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Hemiparasitic shrubs increase resource availability and multi-trophic diversity of eucalypt forest birds

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Summary

1. Parasitic plants are components of many habitats and have pronounced effects on animal diversity; shaping distributions, influencing movement patterns and boosting species richness. Many of these plants provide fleshy fruit, nectar, foliar arthropods and secure nest sites, but the relative influence of these nutritional and structural resources on faunal species richness and community structure remains unclear.
2. To disentangle these factors and quantify the resources provided by parasitic plants, we focused on the hemiparasitic shrub *Exocarpos strictus* (Santalaceae). Twenty-eight *Eucalyptus camaldulensis* forest plots were studied in the Gunbower-Koondrook forest in southeastern Australia, comparing riparian forests with an *Exocarpos*-dominated understorey with otherwise similar habitats with or without equivalent cover of the non-parasitic *Acacia dealbata*. Analyses of avian richness and incidence (overall and in six feeding guilds) were complemented by explicit measures of resources in both shrub types; foliage density, standing crop of fleshy fruit and foliar arthropod abundance and biomass.
3. Avian species richness was *c.* 50% greater and total incidences for five guilds were significantly greater in forests with the parasitic shrub, with no appreciable differences between the other two habitat types. In addition to plentiful fleshy fruits, *Exocarpos* supported abundant arthropods in their foliage – significantly higher in biomass than for equivalent volumes of *Acacia* foliage. *Exocarpos* had a shorter and denser structure, providing a greater range of microhabitats than the more open growing *Acacia*.
4. Our results demonstrate that structural and nutritional resources (both direct and indirect) provided by *Exocarpos* affect diversity and community composition, with each set of resources affecting different organismal groups. Rather than an exceptional system or an aberrant result, we suggest the influence of *Exocarpos* on species richness relates to their parasitic habit, supporting the hypothesis that parasitic plants mobilize resources from their hosts and make them available to a range of trophic levels.

Key-words: canopy, *Exocarpos strictus*, habitat heterogeneity, hemiparasite, physiognomy, Santalaceae, species richness, tri-trophic interactions

Introduction

The effects of parasitic plants on their hosts, neighbours and communities have attracted considerable attention (Press & Phoenix 2005; Grewell 2008; Quested 2008). Initial studies comparing infected hosts with otherwise similar plants lacking parasites documented decreased vigour and survivorship of hosts, becoming more pronounced as parasite densities increased (e.g. Room 1973). Moving beyond pair-wise host–parasite interactions, other workers have noted overlaps in host and parasite pollinators (Gómez 1994; Ollerton *et al.* 2007), improved dispersal of infected hosts (van Ommeren & Whitham 2002; Carlo & Aukema 2005), increased litterfall beneath infected hosts (Quested *et al.* 2003; March & Watson 2007), increased ectomycorrhizal colonization (Mueller & Gehring 2006) and higher functional diversity of fungal communities beneath infected hosts (Cullings & Hanely 2010). At stand and patch-scales, these networks of interactions can alter nutrient cycling dynamics, facilitate growth of understorey plants, modify

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successional dynamics and boost species richness of plants (Quested 2008; Watson 2009).

Animals are also affected by parasitic plant occurrence. The dense structure and modified microclimate associated with the semi-succulent foliage of mistletoes and other woody parasitic plants increases the availability of favoured nesting and roosting sites for birds and mammals (Parks *et al.* 1999; Cooney & Watson 2005) with a wide range of species recorded using these structures (Watson 2001; Cooney, Watson & Young 2006). Many groups of parasitic plant use animals for directed seed dispersal (Heide-Jørgensen 2006), providing abundant fruit high in fats, carbohydrates and/or amino acids to attract frugivores – both dietary specialists and generalists. Likewise, most parasitic plant groups use animals (generalist nectarivorous birds and insects) as pollen vectors, rewarding pollinators with abundant nectar rich in available carbohydrates. Finally, their nutrient and water-rich foliage is widely consumed by mammalian and arthropod folivores (Watson 2001, 2009), with increased prey availability (especially herbivorous insects; Anderson & Braby 2009; Burns, Cunningham & Watson 2011) potentially having indirect effects on higher trophic levels, especially spiders (Burns 2009, Halaj, Ross & Moldenke 2000; Shaw, Watson & Mathiason 2004) and insectivorous birds (Turner 1991; Watson 2002).

While observational and experimental data with aerial hemiparasites have documented positive relationships between mistletoe density and avian species richness (Bennetts *et al.* 1996; Watson 2002; Mathiasen *et al.* 2008), it is unclear which resources contribute to this response – structure, direct nutritional resources (leaves, fruit, nectar) or indirect nutritional resources (foliar arthropods, litter-dwelling prey). Previous studies have used either natural variation in parasite density (e.g. Turner 1991; Bennetts *et al.* 1996) or patch-scale removal experiments (e.g. Watson 2002; Watson & Herring 2006) and, although reporting broad-based changes in diversity and community composition associated with hemiparasite occurrence, they have been unable to attribute recorded variation in richness with particular resources. Moreover, background variation in the same structural and nutritional resources is rarely considered, preventing estimation of the community-level influence of parasitic plants on resource availability and constraining our understanding of their ecological function.

Here, we include habitat-scale measures of structural complexity, fruit abundance and arthropod availability in habitats with and without hemiparasites to distinguish determinants of faunal community structure and species richness. To quantify the effects of resource availability on higher trophic levels, we focused on forest-dependent birds – a group with sufficient dietary breadth to make meaningful interpretations about resource use and underlying mechanisms. The focus of our study was *Exocarpos strictus* (Santalales; Santalaceae, Fig. 1), a poorly known root-parasitic shrub that occurs in high densities in riparian *Eucalyptus camaldulensis* (river red gum) forests. Forests with understoreys dominated by *Exocarpos* were compared with otherwise similar habitats, either lacking shrubs altogether or with an understorey dominated by the non-parasitic shrub *Acacia dealbata*. To estimate differences in resources offered by these two shrub species, three resources available to birds were measured directly: structural complexity, standing crop of fruit and number and biomass of foliar arthropods. Comparisons of avian occurrence in the three habitat types were performed using species richness and incidence, both overall and for six foraging guilds; species-specific comparisons were also conducted but these will be presented elsewhere. Finally, we examined whether *Exocarpos* had indirect effects on bird diversity through modifying the condition of other vegetation components; both canopy and ground-level composition.

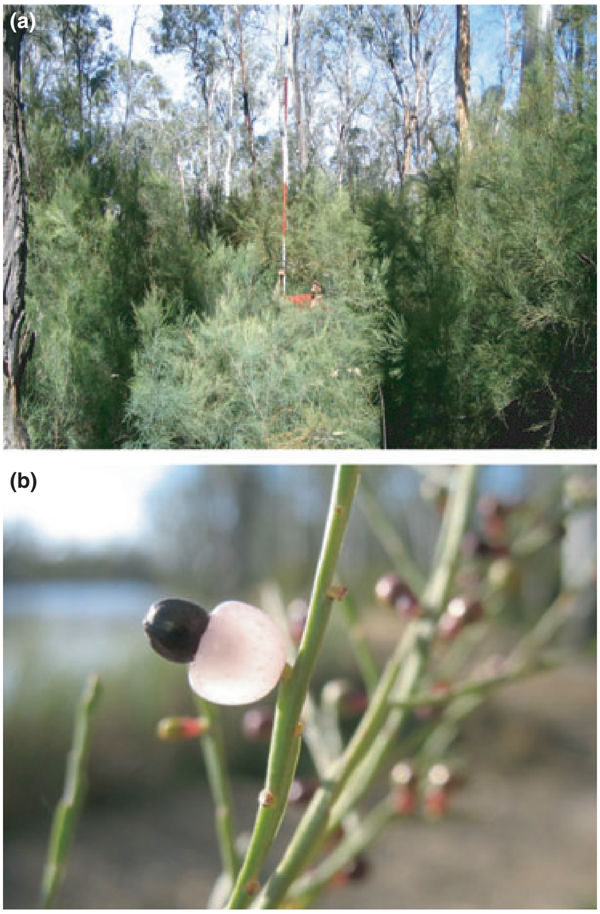

Fig. 1. (a) Thicket of *Exocarpos strictus* plants with pole used to measure shrub structure using number and height distribution of foliage intercepts. (b) *E. strictus* fruit, showing black drupe borne on swollen translucent pedicel. Both photographs by H. W. McGregor.

Materials and methods

STUDY AREA AND DESIGN

This study was conducted in two sections of Gunbower-Koondrook forest – Campbell's Island State Forest and Gunbower Island State Forest (Fig. 2) – located on the floodplain of the Murray River in south-eastern Australia. River regulation began in the 1920s,

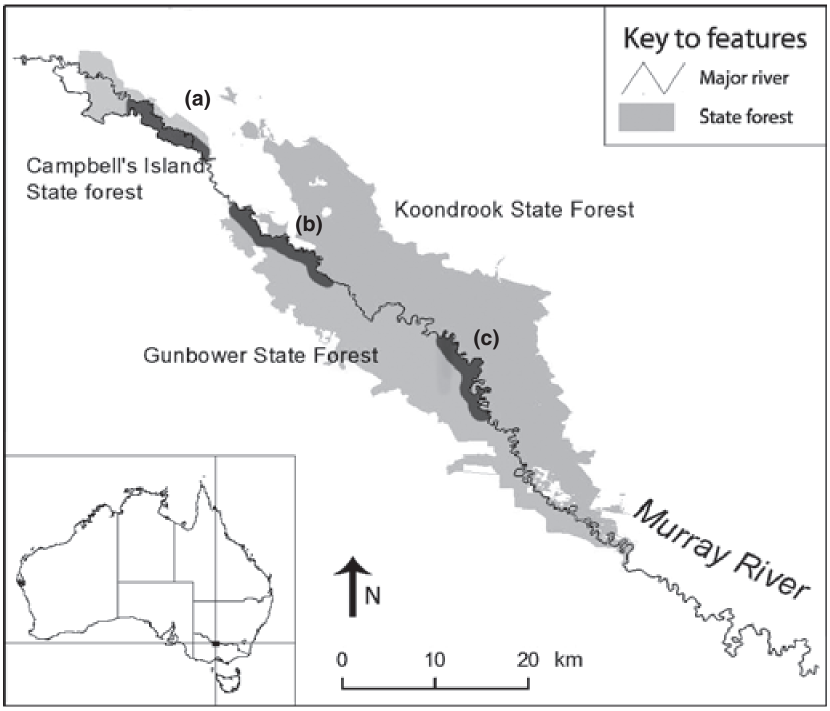

Fig. 2. Location of the Gunbower-Koondrook forest block. Areas shaded grey represent the three study regions; Campbell's Island State Forest in New South Wales (a); north Gunbower Island State Forest (b); and central Gunbower Island State Forest (c), both south of the Murray River in Victoria.

dramatically reducing the size and frequency of floods in these forests, resulting in areas further from the channel (in both linear distance and elevation) receiving less water (Bren 1988). Annual rainfall ranges from 280 to 580 mm, most falling during winter (long-term average of 120 mm) and the least falling during summer (80 mm). Sampling was conducted during a protracted drought: local rainfall for summer 2006–2007 was 75% below the average (Echuca station, Bureau of Meteorology 2007).

Gunbower-Koondrook forest is dominated by *E. camaldulensis* growing in dense monodominant stands, with scattered shrubs found in the slightly elevated parts of the floodplain (natural river levees and stabilized dunes). *A. dealbata* Link is a nitrogen-fixing shrub/small tree (3–8 m in height) with bipinnate phyllodes and abundant insect-pollinated flowers borne in spring, developing into seed pods. *E. strictus* R. Br. is a root-parasitic shrub (1–5 m in height; Fig. 1a) with minute scale-like leaves and abundant vertical branchlets giving a cypress-like appearance. In summer, abundant black drupes (2·5–4 mm) are borne on enlarged red or white pedicels (McGregor 2007; Fig. 1b). The species is presumed to be dispersed by frugivorous birds, but the plants life-history, interactions and autecology have not been studied previously. Historic accounts and palynological data indicate that both shrub species have increased in extent and density along the Murray River over the last 50 years (Kenyon & Rutherford 1999; Sinclair 2006), presumably due to altered flooding and fire frequencies since European settlement (Dexter 1978; Bren 1988)

To minimize the confounding effects of variation in canopy composition, soil type and soil water content, the study area was confined to forest > 80% canopy cover of *E. camaldulensis* with comparable management histories (MDBC 2006), adjacent to the Murray River (5 m from river bank). Initial field mapping within this forest area quantified the distribution of three main habitat types: less than 5% shrub cover of all shrub species ('Nil' understorey); greater than 50% cover of *Acacia* and greater than 50% cover of *Exocarpos*. A stratified random sampling approach was then used to locate fixed-area plots (2 ha) within each habitat type, separated by at least 500 m. Plot dimensions were set at 100 × 200 m, occasionally varying slightly to avoid clearings and maximize understorey homogeneity (e.g. 80 × 250 m). The three habitat types were not evenly represented within the study area, with all available shrub-dominated habitats sampled, yielding a total of 28 plots (12 Nil plots, 7 *Acacia* plots, and 9 *Exocarpos* plots).

BIRD SURVEYS

To compare the species richness of birds between the three habitat types, we used fixed-effort surveys in which all bird species clearly heard or directly observed to alight or feed within the 2 ha plot were recorded (after Loyn 1986). Nine 20 min surveys were conducted per plot (after Watson 2004b), spread evenly over three non-sequential days. This method was selected as it reliably estimates richness of forest-dependent birds (including cryptic and elusive species) and is well-suited to surveying birds in dense vegetation (Recher 1988; Watson 2004b). All surveys were conducted in the austral summer from 12 December 2006 to 16 January 2007, between 05:30 hours and 12:30 hours (Australian Eastern Daylight Savings Time). To reduce systematic bias, sampling was restricted to days with mild weather, the same observer conducted all surveys (HM), the first plot sampled each day was selected randomly and visitation order for subsequent plots based solely on proximity and logistics.

Bird species were classified into six dietary guilds based on their primary food source and the vertical stratum where they forage most frequently: birds of prey (vertebrates); granivores (seeds); frugivores/omnivores (either primarily fruit or generalized diet supplemented with fruit); ground insectivores (invertebrates, taken at ground level); aerial foragers (invertebrates, taken by sallying or hawking in mid-air); and gleaners (invertebrates, taken either on or next to foliage, branches or trunks) using published information (Higgins & Peter 2002; Appendix S1, Supporting information). Species observed in single plots and non forest-dependent species (e.g. emu

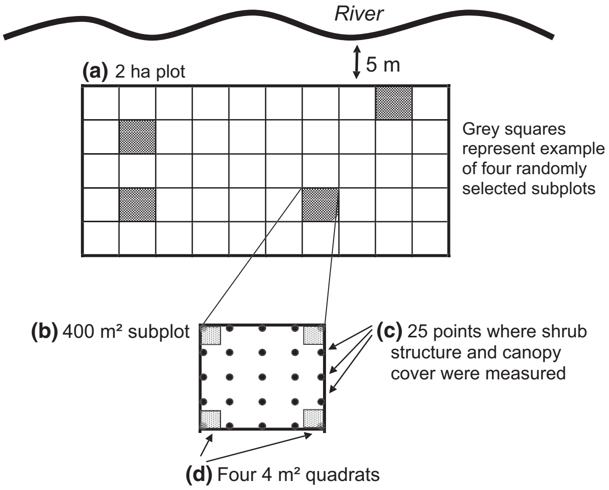

Fig. 3. Details of the placement, scale, shape and number of plots used in this study.

Dromaius novaehollandiae, azure kingfisher *Alcedo azurea*) were excluded from analysis (see McGregor 2007 for complete data). Incidences for each species were calculated as proportions of the nine samples in which they were recorded as present and guild incidences calculated for each plot by summing incidences of all species in each guild represented (Appendix S1).

RESOURCE ESTIMATES

Structural characteristics of the shrub-layer were measured in a subsample of each plot – four randomly placed 400 m^2 subplots (Fig. 3b). In all four subplots, density and vertical structure of shrub foliage was recorded at 25 pre-determined locations arranged 5 m apart in a systematic grid (Fig. 3c). At each point, a 5 m pole (20 mm diameter) was deployed vertically from ground level and the number of foliage or branch intercepts between each 1 m height increment recorded. The number and height distribution of these intercepts were used to calculate foliage density and foliage height profiles respectively. In addition to *Exocarpos* and *Acacia*, data were recorded for *E. camaldulensis* saplings (Eucalypt intercepts) and for various exotic shrub species occurring at low densities in all three plots types (Exotic shrub intercepts).

To estimate nutritional resources provided by the two shrubs, foliar arthropods were sampled in both understorey substrates: *Acacia* foliage and *Exocarpos* foliage. Samples were collected in December 2006 (13–31, inclusive) from selected branches of 40 *Acacia* plants and 40 *Exocarpos* plants, located throughout the study area. Pythrethrum-based insecticide was applied as an aerosol to bagged branches, with 5 min of vigorous agitation minimizing adhesion of arthropods to leaves and branchlets. Samples were field-sorted in large white trays; all arthropods > 1 mm in length transferred to vials and stored in 70% ethanol. Final sorting in the laboratory yielded the number of individuals and dry mass (to 0·0001 g) following drying in a 65 °C oven for 48 h. As few insectivorous birds eat ants (Barker & Vestjens 1990), ants were counted and weighed separately, although we recognize that remaining arthropods are not uniform in nutritional value or palatability. The number and dry mass of arthropods were expressed as functions of the volume of sampled branches, normalized to a standard volume (1 m^3). For each *Exocarpos* branch sampled ($n = 40$), the number of fruits was counted (to the nearest 10), to allow estimation of the standing crop of available fruit.

VEGETATION AND LANDSCAPE ATTRIBUTES

As plots were selected on the basis of shrub cover (> 50% of either species), further data on shrub density per unit area are not presented, as it would not be representative of overall variation in shrub occurrence. To quantify variation in other habitat attributes (both within and between habitat types) for comparison with the effects of understorey shrubs, a nested approach was used (Fig. 3a). Tree characteristics were measured in the same 400 m^2 subplots used for structural measurement of shrubs, where all trees > 5 m in height were assigned to a size class based on d.b.h. (0·01–0·3 m, 0·31–0·6 m, 0·61–1 m, or > 1 m) and to a health-rating class based on the proportion of foliage to branch/twig cover ('dead'; 1–25% green foliage/branches; 25–50% green foliage/branches; 50–75% green foliage/branches; and 75–100% green foliage/branches). Estimates of canopy cover were taken in each subplot at the same 25 points as shrub measurements (Fig. 3c) by estimating the percentage of sky obscured by foliage while looking through a thin tube (110 mm long, 16 mm diameter; after MacDonald *et al.* 1990). Mistletoe abundance was recorded by estimating the number of mistletoes in each 2 ha plot (none, 1–10, 11–25, 26–50, 51–100, 101 +). Ground-cover variables were measured in 4 m^2 quadrats (Fig. 3d) located in the four corners of each subplot (Fig. 3b). In each quadrat, the percent cover of grasses, herbaceous plants (herbs and forbs), litter and fine woody debris (< 20 mm diameter), coarse woody debris (> 20mm diameter) and bare ground was visually estimated to the nearest 5% (Mueller-Dombois & Ellenberg 1974). Finally, three landscape variables were measured for each plot from a digitized vegetation map based on remotely sensed data (D. I. T. M. 2000) using ESRI Arcview v.3·2 and field-maps compiled by HM: area of the overall shrub patch (contiguous forest with uninterrupted shrubby understorey), distance to nearest edge between forest and farmland, and distance to the nearest town.

ANALYSIS

All foraging guild incidences (except ground insectivores) were compared among habitat types using parametric one-way analysis of variance after data were square-root transformed (to fulfil assumptions of normality and equal variances), with differences between habitats tested using Tukey's *post hoc* tests. For bird species richness and the ground insectivore guild, assumptions of normality and equal variance were not met, so Kruskal–Wallis rank sum tests were used and Wilcoxon's rank sum tests to assess differences between habitat types. To compare vegetation attributes of the three habitat types, one-way analysis of variance with Tukey's *post hoc* tests were used if the assumptions of normality and equal variances were met, otherwise Kruskal–Wallis rank sum tests were used. Number and dry mass of arthropods, standardized by branch volume, were compared using one-tailed Mann–Whitney tests to evaluate whether more arthropods were associated with *Exocarpos* foliage. Differences in bird occurrence, vegetation attributes and resource estimates between the three habitat types were deemed significant at $P < 0{\cdot}05$ and highly significant at $P < 0{\cdot}001$ (using PASW v.17).

An information theoretic approach using Akaike's Information Criteria (hereafter AIC) was used to infer which habitat characteristics had the greatest individual and combined influence on differences in bird occurrence between habitat types, calculated using AIC$_c$

Table 1. Variables used in the AIC_c model selection, their abbreviation, description and the bird response variables they were used to model against (SR, species richness; BOP, birds of prey; Gran, granivores; F/O, frugivores/omnivores; GI, ground insectivores; AF, aerial foragers; FGlean, foliage gleaners; All, all bird response variables)

Variables	Description	Response variables modelled against
Shrubs		
Ex	Average no. of *Exocarpos* intercepts per subplot	All
Ac	Average no. of *Acacia* intercepts per subplot	All
Shrub	Average no. of shrub intercepts per subplot	All
Scov	Percent of poles with shrub intercept (%)	BOP
Exotic	Average no. of exotic shrub intercepts per subplot	F/O
Trees		
Can	Average canopy cover per plot (%)	All
CanVar	Canopy cover standard deviation	SR, AF, FGlean,
Health	Average tree health rating (%)	SR, AF, FGlean,
Den	Canopy tree density (n/ha)	SR, AF, FGlean,
Lg	Number of large trees (DBH > 0·7 m) (n/ha)	SR, BOP
Trunk	Estimated trunk surface area at breast height (m)	FGlean
Mtoe	Number of mistletoe clumps per plot (0–5 scale)	F/O
Ground cover		
Gcov	Average grass cover per 4 m^2 quadrat (%)	SR, Gran, FG
Gvol	Average grass volume per 4 m^2 quadrat (m^3/20 m)	
Leaf	Average leaf litter cover per 4 m^2 quadrat (%)	BOP, GI
BG	Average bare ground cover per 4 m^2 quadrat (%)	Gran
Ftim	Average fallen timer cover per 4 m^2 quadrat (%)	SR, BOP, GI
Landscape		
Region	Study region plot was located in (nominal)	SR, Gran
LogPatch	(Log) shrub patch size (ha)	SR, FG
DisFarm	Distance to farmland (km)	SR, AF
DisTshp	Distance to township (km)	F/O

(appropriate for models with a low sample size Burnham & Anderson 2001). A brief description of all variables used is provided in Table 1. The relative strength of evidence for each model was determined by subtracting the value of the minimum AIC from each model (hereafter Δ_i), where the higher the value Δ_i the less strength of evidence. From Δ_i, an evidence ratio (Akaike weights: W_i) was obtained and converted to a 0–1 scale: the probability that each model was the 'best' of the set (Johnson & Omland 2004). To assess the amount of variation explained by each model (VE), each model's maximized log-likelihood was divided by the maximized log-likelihood of the null model and converted to a percentage, equivalent to an r^2 (Quinn & Keough 2002). Models used in the AIC_c analyses were loglinear assuming a Poisson distribution, as data were counts from independent plots (Table 1). For bird species richness and foraging guilds, appropriate and ecological meaningful candidate models were determined based on *a priori* hypotheses and the results of null-hypothesis tests (after Johnson & Omland 2004; Stephens *et al.* 2005). Having two variables in a model set with a correlation greater than ±0·5 was avoided to guard against co-linearity. The global model was always entered and interpreted as the full amount of variation explained by all variables and combinations.

Results

AVIAN RICHNESS IN DIFFERENT HABITATS

After 114 h of bird surveys, 69 bird species were recorded, with 51 forest-dependent species sufficiently abundant for quantitative analysis (Appendix S1, McGregor 2007). Bird species richness was significantly greater in *Exocarpos* plots compared with both *Acacia* plots (mean difference: 10 ± 2, Wilcoxon rank sum: $P < 0{\cdot}001$) and Nil plots (mean difference: 9 ± 2, $P < 0{\cdot}001$), and did not differ significantly between Nil and *Acacia* plots (mean difference: 1·6 ± 1·7, $P > 0{\cdot}05$).

To compare the influence of *Exocarpos* on bird communities with other vegetation attributes which varied across the 28 plots, AIC_c criteria were used. The model containing the single variable *Exocarpos* foliage intercepts had the best fit to the data, explaining 76% of the variation in estimated bird richness ($W_i = 0{\cdot}732$; Table 2). The inclusion of all other habitat variables in the global model explained an additional 8% variation (Table 2).

FORAGING GUILDS

To evaluate which ecological groups of birds contributed most to this overall pattern, separate analyses were conducted for six dietary guilds.

Bird of prey incidence was not significantly different between the three habitat types (ANOVA: $F_{2,25} = 2{\cdot}8706$, $P = 0{\cdot}0754$), but was greatest in Nil plots (mean difference with *Acacia* plots: 4 ± 2, mean difference with *Exocarpos* plots: 3 ±2, Fig. 4). The model with shrub cover (negative relationship) best described the sum of incidence for birds of prey ($W_i = 0{\cdot}507$), explaining 18% of the variation, with a further 10% explained by the global model (VE = 28, Table 2).

Granivore incidence was significantly greater in *Exocarpos* plots than in both Nil plots (mean difference: 6 ± 2, Tukey's *post hoc*: $P < 0{\cdot}05$) and *Acacia* plots (mean difference: 6 ± 2, $P < 0{\cdot}05$, Fig. 4). Using AIC_c criteria, models with shrub foliage intercepts and study region (greatest in Campbell's Island plots) best explained granivore incidence, with

Table 2. Habitat model selection using AIC$_c$ criteria for bird species richness and foraging guilds

	Results of model selection†						
Foraging guild	Model	−log(L)	*K*	AIC$_c$	Δ_i	W_i	VE (%)
Bird species richness	Ex	7·65	1	9·81	0·00	0·732	76
	Ex + Can	7·63	2	12·11	2·30	0·232	76
	Global	5·10	10	38·04	28·23	0·000	84
Birds of prey	Scov	45·56	1	47·72	0·00	0·507	18
	Global	40·18	5	52·91	5·19	0·038	28
Granivores	Gcov + Shrub + Region	37·86	3	44·86	0·00	0·413	77
	Shrub + Region	40·49	2	44·97	0·11	0·391	76
	Global	35·03	7	54·63	9·78	0·003	79
Frugivores/omnivores	Ex + Can + Mtoe	44·63	3	51·63	0·00	0·898	66
	Global	36·54	7	56·14	8·46	0·011	72
Ground insectivores	Scov	80·61	1	82·76	0·00	0·725	12
	Global	78·77	5	91·50	8·73	0·009	14
Aerial foragers	Ex + Ac	51·98	2	56·46	0·00	0·574	35
	Ex	56·16	1	58·31	1·85	0·228	29
	Global	51·66	5	64·39	7·93	0·011	35
Foliage gleaners	Shrub	20·26	1	22·42	0·00	0·367	72
	Shrub + Ex	18·97	2	23·45	1·04	0·219	74
	Shrub + Can	19·33	2	23·81	1·39	0·183	74
	Shrub + Ex + Can	16·87	3	23·87	1·45	0·178	78
	Global	16·54	6	32·54	10·13	0·002	78

†Only the global models and models representing the highest likelihood presented ($\Delta_i < 4$).
Ex, *Exocarpos strictus* foliage < 5 m; Ac, *Acacia dealbata* foliage < 5 m, Shrub: all shrub foliage < 5 m; Scov, shrub cover; Mtoe, mistletoe clumps, Gcov, grass cover; Can, canopy cover; Region, study region.

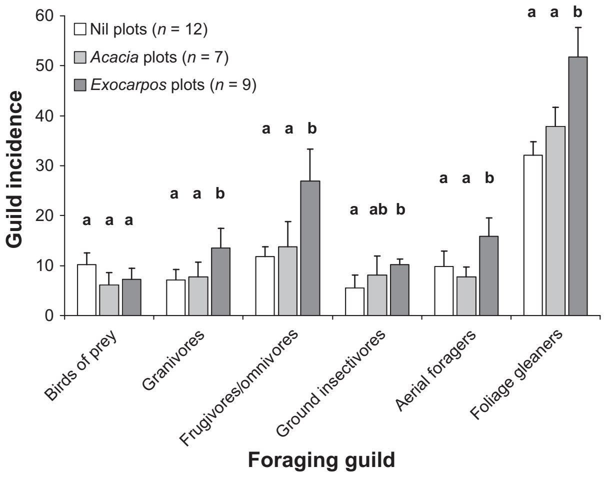

Fig. 4. Foraging guild incidence between plots with different shrub strata: Nil, *Acacia* and *Exocarpos* (means, 95% confidence intervals, a and b indicate homogenous subsets revealed by Tukey's *post hoc* test, or Wilcoxon rank sum test for ground insectivores).

grass cover (positive relationship) accounting for an extra 1% variation (Table 2).

Frugivore/omnivore incidence was significantly greater in *Exocarpos* plots than in both Nil plots (mean difference: 15 ± 3, Tukey's *post hoc*: $P < 0{\cdot}001$) and *Acacia* plots (mean difference: 13 ± 3, Tukey's *post hoc*: $P < 0{\cdot}05$, Fig. 4). Using AIC$_c$ criteria, *Exocarpos* foliage intercepts, mistletoe abundance and canopy cover (all positive relationships) comprised the best model ($\Delta_i = 0$, $W_i = 0{\cdot}898$, Table 2) explaining frugivore/omnivore incidence, but *post hoc* examination of the Poisson assumption of similar variances and means revealed that incidence was overdispersed (variance/mean = 4·2), consistent with aggregation around high densities of fruiting plants.

Ground insectivore incidence was significantly greater in *Exocarpos* plots than Nil plots (mean difference: 5 ± 2, Wilcoxon rank sum: $Z = 2{\cdot}63$, $P = 0{\cdot}009$; Fig. 4). Using AIC$_c$, the model consisting solely of shrub cover (positive relationship) best explained the sum of incidence for ground insectivores; but it only explained 12% of the variation (Table 2). This guild was dominated by the superb fairy-wren *Malurus cyaneus* (83% of incidences), so the response of this guild likely reflects this single species.

Aerial forager incidence was significantly greater in *Exocarpos* plots than in both Nil plots (mean difference: 6 ± 3, Tukey's *post hoc*: $P < 0{\cdot}05$) and *Acacia* plots (mean difference: 8 ± 2, $P < 0{\cdot}05$, Fig. 4). Models including *Exocarpos* and *Acacia* foliage intercepts ($W_i = 0{\cdot}547$) best explained aerial forager incidence, the global model explaining < 1% extra variation (Table 2). The relationship between the incidence of aerial foragers and *Exocarpos* foliage intercepts was positive, while the relationship with *Acacia* foliage was negative.

Foliage gleaner incidence was significantly greater in *Exocarpos* plots than both Nil (mean difference: 20 ± 3, Tukey's *post hoc*: $P < 0{\cdot}001$) and *Acacia* plots (mean difference: 14 ± 3, $P < 0{\cdot}001$, Fig. 4). Using AIC$_c$ criteria, models including shrub foliage intercepts best explained the sum of incidence for foliage gleaners (positive relationship; Table 2), with *Exocarpos* foliage intercepts and canopy cover combined explaining 6% extra variation.

Table 3. Comparison of means and 95% confidence intervals (CI) of habitat and landscape variables between the three shrub strata, and results of ANOVA between shrub strata (Kruskal–Wallis rank sum test if denoted by $^{\text{K–W}}$)

Variable type Variable name	Nil plots mean ± CI	*Acacia* plots mean ± CI	*Exocarpos* plots mean ± CI	*P*-values
Shrubs				
Exocarpos intercepts	0·2 ± 0·1	1 ± 0·7	228 ± 169	** < 0·001$^{\text{K–W}}$
Acacia intercepts		117 ± 87	6 ± 4	** < 0·001$^{\text{K–W}}$
Eucalypt intercepts < 5 m	3 ± 1	5 ± 4	3 ± 2	0·857$^{\text{K–W}}$
Exotic shrub intercepts	0·8 ± 0·7	0·1 ± 0·2	2 ± 2	0·387$^{\text{K–W}}$
Trees				
Canopy cover (%)	32 ± 6	36 ± 3	23 ± 6	*0·024
Average tree health (%)	35 ± 7	41 ± 8	25 ± 5	*0·017
Density (n/ha)	340 ± 58	297 ± 93	338 ± 76	0·675
No. of large trees (n/ha)	38 ± 12	54 ± 25	39 ± 12	0·086
Trunk surface area (m)	14 ± 2	12 ± 3	13 ± 2	0·494
Mistletoe (0–4 scale)	2·5 ± 0·5	2·5 ± 0·5	3·5 ± 0·5	*0·017
Ground cover				
Annual grass (% cover)	8 ± 6	10 ± 7	20 ± 12	0·161
Perennial grass (% cover)	17 ± 12	28 ± 13	29 ± 13	0·352
Grass (% cover)	25 ± 11	38 ± 14	48 ± 9	*0·001
Leaf litter (% cover)	59 ± 11	50 ± 14	37 ± 7	*0·019
Herbs (% cover)	2 ± 2	0·5 ± 0·5	0·8 ± 0·8	0·355$^{\text{K–W}}$
Bare ground (% cover)	8 ± 5	3 ± 3	9 ± 4	0·298
Fallen timber (% cover)	6 ± 3	5 ± 3	8 ± 3	0·507
Landscape				
Shrub patch size (ha)	N/A	8 ± 7	70 ± 49	*0·016
Distance to farmland (km)	2 ± 1	3 ± 2	1 ± 1	0·239$^{\text{K–W}}$
Distance to town (km)	11 ± 2	8 ± 3	7 ± 3	0·109$^{\text{K–W}}$

$^{*}P < 0·05$, $^{**}P < 0·001$

VEGETATION STRUCTURE IN DIFFERENT SHRUB STRATA

Exocarpos strictus plants formed dense (228 ± 169 foliage intercepts per 25 poles) low (91% of intercepts between 0 and 3 m high) thickets, whereas *Acacia* stands were more open (117 ± 87 foliage intercepts) and taller (92% of intercepts between 1 and 5 m high; Table 3), highlighting fundamental structural differences between these two habitat types. Assessment of the other habitat attributes (Table 3) showed that *Exocarpos* plots had significantly less eucalypt canopy cover (ANOVA: $F_{2,25} = 4·32$, $P = 0·02$) and lower average tree health ($F_{2,25} = 4·596$, $P = 0·02$) than Nil and *Acacia* plots (Table 3). *Exocarpos* plots also had significantly greater grass cover ($F_{2,25} = 4·699$, $P = 0·001$), more mistletoe ($F_{2,25} = 4·628$ $P = 0·017$) and significantly less litter cover ($F_{2,25} = 4·616$, $P = 0·019$) than Nil and *Acacia* plots. There were few differences in landscape variables between shrub strata except for shrub patch size, where mean *Exocarpos* patch size was significantly larger than that of *Acacia* (Table 3).

FOLIAGE-INVERTEBRATES

Arthropod samples from 40 *Exocarpos* branches and 40 *Acacia* branches were compared in terms of number of individuals > 1 mm and dry mass, standardized by branch volume. There were no more individuals in *Exocarpos* samples, either for all arthropods (Mann–Whitney $U = 777·0$, one-tailed $P = 0·413$), or excluding ants (Mann–Whitney $U = 705$, one-tailed $P = 0·180$). In terms of dry mass, however, arthropod samples from *Exocarpos* foliage were significantly greater, both for total samples (Mann–Whitney $U = 514$, $P = 0·003$) and with ants excluded (Mann–Whitney $U = 527·5$, $P = 0·005$). The most abundant arthropod associated with *Exocarpos* foliage was a large aposematically coloured hemipteran, exclusively found on fruiting branches. No birds were observed feeding on this distinctive insect so, to evaluate whether this insect was solely responsible for observed differences in arthropod biomass, individuals of this species were excluded and the comparisons recalculated, and found to remain significant (Mann–Whitney $U = 576·5$, one-tailed $P = 0·016$).

FRUIT

Exocarpos was the only plant in the study area that provided abundant fleshy fruits during the study period. Several species of mistletoe occurred in both *Exocarpos* and *Acacia* plots, but few were fruiting during the sampling period, so no formal analyses could be conducted. Of the forty *Exocarpos* shrubs sampled, 17 had zero or very few fruit, with no fruit on the branch being sampled. Five plants had 50–70 fruit on the branch being sampled, yielding an overall mean of 15·13 fruit per branch.

Discussion

Overall, we found clear evidence that eucalypt forests with an understorey of *E. strictus* support a more diverse assemblage of birds. Forests with *Exocarpos*-dominated understoreys contained *c*. 50% more bird species than those with *Acacia*-dominated or open understoreys (Appendix S1). Interestingly, these latter two habitat types (the two most common forest types throughout the region) did not differ significantly in species richness. Aside from shrub foliage generally and *Exocarpos* foliage in particular, no other habitat or landscape variable measured had a comparable influence on avian occurrence. While the habitat types differed in several other respects, this only accounted for an additional 8% of variation in bird richness, compared with 76% for *Exocarpos* foliage alone. The importance of this shrub is particularly striking when compared with other studies of eucalypt woodland and forest bird assemblages (e.g. Mac Nally 1994; Jansen & Robertson 2001; Antos & Bennett 2006), none of which reported any association with particular understorey plants, parasitic or otherwise. The only comparable data come from studies that recorded mistletoe occurrence, and these studies found similar effects of parasitic plants, with notably higher richnesses associated with increased mistletoe densities (Watson 2002; see also Bennetts *et al.* 1996; Watson 2001 and references therein).

Although the second most diverse group of parasitic plant, mistletoes have a unique growth habit that precludes comparisons with structurally similar non-parasitic plants. In this study, we focused on understorey shrubs, and compared habitats containing two structurally similar species, one of which was root-parasitic. Thus, as well as providing an additional example of a parasitic plant affecting faunal diversity, our study differs from previous descriptive studies by the inclusion of explicit resource measures, yielding insight into the underlying basis of differing diversities.

DETERMINANTS OF BIRD OCCURRENCE

To reveal the processes underlying the markedly higher species richness associated with *Exocarpos* and infer which resources were better represented in *Exocarpos*-dominated forests, the responses of various feeding guilds were informative. Except for birds of prey, all guilds examined had significantly more records in *Exocarpos* than either *Acacia* plots, open forest plots or both (Fig. 4), suggesting the pattern was driven by broad-based differences in available resources. Frugivores/omnivores were most frequently recorded in *Exocarpos*-dominated forests plots and all species within this guild were frequently observed eating *Exocarpos* fruits. The increased incidence of aerial foragers in *Exocarpos*-dominated patches was probably not related to foliage cover directly, but more likely influenced by co-varying factors such as more favourable perches for sallying (Antos & Bennett 2006) or higher quality invertebrate assemblages (e.g. Hunter, Ohmart & Anderson 1988). The ground insectivore guild was dominated by one bird species (superb fairy-wren *M. cyaneus*) that clearly favoured *Exocarpos*-dominated habitats, either due to the increased cover afforded by the low, dense foliage or greater availability of arthropod prey. Granivore incidence was greatest in *Exocarpos*-dominated plots, in contrast to other studies (e.g. Barbaro, Dutoit & Cozic 2001; Coppedge *et al.* 2001) that attributed detected declines in granivorous birds to substantial reductions of grass cover associated with increased shrub cover. As six of the eight species in this guild forage primarily on the forest floor (Appendix S1), our findings suggest that increased shrub foliage may also lead to changes in leaf litter dynamics and associated arthropods (see Watson 2011a). Alternatively, and as discussed in more depth below, the root parasite may facilitate the growth of grasses, yielding greater food resources for these seed eating species.

The incidence of foliage gleaners was greatest in forest plots with *Exocarpos*-dominated understoreys and best modelled by shrub foliage. Shrubs provide extra foraging substrate for foliage gleaning species, and additional foraging niches for different species to exploit (Mac Nally 1994; Jansen & Robertson 2001; Whelan 2001). That foliage gleaner incidence was best explained by shrub foliage rather than canopy cover is surprising, as canopy trees represented a far greater habitat component, in terms of both biomass and leaf area. Foliage gleaning birds may have been more strongly influenced by shrubs then canopy foliage as the former could have supported a more preferable invertebrate prey. Also, insects may have been easier to hunt on shrub foliage, or these foliage gleaning birds responded to variation in canopy cover at larger scales.

While the marked influence of *Exocarpos* on occurrence patterns of birds could be considered a short-term response to the severe drought affecting the region (leading to aggregations of animals in the relatively mesic riverside habitats studied), we consider this unlikely, as all plots were located adjacent to a regulated river that was flowing throughout the study period. An alternative interpretation of these data could invoke differing detectabilities of birds in these habitat types as either confounding comparisons or accounting for the patterns reported (Kissling & Garton 2006). Since *Exocarpos* plots with the densest foliage consistently yielded the highest richness estimates, we are confident that systematic differences in detectability did not have a dominant influence on our overall findings and cannot explain the far greater incidences associated with *Exocarpos*-dominated forests. If differing detectabilities did confound our comparisons, it is more likely that they led to underestimation of incidences in *Exocarpos*-dominated plots, lessening the inferred influence of these plants on bird occurrence. Thus, the fact that significant effects were found overall and for most feeding guilds suggests the result reflects fundamental differences in resource availability. Likewise, although patch areas of *Acacia* and *Exocarpos* understoreys differed, all data were gathered in fixed-area plots, effectively controlling for any influence of habitat area (Watson 2004b).

RESOURCE DIFFERENCES BETWEEN HABITATS

Whereas *Exocarpos* fruit was abundant during the study period, *Acacia* was neither flowering nor seeding, and no other understorey plants (native or exotic) were bearing fruit. The only other fleshy fruit available during this period were small sticky fruits of the mistletoe *Amyema miquelii* (Loranthaceae) growing on eucalypt hosts, occurring at slightly higher densities in the *Exocarpos* plots. Hence, the overall amount of fruit available in *Exocarpos*-dominated forests was far greater than in other habitat types within the region. As a parasite, *Exocarpos* is not as constrained by the availability of water or nutrients as autotrophic plants, bearing fruit during the warmest, driest times of the year when few other fruit are available. Mistletoes have been noted exhibiting similar phenologies (Watson 2004a), interpreted as a strategy to maximize fruit removal to enhance seed dispersal by birds (Watson 2001, 2011b). The occurrence patterns of frugivores coincide with this pattern of availability, but likely represent a seasonal influx, birds moving into these riparian forests from other habitats to exploit this temporarily abundant resource (see Moegenburg & Levey 2003).

While seeds were not measured directly, grasses represent one of the main seed sources in these forests, and grass cover was markedly greater in *Exocarpos*-dominated forests. Shrubs with dense foliage normally restrict the growth of grasses under and around their canopies (Homlgren, Scheffer & Huston 1997; Costello, Lunt & Williams 2000) by limiting the amount of light available (Lett & Knapp 2003). Previous studies have noted greater cover of annual grasses beneath parasitic plants (Hobbs & Atkins 1991) likely facilitated by their abundant, nutrient-rich litter (Quested *et al.* 2003; March & Watson 2007; Quested 2008). Although significantly less litter cover was noted in *Exocarpos* plots, enriched litter can alter decomposition rates, confounding quantitative comparisons. Further research is needed to unravel the direct and indirect effects of parasitic plants on grass cover, and may confirm that habitat quality for granivores and grazers is enhanced by hemiparasites.

Those resources directly provided by the parasitic plants were matched with indirect nutritional resources – foliar arthropods – with significantly greater biomass of arthropod prey associated with *Exocarpos* foliage than *Acacia* foliage. This result was noteworthy, given that *Acacia* species are characterized by abundant extra-floral nectaries and high N foliage. While the greater arthropod prey base is consistent with the greater numbers of insectivorous birds recorded in *Exocarpos*-dominated forests, these results should best be regarded as preliminary, as not all arthropods are equally palatable or contain comparable nutritional value.

In addition to nutritional resources, forests with an *Exocarpos*-dominated understorey also had a different physiognomy, with lower, denser thickets of shrubs offering greater cover than the sparse open canopies of both *Acacia* and *E. camaldulensis*. These were highly favoured roosting and nesting location for many species, with every nest of the vulnerable Gilbert's whistler *Pachycephala inornata* located within *Exocarpos* plants (McGregor 2007). Similar patterns have been noted for mistletoe (Cooney, Watson & Young 2006), a wide range of animals recorded using these dense evergreen structures as nest sites and several species demonstrating preference for the substrate (Cooney & Watson 2005). An experimental study compared artificial nests in mistletoe with those in host foliage: mistletoe nests having significantly lower predation rates (Cooney & Watson 2008). Comparing nest success in *Exocarpos* and other substrates (both understorey species generally, and Gilbert's Whistler in particular) would clarify whether differences in occurrence are matched by differences in reproductive success.

INFLUENCE OF PARASITIC PLANTS ON COMMUNITIES

The markedly greater richness of bird species in *Exocarpos* plots lends support to the claim by Press (1998) that parasitic plants can act as 'Robin Hood'; taking from their host(s) and providing resources to a suite of other needy organisms (see also Watson 2001; Quested *et al.* 2003; Press & Phoenix 2005). Originally applied to mistletoes, this is the first study to demonstrate that root parasites can represent important resources for birds and many other animal groups. The greater number of frugivores associated with *Exocarpos* is not surprising given the absence of other sources of fleshy fruit during summer. The fact that more birds from other guilds were also found in *Exocarpos*-dominated forests highlights the influence of other resources provided by these plants, with changes in insectivore numbers and arthropod biomass showing congruent patterns. However it is important to note that eucalypts exhibited lower health scores in *Exocarpos*-dominated forests than those without a shrubby understorey by 6·5–13·5% (comparable to results reported by Sinclair 2006) with additional insects possibly associated with weakened Eucalypts (Heatwole & Lowman 1986). Whether this decline in tree health is due directly to *Exocarpos* parasitism or covarying differences in flooding history is equivocal and warrants further investigation.

Combining the findings reported herein with other studies of root parasites (Quested *et al.* 2003; Press & Phoenix 2005 and references therein), broad parallels are evident with mistletoes, a group that has attracted much attention in a far wider range of systems. While this latter group is considered to function as a keystone resource, there is insufficient information to evaluate whether their root-parasitic analogues have a similar role (Quested 2008). Unlike mistletoes, many of the woody root parasites are long-lived plants that can parasitize multiple hosts simultaneously, making it more complex to discern host–parasite interactions and unravel patterns of dependence. To elucidate these patterns a stoichiometric approach would be a useful complement to experimental manipulations, determining the sources of parasitic plant nutrients and tracking their contribution to overall ecosystem-scale trophic structure. This approach would establish whether the additional resources associated with parasitic plants (including fruit, dense structure and nutrient-rich litter) are necessarily acquired from the host, or from increased external inputs (e.g. via bird droppings) from heightened faunal activity associated with parasitic plants.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Bird foraging guilds.

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