COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Mistletoes and their eucalypt hosts differ in the response of leaf functional traits to climatic moisture supply

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Abstract

Trade-offs between photosynthesis and the costs of resource capture inform economic strategies of plants across environmental gradients and result in predictable variation in leaf traits. However, understudied functional groups like hemiparasites that involve dramatically different strategies for resource capture may have traits that deviate from expectations. We measured leaf traits related to gas exchange in mistletoes and their eucalypt hosts along a climatic gradient in relative moisture supply, measured as the ratio of precipitation to pan evaporation (P/E_p), in Victoria, Australia. We compared traits for mistletoes vs. hosts as functions of relative moisture supply and examined trait–trait correlations in both groups. Eucalypt leaf traits responded strongly to decreasing P/E_p, consistent with economic theory. Leaf area and specific leaf area (SLA) decreased along the P/E_p gradient, while C:N ratio, leaf thickness, N per area, and $\delta^{13}C$ all increased. Mistletoes responded overall less strongly to P/E_p based on multivariate analyses; individual traits sometimes shifted in parallel with those of hosts, but SLA, leaf thickness, and N per area showed no significant change across the gradient. For mistletoes, leaf thickness was inversely related to leaf dry matter content (LDMC), with no relationship between SLA and mass-based N. In mistletoes, reduced costs of transpiration (reflecting their lack of roots) and abundant succulent leaf tissue help account for observed differences from their eucalypt hosts. Trait-based analysis of atypical functional types such as mistletoes help refine hypotheses based on plant economics and specialized adaptations to resource limitation.

Keywords Aridity gradient · *Eucalyptus* · Hemiparasitism · Leaf economics · Succulence

Introduction

Over evolutionary time, plants have developed a wide array of ecological strategies to maximize growth and fitness in response to climate and resource availability. Broad environmental gradients in water, nutrients, temperature,

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and light combined with the energetic trade-offs involved in maximizing whole-plant growth and competitive ability (Givnish 1979, 1986b; Mooney and Gulman 1979; Tilman 1988; Buckley et al. 2002; Walker et al. 2014), result in a spectrum of co-varying morphological and physiological traits (Reich et al. 1998; Westoby et al. 2002; Wright et al. 2004; Reich 2014; Kramer-Walter et al. 2016; Bruelheide et al. 2018). Different resource allocation patterns and leaf, stem, and root traits maximize growth under different environmental conditions, giving rise to a diversity of growth strategies. These strategies can be categorized as running from "slow" to "fast"—where "slow" plants make efficient use of scarce water and nutrients but grow slowly, while "fast" plants allocate more resources to growth-promoting processes but use resources less efficiently. The slow–fast economic spectrum is remarkably consistent across environments and taxonomic groups (Wright et al. 2004; Díaz et al. 2016). Both within and among species, multiple leaf, stem, and root traits exhibit coordinated economic and

environmental responses (Givnish 1986b, 2002; Vile et al. 2005; Reich 2014). The study of trait–trait relationships like these within and among species and life forms can identify key economic trade-offs that separate ecological strategies, while trait–environment relationships can help us understand plant adaptations to resource availability following environmental gradients (Wright et al. 2005; Reich et al. 2007; Šímová et al. 2018).

Water is a limiting resource for many land plants. Leaves display numerous adaptations to reduced water supply and increased evaporative demand, including thicker and narrower leaves, lower stomatal conductance, higher reflectance, and increased incidence of CAM or C_4 photosynthetic pathways (Givnish and Vermeij 1976; Cowan and Farquhar 1977; Ehleringer and Mooney 1978; Givnish 1979, 1986b; Medlyn et al. 2011; Osborne and Sack 2012; Crayn et al. 2015; Murray et al. 2019). These traits reduce water loss but at the cost of reduced photosynthesis, so adaptation requires maximizing the difference between photosynthetic benefits and transpirational costs to maximize whole-plant growth and competitive ability—the economics of gas exchange (Givnish 1986b). Transpiration becomes more costly as water becomes scarcer because greater allocation to roots is required or lower leaf water potential reduces photosynthetic capacity. Consequently, as water supply declines and the costs of replacing water lost to transpiration increase, we would expect leaf thickness and reflectance to increase and stomatal conductance to decrease to maximize net whole-plant carbon uptake (Givnish 1979, 1986b; Wright et al. 2001). In general, such leaf adaptations reduce whole-plant growth as moisture supply declines. Plants in drier habitats typically have thicker leaves that contain more nitrogen per unit area (Cunningham et al. 1999; Wright et al. 2004; Prentice et al. 2011), as expected from the linked optimization of water and nitrogen use (Buckley et al. 2002).

Despite widely recognized trait patterns across plants globally, co-occurring life forms can vary considerably in their trait–trait relationships (Santiago and Wright 2007) and in how traits respond to environmental gradients (Schellenberger Costa et al. 2018). Here, we consider whether hemiparasitism in mistletoes alters trait–trait and trait–environment relationships by changing the economic trade-offs facing plants. Mistletoes are aerial stem hemiparasites including some 1,500 species in three families of Santalales found on all continents except Antarctica (Mathiasen et al. 2008). In place of roots, mistletoe xylem is connected to that of their hosts via haustoria, specialized structures that allow redirection of water and nutrients into the mistletoe (Mathiasen et al. 2008). Mistletoes, thus, avoid the carbon and nutrient costs of roots (Givnish 1986a), as well as the carbon costs of extensive stem construction to reach the light environment of the forest canopy (Těšitel 2016). Their carbon budgets may be supplemented through acquisition of heterotrophic

carbon from hosts (Marshall and Ehleringer 1990; Marshall et al. 1994).

In parallel with differences in water acquisition, mistletoes generally transpire faster at a given rate of photosynthesis (Schulze and Ehleringer 1984; Ullmann et al. 1985; Ehleringer et al. 1985), have shorter leaf lifespans (March and Watson 2007), and have succulent leaf tissue with high water content (Popp et al. 1995; Glatzel and Geils 2009). High transpiration and stomatal conductance at a given photosynthetic rate in mistletoes have been posited to reflect adaptation for either nitrogen piracy from the host xylem stream (Schulze et al. 1984) or the low costs of transpiration in rootless plants (Givnish 1986a). Despite such physiological differences, there is often considerable visual similarity between the leaves of mistletoes and their hosts, leading some to suggest that mistletoe leaf form is occasionally driven by mimicry of host leaves as crypsis against vertebrate herbivory (Barlow and Wiens 1977). Leaf mimicry could cause similarities between mistletoe and host leaves for some traits and may lead them to respond to environmental conditions in similar ways. Even so, based on the economics of gas exchange, mistletoes should exhibit trait–trait and trait–environment relationships that differ in specific ways from those seen in non-hemiparasites.

Previous studies on trait–environment responses in mistletoes vs. hosts (e.g., Scalon and Wright 2017) were not conducted along spatially continuous environmental gradients, precluding powerful analyses in a regression framework. Past research indicates that mistletoes exhibit more transpiration and respiration at a given photosynthetic rate than their hosts (Küppers 1992; Scalon and Wright 2017) and weaker responses of stomatal conductance to aridity (Ullmann et al. 1985). However, many trait–trait relationships remain unexamined and we lack a complete understanding of how hemiparasitism affects economic trade-offs that underlie trait responses to the environment.

Here, we compare leaf functional traits in mistletoes and their *Eucalyptus* (Myrtaceae) hosts in response to a climatic gradient of relative moisture supply from tall wet sclerophyll forest and temperate rainforest to arid mallee in Victoria, Australia (Fig. 1). We quantified relative moisture supply as the ratio of annual precipitation to pan evaporation (P/E_p; Givnish et al. 2014). This metric reflects water stress induced by both declining rainfall and increasing evaporative demand. Relative moisture supply strongly influences eucalypt leaf traits such as specific leaf area, leaf thickness, photosynthetic rate, and water-use efficiency (Warren et al. 2006; Cernusak et al. 2011; Givnish et al. 2014). We ask two core questions: (1) Do mistletoes differ from eucalypts in their leaf traits and the steepness of trait responses to P/E_p—that is, do mistletoes and eucalypts differ in their trait–environment relationships; and (2) Do trait–trait relationships in mistletoes and eucalypts show evidence

Fig. 1 Map of study sites in Victoria, Australia, including **a** Rubicon State Forest, **b** Pyrenees State Forest, **c** Bealiba–Barp State Forest, **d** Little Desert National Park, and **e** Hattah State Forest/ Hattah-Kulkyne National Park. Background indicates relative moisture supply gradient in terms of P/E_p (modified from Givnish et al. 2014)
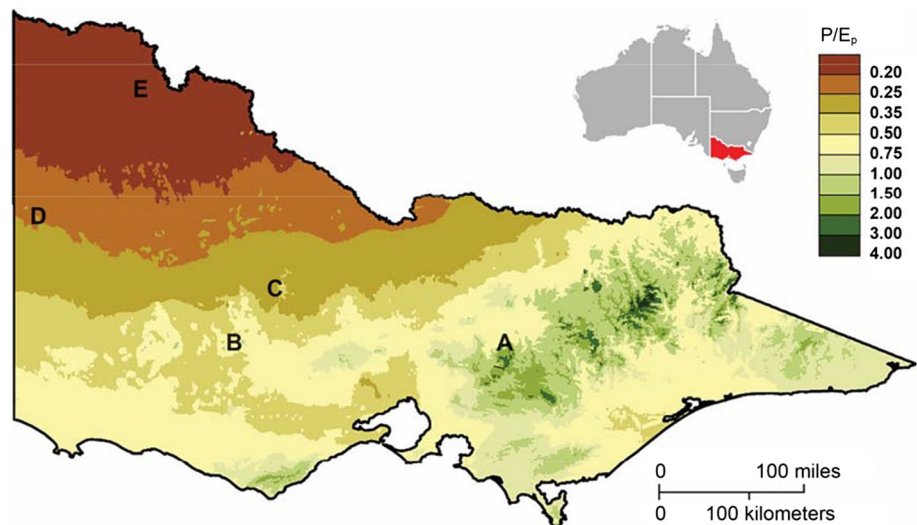
of different economic strategies driven by differences in resource acquisition and use?

We focused our analysis on leaf traits related to gas exchange: carbon isotope ratio ($\delta^{13}C$), leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf thickness, leaf nitrogen per mass and per area (N_{mass} and N_{area}, respectively), leaf chlorophyll per area, and carotenoid:chlorophyll ratio. Based on the economics of gas exchange, eucalypt traits should generally respond more steeply than mistletoe traits to increases in relative moisture supply, including steeper increases in leaf area, SLA, N_{mass}, and chlorophyll content, and steeper declines in leaf thickness, LDMC, C:N ratio, and $\delta^{13}C$. These dampened responses of mistletoes to P/E_p should arise due to their lower costs of transpiration. The slopes of trait–trait relationships in mistletoes should differ from those in eucalypts based on lower investments in water and nutrient acquisition by hemiparasites. Mistletoe succulence should also contribute to differences in leaf construction.

Methods

Study location

Our study sites followed a climatic aridity gradient in Victoria, Australia (Fig. 1). Victoria has three advantages for studying mistletoe vs. host responses to aridity: (1) rainfall and evapotranspiration change quite substantially over short distances; (2) several species of mistletoes and eucalypts are native to the area; and (3) native *Eucalyptus* species there diverged across rainfall regimes over a wide range of times (~ 0.5–50 Mya Thornhill et al. 2019) making it unlikely that trait differences among eucalypts are strongly constrained by phylogeny.

In August 2018, we collected leaf samples from 55 mistletoe–host pairs (Table S1), including four species of mistletoes (*Amyema miraculosum, A. miquelii, A. pendula, Muellerina eucalyptuoides* [Loranthaceae]) and 17 of *Eucalyptus* (*E. arenacea, E. dives, E. dumosa, E. gracilis, E. leptophylla, E. leucoxylon, E. macrocarpa, E. macrorhyncha, E. melliodora, E. polyanthemos, E. radiata, E. regnans, E. tricarpa, E. viminalis,* and three unidentified species)*, at nine well-drained, upland sites in five state forests and national parks that span a substantial gradient in relative moisture supply (Table 1). Research was permitted under permit NW11041F for Victoria State Forests and permit 10008794 for Victorian National Parks. We defined relative moisture supply as the ratio of mean annual precipitation (P) to annual pan evapotranspiration (E_p); P/E_p is, in essence, an index of moisture supply relative to demand, and an inverse measure of aridity. To calculate P/E_p, we used GPS coordinates for each mistletoe–host pair to obtain mean annual precipitation from WorldClim (Fick and Hijmans 2017) and mean annual pan evaporation (Australian Bureau of Meteorology 2016). The layers have spatial resolution of 30 s for precipitation and 0.25 degrees for pan evaporation. Across our study sites, P/E_p increased more than eightfold from northwest to the southeast.

Sample collection

We haphazardly selected mistletoe–host pairs along road-sides at each site. To collect leaves, we launched weight bags attached to a line by hand or slingshot over infected tree branches with sun-exposed leaves, and then pulled mistletoe and eucalypt branches to the ground. Eucalypt leaves were always collected from the mistletoe host plant, but not always from the same branch infected by the mistletoe. From each branch, we collected five healthy, fully

Table 1 Site vegetation and climate characteristics at (A) Rubicon State Forest, (B) Pyrenees State Forest, (C) Bealiba–Barp State Forest, (D) Little Desert National Park, and (E) Hattah State Forest/Hattah-Kulkyne National Park

Site	Vegetation	Coordinates	Elevation (m)	MAT (°C)	MAP (mm)	PET (mm)	P/E_p
A – upper elevation	Temperate rainforest	37°19′S 145°54′E	731	11.0	1565	1102	1.421
A – mid elevation	Temperate rainforest	37°18′S 145°53′E	495	11.7	1377	1153	1.194
A – lower elevation	Woodland	37°17′S 145°52′E	368	13.1	1018	1153	0.883
B – upper elevation	Woodland	37°03′S 143°15′E	500	12.6	739	1411	0.524
B – lower elevation	Woodland	37°02′S 143°16′E	363	13.2	662	1411	0.469
C	Woodland	36°43′S 143°36′E	293	14.0	557	1462	0.381
D	Mallee	36°27′S 141°39′E	156	14.3	461	1604	0.287
E – east site	Mallee	34°44′S 142°19′E	56	16.6	332	1967	0.169
E – west site	Mallee	34°44′S 142°10′E	43	16.7	326	1967	0.166

expanded leaves. Flowers or fruits, if present, were collected to aid in species identification. All samples were placed in plastic bags and kept in insulated containers prior to trait measurements.

Leaf trait measurements

We measured leaf thickness (mm), leaf area (cm^2), specific leaf area (cm^2 leaf area g^{-1} dry mass), leaf dry matter content (mg dry mass g^{-1} fresh mass), leaf N per mass (g N g^{-1} dry mass), leaf N per area (g N cm^{-2} leaf area), leaf C per mass (g C g^{-1} dry mass), C:N ratio (g C g^{-1} N), δ^{13}C, δ^{15}N, chlorophyll content index, and carotenoid:chlorophyll ratio index. We also calculated leaf density (g dry mass cm^{-3}) and saturated water content ([g fresh mass−g dry mass]/g^{-1} dry mass). Using fresh leaves, we measured leaf thickness in three places along the lamina using a thickness gauge micrometer (B.C. Ames). To determine SLA, each dried leaf was weighed and area calculated from a photograph of the fresh leaf using ImageJ (version 1.52 h, National Institutes of Health). Photos were corrected for lens distortion using PTLens (ePaperPress). To provide proxies for chlorophyll concentration and carotenoid:chlorophyll ratio, we calculated the modified normalized difference index (mND$_{705}$) and photochemical reflectance index (PRI) (Sims and Gamon 2002). These indices use % leaf reflectance at 445, 531, 570, 705, and 750 nm, which we measured on both sides of each fresh leaf using a UniSpec spectral analyzer (PP Systems). mND$_{705}$ shows a positive, plateauing response to chlorophyll concentration per unit area; PRI decreases linearly with the carotenoid:chlorophyll ratio (Sims and Gamon 2002).

After initial measurements, leaves were dried in silica gel and transported to Wisconsin, USA where they were oven-dried at 50 °C for 72 h, then weighed on a Mettler Toledo analytical balance. After drying, one leaf per plant was randomly selected for elemental analysis. We prepared each sample by grinding in a Wiley Mill, packing 3–5 mg

of leaf grounds in tin capsules, and sending them to the Idaho State University Stable Isotope Lab for leaf carbon, nitrogen, δ^{13}C, and δ^{15}N analysis. Analyses used a 2010 ThermoFisher Delta V Plus continuous flow isotope ratio mass spectrometer coupled with ConFlo IV/EA, TC/EA, and GasBench II.

Analysis

We used principle components analysis (PCA) to assess multivariate trait differences between mistletoes and eucalypt hosts, aggregated across climatic conditions. Traits with multiple values per individual were averaged before entry into the PCA. Leaf density and saturated water content were excluded because they re-expressed other variables. We tested for differences in centroids between life forms using permutational analysis of variance (PERMANOVA). To test whether mistletoes or eucalypts varied more across all traits, we calculated convex hull volume of the PCA points for each group using the significant PC axes and the *convhulln* function from the 'geometry' package (Roussel et al. 2019) in R. PCA was performed using the *prcomp* function in R using scaled and centered trait values. We tested correlation between each PC axis and P/E_p using Pearson's product-moment correlation.

We used linear mixed effects models to test for significant responses of leaf traits and PC axes to P/E_p for each life form. We evaluated variation in each trait, PC1, and PC2 separately using P/E_p, life form (mistletoe or eucalypt), and their interaction as fixed effects. We included random effects of mistletoe–host pair identity, site, and species to account for nonindependence in the sampling design. Where necessary, trait values were log-transformed to meet assumptions of normality. We fitted models using the R package 'lme4′ (Bates et al. 2019).

We used standardized major axis regressions (SMA; Warton et al. 2006) to assess whether trait–trait relationships differed significantly between eucalypts and mistletoes.

We assessed differences in slopes for various relationships among SLA, LDMC, leaf thickness, N_{mass}, N_{area}, and $\delta^{13}C$ in mistletoes and eucalypts along with whether the slopes of N_{mass} and $\delta^{13}C$ in mistletoes vs. their eucalypt hosts differed from one and intercepts differed from zero (i.e., do leaf nutrients in individual mistletoes vary from those of the host tree they occupy). All SMA analyses were conducted using the R package 'smatr' (Warton et al. 2012).

Finally, we used variance partitioning to examine differences in intraspecific variation between mistletoes and eucalypts to assess the sources of trait variation in each group. We used the R packages 'nlme' (Pinheiro et al. 2020) and 'ape' (Paradis et al. 2019) to partition the variance composition of each trait within each lifeform among species, within species, and within individuals. We also calculated the total percent variation within lifeforms for each trait.

Results

Trait–environment relationships

Responses of eucalypt traits to the P/E_p gradient largely matched theoretical predictions and empirical patterns for other fully autotrophic plants. Specifically, eucalypts show significant increases in SLA and N_{mass} with increasing P/E_p, and significant declines in LDMC, $\delta^{13}C$, and N_{area} (Fig. 2; Table S2). Eucalypts also showed substantial but statistically insignificant increases in leaf area with P/E_p, and similar declines in leaf C:N and $\delta^{15}N$. Mistletoes show the same directionality of P/E_p responses as eucalypts in six of 12 traits: for leaf area, $\delta^{13}C$, and $\delta^{15}N$, the trends were significant, while those for LDMC, N_{mass}, and C:N were not.

Mistletoe P/E_p responses deviated significantly from those of eucalypts for five traits (Fig. 2; Table S2). We found significant interactions between P/E_p and life form for SLA ($t = 7.54$, $P < 0.001$), leaf thickness ($t = -5.99$, $P < 0.001$), and N_{area} ($t = -4.49$, $P < 0.001$), where mistletoes showed no significant response to P/E_p. There were also significant interactions for the chlorophyll index ($t = -7.05$ $P < 0.001$) and carotenoid:chlorophyll index ($t = 3.93$, $P < 0.001$), where mistletoes responded more steeply to P/E_p than eucalypts. LDMC, N_{mass}, $\delta^{13}C$, and C:N ratio differed significantly between lifeforms (LDMC: $t = 4.87$, $P < 0.001$; N_{mass}: $t = 8.62$, p < 0.001; $\delta^{13}C$: $t = 5.98$, $P = 0.003$; C:N: $t = -8.68$, $P < 0.001$).

When mistletoes and hosts were considered together, $\delta^{13}C$ and C:N ratio responded weakly to the P/E_p gradient ($\delta^{13}C$: $t = -2.25$, $P = 0.05$; C:N: $t = -2.44$, $P = 0.03$), while LDMC and N_{mass} did not show significant responses. Leaf area and $\delta^{15}N$ were similar for both life forms and responded significantly to P/E_p (leaf area: $t = 3.11$, $P = 0.01$; $\delta^{15}N$: $t = -2.68$,

$P = 0.02$). Carbon content showed no response to life form or P/E_p (full results are presented in Table S2).

Mistletoes and eucalypts also showed differences in multidimensional trait space. The first principal component axis accounted for 48.0% and the second axis 19.5% of overall trait variance; only these axes made significant contributions to trait variation (Fig. 3a). Leaf thickness and the carotenoid:chlorophyll index increased with PC1, while N_{mass}, %C, and chlorophyll content decreased. LDMC and $\delta^{13}C$ increased with PC2, while leaf area and SLA decreased. Mistletoes and eucalypts showed significant differences in centroids (PERMANOVA: $f = 113.44$, $P < 0.001$). Eucalypt leaves occupied slightly (13.3%) more trait space than mistletoes (convex hull area: eucalypts = 11.9, mistletoes = 10.4), primarily reflecting the greater range of eucalypts on PC2. P/E_p was correlated with both axes, albeit more strongly with PC2 ($r = -0.70$, $P < 0.001$) than PC1 ($r = -0.20$, $P = 0.04$). PC2 reflected significant interactions between P/E_p and life form, with eucalypts showing a steeper response and PC2 being more strongly correlated (Fig. 3c). PC1 showed significant responses to both life form and P/E_p, with mistletoes and eucalypts showing essentially the same steepness of response to P/E_p (Fig. 3b). Thus, overall, mistletoes exhibited a more muted multivariate trait response to P/E_p than eucalypts.

Trait–trait relationships

Mistletoe and eucalypt leaves also differed in relationships between traits. Leaf thickness declined with SLA for both groups but declined more steeply in eucalypt leaves (Fig. 4a) than in mistletoes. Eucalypts also showed a stronger decline in LDMC with SLA (Fig. 4b). LDMC for mistletoe leaves was consistently less than that of eucalypt leaves for a given thickness, confirming that mistletoes had low leaf tissue density and greater saturated water content, that mistletoes stored 50–100% more water per unit leaf mass, and that (surprisingly) saturated water content in both mistletoes and eucalypts increased with P/E_p (Fig. S2). Mistletoes and eucalypts displayed opposing relationships between leaf thickness and LDMC (Fig. 4c). Leaf thickness increased with LDMC in eucalypts and decreased in mistletoes. SLA increased significantly with N_{mass} in eucalypts but not in mistletoes (Fig. 4d). Arguably, however, mistletoes and eucalypts were part of the same data cloud, showing a positive relationship of SLA to N_{mass}. $\delta^{13}C$ varied significantly with both SLA (Fig. 4e) and N_{area} (Fig. 4f) in eucalypts but showed no significant change in mistletoes.

N_{mass} of mistletoe leaves was consistently less than that of their hosts, and significantly but weakly related to host N_{mass} (Fig. 5a), with a slope significantly less than 1 ($P = 0.003$) indicating a greater divergence from host leaves with high N_{mass}. Mistletoe $\delta^{13}C$ increased

Fig. 2 Leaf traits of eucalypt hosts (triangles) and mistletoe hemiparasites (circles) along a gradient in relative moisture supply represented by P/E_p for **a** leaf area (cm^2); **b** specific leaf area ($cm^2\ g^{-1}$); **c** leaf thickness (mm); **d** leaf dry matter content ($mg\ g^{-1}$); **e** leaf C per mass (g g^{-1}); **f** $\delta^{13}C$ (‰); **g** leaf N per mass (g g^{-1}); **h** leaf N per area (g cm^{-2}); **i** carbon:nitrogen ratio (g g^{-1}); **j** $\delta^{15}N$ (‰); **k** chlorophyll content index (mND_{705}); and **l** carotenoid:chlorophyll index (PRI). Significant predictors are displayed at the top of each panel; "P" represents a significant main effect of precipitation/pan evaporation, "L" represents a significant main effect of life form (i.e., eucalypt or mistletoe), "I" represents a significant interaction between precipitation/pan evaporation and life form, and "*n.s.*" represents no significant effect. *$P \le 0.05$, **$P \le 0.01$, ***$P \le 0.001$. See Table S1 for statistics detail
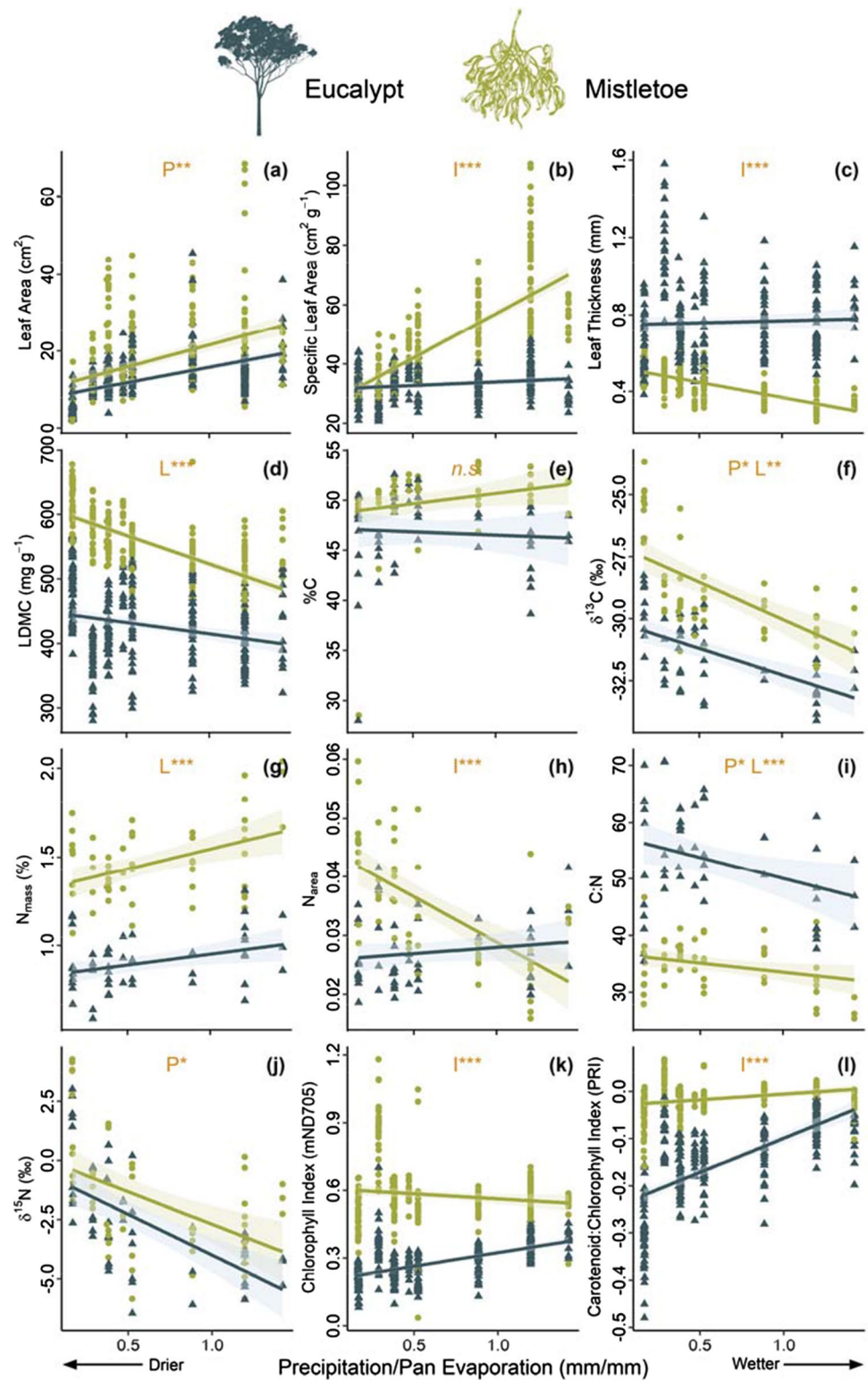
significantly and more strongly with that of eucalypt hosts, but the slope of that relationship was also significantly less than 1 ($P = 0.005$; Fig. 5b). Differences between hosts and mistletoes increased at higher values of $\delta^{13}C$ and N_{mass}, corresponding to greater divergence in N_{mass} under wetter conditions, and greater divergence in $\delta^{13}C$ under drier conditions. We found no significant relationship between $\delta^{13}C$ and N_{mass} within either group, between host N and mistletoe $\delta^{13}C$, or between the host–mistletoe $\delta^{13}C$ difference and host N_{mass} (Fig. S1).

Fig. 3 a Principal components analysis of leaf traits in mistletoes (circles) and eucalypts (triangles). The first two axes represent 71.1% of the variation across nine leaf traits. Arrows represent the relative magnitude of correlation between each PC axis and each trait. **b** Correlations between PC1 and P/E_p gradient, showing significant difference between mistletoes and eucalypts ($t = -17.90$ $P < 0.001$) and a weak effect of P/E_p ($t = -3.39$, $P = 0.008$). **c** Correlations between PC2 and P/E_p gradient, showing a significant interaction between lifeform and P/E_p ($t = -3.94$, $P = 0.002$)
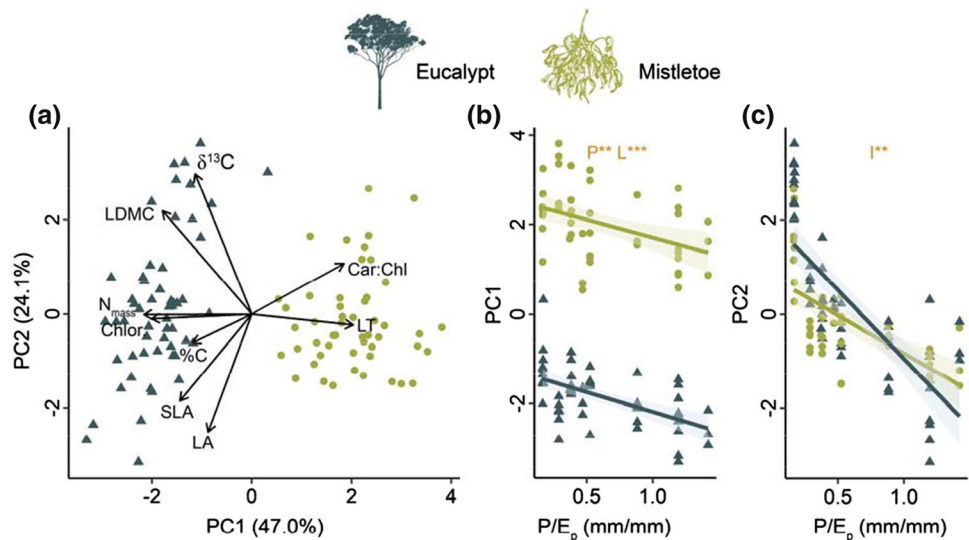
Discussion

Our results reveal both consistent and contrasting patterns in mistletoes vs. eucalypt hosts in response to moisture availability. While both groups showed similar responses to relative moisture supply in some traits, such as $\delta^{13}C$ and leaf area, indicating a shift to more conservative water use and reduced carbon gain in drier regions, other traits, such as SLA and N_{area}, revealed opposing patterns between lifeforms. Trait–trait relationships also showed some similarities in mistletoes and eucalypts (e.g., SLA vs. N_{mass}), as well as some striking differences (e.g., SLA and leaf thickness vs. LDMC and SLA vs. $\delta^{13}C$) which appear to implicate differences in leaf construction. In what follows, we explore potential explanations for these similarities and differences, including the role of transpiration in N capture, the cost of acquiring water, and the significance of succulent leaf tissue in mistletoes.

### Consistent trait responses to relative moisture supply

Mistletoes and eucalypts showed similar responses to relative moisture supply (P/E_p) for four traits ($\delta^{13}C$, leaf area, C:N ratio, $\delta^{15}N$) and a similar trend in N_{mass} (Fig. 2). Most of these patterns can be understood in terms of the economics of gas exchange and hydraulic adaptations. Both lifeforms

showed less negative $\delta^{13}C$ values under drier conditions, corresponding to lower average stomatal conductance relative to photosynthetic capacity (Farquhar et al. 1982). $\delta^{13}C$ declines with increasing precipitation worldwide (Kohn 2010; Prentice et al. 2011; Givnish et al. 2014), a pattern consistent with optimizing the balance of transpiration and photosynthesis (Givnish and Vermeij 1976; Cowan and Farquhar 1977). Yet, mistletoes maintained more negative values of $\delta^{13}C$ than their hosts across all sites, suggesting that they maintain a higher stomatal conductance than their hosts under any given condition (Ullmann et al. 1985; Scalon and Wright 2017).

Worldwide, leaf area shows a positive relationship with annual precipitation. Smaller leaves have a thinner boundary layer, which aids in convective cooling at drier, sunnier sites, while plants at wetter sites have lower transpirational costs associated with evaporative cooling, allowing for larger leaves (Givnish and Vermeij 1976; Cunningham et al. 1999; Wright et al. 2017). Both lifeforms follow this pattern. The lack of a difference in leaf area between lifeforms at any P/E_p is surprising, however, given the lower transpirational costs expected in mistletoes.

Both groups also displayed decreasing C:N ratios with P/E_p. This pattern may relate either to evolution of thicker cell walls and/or smaller cell diameters to avoid cell collapse under more negative water potentials in drier areas or to selection for greater leaf N at wetter sites (Givnish 1978; Givnish et al. 2014). While we observed trends toward higher leaf N at higher P/E_p in both lifeforms, they were not significant. Variation in N_{mass} is directly related to SLA and N_{area} ($N_{mass} = N_{area} * SLA$), both of which showed the expected shifts with P/E_p in eucalypts but not in mistletoes (Fig. 2b, h). Finally, in fully photosynthetic plants, higher $\delta^{15}N$ values are observed globally in areas of lower annual rainfall, apparently due to increased loss of N (and thus,

Fig. 4 Trait–trait correlations in mistletoes (circles) and eucalypts (triangles) based on standardized major axis regression for: **a** leaf thickness and SLA (mistletoe slope $= -1.55$, $R^2 = 0.55$, $P < 0.001$, eucalypt slope $= -0.66$, $R^2 = 0.86$, $P < 0.001$; slope difference: $LR_{df} = 270.3_1$, $P < 0.001$); **b** LDMC and SLA (mistletoe slope $= 0.81$, $R^2 = 0.02$, $P = 0.01$, eucalypt slope $= -0.30$, $R^2 = 0.64$, $P < 0.001$; slope difference: $LR_{df} = 182.0_1$, $P < 0.001$); **c** leaf thickness and LDMC (mistletoe slope $= -1.92$, $R^2 = 0.54$, $P < 0.001$, eucalypt slope $= 2.19$, $R^2 = 0.36$, $P < 0.001$; slope difference: $LR_{df} = 4.22_1$ $P = 0.04$); **d** SLA and N_{mass} (mistletoe slope $= 0.46$, $R^2 = 0.04$, $P = 0.14$, eucalypt slope $= 0.63$, $R^2 = 0.17$, $P = 0.002$; slope difference: $LR_{df} = 2.55_1$, $P = 0.11$); **e** $\delta^{13}C$ and SLA (mistletoe slope $= 0.05$, $R^2 = 0.003$, $P = 0.66$, eucalypt slope $= -0.07$, $R^2 = 0.44$, $P < 0.001$; slope difference: $LR_{df} = 5.18_1$, $P = 0.02$); and **f** $\delta^{13}C$ and N_{area} (mistletoe slope $= -16.33$, $R^2 = 0.01$, $P = 0.46$, eucalypt slope $= 15.08$, $R^2 = 0.35$, $P < 0.001$; slope difference: $LR_{df} = 0.19_1$, $P = 0.66$)
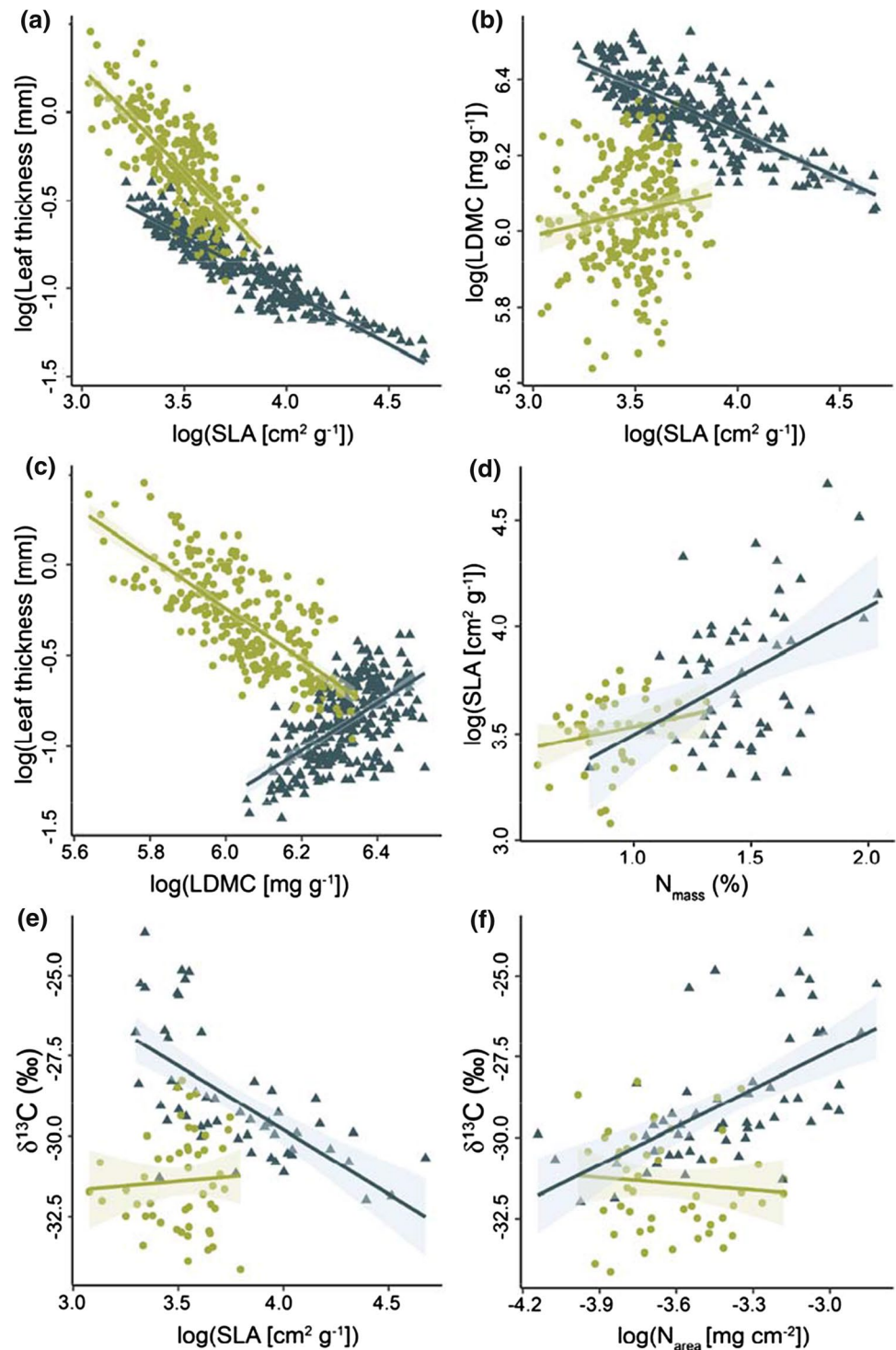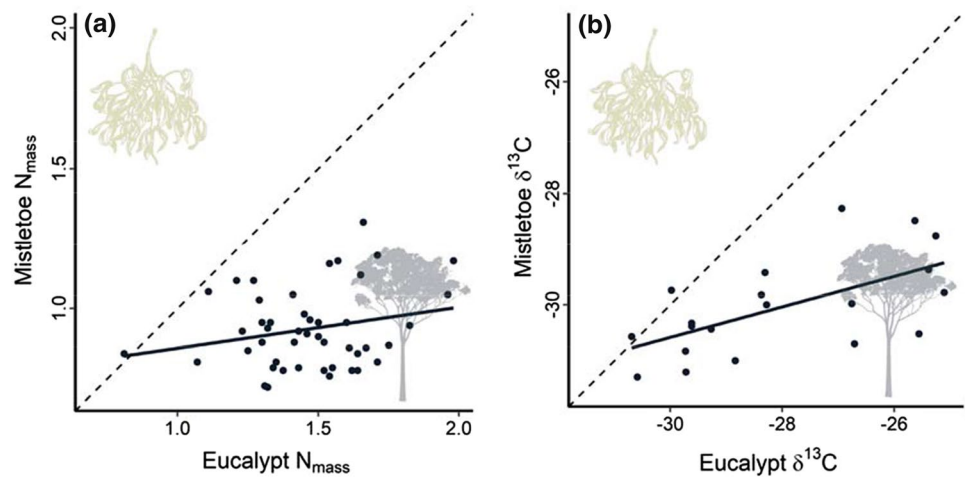
Fig. 5 Difference within eucalypt–mistletoe pairs based on standardized major axis regression in **a** N_{mass} (slope = 0.66, $R^2 = 0.09$, $P = 0.03$, slope different than 1: $P = 0.003$) and **b** $\delta^{13}C$ (slope = 0.73, $R^2 = 0.48$, $P < 0.001$, slope different than 1: $P = 0.005$). The dashed line demarks no difference within eucalypt–mistletoe pairs

preferential retention of ^{15}N) in drier sites due to greater ammonium volatilization, nitrification, and/or denitrification (Craine et al. 2009). Both lifeforms follow this pattern and the lack of difference in $\delta^{15}N$ between them indicates that mistletoes rely on the same sources of nitrogen as their hosts.

Trait differences between lifeforms

Four traits (LDMC, C:N ratio, N_{mass}, $\delta^{13}C$) showed clear differences between mistletoes and eucalypts, whether or not they responded to P/E_p; another five (SLA, leaf thickness, N_{area}, chlorophyll index, carotenoid:chlorophyll index) showed a significant interaction between lifeform and P/E_p (Fig. 2). These differences—as well as most differences in trait–trait relationships between lifeforms (Fig. 4)—trace back to the succulence of mistletoe leaves, with abundant water storage tissue (Popp et al. 1995; Glatzel and Geils 2009). Mistletoes had thicker leaves with lower LDMC and SLA than eucalypts—and higher C:N—across the entire gradient, with lower leaf density and higher saturated water content, suggesting that these traits in mistletoes reflect abundant, thin-walled, N-poor water storage tissue. High LDMC in eucalypts may also reflect selection for thick cell walls and tough leaves to deter herbivory on nutrient-poor substrates; lower LDMC in mistletoes supports previous reports of short leaf lifespans (March and Watson 2007) and poor defenses against herbivory (Canyon and Hill 1997). The unexpected inverse relationship between leaf thickness and LDMC in mistletoes (Fig. 3c) suggests a spectrum of capacitance that facilitates their ability to maintain higher stomatal conductance than their hosts across a wide range of moisture availability.

We found lower N_{mass} in mistletoes than their hosts (Küppers 1992), and mistletoe photosynthetic capacity consistently has been documented as less than that of their host trees (Ehleringer et al. 1986; Davidson et al. 1989; Strong 2000). Critically, low leaf N content—on both a mass and

area basis—in mistletoes may not result from N shortage due to reliance on N-poor xylem flows in their host (as hypothesized by Schulze et al. 1984), but may simply reflect more non-photosynthetic, N-poor water storage tissue in mistletoes. Large amounts of non-photosynthesizing water storage tissue inevitably lead to reduced leaf N and photosynthetic capacity per unit leaf mass. Rapid turnover in mistletoe leaves may also contribute to lower N content compared with hosts (March and Watson 2007). The differences in C:N ratio between lifeforms are primarily driven by differences in nitrogen since carbon content did not vary with P/E_p (Xu et al. 2020).

Greater leaf thickness and lower SLA should be favored on drier sites based on selection to maximize whole-plant growth and the difference between photosynthesis and transpirational costs (Givnish 1978, 1979; Cunningham et al. 1999; Prentice et al. 2011; Givnish et al. 2014), and we saw this pattern in eucalypts but not in mistletoes. Lower values of $\delta^{13}C$ in mistletoes are inconsistent with their lower SLA, but could reflect their lower N_{area} than eucalypts over much of the rainfall gradient (Turner et al. 2008). Decline in N_{area} with P/E_p observed in eucalypts is predicted under selection to maximize photosynthesis for given total water and N supplies (Farquhar et al. 2002) and consistent with other observations along rainfall gradients (Prentice et al. 2011; Givnish et al. 2014). Interestingly, though, $\delta^{13}C$ values did not track shifts in SLA and N_{area} in mistletoes (Fig. 4e, f), a pattern documented in multiple plant groups (Turner et al. 2008; Prentice et al. 2011). Mistletoe $\delta^{13}C$ values only spanned ~ 4‰, which suggests the internal CO_2 concentration was high throughout the gradient and is consistent with mistletoes maintaining higher stomatal conductance than eucalypts.

Increasing carotenoid:chlorophyll index in mistletoes toward drier sites (Fig. 2l; PRI decreases with the ratio) suggests greater photoprotection in mistletoes on brightly lit sites, which may be related to a greater midday drawdown

of leaf water potential driven by their high stomatal conductance and the high VPD at such sites. Increasing chlorophyll content with P/E_p in mistletoes—despite an increase in water storage tissue—could reflect adaptation to shadier conditions as forests become more closed on rainier sites. Eucalypts showed no change in either pigment trait across the gradient.

Adaptive significance of differences between mistletoes and their eucalypt hosts

The N piracy hypothesis advanced by Schulze et al. (1984) can be interpreted as requiring that the difference in transpiration between mistletoe and host become greater as host N supply becomes more limited, so that mistletoes can draw sufficient N from the host xylem sap (Ehleringer et al. 1985; Bannister and Strong 2001). Along with Scalon and Wright (2015), we found little evidence for this hypothesis in our data—in fact, differences between mistletoes and hosts in N_{mass} were least when host N levels were lowest (Fig. 5a). Others have suggested that high transpiration rates help mistletoes acquire phosphorus from their hosts at P-limited sites (Scalon and Wright 2017) or greater amounts of heterotrophic carbon (Marshall et al. 1994; Bannister and Strong 2001). Bannister and Strong (2001) used the relationship between $\delta^{13}C$ and $\delta^{15}N$ to calculate heterotrophic carbon gains by mistletoes from their hosts. Our data do not support such a phenomenon (Fig. S3). Overall, we found little evidence of transpiration-controlled nutrient acquisition in mistletoes, indicating that high transpiration in mistletoes seems more likely to reflect other physiological processes.

Mistletoes make no investments in roots for the same gains in water and nutrients as their hosts, and only small amounts in haustoria, reducing the costs associated with a given amount of transpiration. Givnish (1986a) proposed that mistletoes may be less sensitive to water supply because their investment in acquiring water does not need to increase in more arid environments (i.e., haustorium construction should cost approximately the same in all environments, whereas trees require additional investment in roots as resources become scarcer). Lower costs for a given amount of transpiration should favor high stomatal conductance and high rates of transpiration per unit photosynthesis, both of which have been reported in mistletoes (Ullmann et al. 1985; Küppers 1992). Subsequently, Scalon and Wright (2017) concluded that the costs of acquiring water may not be less for mistletoes at drier sites based on their observations that mistletoe photosynthetic traits, SLA, and nutrient concentrations shifted in parallel with those of their hosts between "wet" and "dry" sites. We did not find the parallel changes in SLA and N_{area} in mistletoes that Scalon and Wright (2017) reported, but our results are consistent with Givnish's (1986a) transpirational costs hypothesis, suggesting that, in economic terms, mistletoes incur fewer costs in

acquiring water than their eucalypt hosts. The lower leaf N seen in mistletoes at any given level of P/E_p (Fig. 5g) almost surely reflects the large amount of water storage tissue in thick, succulent mistletoe leaves rather than a limitation on the amount of N that can be diverted from the host xylem stream.

Irrespective of water supply, mistletoe leaves displayed characteristic traits and trait–trait relationships of succulent plants (Vendramini et al. 2002). Mistletoe leaves contain succulent non-photosynthesizing water storage tissue (Popp et al. 1995; Glatzel and Geils 2009) not present in *Eucalyptus*. These succulent tissues increase leaf thickness, reduce SLA, and reverse the relationship between thickness and dry matter content (Fig. 3). Rather than enhanced rigidity to tolerate more negative water potentials, succulence increases hydraulic capacitance, helping mistletoes buffer declines in leaf water potential and maintain stomatal opening (Glatzel and Geils 2009). Extensive water storage tissue should be favored in mistletoes to cope with rapid short-term drawdowns of leaf water content associated with high stomatal conductance and hydraulic bottlenecks in the haustorium (Davidson et al. 1989). Mistletoe succulence provides a unified explanation for many of the observed differences between mistletoes and eucalypts irrespective of P/E_p, including lower SLA, greater leaf thickness, lower LDMC, lower N_{mass}, higher C:N ratio, and lower chlorophyll content, as well as lower leaf density and greater saturated water content (Figs. 2, S2). Additionally, the abundance of non-photosynthetic water storage tissue can make mass-based measures of photosynthesis artificially low. More investigation into carbon metabolism and hydraulic conductance in mistletoes is needed to complete the picture of atypical trait relationships and economic tradeoffs, particularly in relation to the effects of succulent tissue on leaf physiological processes.

Conclusions and future directions

We found both similarities and differences in trait–environment and trait–trait relationships between mistletoes and their host trees. Our results show that mistletoe traits often respond differently to relative moisture supply than their hosts, which may be related to lower costs of acquiring water in drier environments and leaf construction involving extensive succulent tissue. We found some intriguing deviations in mistletoe trait–trait relationships from those of eucalypts (and those presumed for most other plants). Some of these differences may be driven by leaf succulence and some by the low costs of transpiration, but all merit further investigation. Mistletoes also displayed less interspecific variability but more intraspecific and intra-individual variability in traits, while levels of variation in eucalypts

reflected previously reported patterns for major plant groups. Mistletoes and other less common functional types should be included in global analyses and studied individually to understand not only the typical patterns in plant strategies and economic relationships, but the range of exceptions. We recommend investigating the trait patterns of functional groups including other hemiparasites, holoparasites, succulents, epiphytes, climbers, and non-vascular plants, all of which have been conspicuously underrepresented or absent from global trait analyses to date.

References

Australian Bureau of Meteorology (2016) Australian climate averages-evaporation (Climatology 1975–2005). http://www.bom.gov.au/jsp/ncc/climate_averages/evaporation/index.jsp?period=an#info. Accessed 5 Dec 2019

Bannister P, Strong GL (2001) Carbon and nitrogen isotope ratios, nitrogen content and heterotrophy in New Zealand mistletoes. Oecologia 126:10–20. https://doi.org/10.1007/s004420000495

Barlow BA, Wiens D (1977) Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. Evolution 31:69–84. https://doi.org/10.1111/j.1558-5646.1977.tb00983.x

Bates D, Maechler M, Bolker B, et al (2019) lme4: linear mixed-effects models using "Eigen" and S4. Version 1.1–21URL https://CRAN.R-project.org/package=lme4

Bruelheide H, Dengler J, Purschke O et al (2018) Global trait–environment relationships of plant communities. Nat Ecol Evolut 2:1906–1917. https://doi.org/10.1038/s41559-018-0699-8

Buckley T, Miller J, Farquhar GD (2002) The mathematics of linked optimisation for water and nitrogen use in a canopy. Silva Fennica. https://doi.org/10.14214/sf.531

Canyon DV, Hill CJ (1997) Mistletoe host-resemblance: a study of herbivory, nitrogen and moisture in two Australian mistletoes and their host trees. Austral Ecol 22:395–403. https://doi.org/10.1111/j.1442-9993.1997.tb00689.x

Cernusak LA, Hutley LB, Beringer J et al (2011) Photosynthetic physiology of eucalypts along a sub-continental rainfall gradient in northern Australia. Agric For Meteorol 151:1462–1470. https://doi.org/10.1016/j.agrformet.2011.01.006

Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment. Symp Soc Exp Biol: 471–505

Craine JM, Elmore AJ, Aidar MPM et al (2009) Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytol 183:980–992. https://doi.org/10.1111/j.1469-8137.2009.02917.x

Crayn DM, Winter K, Schulte K, Smith JAC (2015) Photosynthetic pathways in Bromeliaceae: phylogenetic and ecological significance of CAM and C_3 based on carbon isotope ratios for 1893 species. Bot J Linn Soc 178:169–221

Cunningham SA, Summerhayes B, Westoby M (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecol Monogr 69:569–588. https://doi.org/10.1890/0012-9615(1999)069[0569:EDILSA]2.0.CO;2

Davidson NJ, True KC, Pate JS (1989) Water relations of the parasite: host relationship between the mistletoe *Amyema linophyllum* (Fenzl) Tieghem and *Casuarina obesa* Miq. Oecologia 80:321–330. https://doi.org/10.1007/BF00379033

Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. Nature 529:167–171. https://doi.org/10.1038/nature16489

Ehleringer JR, Mooney HA (1978) Leaf hairs: Effects on physiological activity and adaptive value to a desert shrub. Oecologia 37:183–200. https://doi.org/10.1007/BF00344990

Ehleringer JR, Schulze ED, Ziegler H et al (1985) Xylem-tapping mistletoes: water or nutrient parasites? Science 227:1479–1481. https://doi.org/10.1126/science.227.4693.1479

Ehleringer JR, Cook CS, Tieszen LL (1986) Comparative water use and nitrogen relationships in a mistletoe and its host. Oecologia 68:279–284. https://doi.org/10.1007/BF00384800

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Funct Plant Biol 9:121. https://doi.org/10.1071/PP9820121

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol 37:4302–4315. https://doi.org/10.1002/joc.5086

Givnish TJ (1978) Ecological aspects of plant morphology: leaf form in relation to environment. Acta Biotheor 27:83–142

Givnish TJ (1979) On the adaptive significance of leaf form. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Columbia University Press, New York, pp 375–407

Givnish TJ (1986a) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. In: Givnish TJ (ed) On the Economy of Plant Form and Function. Cambridge University Press, pp 171–213

Givnish TJ (2002) Adaptive significance of evergreen vs. deciduous leaves: Solving the triple paradox. Silva Fennica 36:703–743. https://doi.org/10.14214/sf.535

Givnish TJ, Vermeij GJ (1976) Sizes and shapes of liane leaves. Am Nat: 743–778

Givnish TJ, Wong SC, Stuart-Williams H et al (2014) Determinants of maximum tree height in *Eucalyptus* species along a rainfall gradient in Victoria, Australia. Ecology 95:2991–3007

Givnish TJ (ed) (1986b) On the economy of plant form and function. Cambridge University Press

Glatzel G, Geils BW (2009) Mistletoe ecophysiology: Host–parasite interactions. Botany 87:10–15. https://doi.org/10.1139/B08-096

Kohn MJ (2010) Carbon isotope compositions of terrestrial C$_3$ plants as indicators of (paleo)ecology and (paleo)climate. Proc Natl Acad Sci 107:19691–19695. https://doi.org/10.1073/pnas.1004933107

Kramer-Walter KR, Bellingham PJ, Millar TR et al (2016) Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. J Ecol 104:1299–1310. https://doi.org/10.1111/1365-2745.12562

Küppers M (1992) Carbon discrimination, water-use efficiency, nitrogen and phosphorus nutrition 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. https://doi.org/10.1007/BF00225226

March WA, Watson DM (2007) Parasites boost productivity: effects of mistletoe on litterfall dynamics in a temperate Australian forest. Oecologia 154:339–347. https://doi.org/10.1007/s00442-007-0835-7

Marshall JD, Ehleringer JR (1990) Are xylem-tapping mistletoes partially heterotrophic? Oecologia 84:244–248. https://doi.org/10.1007/BF00318279

Marshall JD, Ehleringer JR, Schulze ED, Farquhar GD (1994) Carbon isotope composition, gas exchange and heterotrophy in Australian mistletoes. Funct Ecol 8:237. https://doi.org/10.2307/2389907

Mathiasen RL, Nickrent DL, Shaw DC, Watson DM (2008) Mistletoes: pathology, systematics, ecology, and management. Plant Dis 92:988–1006. https://doi.org/10.1094/PDIS-92-7-0988

Medlyn BE, Duursma RA, Eamus D et al (2011) Reconciling the optimal and empirical approaches to modelling stomatal conductance. Glob Change Biol 17:2134–2144. https://doi.org/10.1111/j.1365-2486.2010.02375.x

Mooney HA, Gulman SL (1979) Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Columbia University Press, New York, pp 316–337

Murray M, Soh WK, Yiotis C et al (2019) Convergence in maximum stomatal conductance of C$_3$ woody angiosperms in natural ecosystems across bioclimatic zones. Front Plant Sci. https://doi.org/10.3389/fpls.2019.00558

Osborne CP, Sack L (2012) Evolution of C$_4$ plants: a new hypothesis for an interaction of CO$_2$ and water relations mediated by plant hydraulics. Philos Trans R Soc B Biol Sci 367:583–600. https://doi.org/10.1098/rstb.2011.0261

Paradis E, Blomberg S, Bolker [aut B, et al (2019) ape: analyses of phylogenetics and evolution. Version 5.3URL https://CRAN.R-project.org/package=ape

Pinheiro J, Bates D, DebRoy S, Sarkar D (2020) nlme: linear and nonlinear mixed effects models

Popp M, Mensen R, Richter A et al (1995) Solutes and succulence in southern African mistletoes. Trees 9:303–310. https://doi.org/10.1007/BF00202493

Prentice IC, Meng T, Wang H et al (2011) Evidence of a universal scaling relationship for leaf CO$_2$ drawdown along an aridity gradient. New Phytol 190:169–180. https://doi.org/10.1111/j.1469-8137.2010.03579.x

Reich PB (2014) The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. J Ecol 102:275–301. https://doi.org/10.1111/1365-2745.12211

Reich PB, Ellsworth DS, Walters MB (1998) Leaf structure (specific leaf area) modulates photosynthesis-nitrogen relations: evidence from within and across species and functional groups. Funct Ecol 12:948–958. https://doi.org/10.1046/j.1365-2435.1998.00274.x

Reich PB, Wright IJ, Lusk CH (2007) Predicting leaf physiology from simple plant and climate attributes: a global GLOPNET analysis. Ecol Appl 17:1982–1988. https://doi.org/10.1890/06-1803.1

Roussel J-R, Barber CB, Habel K, et al (2019) geometry: mesh generation and surface tessellation. Version 0.4.5URL https://CRAN.R-project.org/package=geometry

Santiago LS, Wright SJ (2007) Leaf functional traits of tropical forest plants in relation to growth form. Funct Ecol. https://doi.org/10.1111/j.1365-2435.2006.01218.x

Scalon MC, Wright IJ (2015) A global analysis of water and nitrogen relationships between mistletoes and their hosts: broad-scale tests of old and enduring hypotheses. Funct Ecol 29:1114–1124. https://doi.org/10.1111/1365-2435.12418

Scalon MC, Wright IJ (2017) Leaf trait adaptations of xylem-tapping mistletoes and their hosts in sites of contrasting aridity. Plant Soil 415:117–130. https://doi.org/10.1007/s11104-016-3151-3

Schellenberger Costa D, Zotz G, Hemp A, Kleyer M (2018) Trait patterns of epiphytes compared to other plant life-forms along a tropical elevation gradient. Funct Ecol 32:2073–2084. https://doi.org/10.1111/1365-2435.13121

Schulze E-D, Ehleringer JR (1984) The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes. Planta 162:268–275. https://doi.org/10.1007/BF00397449

Schulze ED, Turner NC, Glatzel G (1984) Carbon, water, and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant, Cell Environ 7:293–299. https://doi.org/10.1111/1365-3040.ep11589756

Šímová I, Violle C, Svenning J-C et al (2018) Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. J Biogeogr 45:895–916. https://doi.org/10.1111/jbi.13171

Sims DA, Gamon JA (2002) Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. Remote Sens Environ 81:337–354. https://doi.org/10.1016/S0034-4257(02)00010-X

Strong G (2000) Are mistletoes shade plants? CO$_2$ assimilation and chlorophyll fluorescence of temperate mistletoes and their hosts. Ann Bot 85:511–519. https://doi.org/10.1006/anbo.1999.1098

Těšitel J (2016) Functional biology of parasitic plants: a review. Plant Ecol Evolut 149:5–20. https://doi.org/10.5091/plecevo.2016.1097

Thornhill AH, Crisp MD, Külheim C et al (2019) A dated molecular perspective of eucalypt taxonomy, evolution and diversification. Aust Syst Bot. https://doi.org/10.1071/SB18015

Tilman D (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Turner NC, Schulze E-D, Nicolle D et al (2008) Annual rainfall does not directly determine the carbon isotope ratio of leaves of *Eucalyptus* species. Physiol Plant 132:440–445. https://doi.org/10.1111/j.1399-3054.2007.01027.x

Ullmann I, Lange OL, Ziegler H et al (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. Oecologia 67:577–587. https://doi.org/10.1007/BF00790030

Vendramini F, Díaz S, Gurvich DE et al (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. New Phytol 154:147–157. https://doi.org/10.1046/j.1469-8137.2002.00357.x

Vile D, Garnier É, Shipley B et al (2005) Specific leaf area and dry matter content estimate thickness in laminar leaves. Ann Bot 96:1129–1136. https://doi.org/10.1093/aob/mci264

Walker AP, Beckerman AP, Gu L et al (2014) The relationship of leaf photosynthetic traits - V_{cmax} and J_{max} - to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. Ecol Evolut 4:3218–3235. https://doi.org/10.1002/ece3.1173

Warren CR, Dreyer E, Tausz M, Adams MA (2006) Ecotype adaptation and acclimation of leaf traits to rainfall in 29 species of

16-year-old Eucalyptus at two common gardens. Funct Ecol 20:929–940. https://doi.org/10.1111/j.1365-2435.2006.01198.x

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biol Rev 81:259. https://doi.org/10.1017/S1464793106007007

Warton DI, Duursma RA, Falster DS, Taskinen S (2012) smatr 3- an R package for estimation and inference about allometric lines: The smatr 3 - an R package. Methods Ecol Evol 3:257–259. https://doi.org/10.1111/j.2041-210X.2011.00153.x

Westoby M, Falster DS, Moles AT et al (2002) Plant ecological strategies: some leading dimensions of variation between species. Annu Rev Ecol Syst 33:125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wright IJ, Reich PB, Westoby M (2001) Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Funct Ecol 15:423–434. https://doi.org/10.1046/j.0269-8463.2001.00542.x

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Wright IJ, Reich PB, Cornelissen JHC et al (2005) Modulation of leaf economic traits and trait relationships by climate: modulation of leaf traits by climate. Glob Ecol Biogeogr 14:411–421. https://doi.org/10.1111/j.1466-822x.2005.00172.x

Wright IJ, Dong N, Maire V et al (2017) Global climatic drivers of leaf size. Science 357:917–921. https://doi.org/10.1126/science.aal4760

Xu S, Sardans J, Zhang J, Peñuelas J (2020) Variations in foliar carbon:nitrogen and nitrogen:phosphorus ratios under global change: A meta-analysis of experimental field studies. Sci Rep. https://doi.org/10.1038/s41598-020-68487-0