

Hemiparasites drive heterogeneity in litter arthropods: Implications for woodland insectivorous birds

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Abstract Providing fruit, nectar, leaves and litter, mistletoes represent important resources for many organisms, linking above-ground patterns with below-ground processes. Here, we explore how mistletoe litter affects arthropod availability, especially those taxa preferentially consumed by ground-feeding insectivorous birds, a group that has undergone widespread declines. We estimated the influence of mistletoe on arthropod occurrence by sampling arthropod communities beneath infected and uninfected trees with pit-fall traps. Then, we experimentally isolated direct effects of mistletoe litter on arthropods with a litterbag study. Soil arthropod communities beneath infected trees had consistently greater abundance and biomass – total arthropods and the subset of arthropods preferentially consumed by ground-foraging insectivores – compared to otherwise comparable uninfected trees. Arthropods showed a weak response to litter addition, with maximum abundances recorded from bags with low mistletoe litter, significantly lower abundances associated with higher mistletoe fractions and pure tree litter (after 5 months). Our findings confirm that mistletoe occurrence has a significant positive impact on arthropod availability, especially on those preferred by ground-foraging bird insectivores. However, only a minor part of this impact is due to the direct, short-term effects of mistletoe litter, which suggests that additional mistletoe-mediated effects (e.g. local changes in structural or microclimatic factors, cumulative effects over multiple years) play significant roles. By altering arthropod assemblages within leaf litter and increasing the heterogeneity of resource availability on forest floors, mistletoe plays an important role in improving habitat quality for declining insectivores.

Key words: facilitation, insectivores, keystone resource, mistletoe, trophic cascade.

INTRODUCTION

Although parasitic plants rely on other plants for their nutrition, a growing body of research has uncovered a network of other interactions that increase productivity and diversity at stand- and patch-scales (Watson & Herring 2012; Watson 2015; Mellado & Zamora 2017). By reallocating nutrients from competitively dominant host plant species and increasing nutrient availability to adjacent non-hosts via litterfall, hemiparasites push successional dynamics away from monodominance (DiGiovanni *et al.* 2017). The abundant litter shed by hemiparasites increases small-scale heterogeneity in nutrient inputs, facilitating coexistence and increasing plant understory diversity (Davies *et al.* 1997; Press 1998). In addition to explaining observed patterns of plant co-occurrence and complementarity (Pennings & Callaway 1996), this understanding has been applied to vegetation management – hemiparasites have been used to promote herb-rich meadows in old-field and

prairie restoration (Pywell *et al.* 2004; DiGiovanni *et al.* 2017).

As well as modifying plant–plant interactions, nutrients mobilised by parasitic plants become available to visiting animals (Mellado & Zamora 2015; Watson 2016). Greater numbers of fleshy fruited understory shrub seeds were found beneath infected pine trees than under otherwise comparable uninfected trees in southern Spain, reflecting differential habitat use by frugivorous birds (Mellado & Zamora 2015). The increased nutrient inputs from bird droppings, together with mistletoe litter, effected dramatic improvements in understory seedling establishment and growth (Mellado & Zamora 2017), driving large-scale successional dynamics. These effects were directly quantified in a patch-scale experiment in south-eastern Australia, with the richness of resident bird species dropping by 36% 3 years after mistletoes were removed (Watson & Herring 2012). Rather than affecting nectar feeders, frugivores or other guilds directly feeding on mistletoes, ground-foraging insectivores drove this response, interpreted to reflect reductions in litter-dependent arthropod prey (Watson 2015). This guild is of conservation concern,

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having undergone widespread range reductions and population declines worldwide (Bennett & Watson 2011; Watson 2015), a symptom of land-use intensification diverting productivity and disrupting food webs (Watson 2011a,b; Barnes *et al.* 2017).

To date, the only research conducted on the effects of hemiparasites on epigeic arthropods (i.e. arthropods that live on the soil surface) is from monsoonal woodlands in southern Africa (Ndagurwa *et al.* 2014) and from grasslands of southern England (Hartley *et al.* 2015), which showed greater diversity and abundance of arthropods beneath infected Acacias or within grassland infected patches. Besides the significant impact, the mechanisms driving arthropod's response to parasitism are still poorly known. As agents of change in their immediate biotic and abiotic environment, hemiparasites can indirectly affect the arthropod community via shifts in the plant community or in microclimatic conditions. In African savannahs, for example, soil moisture content was lower under infected Acacias (Ndagurwa *et al.* 2014) – probably due to greater water use by the host (Sala *et al.* 2001) – where maximum abundances of epigeic arthropods were found. In grasslands, however, greater arthropod numbers were associated with lower plant cover and reduced grass biomass (Hartley *et al.* 2015), reflecting both host preferences and individual effects of parasitism on host vigour. Although comparing arthropods beneath infected and uninfected plants likely reflects the influence of the hemiparasite, any initial variation in microclimate, soil or the plants themselves that led to only some becoming initially infected (including host quality, Watson 2008) may confound the mechanistic interpretation of these comparisons. The direct effect of hemiparasite litter – characterised by its enriched composition, spatial aggregation and extended availability – upon arthropod community structure and function has not yet been quantified, constraining our understanding of broader trophic effects of hemiparasites.

To disentangle the direct and indirect effects of parasitic plants on food webs, we undertook two studies to estimate the influence of mistletoe occurrence on arthropod availability to insectivores. In addition to comparing arthropod assemblages in sites with differing mistletoe abundance, we used litterbags to manipulate litter composition, enabling the direct effects of mistletoe litter to be isolated. As well as total arthropod abundance, we build on previous work that identified those groups of litter-dwelling arthropods preferentially consumed by ground-foraging insectivorous birds (Razeng 2011; Razeng & Watson 2012; Razeng and Watson 2015). Having estimated the effect of mistletoe litter on arthropods, we discuss the implications of altered arthropod assemblages on ecosystem function and

consider the potential role of mistletoe in improving habitat quality for declining woodland birds and other ground-foraging insectivores of conservation concern.

METHODS

This research was carried out in temperate eucalypt-dominated woodland at two sites in the south-west slopes region of New South Wales (Australia), sampling periods timed to coincide with the breeding season of resident woodland birds (late Spring) when differences in availability of nutritional resources matter most for insectivores (Hobby 2015). The region is characterised by hot summers (December–February) and cool winters (June–October) with rainfall concentrated in winter and spring (March & Watson 2007, 2010). An estimated 85% of the original woodland was cleared over the last two centuries for agriculture, with present land-use predominantly cereal cropping and grazing sheep and cattle on improved pasture. Most remaining stands of temperate woodland are small remnants on roadsides and private land, with many of the largest remnants the focus of conservation management and restoration.

To estimate the influence of mistletoe infection on arthropod occurrence, comparisons of arthropod communities beneath infected and uninfected eucalypts were made at Slate Hill, near Woomargama (−35.842758, 147.205829), using pit-fall traps. The study site is located in a stand of *Eucalyptus bridgesiana* and *Eucalyptus blakelyi*, with occasional *Eucalyptus polyanthemus*, *Eucalyptus melliodora* and *Eucalyptus albens*. The shrub layer mainly consists of scattered *Acacia dealbata* and *Acacia implexa*, while the grassy ground layer contains abundant herbs and forbs. To isolate the direct influence of mistletoe litter on arthropod occurrence, a litterbag study was carried out at Yabtree West (−35.093084, 147.775546). The study site is located within a 10 ha patch of remnant box-gum grassy woodland dominated by *E. blakelyi*, *A. dealbata* and *E. albens* with *Allocasuarina verticillata* growing along the ridge. The understorey is open, and the ground layer dominated by annual grasses.

At both sites, remnant grassy box woodlands are dominated by *E. blakelyi*, one of the principal hosts of the mistletoe *Amyema miquelii*. This large loranthaceous mistletoe grows to 2.5 × 1 m, previously demonstrated to increase overall litterfall by up to 189%, the amount of litter being proportional to the mistletoe biomass in the canopy (March & Watson 2007). Comprehensive bird surveys at both sites (Razeng 2011, Gorman *in litt*) indicate they support comparable assemblages of woodland birds, many of which, including the Speckled Warbler (*Pyrhholaeus sagittatus*), Hooded Robin (*Melanodryas cucullata*), Red-capped Robin (*Petroica goodenovii*) and Brown Tree-creeper (*Climacteris picumnus*) are ground-foraging insectivores considered to be experiencing widespread declines (Watson 2011a,b). In addition to evaluating variation in the overall assemblage of epigeic arthropods for both pit-fall and litterbag components, those groups previously demonstrated to be the preferred prey of ground-foraging insectivorous birds (Razeng & Watson 2012) were distinguished and analysed separately.

Pit-fall trap experiment

Abundance and biomass of epigeic arthropods were compared between infected and non-infected eucalypts using pit-fall traps during the Austral spring (September–October) of 2012. Ten pairs of infected and uninfected Blakely's red gum (*E. blakelyi*) and another 10 pairs of Apple box (*E. bridgesiana*) were used for the experiment (a total of 40 trees), both species representing principal hosts for *A. miquelii*. Trees were chosen based on their structural similarities (i.e. size and canopy configuration) and spatial proximity, paired trees selected within a maximum distance of 20 m to minimise bias due to differences in environmental factors (e.g. habitat structure, soil properties, adjacent vegetation, etc.) but at least 10 m apart to keep trees as independent sampling units. For each focal tree, we measured crown coverage (m^2), trunk perimeter (cm) and the percent of grass coverage beneath the canopy.

Eight pit-fall traps were installed beneath each infected and uninfected tree, consisting of plastic cups 80 mm in diameter and 130 mm deep, arranged in a circle approximately $2/3$ along the radius of the tree crown from the trunk. We used a solution of ethylene glycol with water, in a proportion of 1:6, respectively (166 g L^{-1}), as a preservative fluid. After 40 days, pit-fall traps were removed, the contents of each trap rinsed with water and stored in 70% ethanol solution prior to sorting and further analysis. As well as total numbers, individuals from those five more palatable and nutritive orders most preferred by ground-foraging insectivorous birds (Coleoptera, Lepidoptera, Araneae, Hemiptera and Orthoptera; after Razeng & Watson 2012, 2014) were grouped together and considered separately ('preferred arthropods' hereafter) to estimate prey availability. Once counted and classified, arthropod samples were dried at 60°C for 72 h then weighed using an analytic balance to the nearest 0.0001 g. Arthropod availability was analysed in terms of abundance (number of individuals $\text{trap}^{-1}\text{ day}^{-1}$) and dry biomass ($\text{mg trap}^{-1}\text{ day}^{-1}$).

Litterbag experiment

We performed a litterbag experiment to assess whether different mixtures of mistletoe and host litter affect arthropod abundance. Leaf litter was collected from the Yabtree West study site in August 2014. To avoid confounding the experiment by contaminating litterbags with fungi or bacteria associated with mistletoe litter decomposition beneath infected hosts, mistletoe foliage was removed from live *A. miquelii* plants, air dried in a sun-lit green house for 4 weeks. Eucalypt litter was collected separately from freshly fallen leaves of uninfected *E. blakelyi*, *E. dealbata* and *E. albens*. Litter bags ($200 \times 200\text{ mm}$) were made from $10 \times 10\text{ mm}$ nylon orchard mesh and filled with 20 g of leaf litter in various ratios of mistletoe and mixed *Eucalyptus* species (0:100, 15:85, 30:70, 45:55, 60:40, 75:25, 100:0). Seven litterbags (one from each litter mix ratio) were installed beneath 32 eucalypt trees in September 2014 (total of 224 bags deployed), ensuring all trees contained no mistletoe plants and were isolated from the nearest tree by $>10\text{ m}$. Litterbags were placed directly on the ground, atop any existing grass or litter, pinned in place with an

aluminium tent-peg. Tree diameter at breast height and percentage of ground cover were noted. Litterbags were collected in February 2015, a sheet of stiff plastic slid beneath litter bags to prevent any arthropods falling through, the contents then placed in a plastic bag, sealed and transferred to a -17°C storage freezer. All arthropods were counted and identified to order. As in the pit-fall trapping comparisons, arthropods were classified as 'preferred', 'other' and 'total' arthropods.

Statistical analysis

Analyses were carried out using the open source software R version 3.3.1 (R Development Core Team, 2016). To analyse the effect of mistletoe infection and tree species on arthropod abundance and biomass, we used linear mixed models (LMM's) with Gaussian error distribution including tree condition (infected, uninfected) and tree species (*E. bridgesiana*, *E. blakelyi*) as fixed factors and pair as a random factor. Using this same statistical approach, we also analysed the effect of mistletoe occurrence on the different groups of arthropods. Finally, to analyse the effect of different mistletoe: eucalypt litter proportions on arthropod counts, we used GLMM's with negative binomial error distribution and log-link function, including the seven categories of mistletoe: eucalypt litter as a fixed factor and individual trees as a random factor. All response variables used in LMM's met the assumptions of normality and homoscedasticity, except for tree perimeter and the percentage of grass cover – used as descriptive variables of the study plots – that were transformed prior to analysis. GLMM's and LMM's were run using the *glmer*, *glmer.nb* and *lmer* functions of the package *lme4* (Bates *et al.* 2015). Chi-square values (χ^2), *F*-values (*F*), degrees of freedom (d.f.) and significance (*P*) come from the ANOVA tables of the fitted GLMM's and LMM's, calculated with the *Anova* function of the package *car* (Fox & Weisberg 2011). Tukey's pairwise comparisons with 95% confidence level were conducted with *lsmeans* function of the package *lsmeans* (Russell 2016). Results are presented as mean \pm 1 SE, unless otherwise specified.

RESULTS

A total of 11 784 individual arthropods were recovered from the 40 pit-fall trap arrays belonging to 19 groups (17 orders, the family Formicidae and larval stages; Table 1). The group of 'preferred arthropods' included Coleoptera, Lepidoptera (adults and litter-dwelling larvae), Araneae, Hemiptera and Orthoptera, representing 55% of the total community. Other arthropods belonged to Hymenoptera, Diptera, Isopoda, Blattodea, Neuroptera, Diplopoda, Dermaptera, Chilopoda, Scorpionida, Hirudinea, Collembola and Trichoptera. Formicidae was very numerous (8291 individuals), those pit-fall traps located near ant nests containing far more individuals, with no effects of litter (LMM: Infection status, $F_{1,16} = 0.05$,

Table 1. Mean \pm SE arthropod abundance (number of individual trap⁻¹ day⁻¹) and biomass (mg trap⁻¹ day⁻¹) collected by pit-fall traps beneath mistletoe *Anyema miquelii* infected and uninfected eucalypt trees in a temperate eucalypt forest of south-eastern Australia

	Abundance			Biomass		
	Uninfected	Infected	<i>P</i> -value	Uninfected	Infected	<i>P</i> -value
Preferred taxa						
Araneae	0.077 \pm 0.015	0.131 \pm 0.024	0.046	0.388 \pm 0.081	0.598 \pm 0.099	0.059
Coleoptera	0.044 \pm 0.100	0.079 \pm 0.009	0.005	0.419 \pm 0.088	1.312 \pm 0.243	0.002
Hemiptera	0.011 \pm 0.005	0.009 \pm 0.003	0.499	0.007 \pm 0.003	0.023 \pm 0.008	0.071
Lepidoptera larvae	0.021 \pm 0.004	0.033 \pm 0.006	0.078	0.175 \pm 0.070	0.324 \pm 0.097	0.081
Lepidoptera adults	0.0004 \pm 0.0003	0.0007 \pm 0.0005	0.832	0.0008 \pm 0.0006	0.0017 \pm 0.0012	0.492
Orthoptera	0.007 \pm 0.003	0.005 \pm 0.002	0.973	0.034 \pm 0.018	0.026 \pm 0.009	0.919
Other taxa						
Blattodea	0.014 \pm 0.004	0.017 \pm 0.003	0.365	1.132 \pm 0.338	1.505 \pm 0.376	0.365
Chilopoda	0.003 \pm 0.001	0.003 \pm 0.001	0.642	0.014 \pm 0.009	0.084 \pm 0.069	0.354
Collembola	0.004 \pm 0.002	0.004 \pm 0.002	0.838	0.0005 \pm 0.0002	0.0005 \pm 0.0003	0.816
Dermoptera	0.012 \pm 0.004	0.018 \pm 0.004	0.186	0.078 \pm 0.023	0.113 \pm 0.027	0.270
Diplopoda	0.038 \pm 0.007	0.066 \pm 0.009	0.005	2.989 \pm 0.575	4.664 \pm 0.678	0.028
Diptera	0.034 \pm 0.006	0.042 \pm 0.009	0.394	0.021 \pm 0.006	0.058 \pm 0.015	0.022
Formicidae	1.096 \pm 0.317	0.771 \pm 0.122	0.623	1.792 \pm 0.573	1.566 \pm 0.301	0.885
Gasteropoda	–	–	–	–	–	–
Hirudinea	0.015 \pm 0.006	0.018 \pm 0.006	0.322	0.139 \pm 0.061	0.202 \pm 0.087	0.262
Hymenoptera	0.017 \pm 0.004	0.015 \pm 0.004	0.462	0.260 \pm 0.085	0.080 \pm 0.022	0.174
Isopoda	0.004 \pm 0.002	0.005 \pm 0.002	0.468	0.067 \pm 0.037	0.143 \pm 0.079	0.265
Neuroptera	–	0.0002 \pm 0.0002	0.326	–	0.0003 \pm 0.0003	0.335
Psychidae	0.0014 \pm 0.0006	0.0004 \pm 0.0003	0.133	0.028 \pm 0.021	0.014 \pm 0.014	0.446
Scorpionida	0.0006 \pm 0.0003	0.0009 \pm 0.0005	0.668	0.054 \pm 0.039	0.147 \pm 0.109	0.459

Significant *P*-values ($P < 0.05$) are in boldface; $N = 20$.

$P = 0.821$; Species, $F_{1,16} = 0.39$, $P = 0.540$; Interaction, $F_{1,16} = 0.91$, $P = 0.353$). Given their highly skewed distribution, ants were excluded from analyses to prevent masking comparisons.

Overall, arthropod abundance and biomass increased significantly beneath trees infected by mistletoe, but was unaffected by tree species (Fig. 1; Table 2). Total arthropod abundance beneath infected eucalypts was 47.1% higher than uninfected trees, this difference more pronounced (60.4%) for preferred prey taxa. The same pattern was reflected in arthropod biomass, total arthropods (excluding ants) increasing by 59.4% and preferred arthropods by 123.8% beneath infected trees. Within specific taxa, there were significant effects of mistletoe occurrence on the abundance of Araneae, Coleoptera and Diplopoda (Table 1).

Pit-fall arrays beneath mistletoe-infected trees had significantly greater biomass of Coleoptera, Araneae, Diptera and Diplopoda than beneath uninfected trees (Table 1). Since infected and uninfected trees were similar in all measured characteristics (perimeter of the tree trunk ($P = 0.089$), surface of the tree canopy ($P = 0.568$) and per cent cover of grass beneath the tree canopy ($P = 0.247$)), detected differences in the arthropod community are likely due to mistletoe infection.

Despite the low average number of arthropods in litterbags (0.57 ± 0.07 individuals) and the high within-group variance, total and preferred arthropod abundances differed significantly among litter bags containing different litter proportions (Total: $\chi^2 = 13.22$, d.f. = 6, $P = 0.0396$; Preferred: $\chi^2 = 20.08$, d.f. = 6, $P = 0.0026$; Others: $\chi^2 = 7.82$, d.f. = 6, $P = 0.2516$), with maximum numbers found in bags containing low proportions (15%) of mistletoe litter (Fig. 2), equating to approximately one mistletoe per 14 trees (calculated using rates of litterfall from March & Watson 2007). Trunk circumference (148.92 ± 16.86 cm) and per cent cover of grass ($20.31 \pm 3.31\%$) were similar among selected trees.

DISCUSSION

This study demonstrates a strong positive effect of mistletoe litter on the abundance and biomass of selected epigeic arthropod groups. The influence of mistletoe infection was evident for different tree species, with infected eucalypts having much greater arthropod abundance and biomass (both total and preferred prey groups) compared to uninfected trees (Fig. 1). The litterbag experiment revealed a weak

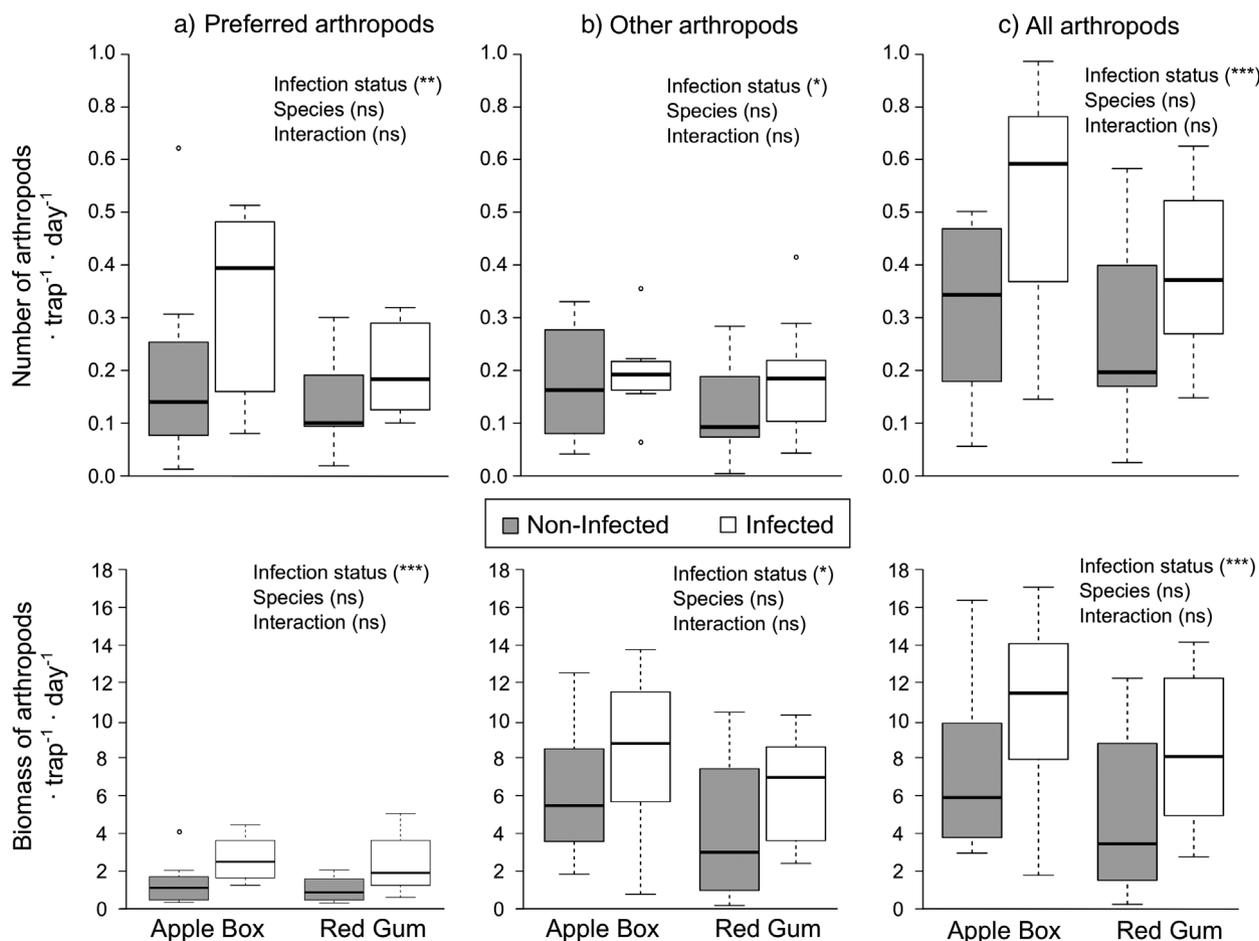


Fig. 1. Abundance and biomass (mg) of epigeic arthropods caught in pit-fall traps beneath mistletoe *Amyema miquelii* infected (white) and uninfected (grey) red gum (*Eucalyptus blakelyi*) and Apple box (*E. bridgesiana*), differentiating those groups highly preferred by ground-dwelling insectivorous birds (a); ('preferred arthropods'), less preferred arthropods (b); ('other arthropods') and (c); total arthropods. Horizontal lines represent median values, the top and bottom lines of each box indicate the lower and upper quartiles, points denote outliers. Statistical differences are indicated as * $P < 0.01$, ** $P < 0.001$; *** $P < 0.0001$; $N = 10$.

direct response to short-term mistletoe litter addition (Fig. 2), suggesting that additional mistletoe-mediated mechanisms might play a significant role. Integrating these findings with disproportionate declines of insectivores following experimental mistletoe removal (Watson & Herring 2012; Watson 2015) provides direct evidence that mistletoe can improve habitat quality for ground-feeding insectivorous birds via boosted prey availability, consistent with the productivity-based explanation of declining insectivores (Watson 2011a,b, 2015).

Previous work on the role of *A. miquelii* in litter dynamics indicated that mistletoe has characteristically higher rates of leaf turnover compared to its host trees, leading to accumulations of litter beneath infected eucalypts (March & Watson 2007). In addition to increasing litter quantity, mistletoe contains a unique leaf nutrient profile – particularly rich in

nitrogen, potassium and phosphorous (Patykowski *et al.* 2018) – and constitutes a high quality food source for litter-foraging arthropods (March & Watson 2010) compared to the heavily lignified leaves of eucalypt hosts. Further, in the Mediterranean pinelands of south Spain, it has been recently demonstrated that mistletoe-infected pines have significantly greater secondary compounds and lower amounts of nitrogen than non-infected ones (Lázaro-González *et al.* 2019), making host leaves less attractive for herbivorous insects (Lázaro-González *et al.* 2019). These differences in resource quantity and quality can be expected to increase the abundance of herbivores and detritivores likely represented in the most responsive arthropod groups found in pit-fall traps – that is, Coleoptera, Hemiptera, Diplopoda, and litter-dwelling Lepidoptera larvae. In turn, greater prey availability would sustain higher numbers of spiders (Table 1).

Table 2. Effect of mistletoe *Amyema miquelii* infection and tree species on arthropod abundance and biomass

Arthropods	Variable	Abundance (individuals trap ⁻¹ day ⁻¹)						Biomass (mg trap ⁻¹ day ⁻¹)					
		Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr (>F)
Preferred	Infection status	6407.2	6407.2	1	31	115.294	0.0018	0.8290	0.8291	1	15.945	176.619	0.0007
	Species	1355.7	1355.7	1	31	24.395	0.1285	0.0025	0.0025	1	16.126	0.0526	0.8214
	Infection status: Species	1305.6	1305.6	1	31	23.494	0.1355	0.0111	0.0111	1	15.945	0.2370	0.6330
Others	Infection status	1145.83	1145.83	1	15.917	43.545	0.0533	258.888	258.888	1	16.201	53.576	0.0340
	Species	31.40	31.40	1	16.401	0.1193	0.7341	0.6111	0.6111	1	16.387	12.647	0.2769
	Infection status: Species	121.41	121.41	1	15.917	0.4614	0.5067	0.0144	0.0144	1	16.201	0.0298	0.8651
Total	Infection status	12927.9	12927.9	1	16.303	86.705	0.0094	63.489	63.489	1	16.232	87.895	0.0091
	Species	1861.0	1861.0	1	16.380	12.481	0.2800	0.6926	0.6926	1	16.416	0.9589	0.3416
	Infection status: Species	607.8	607.8	1	16.303	0.4076	0.5321	0.0509	0.0509	1	16.232	0.0705	0.7940

Linear mixed models (LMM's) were used, including tree infection status (infected, uninfected) and tree species (Apple box, red gum) as fixed factors and paired trees as a random factor. Significant *P*-values (*P* < 0.05) are in boldface.

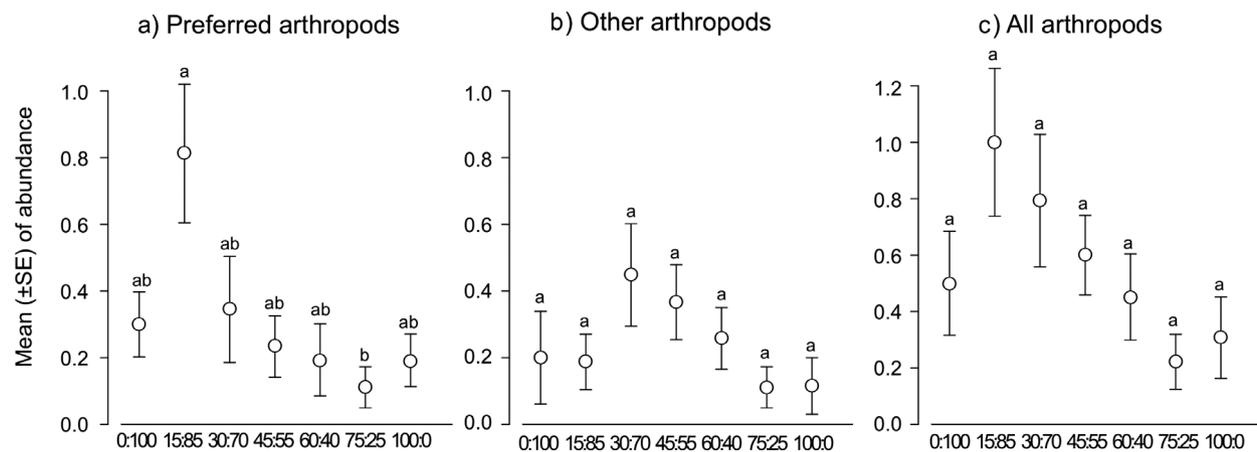


Fig. 2. Average number (\pm SE) of arthropods per litterbag with variable percentages of mistletoe: eucalypt litter, differentiating those groups highly preferred by ground-dwelling insectivorous birds (a); ('preferred arthropods'), less preferred arthropods (b); ('other arthropods') and (c); total arthropods. Different lowercase letters denote significantly different (*P* < 0.05) results, based on post hoc multiple comparisons; *N* = 32.

However, despite the potential direct benefits of mistletoe litter, its addition triggered unexpected responses from arthropods, with small fractions of hemiparasite litter resulting in the greatest increase in arthropod abundance, and higher fractions resulting in no increase in abundance relative to pure eucalypt litter (Fig. 2). This unexpected outcome could be explained by the greater heterogeneity of litter mixtures that could gather a greater number of arthropods (Kaneko & Salamanca 1999). In addition, mistletoe and eucalypt litters could be attracting different assemblages of soil arthropods, reflecting similar patterns to those recently found for canopy-dwelling arthropods, in which mistletoe opens a new habitat

space for a specific arthropod community within the relatively uniform host canopy (Burns *et al.* 2011; Lázaro-González *et al.* 2017). Otherwise, the structural changes naturally created by mistletoe litter accumulating on the forest floor, independent of those proximate mechanisms manipulated with the litterbag experimental approach, could be relevant. Mistletoes generate thick litter beds (March & Watson 2007) comprising a great variety of plant components – for example, fruits, leaves, flowers, etc. (Mellado *et al.* 2016) – under infected trees, providing structural complexity and probably a range of habitats for different epigeic arthropod groups (Bultman & Uetz 1984; Kaspari & Weiser 2007; Barton *et al.* 2010).

Differences between observational (Fig. 1) and experimental (Fig. 2) comparisons could suggest that mistletoe-mediated indirect pathways might come into play. Previous studies have demonstrated that the deposition of mistletoe litter beneath infected trees increases soil nutrient returns (March & Watson 2010), facilitating the growth of understory plants (March & Watson 2007; Mellado & Zamora 2017), thereby raising the availability of food resources for many arthropods (Hartley *et al.* 2015). In addition to altered litter inputs (in terms of quantity, seasonality, C:N ratio and micronutrient enrichment), trees infected by mistletoes are visited by more animals, leading to additional nutrient inputs over time (Mellado *et al.* 2016; Watson 2016). Hemiparasites also increase the abundance and diversity of fungal soil communities (Mueller & Gehring 2006), likely affecting arthropod fungivores. Further, parasitism could improve soil microclimate in a way that it benefits epigeic invertebrates (Ndagurwa *et al.* 2014; Hartley *et al.* 2015).

Regardless of the operating mechanisms (either direct or indirect), the fact that mistletoe occurrence considerably elevates arthropod numbers and biomass beneath infected trees is noteworthy, especially when considering the conservative nature of our approach. Results from the litterbag experiment reflect only a subset of arthropods colonising mistletoe litter within 5 months which are simultaneously present in the mesh bags at the time of collection, excluding burrowing, flying and small-bodied taxa and those groups colonising mistletoe litter decomposing over longer time scales. The same conservative nature applies to pit-fall data, in which sampled assemblages of arthropods include only those individuals left over after insectivores have removed their preferred prey (i.e. standing crop, Hobby 2015) and abundant but relatively immobile species likely under-represented due to the inherent biases of this sampling technique (Woodcock 2005). Therefore, in both study components, estimated arthropod differences were conservative and best treated as minimum stand-scale effects of mistletoe litter on arthropod availability.

Changes induced by *A. miquelii* upon the epigeic arthropod community in eucalypt woodlands were consistent with the two studies previously analysing the impact of hemiparasitic plants on these organisms. The herbaceous *Rhinanthus minor* (Hartley *et al.* 2015) and the African mistletoes *Erianthemum ngamicum*, *Plicosepalus kalachariensis* and *Viscum verrucosum* (Ndagurwa *et al.* 2014) increased arthropod abundance in their proximities, mainly those groups feeding on living or dead plant matter, and spiders depredating other invertebrates. The underlying mechanisms are likely similar for all these species as most hemiparasites studied have similar traits (e.g. nutrient-rich litter, high leaf turn over) and play

similar functional roles (e.g. increase litterfall, nutrient cycling and plant productivity) in their respective habitats (Quested *et al.* 2003; Ndagurwa *et al.* 2013; Mellado & Zamora 2017).

Another important feature shared by most hemiparasites (including mistletoes) is their characteristically patchy occurrence, with patches of uninfected plants intermingled with patches of low or intense parasitism (Aukema 2004). This patchiness likely generates complex litterfall gradients, from hemiparasite litter dominating areas beneath heavily infected hosts to none far away from hosts, affecting the spatial distribution of arthropods (Hartley *et al.* 2015). Thus, rather than a simple increase in arthropod numbers, parasitic plants might best be considered to increase heterogeneity, concentrating herbivores and detritivores in areas of higher resource availability, subsequently attracting spiders and other predatory groups. This heterogeneity could be further accentuated in those systems in which multiple hemiparasite species coexist, making available more diverse litter substrates (Ndagurwa *et al.* 2013) that attract different arthropod assemblages (Ndagurwa *et al.* 2014). Since habitat simplification reduces arthropod occurrence and diversity (Dennis *et al.* 1998), mistletoe may facilitate the ability of insectivores to find and consume their preferred prey by increasing habitat structural complexity through increasing litter quantity, quality and heterogeneity.

Numerous questions remain concerning the magnitude, time frame and underlying mechanisms of parasitic plants' influence on ecosystem processes. Rather than occurring in isolation, the litter-insect interactions we quantified here are embedded within complex food webs. How does increasing prey availability affect insectivore occurrence and microhabitat use and, consequently, community-wide patterns of insect occurrence and stand-scale herbivory? Below ground, how do altered litter inputs, decomposition rates and animal-mediated nutrient return rates affect soil-dwelling bacteria and mycorrhizae and, consequently, moisture retention and plant growth? Collectively, what fraction of the facilitative effects of hemiparasites arises from re-allocation from infected trees within systems, and what fraction comes from external subsidies via animal transport? In addition to replicated litterbag trials over biologically meaningful time frames, inoculation experiments will help clarify these dependencies.

In conclusion, although mistletoes have been widely seen as destructive forest pests (Hawksworth & Wiens 1996; Watson 2011b) a growing body of direct evidence demonstrates that they increase resource availability for many forest- and woodland-dependent organisms. Their bulky structure provides nesting and roosting sites (Cooney *et al.* 2006; Barea & Watson 2013) and their nutritive leaves, fruits,

flowers, nectar and litter feed a great diversity of animals (Watson 2001; Shaw *et al.* 2004; Burns and Watson 2013). Further, by boosting the availability of those arthropod groups of higher nutritional quality (Razeng & Watson 2014), the influence of mistletoe on insectivores extends beyond influencing occurrence, those woodlands with mistletoe supporting higher numbers of the nutritious prey required for breeding success and for maintaining resident insectivore populations (Siikamäki 1998). In addition to boosting prey availability for bird insectivores, changes in abundance and activity of different arthropod groups contribute to key functions (e.g. decomposition, seed dispersal, soil bioturbation, herbivore control *inter alia*) which collectively underpin many aspects of ecosystem health (Watson 2016). Considering the worldwide distribution of hemiparasites, their facilitative influence on epigeic arthropods might be of more generalised significance, both for insectivores and for the proactive management of the multifunctional landscapes upon which many of them depend (Bennett & Watson 2011, and references therein).

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