Invasion of an exotic annual forb affects grass-feeding termites in a semi-arid woodland

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Abstract   Invasive plants are known to have dramatic and generally negative effects on ecosystems. The rapid spread and naturalization of *Carrichtera annua* (wards weed) across large areas of southern Australia has been widely reported, but its effects on biodiversity and ecosystem functions are poorly known. We examined the effects of *Carrichtera* on grass-feeding termites *Drepanotermes* spp. and hypothesized that increasing cover of *Carrichtera* would reduce termite abundance, which we assessed using the density of their above-ground pavements as a proxy for density. Our study was conducted at two spatial scales to explore (i) potential effects of *Carrichtera* invasion under variable intensities of grazing and (ii) differences between invaded and uninvaded sites at a long-ungrazed conservation reserve. Increasing cover of *Carrichtera* was associated with a greater density of pavements, both under grazed conditions and within the conservation reserve. However, increasing grazing intensity tended to be associated with reduced pavement density and size, through indirect reductions in plant biomass. Greater cover of *Carrichtera* was associated with declines in the cover of native plants and biocrusts, but not native plant richness. Pavement size tended to decline with increasing pavement density. Under conservation, *Carrichtera* sites supported more pavements, but densities declined markedly in drought years. The lower resilience to droughts and the fact that pavements in *Carrichtera*-invaded sites tended to be less cemented and contain more ants, suggest that invasion by *Carrichtera* may have long-term functional implications for processes mediated by termites. Increasingly, drier climates in southern Australia may exacerbate reductions in ecosystem functions given the pivotal role played by termites in dryland food webs and ecosystem functions.

Key words: *Carrichtera annua*, *Drepanotermes*, ecosystem functions, termites, weed invasion.

INTRODUCTION

Invasive plant species have been shown to have dramatic effects on ecosystem structure and function, altering habitat quality and leading to the extirpation of other species. A global meta-analysis of 198 studies showed that the effects of invasive plant species on animal abundance, diversity, fitness and ecosystem function were negative (58%) or neutral (44%) but never positive (Schirmel *et al.* 2015). Many invasive plants (weeds) have become naturalized in climatic areas similar to their native ranges and can quickly spread and dominate large areas. These invasions can have irreversible effects on ecosystem functions, such as nutrient cycling (Vanderhoeven *et al.* 2005), the provision of ecosystem services (Eviner *et al.* 2012) and the alteration of fire regimes (Clarke *et al.* 2005). Findings from a global meta-analysis demonstrate that the effects of invasive plant species

can be particularly devastating for arthropods, with 62% of studies finding a decrease in abundance of arthropods in response to plant invasions (Litt *et al.* 2014).

Ward's weed *Carrichtera annua* (L.) DC. an invasive annual forb from the family Brassicaceae, has increased markedly in cover and distribution across large areas of Mediterranean southern Australia over the past half century (Cooke 2003), particularly on alkaline soils. This widespread increase is thought to correspond with prolonged droughts, dispersal of seeds carried in fodder transported by road and potentially, overgrazing by livestock (Cooke *et al.* 2011). The success of *Carrichtera* as a highly invasive weed is thought to be due to its substantial seed production ($>30\,000$ seeds m^{-2}; Cooke 2003) and large aerial seed bank whereby seeds are retained on the plant until their release is triggered by adequate rainfall to ensure survival of the germinants (Zaady *et al.* 1997; Facelli & Chesson 2008). *Carrichtera* also is relatively unpalatable to most herbivores, and displays cyclic dormancy (Cooke 2003;

Cooke *et al.* 2012). The seeds of *Carrichtera* have a mucilaginous coating that allows them to adhere to the soil surface, providing an anchoring point even when soils are degraded or covered with a biological soil crust (biocrust; Zaady *et al.* 1997). Despite its recognition as a significant weed of Mediterranean rangelands, we know relatively little about the effects of *Carrichtera* invasion on biodiversity or ecosystem processes, though anecdotal information suggests that invasion is accompanied by dramatic shifts in plant community composition, and reductions in perennial and biennial grasses such as *Austrostipa* and *Rytidosperma* spp. (Keith 2004; Facelli & Chesson 2008; Cooke *et al.* 2011). Despite its rapid spread over vast areas and subsequent naturalization, there are still few studies from Australia.

The current and predicted distribution of *Carrichtera* in southern Australia is coincident with large areas of semi-arid rangelands occupied by the pavement-forming harvester termite *Drepanotermes perniger* (Froggatt) (Blattodae: Termitidae) (Watson & Perry 1981). Anecdotal evidence suggests that the replacement of perennial grasses, such as *Austrostipa* and *Rytidosperma* by *Carrichtera* may pose a threat to these grass-feeding termites, the main invertebrate decomposers in arid and semi-arid grasslands and woodlands (Whitford 2000). Little is known about the effects of *Carrichtera* on termites. We would expect that increasing density and abundance of *Carrichtera* would reduce termite populations, with unspecified and unexpected effects on soil functions. Pavements represent the above-ground cappings of subterranean colonies of *Drepanotermes*, and vary in size, configuration and condition, and have been used as proxies of termite abundance (Noble *et al.* 1989). Knowing how the presence of *Carrichtera* affects subterranean termites could provide valuable insights into the broader impacts of this invasive weed on ecosystem processes as broad as nutrient flows (Whitford *et al.* 1992), water infiltration (Elkins *et al.* 1986; Eldridge 1994), litter decomposition (Holt & Coventry 1988; Brown & Whitford 2003), carbon mineralization and subsequent plant production (Parker *et al.* 1982; Coventry *et al.* 1988). Changes in plant community composition are likely to lead to structural changes in termite populations (Noble *et al.* 1989). Because termites are also preferred food items for a range of vertebrates and invertebrates, their loss likely has wider trophic level ecosystem effects.

Here we describe a study where we explored the effects of the invasion of *C. annua* into perennial grasslands, and its effects on plants and termites. A hitherto unknown effect of subterranean termites may be a switch from harvesting *Austrostipa* and other perennial grasses to *Carrichtera* as the density and cover of perennial grasses decline with projected reductions in winter rainfall of up to 80% by 2080 (Crimp *et al.* 2010). However, although termites are known to display a high degree of dietary plasticity (Abensperg-Traun 1992), little is known of how changes in plant composition might influence their abundance. For example, some grass species are known to be more strongly preferred by termites (Smith *et al.* 2019), and changes in plant composition can influence the C-to-N ratio of litter and therefore its preference to termites (Freymann *et al.* 2010). Our study used data from two modules: (i) a district-wide assessment of sites with different levels of grazing and pavement densities to explore the potential direct and indirect effects of *Carrichtera* on plants and termites and (ii) a site-specific study within a long-ungrazed conservation reserve, where we compared invaded and uninvaded sites, *a priori*. In both of these modules, we hypothesized that increasing cover of *Carrichtera* would reduce the abundance of termites, which we assessed by measuring the density and size of their pavements. This hypothesis is based on the notion that termites prefer perennial grasses so that any decline in grasses brought about by *Carrichtera* would be associated with termite loss. Increases in bare ground associated with overgrazing are known to reduce foraging by *Drepanotermes tamminensis* (Watson & Perry 1981), leading to declines in termite diversity and grasslands productivity (Holt *et al.* 1996). We predicted therefore that increased grazing would reduce termite abundance by reducing perennial grasses at the expense of the relatively unpalatable *Carrichtera*.

METHODS

Study area

The study was carried out near the town of Mildura in south-eastern Australia ($-34.21°$, $142.12°$). The climate is Mediterranean, with hot summers and cool winters. In summer temperature ranges from a minimum of 14°C to a maximum of 47°C and in winter from a minimum of $-4°C$ to a maximum of 18°C (Bureau of Meteorology 2020). Rainfall is mainly winter dominant with an average of 280 mm annually. Rainfall for the period 2010–2017 very threefold from 214 to 657 mm (Appendix S1). The vegetation is dominated by chenopod shrublands (*Maireana pyramidata*), derived grasslands and herblands, interspersed with open belah (*Casuarina pauper*)-rosewood (*Alectryon oleifolius*) woodland. The soils are classified as Calcarosols (Isbell 1996) or Calcareous Earths, which are characterized by loamy surface textures and high pH.

For module 1, we selected 43 sites within 100 km of Mildura, from open shrublands and woodlands on calcareous soils that are inhabited by harvester termites *Drepanotermes* spp. and susceptible to invasion by *Carrichtera* (Cooke *et al.* 2011). These sites spanned different grazing intensities (ungrazed to moderately grazed) and were selected to

incorporate a range of densities of *Carrichtera* from no (absent) to high (>50%) cover. Ungrazed sites were located in Mallee Cliffs National Park (−34.21°, 142.62°, $n = 31$), a large 58 000 ha reserve about 25 km east of Buronga. Mallee Cliffs National Park has not been grazed by livestock since 1977 but is grazed at low levels by kangaroos (*Macropus* spp.) and European rabbits (*Oryctolagus cuniculus*). The low grazing sites were from a large crown reserve (Kelso Reserve, −34.11°, 142.11°, $n = 6$) that has been ungrazed for less than a decade and supports low numbers of feral goats (*Capra hircus*), kangaroos and rabbits. The remaining sites ($n = 6$) classified as moderately grazed were located on a pastoral (grazing) property where Merino sheep are stocked at average district densities. Within each grazing intensity category (ungrazed, low grazing, moderate grazing) we assessed the level of grazing intensity in the field and chose sites that accurately reflected these categories.

Site methods

At each of the 43 sites we positioned a 200 × 20 m (0.4 ha) plot, away from trees and tall shrubs and any historic ground disturbance. Within each plot, we counted all pavements of *D. perniger* and measured two perpendicular diameters through the centre of each pavement. Colony condition was characterized using three attributes: pavement morphology, pavement shape and level of invasion by ants (*sensu* Noble *et al*. 1989). Shape and surface morphology have been shown to be indicative of the colony condition (Noble *et al*. 1989; Abensperg-Traun & De Boer 1990; Abensperg-Traun & Milewski 1995). To assess surface morphology, we recorded the proportion of the pavement surface covered by compacted (cemented) material (which termites produce by mixing saliva with soil), loose soil, biocrusts and vascular plants. Pavement shape was recorded as convex, flat, or concave. Two core samples were collected near the centre and edge of each pavement to sample the main storage areas outer galleries (Watson & Gay 1970). Samples were collected using a 47 mm diameter corer to a depth of 100 mm from three convex and three concave pavements. The core samples were examined under a dissecting microscope in the laboratory to identify the plant species being harvested by termites.

We also recorded the cover and abundance of all vascular plant species, and total plant, bare soil, biocrust and litter cover, in one 20 m by 20 m plot within the larger 0.4 ha plot. Plant biomass was estimated from five 0.5 × 0.5 m quadrats evenly spaced within the 0.4 ha plot using the comparative yield approach (Friedel & Bastin 1988). This involved estimating biomass with a series of photo-standards based on previously clipped quadrats. One of the five quadrats at a site was clipped, and the material dried and weighed. The weighed samples were used to determine the correlation between estimated and actual biomass.

For Module 2, we selected 10 sites in Mallee Cliffs National Park, five of which were dominated by *Carrichtera* and five by native tussock grasses (*Austrostipa* spp.) at a range of densities. At each site, the density and morphology of termite pavements were assessed twice (2010, 2017) to explore possible differences due to a pronounced drought over that period. Within each of the sites, we also recorded the size and density of native perennial grass butts within a 20 × 1 m sub-plot, and the density of *Carrichtera* seedlings in a single 0.5 × 0.5 m quadrat that was representative of the average density at the site. Six pavements were randomly sampled from each site, three convex and three concave-shaped pavements. Core samples were collected using the methodology described in module 1 to obtain a qualitative and quantitative assessment of the material being harvested by termites. Core samples were sieved in the laboratory, sorted and all vegetative material removed, identified and weighed. We also counted the number of termites and ants in each core sample as a measure of colony health, given that mounds in poor condition are frequently invaded by *Iridomyrmex* spp. ants (Abensperg-Traun & De Boer 1990; Abensperg-Traun *et al*. 1995). We assessed the richness of surface-dwelling invertebrates using small pitfall traps. Ten pitfall traps were located inside the 20 × 20 m vascular plant plot and consisted of 7.5 cm deep × 7 cm wide plastic vials filled with ethyl glycol, arranged in a 5 × 2 m grid, and left open for 10 nights. Captured invertebrates were enumerated and identified to genus or morphospecies.

Data analysis

Prior to analysis, we calculated the richness of different vascular plants groups according to growth form (chenopod, forb, shrub, tussock grass, vine, exotic) and life history (annual, perennial). Invertebrate richness and abundance were calculated for separate broad invertebrate groups (ants, beetles, bugs, spiders). We used general linear models in R (Version 3.4.4, R Core Team, R Foundation for Statistical Computing, Vienna, Austria; R Core Team 2018) to determine the influence of *Carrichtera* cover on native plant cover and richness, cryptogam cover, termite pavement size and abundance and other invertebrate abundance and richness. We removed ants from the analysis of total invertebrate abundance to prevent them obscuring potential differences in other invertebrate groups. In all models, site was used as a random effect. For Module 1, we used regression analysis in R to examine linear and non-linear relationships between the cover of *Carrichtera* and different response variables (e.g., pavement density and size, biocrust and native plant cover and plant richness and biomass). We used AIC to determine the appropriateness of a non-linear over a linear model. For Module 2, we examined significant differences in our variables of interest (native plant cover and richness, cryptogam cover, termite pavement density and size, termite pavement morphology and shape, termite pavement gallery contents) in relation to community type, that is, invaded (*Carrichtera*-dominant) compared with uninvaded (*Austrostipa*-dominant) using a general linear model with community type as a fixed effect. For all analyses, diagnostic tests (Levene's test) were run to check for normality and homogeneity of residuals prior to modelling.

We used structural equation modelling (Grace 2006) to build a system-level understanding on the effects of *Carrichtera* cover and the intensity of livestock and native herbivore grazing on termites, as assessed using pavement

density. To have sufficient statistical power, we used a two-scale measure of grazing, low (*n* = 12, which included the ungrazed and low grazing sites) and moderate (*n* = 21). This designation is reasonable given the even low grazing rate (of kangaroos) in Mallee Cliffs National Park. Structural equation modelling tests the plausibility of an *a priori* model, based on best available information, in explaining how *Carrichtera* and grazing affect termites, while accounting for differences in plant biomass (Appendix S2). Our modelling allowed us to explore the indirect effects of *Carrichtera* and grazing on termites *via* their effects on plant biomass. We used a goodness of fit test to assess the likelihood of our observations based on the structure of the *a priori* model such that high probability values indicate highly plausible causal structures underlying the observed correlations. Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software.

RESULTS

### Effects of *Carrichtera* on termites at the landscape scale

The cover of *Carrichtera* across the 43 sites ranged from 0% to 55% (12.7 ± 2.6%, mean ± SE) and the density of termite pavements from 9 to 290 pavements ha^{-1} (89.9 ± 9.8). Contrary to expectation, we found that the density of termite pavements increased with increasing cover of *Carrichtera* (*r* = 0.44, *P* = 0.003; Fig. 1a) but there were no significant effects on pavement size (*r* = 0.11, *P* = 0.45; Fig. 1b). Increasing cover of *Carrichtera* was also associated with other biotic effects including significant declines in cryptogam cover (*r* = −0.46,

P = 0.002; Fig. 1c), native plant cover (*r* = −0.38, *P* = 0.012; Fig. 1d), but no effect on plant richness (*r* = 0.15, *P* = 0.34; Fig. 1e). Increasing *Carrichtera* *cover* was also associated with strong increases in site-level plant biomass (*r* = 0.37, *P* = 0.014; Fig. 1f), most of which was dominated by *Carrichtera*.

Structural equation modelling identified direct effects of *Carrichtera* cover on pavement density (path coefficient [PC] = 0.31), but no effect on pavement size, after accounting for differences in plant biomass and grazing intensity (Fig. 2). There were no direct effects of increasing grazing intensity on pavement density, but an indirect suppressive effect, by reducing the positive effect of plant biomass, on pavement size and pavement density. *Carrichtera* also had an indirect positive effect on pavement density by increasing plant biomass. There was also evidence that termite pavements tended to be smaller where their density was high (Fig. 2).

Effects of *Carrichtera* on termites in the absence of grazing

We then examined potential effects of *Carrichtera* on termites at a finer spatial scale (module 2) using sites with and without *Carrichtera* in a National Park that has been ungrazed by European livestock for more than half a century, thus removing potential confounding effects of different grazing management. The five sites dominated by *Carrichtera* had 40-times greater cover (41.9 ± 3.4%; mean ± SE) and 30-times greater density (1559 ± 194; mean ± SE) than the grassland sites (1.3 ± 0.3%, 47 ± 16; for cover
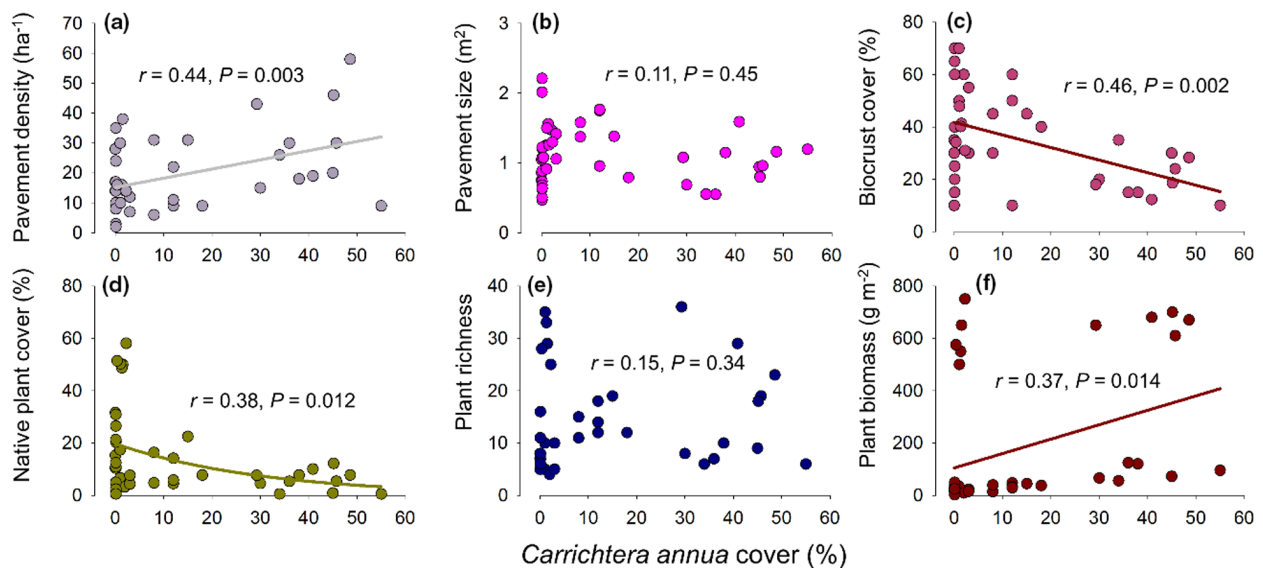
Fig. 1. Influence of ward weed cover on; (a) termite pavement density, (b) termite pavement size, (c) biocrust cover, (d) native plant cover, (e) plant richness and (f) plant biomass.
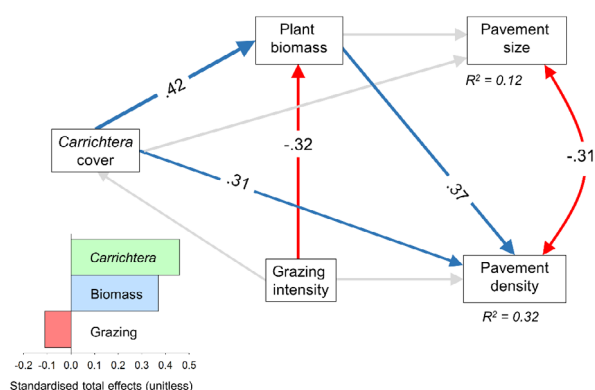
Fig. 2. Structural equation model showing the direct and indirect effects of *Carrichtera* cover, grazing intensity (low, medium, high) and plant biomass on termite pavement size and density. Numbers adjacent to arrows are standardized path coefficients, analogous to partial correlation coefficients, that indicate the effect size of the relationship. Continuous blue and red arrows indicate positive and negative relationships, respectively. The proportion of variance explained (R^2) in pavement size and density is given. Grey lines indicate non-significant pathways. The χ^2 goodness of fit test ($\chi^2 = 0.03$, $P = 0.874$, d.f. = 1) indicates significant support for our *a priori* model. The standardized total effects (sum of all direct and indirect effects) on pavement density is presented in the histograms.

and density, respectively; Table 1). *Carrichtera* sites also had greater cover of annual plants, sparser cover of native plants, more bare soil and litter, but half the cover of cryptogams.

Carrichtera sites had significantly more pavements (196 ha^{-1} ± 33.6; mean ± SE) than grassland sites (94 ha^{-1} ± 24.6) in 2010, but this difference had dissipated by 2017, following a 4-year drought (2012–2015) (116 *cf.* 110; Fig. 3a,b). Pavement size was similar between sites in 2010, but in 2017, were significantly greater in non-invaded sites ($F_{1,8} = 9.89$, $P = 0.014$; Fig. 3b). Pavement morphology was variable within and among sites, although there were some significant differences. At *Carrichtera* sites, pavements had greater plant cover in both 2010 ($F_{1,8} = 6.1$, $P = 0.038$; Fig. 3c) and 2017 ($F_{1,8} = 9.1$, $P = 0.005$, Fig. 3d), while the surfaces at grassland sites were more cemented ($F_{1,8} = 14.0$, $P = 0.005$; Fig. 3d). More termite pavements at *Carrichtera* sites were concave-shaped ($F_{1,8} = 8.0$, $P = 0.022$; Fig. 3e) but only in 2017. We also found some differences in the contents of termite galleries. Cores from the pavements at *Carrichtera* sites contained more ants (*Iridomyrmex* spp.; $F_{1,8} = 8.10$, $P = 0.02$), and contrary to expectation, contained more chaff ($F_{1,8} = 5.20$, $P = 0.05$; Fig. 3f).

Table 1. Differences in plant cover and richness and invertebrate abundance and richness between sites *Carrichtera* sites and grassland sites

Attribute	Carrichtera invaded		Grassland uninvaded		*F*-value	*P*-value
	Mean	SE	Mean	SE		
Cover attributes						
Carrichtera cover (%)	41.9	3.3	1.3	0.3	315.6	**<0.001**
Carrichtera density (plants m^{-2})	1358.8	193.9	46.6	16.3	78.6	**<0.001**
Exotic plant cover (%)	52.5	1.9	2.0	0.6	438.9	**<0.001**
Native plant cover (%)	8.6	1.1	51.7	1.6	187	**<0.001**
Annual plant cover (%)	52.6	1.6	2.5	0.8	173.2	**<0.001**
Perennial plant cover (%)	8.5	1.0	51.2	1.7	153.6	**<0.001**
Native grass butt density (m^{-2})	1.4	0.6	9.7	1.2	27.2	**<0.001**
Native grass butt diameter (cm)	4.2	0.4	9.5	0.8	33	**<0.001**
Biomass 2010 (g m^{-2})	508.0	46.5	428.8	53.1	1.4	0.27
Bare soil cover (%)	9.8	1.5	4.1	0.3	17.6	**0.003**
Cryptogam cover (%)	20.2	2.7	38.8	2.9	18.1	**0.002**
Litter cover (%)	9.9	0.9	6.2	0.8	10.8	**0.01**
Invertebrate attributes						
Invertebrate abundance (excl ants)	204.2	25.1	83.0	11.9	20.1	**0.002**
Beetle abundance	16.4	5.6	4.4	1.1	10.0	**0.013**
Bug abundance	11.6	6.1	5.4	1.4	0.8	0.37
Spider abundance	26.2	6.9	16.0	1.4	1.5	0.24
Ant abundance	1588.6	842.6	423.4	258.6	4.0	0.07
Invertebrate richness	26.8	2.4	26.8	1.7	0.0	0.82
Beetle richness	4.2	0.9	2.0	0.5	3.1	0.24
Bug richness	3.2	0.3	2.6	0.2	1.3	0.28
Spider richness	7.0	1.30	8.8	0.9	1.3	0.28
Ant richness	9.2	1.5	10.0	1.3	0.2	0.66

Bold font indicates statistical significance.
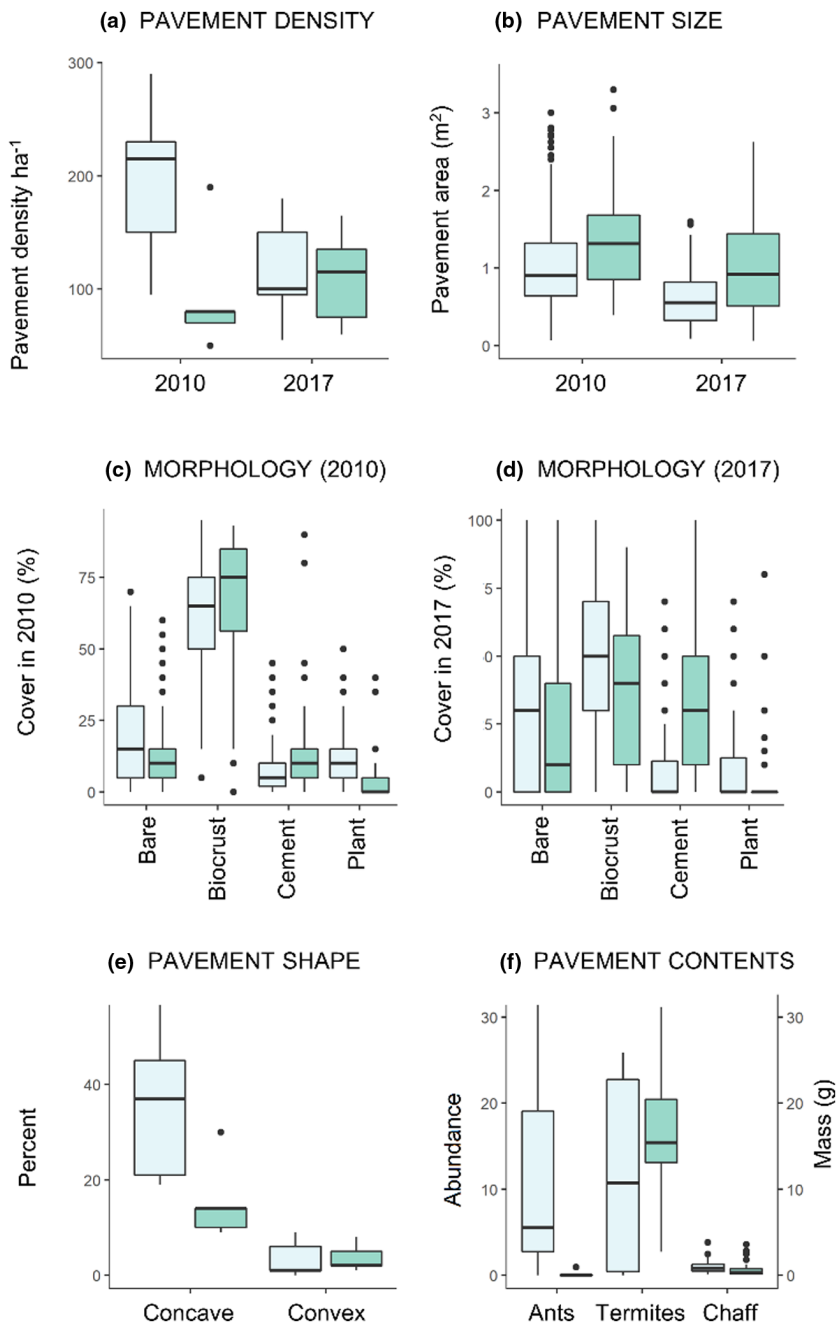
Fig. 3. Box plots representing invaded and uninvaded sites in relation to: (a) density of pavements, (b) pavement size, (c) pavement morphology in 2010, (d) pavement morphology in 2017, (e) pavement shape and (f) gallery contents. Light shade invaded, dark shade uninvaded.

DISCUSSION

We found that increasing cover of the invasive forb *C. annua* was associated with declines in ecosystem quality including lower cover of biocrusts and reductions in native plant cover, as well as an increase in weedy biomass. Contrary to expectation, however, increased *Carrichtera* was associated with a greater density of termite pavements, but no significant difference in their size. Declines in the cover and biomass of perennial native grasses did not seem to have any significant effect on termite populations, as assessed by the density of their pavements.

We expected that landscapes dominated by perennial native grasses would support higher densities of subterranean termites, but this was not the case. Although largely a grass harvesting species (Garnett 1977), *D. perniger* harvests a wide range of plant material, depending on its availability (Watson *et al.* 1973; Noble *et al.* 1989), consistent with other pavement builders (e.g., *Drepanotermes tamminesis*) that have a flexible diet according to seasonal availability of plant material (Watson & Perry 1981; Park

et al. 1993). Previous research has shown that *D. perniger* can shift from grass feeding to leaf harvesting during dry periods when grass is not readily available (Watson & Gay 1970). At some sites invaded by *Carrichtera*, the density of *Carrichtera* plants was >1000 plant m^{-2} producing a large amount of biomass, with estimates in our study ranged from 2 to 630 g m^{-2}. *Carrichtera* may have high suitability to termites because, unlike other less woody annual plants, much of its biomass (stalks, branches, seed pods) remains intact, albeit often dead, throughout the year, and this material is therefore available for harvesting. Our sampling of termite pavements confirmed that *D. perniger* mounds contained galleries with *Carrichtera* stems and capsules, providing direct evidence that they are foraging for this plant. However, core sampling also indicated some signs of declining pavement condition at invaded sites. For example, despite containing more foraging material, galleries at *Carrichtera* sites contained significantly more ants *Iridomyrmex* spp. Competition between ants and termites for forage is intense and there is some suggestion that *Iridomyrmex* spp. may be able to exploit weakened termite populations (Wood & Lee 1971). The mounds of *D. tamminensis* in poor condition were crumbly, ill maintained and frequently cohabitated by ants, *Iridomyrmex* spp. (Abensperg-Traun & De Boer 1990). We also found more beetles associated with *Carrichtera* sites, possibly due to the greater cover of bare soil, which is important habitat for beetles (Cameron & Leather 2012).

Our broad regional study (Module 1) demonstrated the highly variable density of termite pavements, ranging from 9 to 290 pavements ha^{-1}. Significant spatial variation in density has been noted elsewhere (Noble *et al.* 1989), although at densities about a third of what we detected in southern New South Wales. Watson and Gay (1970) recorded densities up to 350 mounds per ha in degraded *Acacia aneura* woodlands in southwestern Queensland. In *Acacia* communities, high variability might be associated with surface water run-off and run-on (Noble *et al.* 1989), since most grasses tend to occur in run-on areas where water accumulates and landscape productivity is greatest (Tongway & Ludwig 1994). Given the longevity of termite structures, up to 60 years after abandonment (Watson & Gay 1970), there is likely a large legacy effect between changes in environmental conditions (rainfall, plant biomass) and growth or attraction of pavements. Variability in pavement density may also be due to subtle differences in soil chemistry which can influence site occupancy (Spain & McIvor 1988), although we did not account for this in our study.

Legacy effects might also explain why we failed to find an effect of current livestock grazing intensities,

albeit at qualitative levels, on either pavement density or size. Our only significant effect of grazing was the negative association between increasing grazing intensity and plant biomass, which was itself positively correlated with pavement density. Although these results are correlated, they suggest that grazing could act indirectly on termites by reducing the availability of forage material, thereby reducing termite-carrying capacity. Support for this proposition is, however, ambivalent. For example, Watson and Perry (1981) found a higher incidence of *D. tamminensis* mounds in grazed plots, suggesting that supply of foraging material is not a limiting factor, but that shade and an increase in bare ground may favour unimpeded harvesting. Likewise, Abensperg-Traun (1992) found that despite the reduced litter cover and plant cover in grazed plots, the abundance and diversity of termites was not significantly less than in the ungrazed plots. In contrast, the incidence of mound abandonment has been shown to be greater for harvester (*Drepanotermes*) than wood eating termite colonies in small grazed remnants (Abensperg-Traun & Smith 1999).

As a test of the usefulness of pavement density as a proxy for termite populations, we classified pavements based on their surface type and morphology (*sensu* Noble *et al.* 1989). Pavement morphology was variable within and among sites, but in general, invaded sites had more concave pavements and more were colonized by vascular plants. Conversely, those at grass-dominated sites tended to be heavily cemented and convex in shape. Termites tend to maintain the integrity of the pavement by using mucilaginous secretions to cement the uppermost layers, resulting in an impermeable surface that repels water and prevents the growth of vascular plants. Thus, healthy pavements are generally convex-shaped, which drives run-off water to the annular zone surrounding the pavement (Eldridge 1994). At grasslands sites, a greater proportion of the pavement surface was covered in cement and pavements were more frequently convex. Concave-shaped pavements and those colonized by vascular plants are likely indicative of declining colony condition, reduced termite activity or perhaps signs of retraction of the colony from pavements. In contrast, the hard-cemented capping more common at the grassland sites is indicative of recent activity in maintaining the surface of the pavement (Abensperg-Traun & De Boer 1990).

CONCLUSIONS

Overall, our expectation that the spread of *Carrichtera* would suppress the density of the harvester termites *D. perniger* was not supported by this study. Indeed, we found that increasing density of *Carrichtera* resulted

in an increase in the density of termite pavements. When we compared *Carrichtera* dominated sites to grassland sites, we found the density of termite pavements was higher under *Carrichtera*. Our results suggest that *D. perniger* has a flexible diet and is capable of utilizing *Carrichtera* as an alternative to perennial grass. Assessing the status of the termite population during an extended drought demonstrated the fragility of obligate reliance on an annual exotic plant. Termite populations appeared to crash at *Carrichtera*-invaded sites but not at grassland sites. These findings warrant further investigation given the important role that termites play in a range of ecosystem functions. The predicted drier climate may have profound implications for termite populations that are forced to rely on exotic annual forage. This scenario may have significant implications for ecosystem function since termites play a pivotal role in food webs (Abensperb-Traun, 1994) and as ecosystem engineers (Coventry *et al.* 1988). Furthermore, as *Carrichtera* has displaced the native ground cover in shrublands and open woodlands over vast areas in NSW, Victoria and South Australia (Cooke *et al.* 2011), these consequences may extend over large areas.

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AUTHOR CONTRIBUTIONS

James Val: Conceptualization (equal); data curation (lead); formal analysis (supporting); investigation (equal); methodology (equal); project administration (lead); writing – original draft (lead); writing – review and editing (equal). **Dave Eldridge:** Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (equal).

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Rainfall and pavement density over the period of the study.

Appendix S2. Structural equation modelling a priori model.