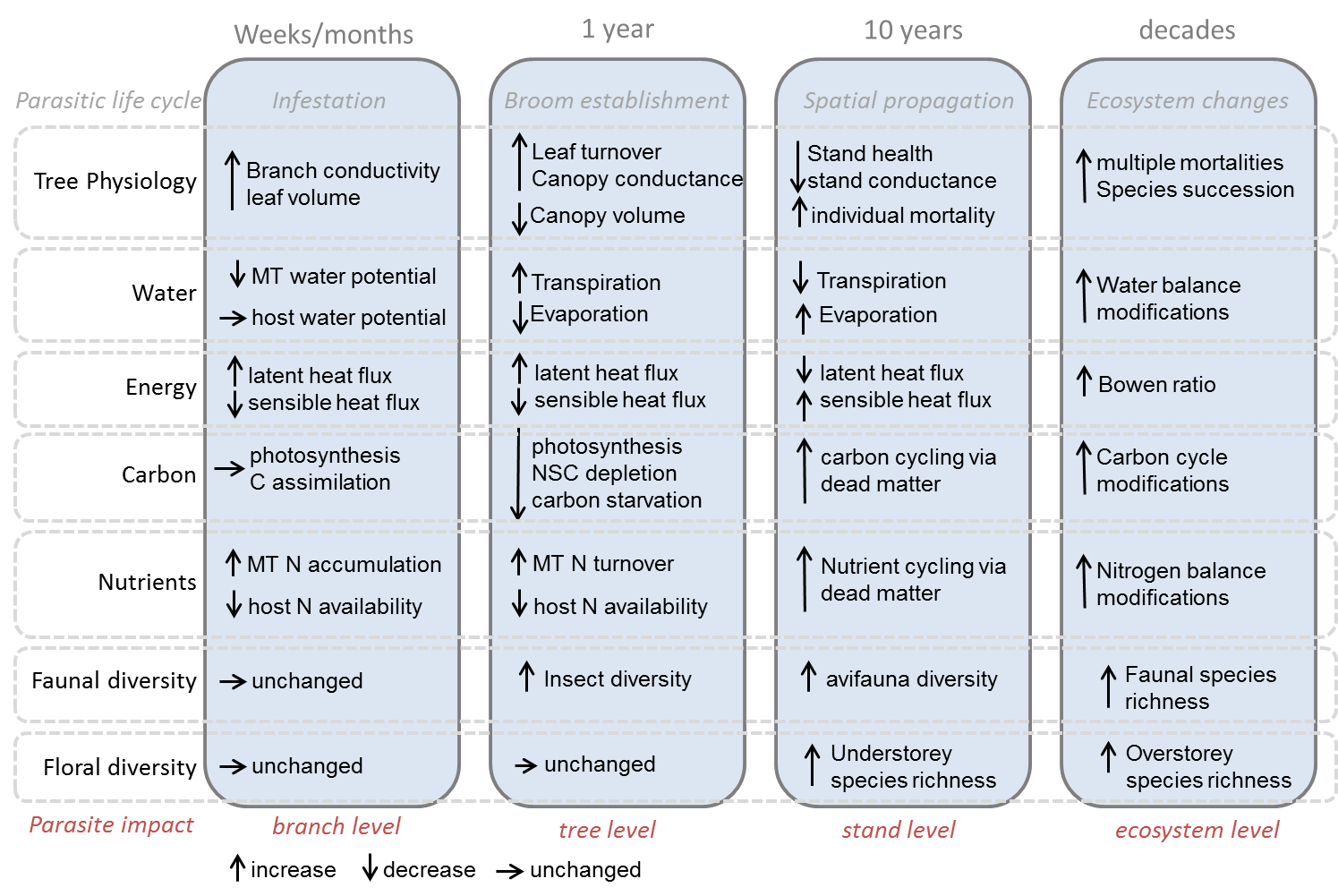


Figure 2. Conceptual figure indicating the temporal dynamics of mistletoe infection from the branch to the ecosystem level with a focus on tree phsysiology, matter and energy fluxes, and floral and faunal diversity.

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 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 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 individuals across the stand (Ward and Paton 2007). At this time step highly infected trees lose vigour, as the canopies increasingly show signs of degradation (Raftoyannis *et al* 2015, Meinzer *et al* 2004). 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 avaialbility enhances floral biodiversity, while faunal diversity is enhanced through the increased availability of mistletoe fruits and shelter (Cooney and Watson 2005, Watson 2009, Bowen *et al* 2009).

On time scales of 10 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 (Carnegie *et al* 2009, Dobbertin and Rigling 2006, Scott and Mathiasen 2012, Zweifel *et al* 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 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).

## Mistletoe and biodiversity

## Although representing a minor canopy constituent in terms of abundance, biomass and species richness, a growing number of studies have found mistletoe contributes disproportionately to species occurrence, community composition and overall ecosystem function. These effects arise from an articulated set of processes resulting 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 litter-fall 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 emphasising how the influence of mistletoe may intersect with climate change.

## As semi-succulent plants with few structural and chemical defences reliant on animal pollinators and seed dispersers, mistletoes are an important food source for many animals. Like other parasitic plants, mistletoe tissues characteristically contain higher cation concentrations than their hosts, and are preferentially browsed by many herbivores. Browsing herbivores may constrain mistletoe abundance, either by nipping off growing stems or, in the case of elephants and rhinoceros, removing entire plants. Likewise, individual animals adjust their movements, diets, territories and breeding sites relative to mistletoe abundance and phenology, culminating in consistently close relationships between mistletoe occurrence and species richness. Heavily-infected hosts may be actively defended, both as a food source (Barea) but also as a reliable source of water (Wahlsberg in Oecologia paper), especially in arid areas where standing water may be unavailable seasonally. Although most research has focused on vertebrates, a large number of arthropod groups have been found associating with mistletoe, both as pollinators and specialist herbivores, with one recent study (Fadini et al.) documenting a three way interaction between a beetle that selectively predated mistletoe seeds on one of several potential host plants, constraining host range post-dispersal.

## Most mistletoe lineages have a densely-branched growth habit, representing distinct structural elements in forest canopies that are used by many animals for shelter. As well as roosting, nesting, hibernating or hiding from predators within the mistletoe plant itself, some animals preferentially occupy infected hosts, most notable in the dwarf mistletoes with systemic infections resulting in contorted branches with densely packed foliage (known as witches’ brooms). This increased structural heterogeneity coupled with the high water content of mistletoe tissues generates a distinct microclimate, measurably cooler and more humid than host canopies during hot weather. As well as safe places to raise young, nocturnal animals with lower tolerances to high temperatures seek out mistletoes during hot weather (Figure 3). 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 (Hemlock, Shaw; Pinus, Mellado and Zamora), “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, Functional Ecology in press).



## Figure 3. An immature Boobook Owl Ninox novaeseelandiae roosting in a mistletoe-infected Acacia on a hot (45 °C) day in southern Australia. With their high water content and densely-branched habit, mistletoe clumps represent a more moderate microclimate used by many animals seeking shelter. Photograph by Skye Wassens (used with permission).

## As with other parasitic plants, mistletoe generate large amounts of enriched litter, precipitating a cascading series of facilitative interactions beneath infected hosts. Convergent findings in Australian eucalypt woodlands, African Acacia savannah and Eurpean pine forests suggest a generalized role of mistletoes as facilitators. 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 nutrient boosting availability. These effects have been noted in epigeic arthropods (Ngurwa, Mellado et al. in review), understorey plants (March), seedling growth, and fungal diversity (Spasojevic).

## While these three classes of interactions are often studied in parallel, they interact at multiple scales to catalyse 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. Three years after mistletoes were removed from woodland canopies, the richness and incidence of birds decreased by up to 36%, treatment effects most pronounced for ground-foraging insectivores. While some of these losses arose from local extirpations post removal, most of the experimental effect was due to the combined effect of mistletoe and drought, whereby bird species preferentially returned to woodlands with mistletoe after the drought (Watson PloS ONE)…

## 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 induced tree mortality is rarely damaging 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.

### 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). Fungi 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). 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 either reduce land degradation and thus increases wildlife and natural enemies, or to identify and plant infection-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 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 rates. This is increasingly complex as parasitic infection on its own is rarely lethal; rather, 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 prolonged 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 adapted 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.

## References

Agne M C, Shaw D C, Woolley T J and Queijeiro-Bolaños M E 2014 Effects of dwarf mistletoe on stand structure of lodgepole pine forests 21-28 years post-mountain pine beetle epidemic in central oregon *PloS one* **9** e107532

Allen C D, Macalady A K, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears D D, Hogg E H, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J H, Allard G, Running S W, Semerci A and Cobb N 2010 A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests *Forest Ecology and Management* **259** 660–84

Ancic M, Pernar R, Bajic M, Seletkovic A and Kolic J 2013 Detecting mistletoe infestation on silver fir using hyperspectral images *Iforest-Biogeosciences and Forestry* **7** 85–91

Barbosa J M, Sebastian-Gonzalez E, Asner G P, Knapp D E, Anderson C, Martin R E and Dirzo R 2016 Hemiparasite-host plant interactions in a fragmented landscape assessed via imaging spectroscopy and lidar *Ecological Applications* **26** 55–66

Barea L P 2008 Nest-site selection by the painted honeyeater (grantiella picta), a mistletoe specialist *Emu* **108** 213–20

Bartels S F and Chen H Y H 2012 Mechanisms regulating epiphytic plant diversity *Critical Reviews in Plant Sciences* **31** 391–400

Bell T L and Adams M A 2011 Attack on all fronts: Functional relationships between aerial and root parasitic plants and their woody hosts and consequences for ecosystems *Tree Physiology* **31** 3–15

Bowen M E, McAlpine C A, House A P N and Smith G C 2009 Agricultural landscape modification increases the abundance of an important food resource: Mistletoes, birds and brigalow *Biological Conservation* **142** 122–33

Brown M, Black T, Nesic Z, Foord V, Spittlehouse D, Fredeen A, Grant N, Burton P and Trofymow J 2010 Impact of mountain pine beetle on the net ecosystem production of lodgepole pine stands in british columbia *Agricultural and Forest Meteorology* **150** 254–64

Canyon D V and Hill C J 1997 Mistletoe host-resemblance: A study of herbivory, nitrogen and moisture in two australian mistletoes and their host trees *Australian Journal of Ecology* **22** 395–403

Carnegie A J, Bi H Q, Arnold S, Li Y and Binns D 2009 Distribution, host preference, and impact of parasitic mistletoes (loranthaceae) in young eucalypt plantations in new south wales, australia *Botany-Botanique* **87** 49–63

Cernusak L A, Pate J S and Farquhar G D 2004 Oxygen and carbon isotope composition of parasitic plants and their hosts in southwestern australia *Oecologia* **139** 199–213

Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichefet T, Friedlingstein P, Gao X, Gutowski W, Johns T, Krinner G, Shongwe M, Tebaldi C, Weaver A and Wehner M 2013 Long-term climate change: Projections, commitments and irreversibility *Climate change 2013: The physical science basis. contribution of working group i to the fifth assessment report of the intergovernmental panel on climate change* ed T Stocker, D Qin, G-K Plattner, M Tignor, S Allen, J Boschung, A Nauels, Y Xia, V Bex and P Midgley (Cambridge, United Kingdom; New York, NY, USA: Cambridge University Press) pp 1029–136

Cooney S J N and Watson D M 2005 Diamond firetails (stagonopleura guttata) preferentially nest in mistletoe *Emu* **105** 317–22

Davidson N J and Pate J S 1992 WATER relations of the mistletoe amyema-fitzgeraldii and its host acacia-acuminata *Journal of Experimental Botany* **43** 1549–55

Davidson N J, True K C and Pate J S 1989 WATER relations of the parasite - host relationship between the mistletoe amyema-linophyllum (fenzl) tieghem and casuarina-obesa miq *Oecologia* **80** 321–30

Dobbertin M and Rigling A 2006 Pine mistletoe (viscum album ssp austriacum) contributes to scots pine (pinus sylvestris) mortality in the rhone valley of switzerland *Forest Pathology* **36** 309–22

Dukes J S, Pontius J, Orwig D, Garnas J R, Rodgers V L, Brazee N, Cooke B, Theoharides K A, Stange E E, Harrington R, Ehrenfeld J, Gurevitch J, Lerdau M, Stinson K, Wick R and Ayres M 2009 Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern north america: What can we predict? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **39** 231–48

Ehleringer J R, Schulze E D, Ziegler H, Lange O L, Farquhar G D and Cowar I R 1985 XYLEM-tapping mistletoes - water or nutrient parasites *Science* **227** 1479–81

Galiano L, Martínez-Vilalta J and Lloret F 2011 Carbon reserves and canopy defoliation determine the recovery of scots pine 4 yr after a drought episode *New Phytologist* **190** 750–9

Hatcher M J, Dick J T A and Dunn A M 2012 Diverse effects of parasites in ecosystems: Linking interdependent processes *Frontiers in Ecology and the Environment* **10** 186–94

Hutley L B, Evans B J, Beringer J, Cook G D, Maier S W and Razon E 2013 Impacts of an extreme cyclone event on landscape-scale savanna fire, productivity and greenhouse gas emissions *Environmental Research Letters* **8** 12

Johnson D M, Buntgen U, Frank D C, Kausrud K, Haynes K J, Liebhold A M, Esper J and Stenseth N C 2010 Climatic warming disrupts recurrent alpine insect outbreaks *Proceedings of the National Academy of Sciences of the United States of America* **107** 20576–81

Kara A, Juan Manuel D, Maria G G, Catherine H, David M, Camila P, Beatriz S-N, Christina M S, Annette T, Skip J V B, Bonnie G W, Xiangtao X and Jennifer S P 2017 Will seasonally dry tropical forests be sensitive or resistant to future changes in rainfall regimes? *Environmental Research Letters* **12** 023001

Kolb T E, Fettig C J, Ayres M P, Bentz B J, Hicke J A, Mathiasen R, Stewart J E and Weed A S 2016 Observed and anticipated impacts of drought on forest insects and diseases in the united states *Forest Ecology and Management* **380** 321–34

Kulakowski D, Seidl R, Holeksa J, Kuuluvainen T, Nagel T A, Panayotov M, Svoboda M, Thorn S, Vacchiano G, Whitlock C, Wohlgemuth T and Bebi P 2017 A walk on the wild side: Disturbance dynamics and the conservation and management of european mountain forest ecosystems *Forest Ecology and Management* **388** 120–31

Küppers M, Küppers B I, Neales T F and Swan A G 1992 Leaf gas exchange characteristics, daily carbon and water balances of the host/mistletoe pair eucalyptus behriana f. muell. and amyema miquelii (lehm. ex miq.) tiegh. at permanently low plant water status in the field *Trees-Structure and Function* **7** 1–7

Lamont B 1983 Germination of mistletoes *The biology of mistletoes* ed P Calder M; Bernhardt (Sydney: Academic Press) pp 129–43

MacRaild L M, Radford J Q and Bennett A F 2010 Non-linear effects of landscape properties on mistletoe parasitism in fragmented agricultural landscapes *Landscape Ecology* **25** 395–406

Maffei H M, Filip G M, Grulke N E, Oblinger B W, Margolis E Q and Chadwick K L 2016 Pruning high-value douglas-fir can reduce dwarf mistletoe severity and increase longevity in central oregon *Forest Ecology and Management* **379** 11–9

March W A and Watson D M 2007 Parasites boost productivity: Effects of mistletoe on litterfall dynamics in a temperate australian forest *Oecologia* **154** 339–47

March W A and Watson D M 2010 The contribution of mistletoes to nutrient returns: Evidence for a critical role in nutrient cycling *Austral Ecology* **35** 713–21

Marshall J D, Ehleringer J R, Schulze E D and Farquhar G 1994 CARBON-isotope composition, gas-exchange and heterotrophy in australian mistletoes *Functional Ecology* **8** 237–41

Mathiasen R L, Hawksworth F G and Edminster C B 1990 Effects of dwarf mistletoe on growth and mortality of douglas-fir in the southwest *The Great Basin Naturalist* 173–9

Mathiasen R L, Nickrent D L, Shaw D C and Watson D M 2008 Mistletoes: Pathology, systematics, ecology, and management *Plant disease* **92** 988–1006

Matsubara S, Gilmore A M, Ball M C, Anderson J M and Osmond C B 2002 Sustained downregulation of photosystem ii in mistletoes during winter depression of photosynthesis *Functional Plant Biology* **29** 1157–69

Meinzer F C, Woodruff D R and Shaw D C 2004 Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection *Plant Cell and Environment* **27** 937–46

Mellado A, Morillas L, Gallardo A and Zamora R 2016 Temporal dynamic of parasite-mediated linkages between the forest canopy and soil processes and the microbial community *New Phytologist* **211** 1382–92

Millar C I, Westfall R D and Delany D L 2007 Response of high-elevation limber pine (pinus flexilis) to multiyear droughts and 20th-century warming, sierra nevada, california, usa *Canadian Journal of Forest Research* **37** 2508–20

Miller A C, Watling J R, Overton I C and Sinclair R 2003 Does water status of eucalyptus largiflorens (myrtaceae) affect infection by the mistletoe amyema miquelii (loranthaceae)? *Functional Plant Biology* **30** 1239–47

Mutlu S, Ilhan V and Turkoglu H I 2016 Mistletoe (viscum album) infestation in the scots pine stimulates drought-dependent oxidative damage in summer *Tree physiology* **36** 479–89

Napier K R, Mather S H, McWhorter T J and Fleming P A 2014 Do bird species richness and community structure vary with mistletoe flowering and fruiting in western australia? *Emu* **114** 13–22

Norton D A and Reid N 1997 Lessons in ecosystem management from management of threatened and pest loranthaceous mistletoes in new zealand and australia *Conservation Biology* **11** 759–69

Pate J S 2001 Haustoria in action: Case studies of nitrogen acquisition by woody xylem-tapping hemiparasites from their hosts *Protoplasma* **215** 204–17

Press M C and Phoenix G K 2005 Impacts of parasitic plants on natural communities *New Phytologist* **166** 737–51

Raftoyannis Y, Radoglou K and Bredemeier M 2015 Effects of mistletoe infestation on the decline and mortality of abies cephalonica in greece *Annals of Forest Research* **58** 55–65

Reed D E, Ewers B E and Pendall E 2014 Impact of mountain pine beetle induced mortality on forest carbon and water fluxes *Environmental Research Letters* **9**

Reichstein M, Bahn M, Ciais P, Frank D, Mahecha M D, Seneviratne S I, Zscheischler J, Beer C, Buchmann N, Frank D C, Papale D, Rammig A, Smith P, Thonicke K, Velde M van der, Vicca S, Walz A and Wattenbach M 2013 Climate extremes and the carbon cycle *Nature* **500** 287–95

Reid N and Shamoun S F 2009 Contrasting research approaches to managing mistletoes in commercial forests and wooded pastures *Botany-Botanique* **87** 1–9

Reid N and Stafford Smith D M 2000 Population dynamics of an arid zone mistletoe (amyema preissii, loranthaceae) and its host acacia victoriae (mimosaceae) *Australian Journal of Botany* **48** 45–58

Reid N, Yan Z and Fittler J 1994 Impact of mistletoes (amyema miquelii) on host (eucalyptus blakelyi and eucalyptus melliodora) survival and growth in temperate australia *Forest Ecology and Management* **70** 55–65

Rigling A, Eilmann B, Koechli R, Dobbertin M and others 2010 Mistletoe-induced crown degradation in scots pine in a xeric environment *Tree Physiol* **30** 845–52

Sangüesa-Barreda G, Linares J C and Camarero J J 2013 Drought and mistletoe reduce growth and water-use efficiency of scots pine *Forest Ecology and Management* **296** 64–73

Sangüesa-Barreda G, Linares J C and Camarero J J 2012 Mistletoe effects on scots pine decline following drought events: Insights from within-tree spatial patterns, growth and carbohydrates *Tree Physiology* **32** 585–98

Schoennagel T, Balch J K, Brenkert-Smith H, Dennison P E, Harvey B J, Krawchuk M A, Mietkiewicz N, Morgan P, Moritz M A, Rasker R, Turner M G and Whitlock C 2017 Adapt to more wildfire in western north american forests as climate changes *Proceedings of the National Academy of Sciences of the United States of America* **114** 4582–90

Scott J M and Mathiasen R L 2012 Assessing growth and mortality of bristlecone pine infected by dwarf mistletoe using dendrochronology *Forest Science* **58** 366–76

Shaw D C, Watson D M and Mathiasen R L 2004 Comparison of dwarf mistletoes (arceuthobium spp., viscaceae) in the western united states with mistletoes (amyema spp., loranthaceae) in australia - ecological analogs and reciprocal models for ecosystem management *Australian Journal of Botany* **52** 481–98

Start A N 2011 Fire responses and survival strategies of mistletoes (loranthaceae) in an arid environment in western australia *Australian Journal of Botany* **59** 533–42

Start A N 2013 Mistletoe flora (loranthaceae and santalaceae) of the kimberley, a tropical region in western australia, with particular reference to fire *Australian Journal of Botany* **61** 309–21

Start A N 2015 The mistletoe flora of southern western australia, with a particular reference to host relationships and fire *Australian Journal of Botany* **63** 636–46

Strong G L and Bannister P 2002 Water relations of temperate mistletoes on various hosts *Functional Plant Biology* **29** 89–96

Turner R J and Smith P 2016 Mistletoes increasing in eucalypt forest near eden, new south wales *Australian Journal of Botany* **64** 171–9

Varga I, Taller J, Baltazár T, Hyvönen J and Poczai P 2012 Leaf-spot disease on european mistletoe (viscum album) caused by phaeobotryosphaeria visci: A potential candidate for biological control *Biotechnology letters* **34** 1059–65

Ward M J and Paton D C 2007 Predicting mistletoe seed shadow and patterns of seed rain from movements of the mistletoebird, dicaeum hirundinaceum *Austral Ecology* **32** 113–21

Watson D M 2009 Determinants of parasitic plant distribution: The role of host quality *Botany-Botanique* **87** 16–21

Watson D M 2002 Effects of mistletoe on diversity: A case-study from southern new south wales *Emu* **102** 275–81

Watson D M 2016 Fleshing out facilitation - reframing interaction networks beyond top-down versus bottom-up *New Phytologist* **211** 803–8

Watson D M 2001 Mistletoe - a keystone resource in forests and woodlands worldwide *Annual Review of Ecology and Systematics* **32** 219–49

Watson D M and Herring M 2012 Mistletoe as a keystone resource: An experimental test *Proceedings of the Royal Society B-Biological Sciences* **279** 3853–60

Watson D M, Milner K V and Leigh A 2017 Novel application of species richness estimators to predict the host range of parasites *International Journal for Parasitology* **47** 31–9

Watson R T, Noble I R, Bolin B, Ravindranath N, Verardo D J and Dokken D J 2000 Land use, land-use change and forestry. a special report of the intergovernmental panel on climate change (ipcc) *Cambridge: Cambridge University*

Way D A 2011 Parasitic plants and forests: A climate change perspective *Tree Physiology* **31** 1–2

Worrall J J, Lee T D and Harrington T C 2005 Forest dynamics and agents that initiate and expand canopy gaps in picea–Abies forests of crawford notch, new hampshire, usa *Journal of Ecology* **93** 178–90

Yan C F, Gessler A, Rigling A, Dobbertin M, Han X G and Li M H 2016 Effects of mistletoe removal on growth, n and c reserves, and carbon and oxygen isotope composition in scots pine hosts *Tree Physiology* **36** 562–75

Yi C X, Pendall E and Ciais P 2015 Focus on extreme events and the carbon cycle *Environmental Research Letters* **10** 8

Yuan W P, Cai W W, Chen Y, Liu S G, Dong W J, Zhang H C, Yu G R, Chen Z Q, He H L, Guo W D, Liu D, Liu S M, Xiang W H, Xie Z H, Zhao Z H and Zhou G M 2016 Severe summer heatwave and drought strongly reduced carbon uptake in southern china *Scientific Reports* **6** 12

Zweifel R, Bangerter S, Rigling A and Sterck F J 2012 Pine and mistletoes: How to live with a leak in the water flow and storage system? *Journal of Experimental Botany* **63** 2565–78