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RESEARCH ARTICLE

Continental-scale interactions of Australian showy mistletoes and their hosts

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Abstract

Premise: Showy mistletoes are obligate hemiparasites of woody plants. Host specificity is therefore a fundamental determinant of mistletoe diversity, persistence, geographic distribution, and abundance. Investigations of host specificity in Australian Loranthaceae have focused mostly on host range (taxon counts), but additional insights into specificity are gained by quantifying mistletoe prevalence on taxa in their host range and by exploring specificity in a phylogenetic context.

Methods: We estimated measures of host specificity to characterize mistletoe–host interactions at a continental scale by using occurrence records in the Atlas of Living Australia. We calculated host taxon richness, mistletoe prevalence, and phylogenetic diversity, and used rarefaction curves to evaluate sampling coverage.

Results: Many mistletoe taxa were represented by few records that listed the host, which often was identified to genus only. Mistletoe genera were recorded on 29 orders and 80 families, and no association was observed between host richness and number of records per genus. Rarefaction curves suggested that additional host orders and families remain to be discovered for *Amylotheca*, *Decaisnina*, *Dendrophthoe*, and *Muellerina*. Four mistletoe genera were most prevalent on Myrtales, one on Fabales, and one on Laurales. Rosids were most often the recorded hosts (84.3% of all records). We found evidence of significant phylogenetic clustering in host use by *Amyema*, *Amylotheca*, and *Decasinina*.

Conclusions: Our results, particularly the high prevalence on rosids, suggest that relationships of mistletoes with rainforest lineages may have been established early in the history of Australian Loranthaceae and that some lineages co-diversified with their hosts in arid regions.

KEYWORDS

Amyema, *Amylotheca*, *Decaisnina*, *Dendrophthoe*, host phylogenetic diversity, host specificity, Loranthaceae, *Lysiana*, *Muellerina*, parasite prevalence

Showy mistletoes (Loranthaceae Juss.) are hemiparasites of woody shrubs and trees. They comprise the largest family in the sandalwood order (Santalales) and include the largest clade of stem parasites in the angiosperms (~1000 species). They are distributed globally throughout tropical and subtropical regions, with some species entering temperate areas of Asia, Europe, and South America. Most mistletoe clades are characterized by inconspicuous flowers, whereas many Loranthaceae bear clusters of larger, often brightly colored flowers pollinated by birds and insects, (Vidal-Russell and Nickrent, 2008b). Three monotypic root-parasitic genera form a basal grade in the family phylogeny: *Atkinsonia ligustrina* (A. Cunn. ex Lindl.) F. Muell., restricted to the Blue Mountains of New South Wales, Australia, *Gaiadendron punctatum* Ruíz & Pavón in Central and South America, and *Nuytsia floribunda* R. Br. ex G. Don, restricted to Western Australia (Vidal-Russell and Nickrent, 2008b; Liu et al., 2018). Loranthaceae originated in Gondwana, and following the origin of the stem-parasitic habit, they diversified in Australia, Central and South America, Southeast Asia, the Caribbean, and Africa (Vidal-Russell and Nickrent, 2008a;

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Liu et al., 2018). Australian Loranthaceae are distributed among *Amyema* Tiegh., *Amylotheca* Tiegh., *Benthamina* Tiegh., *Cecarria* Barlow, *Dactyliophora* Tiegh., *Decaisnina* Tiegh., *Dendrophthoe* Mart., *Diplatia* Tiegh., *Lysiana* Tiegh., and *Muellerina* Tiegh. *Diplatia* (3 spp.), *Lysiana* (8 spp.) and *Muellerina* (5 spp.) are found only in Australia, while the remaining genera also occur outside of Australia: *Amyema* (41 spp. in Australia, 97 total), *Amylotheca* (2 spp. in Australia, 4 total), *Cecarria* (1 sp. total), *Dactyliophora* (1 sp. in Australia, 2 total) *Decaisnina* (7 spp. in Australia, 25 total), and *Dendrophthoe* (6 spp. in Australia, 38 total).

All Loranthaceae are obligate hemiparasites, unable to survive without connecting to the vascular system of their host (Nickrent, 2020). The degree of host specificity in mistletoe–host interactions is thus a fundamental determinant of mistletoe diversity, persistence, geographic distribution, and abundance. A remarkably high degree of host specificity may indicate a history of co-cladogenesis and a limited capacity of the parasite to shift to a new host. High host specificity generally is rare in parasitic plants, including Loranthaceae (Kuijt, 1969). On the basis of field notes, floras, herbarium labels, and regional and taxon-based studies, many Loranthaceae occur on multiple, phylogenetically diverse host species (Monteiro et al., 1992; Yan, 1993; Dean et al., 1994; Barlow, 1997; Downey, 1998; Norton and De Lange, 1999; Dzerefos et al., 2003; Carnegie et al., 2009; Grenfell and Burns, 2009; Kavanagh and Burns, 2012; Start, 2013, 2015; Okubamichael et al., 2014, 2016; Lobo, 2016; Mourão et al., 2016; Watson et al., 2017; Amico et al., 2019; Amico and Vidal-Russell, 2019; Clark et al., 2020). The most comprehensive compilations of host use by Australian mistletoes are those of Downey (1998) and Clark et al. (2020). Downey (1998) compiled data on mistletoe hosts from herbarium labels for Loranthaceae and other stem parasites in Australia and showed that many Loranthaceae previously thought to be highly host-specific occurred on multiple hosts. A study on host use in Australia by Clark et al. (2020), based largely on occurrence records in the Australian Virtual Herbarium (AVH; https://avh.chah.org.au/), confirmed and expanded the findings of Downey (1998). Based on the occurrence records they inferred that Australian Loranthaceae rarely use a single host, and they noted that multiple species had been recorded on well over 100 host species. The root-parasitic *Nuytsia*, for example, is well known to be a generalist parasite, with haustoria that will pierce and obstruct inanimate objects such as underground communication cables and tubing for drip irrigation (Groom and Lamont, 2015). In studies of host specificity, however, it has been noted that the number of host species commonly used by a species of Loranthaceae may be narrower than its reported host range (e.g., Downey, 1998; Watson et al., 2017; Amico et al., 2019; Clark et al., 2020; Atencio et al., 2021). Results from these studies suggest that parasite prevalence in Loranthaceae is influenced by ecological and phylogenetic constraints that are only beginning to be explored.

Several diversity measures are available for characterizing host specificity (e.g., Poulin et al., 2011; Esser et al., 2016; Wells and Clark, 2019). Taxon richness measures the number of hosts used by a mistletoe (host range) and represents the accumulation of historical interactions between a mistletoe and its hosts. In ecology, taxon richness is used to estimate the number of taxa in a community, and here a community is the set of hosts used by a mistletoe taxon. Parasite prevalence is observed when a parasite occurs on multiple hosts, but when it occurs disproportionately on one or a few host taxa. Poulin et al. (2011) referred to this as structural specificity, and it is a feature of many parasite–host systems. The uneven distribution of a parasite between two or more of its host taxa is a fundamental aspect of host specificity, raising several questions about the actual determinants of host use in nature. Which abiotic variables most influence the distribution and persistence of both parasite and host? What are the roles of their phylogenetic and biogeographical histories? What is the role of interactions with other organisms, such as pollinators, dispersers, and herbivores? What traits determine the cost–benefit trade-offs in the parasite–host interaction, and how might these trade-offs change across environments? Are patterns of prevalence geographically structured? In addition to using parasite prevalence to investigate patterns of host specificity, phylogenetic diversity of the community of hosts used by a mistletoe can be used as a measure of host specificity if a host phylogeny is available; phylogenetic diversity can be used to address whether a mistletoe's hosts are more closely related than expected by chance.

The aim of our study was to use multiple measures of host specificity to infer continental-scale patterns of host use by Australian Loranthaceae based on occurrence records from the Atlas of Living Australia (ALA; www.ala.org.au). The ALA aggregates occurrence data digitally provided by all museums and herbaria in Australia and personal observations submitted directly to the Atlas and indirectly through iNaturalist (https://www.iNaturalist.org). The ALA has become Australia's most comprehensive biodiversity database, containing over 146 million occurrence records for Australasian species. There are options to search for taxa, data sets, regions of Australia and adjacent countries, and multiple tools for analyzing the data. Interactive maps can be generated to visualize the location of species records in the context of spatial layers and thus to observe relationships among species distribution, climate, topography, and many other variables. The online access to the extensive records in the Atlas of Living Australia allows researchers to collaborate internationally, expanding opportunities for new findings related to Australia's biodiversity. We used data in the ALA occurrence records on mistletoe–host interactions to (1) estimate the number of host orders and families used by each mistletoe genus in our study (host taxon richness), (2) ask whether mistletoe genera appeared to be more prevalent on one or a few taxa in their host range (parasite prevalence on hosts), and (3) ask whether a particular mistletoe genus occurred on host orders or families that were more closely related than expected (host phylogenetic diversity).

MATERIALS AND METHODS

Data download and cleaning

We downloaded all occurrence records of Loranthaceae from the ALA on 14 October 2021. These records cover accessions of preserved specimens from 26 herbaria, including AD, AK, BRI, CANB, CANU, CBG, CHR, CNS, DNA, ERBG, HO, JCT, LING, LTB, MEL, MELU, NE, NSW, NSW Dept. of Planning, Industry and Environment, NSW Office of Environment and Heritage, NT, NZFRI, PERTH, UNSW, WELT, and WOLL (Index Herbariorum: https://sweetgum.nybg.org/science/ih/). In the initial download of 50,125 occurrence records, 8847 records reported the identity of the mistletoe's host plant or plants, at least to genus. From these, 705 records were removed due to mislabeling or because they referenced a host plant in cultivation (e.g., *Citrus*, *Pinus*, *Nerium*, etc.). We excluded all mistletoe genera in the download that occur only outside of Australia (*Elytranthe*, *Gaiadendron*, *Ileostylus*, *Lepeostegeres*, *Loranthus*, *Macrosolen*, *Peraxilla*, *Trilepidea*, *Tristerix*, and *Tupeia*). Lastly, *Atkinsonia* and *Nuytsia* were removed because host associations for these root parasites are poorly characterized, leaving 8142 records (Table 1). All names were checked for spelling errors and to ensure their current validity in the Australian Plant Names Index (https://www.anbg.gov.au/apni/). Because the number of host records per individual mistletoe species in our data set was often quite small, we estimated measures of host specificity from the interactions of each mistletoe genus with the seed plant orders and families represented by their hosts.

Taxon richness of host communities

Our data set comprised occurrence records for mistletoe individuals on host individuals where both the mistletoe and host were often recorded only to the level of the genus. For many individual mistletoe species in the download, few records referenced a host, suggesting that sampling effort might be insufficient in some cases to obtain robust estimates of host taxon richness. Because estimates of taxon richness are strongly influenced by sampling effort and the probability of finding new host taxa increases with the number of samples added to a collection, we used rarefaction curves to estimate host taxon richness at the ordinal and familial levels. Individual-sample-based rarefaction/extrapolation curves were generated using the R package iNEXT (Chao and Gotelli, 2014; Hsieh et al., 2022). Confidence intervals were obtained in a bootstrap analysis of 1000 replicates randomly selected from host range and abundance data. The curve for each genus was extrapolated to 5000 sampled individuals to account for the genus with the highest number of individual records in the final data set (*Amyema*). Subsequent analyses focused on a data set comprising the interactions between each mistletoe genus and the seed plant orders and families of its recorded host species or genus.

To explore spatial patterns in the ALA's occurrence records for Loranthaceae, we used the available coordinates and QGIS version 3.32 (https://www.qgis.org) to map records in which the host was or was not reported for each mistletoe genus. The process involved utilizing the Field Studies Council (FSC) Biological Recording Tools plugin, with a grid level of 1500 km^2. The compiled data for the reported host records can be found in Table 1.

Parasite prevalence

To estimate parasite prevalence on host orders and families in the occurrence records, we calculated the relative proportions of hosts used by each mistletoe genus. To visualize patterns detected in the records of parasite prevalence on host taxa, we generated circular plots of bipartite networks representing mistletoe-host interactions. Plots were generated by using the R package *circlize* (Gu et al., 2014). Interactions were colored by host order and major seed plant clade to emphasize phylogenetic patterns of host use in the networks. Drawing from a color palette generated in Coolors (https://coolors.co), we assigned colors to host orders based on the larger clades to which the order belongs, using the phylogenetic classification of the Angiosperm Phylogeny Group IV (2016).

TABLE 1 Number of occurrence records in the final data set for each mistletoe genus distributed across major seed plant clades, accompanied by the corresponding number and percentage of records that report the host(s).

Genus	Asterids	Santalales	Rosids	Eudicots	Magnoliids	Conifers	Total with host report	Total with no host report	% With host report
Amyema	224	143	4383	157	13	5	4925	25,206	16.34
Amylotheca	28	0	86	8	46	0	168	472	26.25
Decaisnina	63	0	260	3	5	0	331	383	46.36
Dendrophthoe	23	6	623	54	1	3	710	1732	29.07
Lysiana	188	147	1388	70	0	17	1810	5152	25.99
Muellerina	9	9	125	23	2	22	198	2440	7.52
Total	535	305	6865	315	67	55	8140	35,385	18.70

Phylogenetic specificity

Phylogenetic diversity (PD) is a measure of biodiversity that represents the phylogenetic relationships of the community studied (Faith, 1992). This measure is correlated with taxon richness but takes a phylogeny into account to evaluate the phylogenetic structure of a community. In this study, the community comprises the set of host taxa in continental Australia on which a mistletoe genus has been recorded in the ALA records. We estimated the PD of community host orders and families for each genus, along with its standardized effect size (sesPD), using the seed plant ordinal and familial-level phylogenies (with all tips retained) inferred by Li et al. (2019), and a matrix of mistletoe presence/absence data for each tip. We used packages phytools (Revell, 2012) and phangorn (Schliep, 2011) in R (R Core Team, 2020) to obtain ultrametric trees so that all root-to-tip distances were equal, and distances could be estimated correctly. All PD analyses were conducted in the R package picante (Kembel et al., 2010).

To address whether the hosts recorded for a mistletoe genus in the ALA were more closely related than expected by chance, we calculated the mean phylogenetic distance (MPD) and the mean nearest taxon distance (MNTD) for the host community of each genus. The MPD is an estimate of the average distance between all host taxa within a given host community, whereas the MNTD is an estimate of the distance between each host and its nearest neighbor in the tree. Since MPD and MNTD cannot be compared across host communities for each genus, we also calculated the standardized effect sizes of the MPD (sesMPD) and MNTD (sesMNTD). Here the observed values for MPD and MNTD were compared to expected values based on a null model from a randomization method. Null host communities were generated by randomizing the host data matrix of presence/absence using the algorithm taxa.labels with 1000 runs. Positive values of sesMPD and sesMNTD indicate that hosts in a community are more evenly distributed across the host phylogeny than expected by chance (low phylogenetic specificity or overdispersion), whereas negative values indicate that hosts are more clustered in the phylogeny, i.e., are more closely related than expected (high phylogenetic specificity, or underdispersion) (Webb et al., 2002; Kembel et al., 2010). Statistical significance is inferred if the standardized effect size values are greater than 1.96 or less than −1.96, which represent the 95% confidence intervals (Pérez-Toledo et al., 2022).

RESULTS

Taxon richness of host communities

Our cleaned data sets comprised 8140 records for six mistletoe genera. Numbers of species-level records of mistletoe host use ranged from 168 records for *Amylotheca* to 4925 for *Amyema* (Table 1; Supplementary Table 1, https://doi.org/10.6084/m9.figshare.24396874.v3). There were only two records of *Benthamina* that reported a host. These and the records for *Diplatia* (163) were included in the *Amyema* data set due to evidence that they are likely nested within *Amyema* (e.g., Liu et al., 2018; D. Nickrent, Cornell University, personal communication). *Dactyliophora* was not in the cleaned data set because no records included a report of the host. *Cecarria* was excluded from the final data set due to the limited number of records. The ALA has only 32 occurrence records for *Cecarria*, and this total includes duplicates and sites outside of Australia; of the 20 records in Australia, just seven noted the host. In the final data set, the 8140 records that reported the host at least to genus represented just 18.70% of the records in the download (Table 1). Overall, the ordinal host richness observed across the six genera ranged from 15 orders for *Decaisnina* to 22 orders for *Amyema*, with a mean of 19 ± 1.18 for the host records encompassing all mistletoe genera in the data set (Figure 1A). The overall familial host richness observed across all parasite genera varied from 23 families for *Muellerina* to 66 for *Amyema*, yielding a mean of 39.83 ± 5.49 (Figure 1B).

Rarefaction curves showed that sampling coverage of host taxa varied substantially across mistletoe genera,

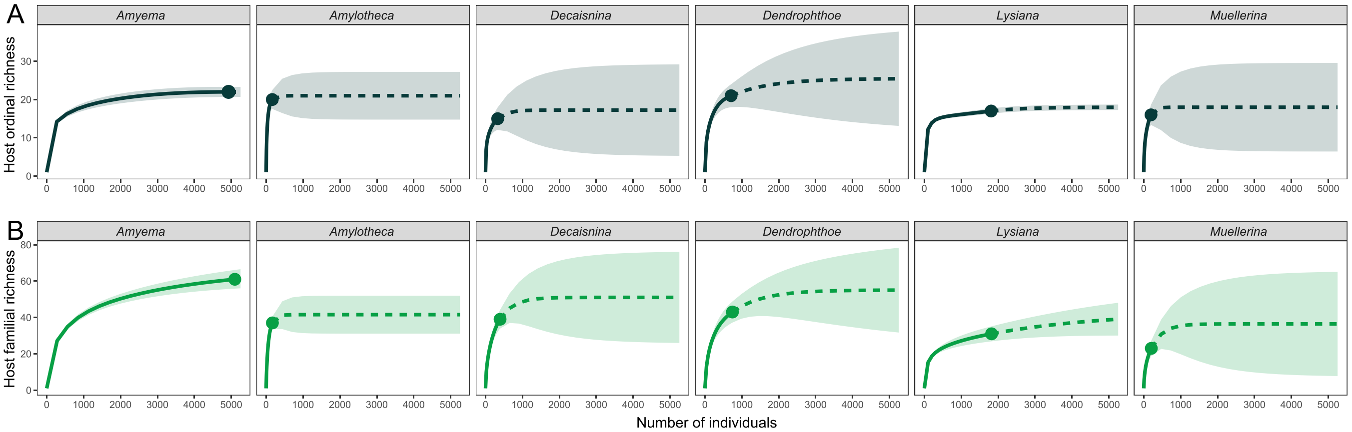

FIGURE 1 Rarefaction/extrapolation curves based on sample size for taxon richness of host communities for each mistletoe genus at the level of (A) order and (B) family. The *x*-axis represents the number of individuals observed for each mistletoe genus. Dark solid lines indicate interpolated data and dashed lines extrapolated estimates. Shaded areas depict 95% confidence intervals calculated in a bootstrap analysis.

whether sampling coverage was estimated for host orders or families (Figure 1). In the cases of *Amyema* and *Lysiana*, levels of host taxon richness increased as the number of individuals in the sample increased until the curve reached a plateau with narrow confidence intervals when extrapolated past the individual records for *Amyema* (Figure 1), particularly for the interactions recorded at the level of host order (Figure 1A). Confidence intervals were narrowest for *Amyema* (observed = 22; estimated = 22 ± 0.7; 95% CI = 22–23.9) and *Lysiana* (observed = 17; estimated = 17.9 ± 2.3; 95% CI = 17.1–31.2). For the other genera, however, the curves did not reach a plateau, and the wide confidence intervals indicated higher uncertainty in the estimates of host ordinal richness for *Amylotheca* (observed = 20; estimated = 20.9 ± 1.9; 95% CI = 20.1–31), *Decaisnina* (observed = 15; estimated = 17.2 ± 3.4; 95% CI = 15.3–33.9), *Dendrophthoe* (observed = 21; estimated = 25.5 ± 7.2; 95% CI = 21.5–61.9), and *Muellerina* (observed = 16; estimated = 17.9 ± 2.6; 95% CI = 16.3–30.3: Figure 1A).

For the occurrences of mistletoe genera on host families, confidence intervals were narrowest for *Amyema* and *Amylotheca* (*Amyema* observed = 66; estimated = 78.3 ± 12.3; 95% CI = 66–102.3 and *Amylotheca* observed = 37; estimated = 41.5 ± 5.4; 95% CI = 37–52.1). For all other genera, the confidence intervals displayed higher uncertainty in the estimates of host familial richness for *Decaisnina* (observed = 39; estimated = 51.1 ± 27.2; 95% CI = 39–104.4), *Dendrophthoe* (observed = 43; estimated = 55.1 ± 16.3; 95% CI = 43–87), *Lysiana* (observed = 31; estimated = 43.2 ± 16.1; 95% CI = 31–74.8) and *Muellerina* (observed = 23; estimated = 39.4 ± 17.2; 95% CI = 23–70.2).

Parasite prevalence of mistletoe genera on host orders and families

Visual representations of mistletoe–host interactions are depicted in Figures 2–5. Figures 2 and 3 show bipartite networks of interactions between mistletoe genera and host order. Figure 2 is a summary network of interactions between all mistletoe genera and their hosts, while Figure 3A–F shows networks for each genus and their hosts. The visual representation of prevalence on hosts was effective for interactions at the level of mistletoe genus on host order, but not for interactions with host families. With the increased number of hosts, detection of many interactions became too difficult to detect. Figures 3 and 4 visualize host prevalence in a phylogenetic context.

The host range for all genera combined comprised 29 orders. No single genus was recorded on all 29 host orders (Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). Occurrence records for each mistletoe genus were unevenly distributed across host orders (Figures 2–4), and the identity of the predominant ordinal host varied across genera. For *Amyema*, *Decaisnina*, *Dendrophthoe*, and *Muellerina*, Myrtales were the most commonly recorded hosts (Figures 3A,C,D,F, 4; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). For *Amylotheca* and *Lysiana*, the most commonly recorded hosts were Laurales and Fabales, respectively (Figures 3B,E, 4; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). When all mistletoe records were considered together, Myrtales and Fabales each accounted for about 33% of the records of mistletoes on hosts in the ALA download (Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3), and the prevalence of Australian mistletoe genera on these two orders was apparent in the bipartite network depicting mistletoe host interactions for all genera (Figure 2).

Similar patterns were observed for host families listed as mistletoe hosts. For *Amyema*, *Decaisnina*, *Dendrophthoe*, and *Muellerina*, Myrtaceae were the most commonly recorded hosts (Figure 5; Supplementary Table 3, https://doi.org/10.6084/m9.figshare.24396874.v3). For *Amylotheca* and *Lysiana*, the most commonly recorded hosts were Lauraceae and Fabaceae, respectively (Figure 5; Supplementary Table 3, https://doi.org/10.6084/m9.figshare.24396874.v3). Considering all records, Fabaceae and Myrtaceae accounted for 31.6% and 30.4% of the records of mistletoe on Australian hosts, respectively (Figure 5; Supplementary Table 3, https://doi.org/10.6084/m9.figshare.24396874.v3).

In the set of occurrence records we analyzed, *Lysiana* was the mistletoe genus most commonly recorded on a host in the sandalwood order (Santalales, 8.9%, Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). A similar percentage of Santalalean hosts was observed for *Muellerina* (7.58%). These two genera thus provided the most evidence of hyperparasitism in Australia. Species records in the data set show that hyperparasitism frequently represents mistletoe occurrences on *Santalum* (Santalaceae) or Loranthaceae, including on congenerics and conspecifics of the mistletoe of record. Beyond Myrtales and Fabales, parasite prevalence was relatively high on Fagales (*Amyema*, *Lysiana*, and *Muellerina*) and on Sapindales (*Amylotheca*, *Decaisnina*, *Dendrophthoe*, and *Lysiana*) (Figure 5, Supplementary Table 3, https://doi.org/10.6084/m9.figshare.24396874.v3). Notably, parasite prevalence on conifers (Cupressales and Araucariales) was relatively high only for *Muellerina* (Figures 3F, 5; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3).

Patterns of parasite prevalence at the level of major seed plant clades are also evident in the bipartite networks (Figures 2 and 3). For each mistletoe genus (Figure 3) and for the summary plot of all genera (Figure 2), the prevalence on rosids (blues) is apparent and is underscored by percentages of all mistletoe records on major clades: rosids, 84.31%; asterids, 6.57%; eudicots, 3.87%; Santalales, 3.74%; magnoliids, 0.82%; and conifers, 0.68% (Table 1).

Phylogenetic diversity of mistletoe host communities

Values of phylogenetic diversity (PD) for host orders in the occurrence records largely corresponded with host richness

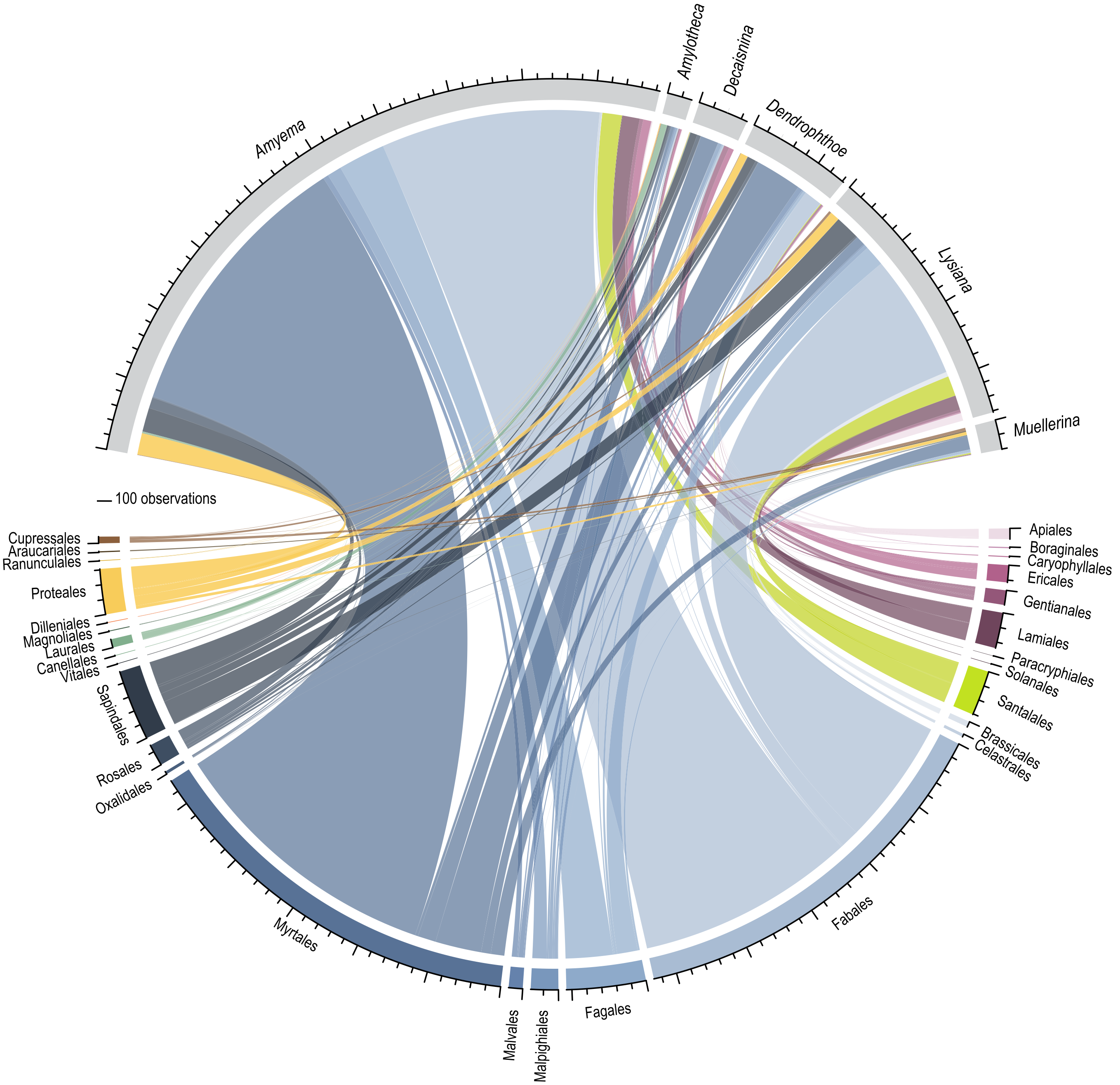

FIGURE 2 Summary bipartite network of mistletoe–host interactions across all mistletoe genera considered (top half). Host orders are colored by major seed plant clade with asterid orders in reds, rosids in blues, basal eudicots in yellows, magnoliids in greens, and conifers in browns. Dilleniales are in orange, Santalales in lime green. Ticks indicate increments of 100 observations.

and ranged from 1.85 for *Decaisnina* to 3.07 for *Amyema* (Figure 6; Supplementary Table 4, https://doi.org/10.6084/m9.figshare.24396874.v3). All values of sesMPD were negative, but sesMPD was significant only for *Amylotheca* (sesMPD = –2.26, $P = 0.003$). Values of sesMNTD were also negative but were significant only for *Amylotheca* (sesMNTD = –2.33, $P = 0.008$) and *Decaisnina* (sesMNTD = –2.08, $P = 0.022$).

Values of phylogenetic diversity (PD) for host families in the occurrence records ranged from 3.13 for *Muellerina* to 5.64 for *Amyema* (Figure 6; Supplementary Table 5, https://doi.org/10.6084/m9.figshare.24396874.v3). Most values of sesMPD were negative, but sesMPD was significant only for *Amylotheca* (sesMPD = –1.96, $P = 0.002$) and *Decaisnina* (sesMPD = –2.68, $P = 0.003$). The sesMPD value for *Muellerina* (sesMPD = 0.88, $P = 0.83$) suggested overdispersion or low phylogenetic specificity at the familial level. Values of sesMNTD were mostly negative but were significant only for *Amyema* (sesMNTD = –2.95, $P = 0.002$), *Amylotheca* (sesMNTD = –2.33, $P = 0.008$), and *Decaisnina* (sesMNTD = –2.08, $P = 0.022$).

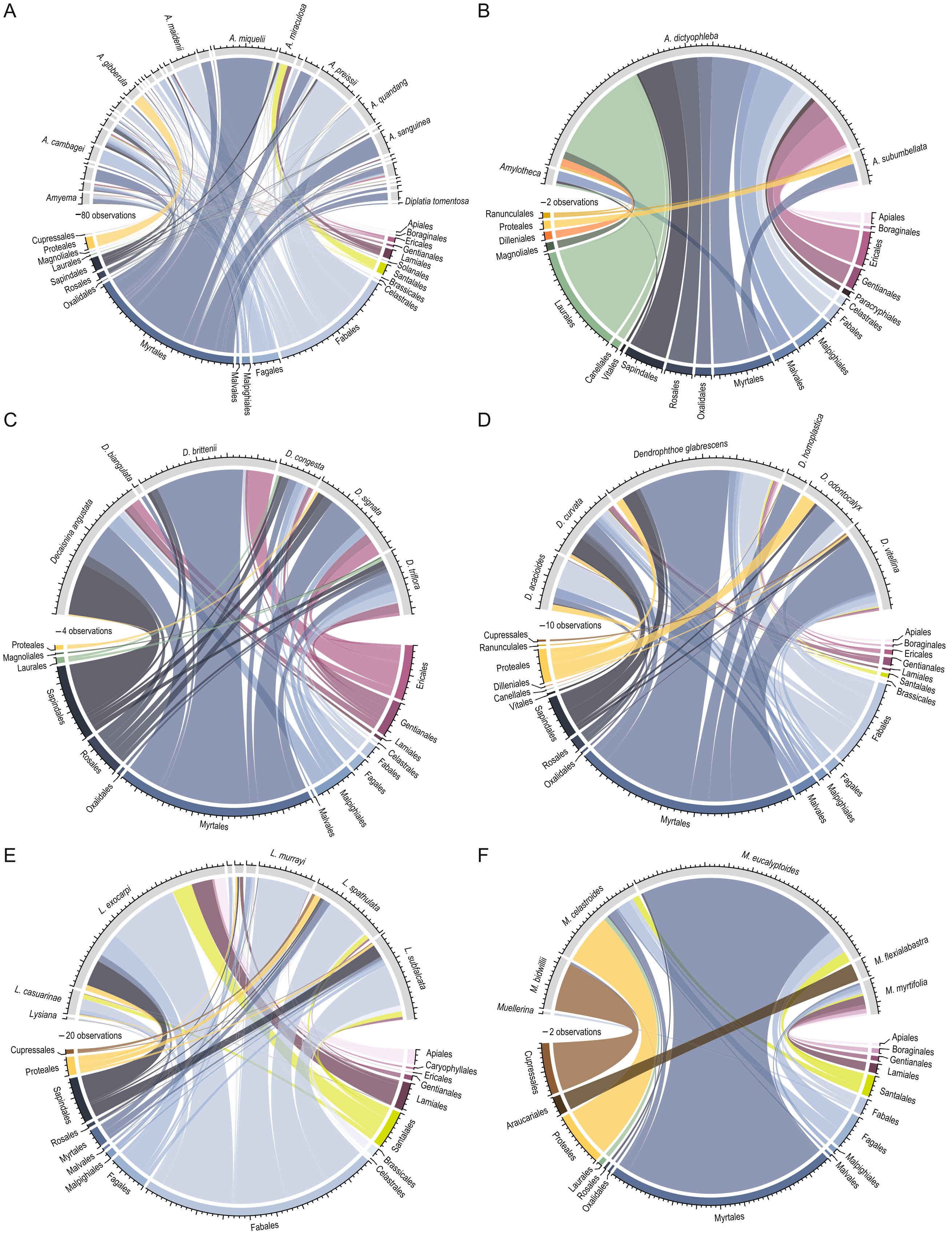

FIGURE 3 Summary bipartite networks of mistletoe–host interactions for (A) *Amyema*, (B) *Amylotheca*, (C) *Decaisnina*, (D) *Dendrophthoe*, (E) *Lysiana*, and (F) *Muellerina*. Mistletoe species are shown in the top half of each circle; records of host orders are shown in the bottom half of each circle. Host orders are colored by major seed plant clade with asterid orders in reds, rosids in blues, basal eudicots in yellows, magnoliids in greens, and conifers in browns. Dilleniales are in orange, Santalales in lime green. Ticks indicate increments in the number of observations and differ by mistletoe genus.

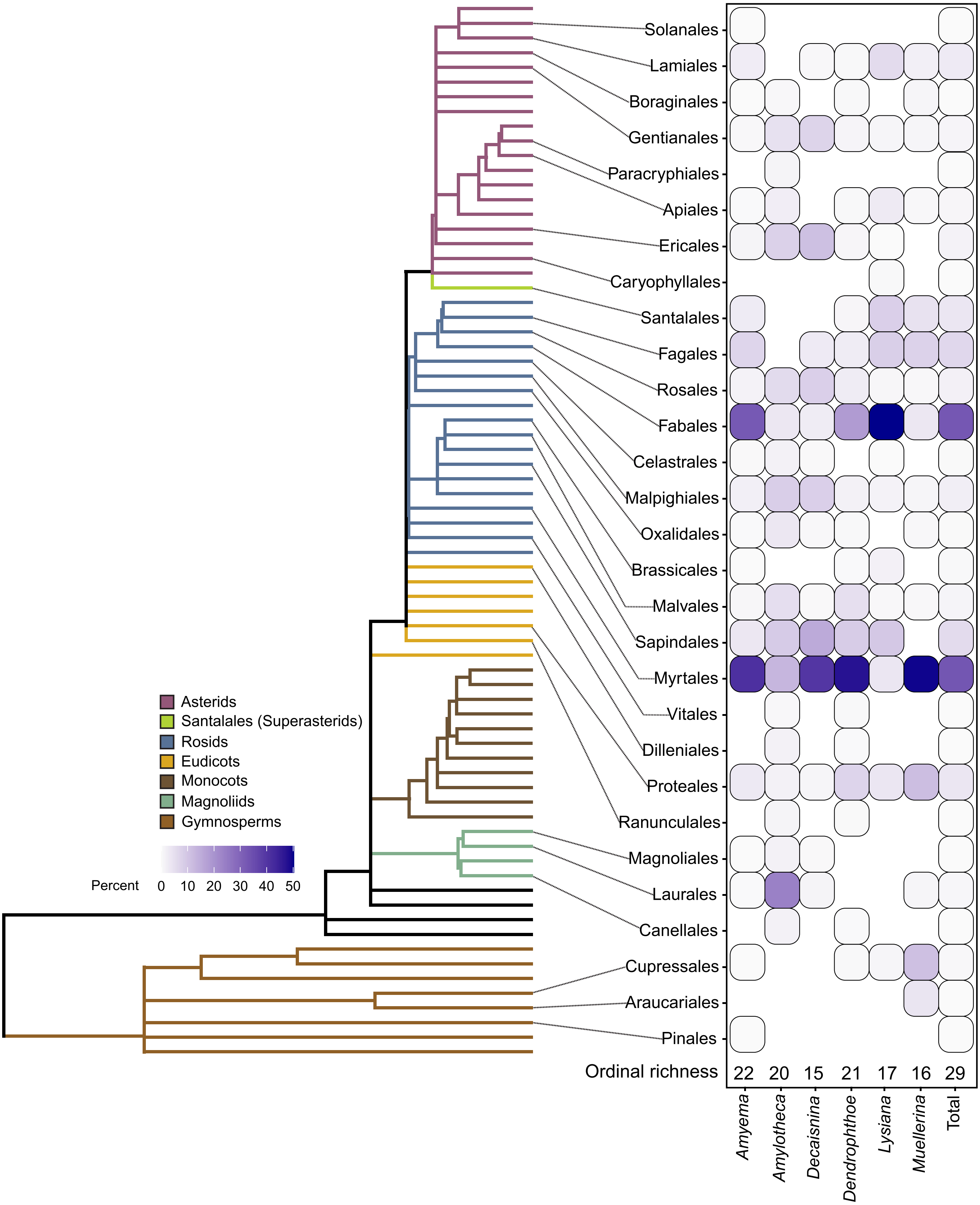

FIGURE 4 The phylogeny of seed plant orders from Li et al. (2019). Tip labels are provided for those orders that are recorded as mistletoe hosts in the ALA data set. Branch colors represent major seed plant clades. Boxes to the right of the tips indicate the presence of genera on host orders; saturation of the box colors indicates percentage of hosts reported per genus.

FIGURE 5 The phylogeny of seed plant families from Li et al. (2019). Tip labels are provided for those families that are recorded as mistletoe hosts in the ALA data set. Branch colors represent major seed plant clades. Boxes to the right of the tips indicate the presence of genera on host families; saturation of the box colors indicates percentage of hosts reported per genus.

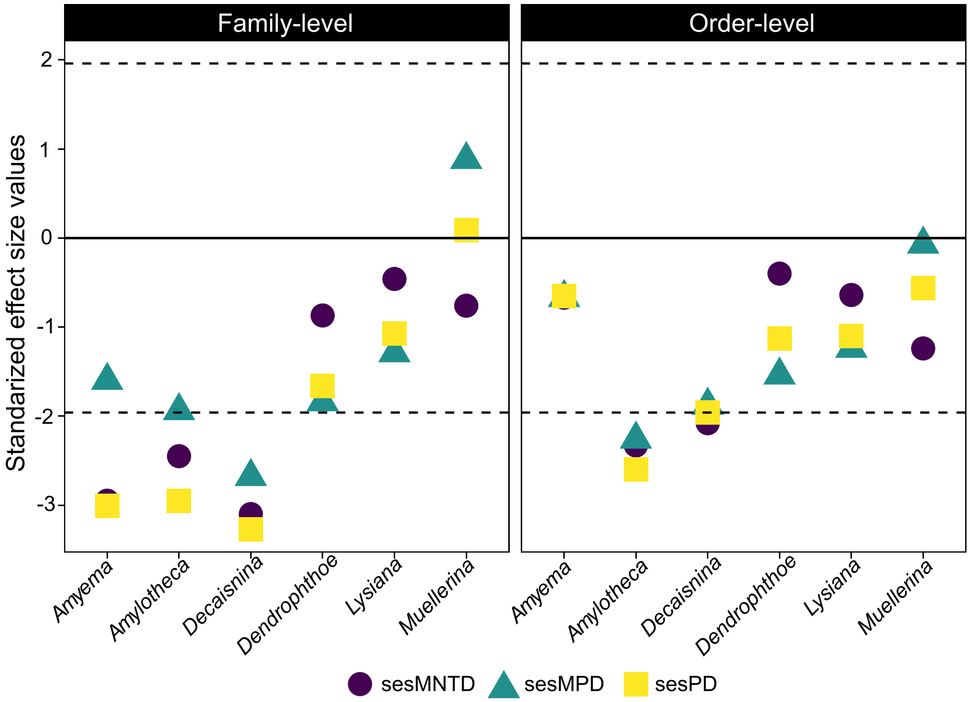

FIGURE 6 Standardized effect size values for phylogenetic distance (PD, yellow), mean phylogenetic distance (MPD, green), and mean nearest taxon distance (MNTD, purple) of the communities of host orders and families for each parasite genus. Positive values indicate phylogenetic overdispersion; negative values indicate phylogenetic underdispersion or clustering. The solid line represents the 0 threshold; the dashed lines indicate the 95% confidence intervals.

DISCUSSION

Taxon richness of host communities

Australian Loranthaceae in the ALA are recorded on hosts representing 29 orders and 80 families from all major clades of seed plants except monocots (Figures 2, 4–6; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). The data set of Clark et al. (2020) included a record (CANB 689739.1) of *Amyema friesiana* (Schumann) Danser on a monocot host *Kuntheria pedunculata* (F. Muell.) Conran & Clifford (Colchicaceae: Liliales). This record, however, lists the host as either *Canarium* or *Kuntheria*. It does not list a species for either and does not cite a voucher specimen of the host. *Kuntheria pedunculata* is an understory herb that has a restricted distribution well south of the occurrences of *Amyema friesiana* in Australia. In contrast, *Canarium* species are a rainforest trees, some of which have overlapping distributions with that of *A. friesiana* in Australia and New Guinea, and that are used as hosts by species of *Amyema* and *Dendrophthoe*. *Canarium* is therefore a much more likely host than *K. pedunculata*. Thus, for Australian Loranthaceae, monocots do not appear to serve as host plants.

Rarefaction analysis suggested that for most Australian Loranthaceae, additional mistletoe–host occurrence records are needed to accurately estimate host ordinal and familial richness from data in the ALA. The exceptions are *Amyema* and *Lysiana*, where rarefaction results suggest that discovery of new mistletoe–host interactions at the level of host order and family have a low likelihood of increasing estimates of taxon richness (Figure 1). These findings contrast with those of Clark et al. (2020). They compared the number of host families, genera, and species that they recorded in a study of Australian Loranthaceae host ranges, with those in an earlier study (Downey, 1998). Based on the percentage increases in numbers of host taxa from the 1998 and the 2020 studies, they predicted that many new host taxa remained to be discovered for all genera. They did not consider, however, that the years from 1998 to 2020 were years of intense activity in specimen digitization across Australian herbaria. Since their data included all data in AVH until 2015 and records in their data set were not restricted to new collections made between 1998 and 2015, the increases might simply reflect the increase in available data for historic collections, rather than new observations from the field.

It was notable that the genus with the fewest host records in the ALA (*Amylotheca*, with 168 records, Table 1) had the third highest estimate of host ordinal richness (20, above the mean of 19 ± 1.18; Figures 4 and 5). Estimates of host ordinal and familial richness were not apparently associated with the number of records per genus in the ALA, nor the number of species in a genus. The highest estimate (22 orders) for *Amyema* (41 species in Australia, 97 total) was not unexpected, but the estimates for *Amylotheca*, *Decaisnina*, and *Muellerina* would not have been predicted based on genus size. Together, observed patterns of host richness may be better explained by phylogenetic constraints in host use, geographic range size of the mistletoes, and variability of environments and plant communities within the range of a genus (Thrall et al., 2007; Mouillot et al., 2008; Watson et al., 2017; Wells and Clark, 2019).

Patterns of parasite prevalence in Australian Loranthaceae

Analyses of occurrence data in the ALA suggested a striking picture of mistletoe host use in Australian Loranthaceae, with rosids emerging as the most frequently used hosts (Table 1, Figures 2, 3, and 5). Rosids comprise a large, heterogeneous clade of about 90,000 species and account for about 40% of species diversity in the eudicot clade of angiosperms (~190,000 species). The rosid clade originated in the Cretaceous and their subsequent diversification underlies the rise of forests dominated by angiosperms (Sun et al., 2020). Others noted the prevalence of mistletoe occurrences on *Acacia* Willd. (Fabaceae: Fabales) and *Eucalyptus* L'Hér. (Myrtaceae: Myrtales; Barlow, 1984; Downey, 1998; Clark et al., 2020), which are the largest and most widely distributed woody genera in Australia. Both genera are members of the rosid clade, but the data in the ALA reveal the relative importance of additional rosid orders, including Fagales, Malpighiales, Malvales, and Sapindales (Figures 2–5).

While mistletoe prevalence estimated from the occurrence records is highest on rosid hosts for all genera together and each genus separately (Figures 2 and 3), the particular rosid host most commonly recorded differs among genera (Figures 3 and 4). For example, parasite prevalences of *Amyema*, *Decaisnina*, *Dendrophthoe*, and *Muellerina* are highest on Myrtales, especially on Myrtaceae, but prevalence of *Lysiana* is highest on Fabales, especially in Fabaceae (Figure 2; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). The pattern of prevalence of *Amylotheca* is unique. Prevalence is highest on rosids, but these occurrences are spread more evenly across several rosid orders, and the single order with the highest percentage of records is not a rosid but a magnoliid angiosperm (Laurales, especially in Lauraceae; Figures 2 and 4; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). Laurales are widespread in the tropics and subtropics, are very diverse in Southeast Asia, and are important components of tropical rainforest communities. The prevalence of *Amylotheca* on Laurales may reflect a rainforest history, which also is consistent with its distribution in Australian rainforests and more generally in mesic habitats along the east coast of Australia (Figure 7). Overall, as noted by others (Downey, 1998; Clark et al., 2020), the patterns of mistletoe prevalence are consistent with levels of diversity and predominance of certain families in the Australian flora, such as Fabaceae and Myrtaceae.

If we exclude from consideration the mistletoe genera for which host interactions are most poorly represented in the Atlas of Living Australia (Figure 1), the signal in the occurrence records of prevalence on rosids remains. For *Amyema* and *Lysiana*, 88.97% and 76.7% of records are on rosid hosts, respectively (cf. Figure 2; Supplementary Table 2, https://doi.org/10.6084/m9.figshare.24396874.v3). Compared with *Amyema*, *Lysiana* has a greater percentage of records on asterids (10% vs. 4.55%). *Lysiana* also has the higher percentage of records on Santalales hosts (8.12% vs. 2.9%), and the most records among all mistletoe genera. *Muellerina* has the second highest percentage of records on species of Santalales (4.55%). Occurrences on Santalales represent cases of hyperparasitism, where the mistletoe's host is another individual, species, or genus of Loranthaceae or a species in Santalaceae, typically *Exocarpos* Labill. or *Santalum* L. Santalales does not appear in the bipartite plots for *Amylotheca* and *Decaisnina* (Figures 2 and 3). These genera appear to use Santalales hosts very rarely, with just eight records for these two genera of occurrences on Santalales in our data set and those of Clark et al. (2020) and Downey (1998) (Figure 4). Krasylenko et al. (2021) suggested that hyperparasitism enhances the compatibility of parasite and host, perhaps due to phylogenetic relatedness. However, given the prevalence of mistletoes on hosts outside of Santalales, being a fellow member of Santalales may not be the most important determinant of mistletoe–host compatibility.

In some cases, mistletoe species appear to have remarkably high prevalence on hosts in a particular host order and family (Figure 2). These include *Amyema cambagei* (Blakely) Danser on Fagales (on species of Casuarinaceae), *A. gibberula* (Tate) Danser on Proteales (on species of *Grevillea* R. Br. ex Knight or *Hakea* Schrad., Proteaceae), *A. miquelii* (Lehm. ex Miq.) Tiegh. on Myrtales (on species of *Eucalyptus* or *Corymbia* K.D. Hill & L.A.S. Johnson, Myrtaceae), *A. quandang* (Lindl.) Tiegh. and *A. maidenii* (Blakely) Barlow (on species of *Acacia*, Fabaceae), and *Muellerina flexialabastra* Downey & C.A. Wilson (on species of *Araucaria* Juss., Araucariaceae), to name a few (Figure 3). The ALA records suggest that several of these mistletoe–host pairs would be excellent systems for detailed studies to investigate the factors contributing to host specificity in Australian Loranthaceae. More detailed studies are needed to characterize patterns of specificity that are less readily observed in our visualization of interactions between mistletoe genera and host orders and families based on occurrence records. For example, *Amyema maidenii* (Blakely) Barlow and *A. hilliana* (Blakely) Danser grow sympatrically on different species of *Acacia* in central Australia. These details are observable in the ALA records, but due to the limited number of recorded mistletoe–host pairs in the ALA sample, the degree of specificity in sympatry is uncertain. And factors contributing to finer scale patterns of specificity can only be explored through methodical field studies of plant communities across mistletoe geographic ranges (see example in Watson et al., 2017). Similarly, studies of mistletoe species that use different host species in different portions of their geographic ranges (e.g., Downey, 2004; Start, 2013) are critical for understanding the relative importance of factors that may contribute to

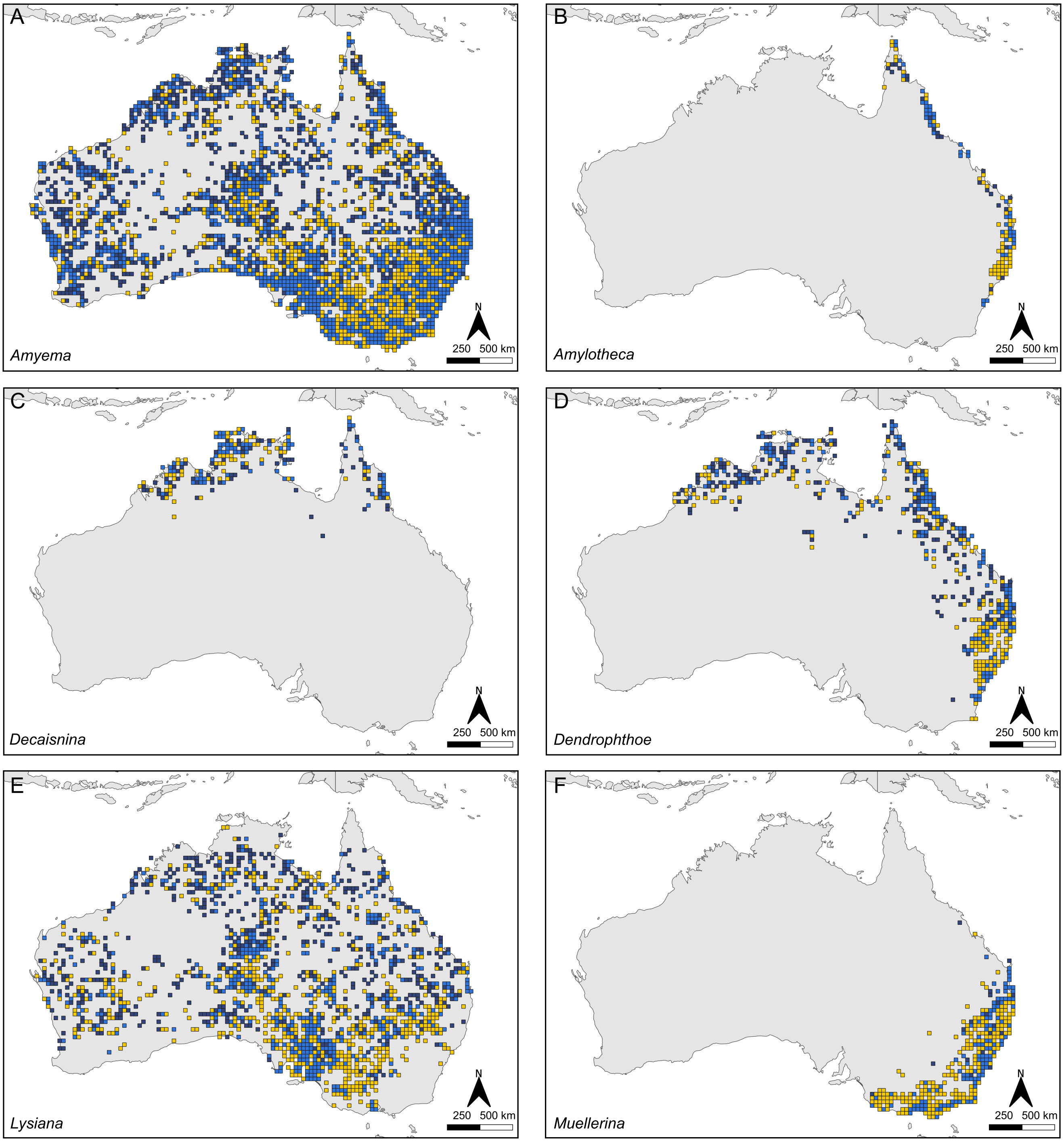

FIGURE 7 Localities in Australia of occurrence records in the ALA for (A) *Amyema*, (B) *Amylotheca*, (C) *Decaisnina*, (D) *Dendrophthoe*, (E) *Lysiana*, and (F) *Muellerina*, illustrating the presence (dark blue), absence (yellow), and combined presence/absence (light blue) of host data in the records.

specificity, including abiotic factors, the general composition of plant communities, interactions with herbivores, and pollinators and dispersers.

Patterns of mistletoe prevalence on host orders, families and major angiosperm clades may reflect the influence that the evolution of the Australian flora has had on mistletoe–host interactions. Of five major biomes in Australia today, the everwet and sclerophyll biomes were present on Gondwana, whereas the arid, monsoonal, and alpine biomes emerged later (Byrne et al., 2008, 2011; Crisp and Cook, 2013). Before the Eocene break-up of Gondwana, when Australia separated from Antarctica and began drifting north to its current position, a rainforest biome predominated. Loranthaceae and several of its host taxa (including members of Myrtales, Proteaceae, Casuarinaceae, and Nothofagaceae) originated in Gondwana (Hill, 2004;

Berger et al., 2016) before the break-up. Araucariaceae was also present at this time and a significant element of the vegetation (Kershaw and Wagstaff, 2001). The presence of Loranthaceae and many of its current host lineages in Gondwana suggests that interactions of Loranthaceae with these host lineages could have been established early in their history. This suggestion is consistent with the observation that Loranthaceae in New Zealand, South America, and Africa parasitize some of these same lineages (Kuijt, 1975, 1988; Monteiro et al., 1992; Norton and De Lange, 1999; Dzerefos et al., 2003; Didier et al., 2008; Kuijt, 2011; Lobo, 2016; Amico and Vidal-Russell, 2019), although it is important to note that in the absence of more detailed and better resolved phylogenies for Loranthaceae, ancestral host ranges cannot be reconstructed. As Australia began to move northward during the Eocene, mesic biomes (rainforest and wet sclerophyll forest) remained dominant (Crisp and Cook, 2013); thus, rainforest lineages more generally may have been the most likely hosts for the first stem-parasitic Loranthaceae, which are estimated to have originated in the Eocene (Liu et al., 2018). Subsequent cooling and drying through the Neogene resulted in contraction of the everwet biome in continental Australia to pockets along the east coast and considerable expansion of Australia's central arid and northern monsoon tropical regions (Byrne et al., 2011). Today, four of the mistletoe genera considered in our study are restricted to Australia's mesic regions, *Amylotheca*, *Decaisnina*, *Dendrophthoe*, and *Muellerina*. *Muellerina* is restricted to southeastern Australia, whereas the first three of these genera are more diverse outside of Australia, extending into tropical regions of Oceania and to the north and west across Malesia and into South Asia (Barlow, 1997). Conversely, *Amyema* and *Lysiana* occur throughout Australia and are diverse and well established in the arid zone and the seasonally dry monsoon tropics (Figure 7). Their apparent prevalence on Fabales and Myrtales could reflect histories of diversification that coincided with the success of both *Acacia* (Fabaceae) and eucalypts (*Corymbia* and *Eucalyptus*, Myrtaceae) in the arid zone, and of eucalypts in the monsoon tropical regions (Crisp and Cook, 2013). Semiarid shrub woodlands are the major type of vegetation in the arid zone, including *Acacia* and mallee eucalypt shrublands (Byrne et al., 2008), and savanna is the most extensive vegetation type in the Australian Monsoon Tropics and is often dominated by eucalypts (Bowman et al., 2010).

Host phylogenetic diversity

Despite notable patterns of parasite prevalence on host orders and families, there was limited evidence in the ALA records of high phylogenetic specificity in host use. Limited evidence of phylogenetic specificity might relate to the fact that mistletoe–host interactions were measured as interactions between mistletoe genus and host order or family, rather than mistletoe species and host species (for which the data mostly were inadequate). We noted that the signal of phylogenetic clustering is higher when phylogenetic specificity of mistletoes on host families (rather than on host orders) is measured (Figure 6). Most host orders are represented by multiple host families. The increase in number of hosts in the family data set will affect patterns of branch lengths in the phylogeny used to estimate phylogenetic diversity metrics and may allow for a more sensitive test of phylogenetic specificity. Our results provide evidence of phylogenetic specificity in host use at the familial level for just three genera, *Amyema*, *Amylotheca*, and *Decaisnina* (Figure 6). All three genera belong to clades with largely tropical distributions (Liu et al., 2018). The majority of *Decaisnina* occur in SE Asian tropical regions, and the few species in Australia are limited to tropical regions of northern Australia. The significant sesMPD value (Figure 6) may reflect deep phylogenetic conservatism in their occurrence on rainforest host lineages. The greater number of significant values for sesMNTD in family-level analyses highlight the need for more detailed records of mistletoes on hosts in Australia. A further challenge to estimating measures of phylogenetic diversity is the current lack of available species phylogenies for the Australasian Loranthaceae. Measures of host phylogenetic diversity have important implications for our understanding of the role of phylogenetic constraints on host switching in the evolution of Australian Loranthaceae.

Advantages and limitations of existing occurrence data on mistletoe-host interactions

We have used presence-only data and simple measures of specificity to explore patterns of host use in Australian genera of Loranthaceae. Biases, errors, and insufficiency are concerns in analyses of occurrence data from natural history collections (Meyer et al., 2016; Daru et al., 2018). One bias relates to the lack of data on the absences of a mistletoe on potential hosts that are present (Vesk et al., 2010). Additionally, geographical biases are inherent in museum data sets (e.g., Williams et al., 2002; Kadmon et al., 2004) and non-geographical biases also have been documented for herbarium data sets (Loiselle et al., 2007; Schmidt-Lebuhn et al., 2013). Furthermore, errors are introduced by misidentification of species and incorrect taxonomy (Graham et al., 2004), and this issue may be especially pronounced in mistletoe-host records. Mistletoes are often collected on host plants in sterile condition, which are difficult to identify. Moreover, the insufficiency of occurrence records, an inherent bias in public digital data sets, is exacerbated for Loranthaceae, where fewer than 20% of the ALA records in the download of >50,000 records contain information about the host.

We found, therefore, that the sample of mistletoe–host occurrence records in the publicly available data in ALA were inadequate for analyses of mistletoe–host interactions at the species level (Figure 1) for Australian Loranthaceae. Our view here differed from that of Clark et al. (2020). They used a data set similar to ours to analyze mistletoe–host interactions at the species level. We found, nevertheless, that for two of the showy mistletoe genera that occur in Australia, *Amyema* and *Lysiana*, publicly available data from the ALA were measurably sufficient to estimate metrics of host specificity when the interactions measured were those between mistletoe genus and host order, and for *Amyema* at the genus–family level. For *Cecarria* and *Dactyliophora*, records in the ALA were too few to include in the analyses, and for the remaining four, *Amylotheca*, *Decaisnina*, *Dendrophthoe*, and *Muellerina*, rarefaction analyses suggested that additional records of mistletoe–host occurrences are needed to increase confidence in estimates of host specificity, even at the ordinal level (Figure 1). Despite the limitations in the data, our approach of analyzing and visualizing mistletoe–host interactions at the genus–order and genus–family levels allowed us to detect the pattern of prevalence on rosid orders for *Amyema* and *Lysiana* and the notable difference between the prevalence of *Amyema* on Myrtales and of *Lysiana* on Fabales (Figure 3A,E). The prevalence on rosid hosts also characterized host use in the other four genera in our analyses and is clearly apparent in the visualization of mistletoe interactions with host orders for all records combined (Figure 2). If this pattern of prevalence reflects conservation in the use of rosid hosts that was established early in the evolution of Loranthaceae stem parasites, increased sampling may not drastically alter this finding of mistletoe prevalence on host orders.

Inferring patterns of parasite prevalence and estimating phylogenetic niche conservatism based on more recent evolutionary histories will, however, require many more observations of mistletoe–host occurrences. Data from the ALA are fundamental to developing a plan to increase sampling strategically and efficiently. The maps we generated from all occurrence records for Loranthaceae in the ALA highlight regions of Australia where mistletoes occur and have been collected, but without recording identities of the host taxa (Figure 7, Table 1). For example, efforts to better document host use in *Amylotheca* and *Dendrophthoe* (Figure 7B,D) might focus on the southern portions of their ranges, while for *Muellerina* (Figure 7F), targets might include several sites across southeast Australia. Further refinement of collection sites to target specific environments that might yield novel host records would be trivial to conduct in the ALA's Spatial Portal. Results would also help identify regional collaborators. Rarefaction analyses to evaluate the sampling effort needed to estimate richness at various taxonomic levels would yield target collection numbers that would be a key component in developing a strategic sampling plan that targets specific geographic regions and environments where sampling would most likely fill gaps in mistletoe–host records. Finally, most Australian stem-parasitic genera in Loranthaceae are distributed beyond Australia, and extending the sampling to include additional individuals and species is an exciting prospect that will lead to a more comprehensive characterization of host use by Australian showy mistletoes.

AUTHOR CONTRIBUTIONS

S.M. conceived and managed the study with input from all authors. J.B., L.Y.S-R., and S.M. contributed to data collection and curation from ALA. J.B. and L.Y.S-R. drafted the first version of the manuscript. L.Y.S-R. performed all the analyses. All authors contributed to the interpretation or results and manuscript revisions.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Complete data set extracted from the Atlas of Living Australia for mistletoes and host occurrence records.

Table S2. Mistletoe prevalence (percentage) by host order for each genus included in the study, alongside the total percentage of hosts represented in the analysis.

Table S3. Mistletoe prevalence (percentage) by host family for each genus included in the study, alongside the total percentage of hosts represented in the analysis.

Table S4. Host ordinal phylogenetic diversity, mean phylogenetic distance, and mean nearest taxon distance per mistletoe genus.

Table S5. Host familial phylogenetic diversity, mean phylogenetic distance, and mean nearest taxon distance per mistletoe genus.

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