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Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity within wet sclerophyll forest in southeastern Australia

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Abstract

Plant invasions of natural communities are commonly associated with reduced species diversity and altered ecosystem structure and function. This study investigated the effects of invasion and management of the woody shrub *Lantana camara* (lantana) in wet sclerophyll forest on the south-east coast of Australia. The effects of *L. camara* invasion and management on resident vegetation diversity and recruitment were determined as well as if invader management initiated community recovery. Vascular plant species richness, abundance and composition were surveyed and compared across *L. camara* invaded, non-invaded and managed sites following *L. camara* removal during a previous control event by land managers. Native tree juvenile and adult densities were compared between sites to investigate the potential effects of *L. camara* on species recruitment. Invasion of *L. camara* led to a reduction in species richness and compositions that diverged from non-invaded vegetation. Species richness was lower for fern, herb, tree and vine species, highlighting the pervasive threat of *L. camara*. For many common tree species, juvenile densities were lower within invaded sites than non-invaded sites, yet adult densities were similar across all invasion categories. This indicates that reduced species diversity is driven in part by recruitment limitation mechanisms, which may include allelopathy and resource competition, rather than displacement of adult vegetation. Management of *L. camara* initiated community recovery by increasing species richness, abundance and recruitment. While community composition following *L. camara* management diverged from non-invaded vegetation, vigorous tree and shrub recruitment signals that long-term community reinstatement will occur. However, secondary weed invasion occurred following *L. camara* control. Follow-up weed control may be necessary to prevent secondary plant invasion following invader management and facilitate long-term community recovery.

Disciplines

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1 **Title**

2 Invasion and management of a woody plant, *Lantana camara* L., alters vegetation diversity
3 within wet sclerophyll forest in south-eastern Australia
4

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Abstract

Plant invasions of natural communities are commonly associated with reduced species diversity and altered ecosystem structure and function. This study investigated the effects of invasion and management of the woody shrub *Lantana camara* (lantana) in wet sclerophyll forest on the south-east coast of Australia. The effects of *L. camara* invasion and management on resident vegetation diversity and recruitment were determined as well as if invader management initiated community recovery. Vascular plant species richness, abundance and composition were surveyed and compared across *L. camara* invaded, non-invaded and managed sites following *L. camara* removal during a previous control event by land managers. Native tree juvenile and adult densities were compared between sites to investigate the potential effects of *L. camara* on species recruitment. Invasion of *L. camara* led to a reduction in species richness and compositions that diverged from non-invaded vegetation. Species richness was lower for fern, herb, tree and vine species, highlighting the pervasive threat of *L. camara*. For many common tree species, juvenile densities were lower within invaded sites than non-invaded sites, yet adult densities were similar across all invasion categories. This indicates that reduced species diversity is driven in part by recruitment limitation mechanisms, which may include allelopathy and resource competition, rather than displacement of adult vegetation. Management of *L. camara* initiated community recovery by increasing species richness, abundance and recruitment. While community composition following *L. camara* management diverged from non-invaded vegetation, vigorous tree and shrub recruitment signals that long-term community reinstatement will occur. However, secondary weed invasion occurred following *L. camara* control. Follow-up weed control may be necessary to prevent secondary plant invasion following invader management and facilitate long-term community recovery.

Key words

Diversity loss, invasive species management, *Lantana camara*, plant invasion, restoration ecology, weed impacts

Introduction

Non-indigenous species are important agents of global environmental change (Vitousek et al., 1996) and recognised as the second greatest threat to global biodiversity after anthropogenic habitat loss and ecosystem destruction (Adair and Groves, 1998; Gurevitch and Padilla, 2004). Plant invaders of natural communities, also termed environmental weeds (Richardson et al., 2000), alter ecosystem structure and function and affect the abundance and diversity of resident vegetation (Weiss and Noble, 1984; Mack and D'Antonio, 1998; Costello et al., 2000; Lindsay and French, 2004; Grice, 2006; Minchinton et al., 2006). Weeds may adversely affect plant species diversity by displacing mature vegetation or limiting juvenile recruitment (Yurkonis et al., 2005). For example, Grant et al. (2003) showed that invasion by the perennial forb *Acroptilon repens* in semiarid grasslands of North America reduced the seed germination and initial survival of resident perennial grass species. The mechanisms limiting resident species recruitment in invaded communities include competition for resources such as light, nutrients and space (Tilman, 1987; Gorchov and Trisel, 2003), as well as non-resource mediated interference, such as allelopathy (Gentle and Duggin, 1997a; Foy and Inderjit, 2001). Recruitment limitation may result in fewer resident juveniles in weed invaded relative to non-invaded vegetation, yet this has not been widely demonstrated (but see Standish et al. (2001)). Field-based quantitative studies that measure the differential effects of plant invaders on resident species growth stages (e.g. juveniles versus adults) may indicate long-term mechanisms by which weeds affect species diversity (Yurkonis, et al., 2005; Ens and French, 2008).

A variety of quantitative procedures are used to assess weed impacts on natural communities, including multi-site comparison, weed removal and weed addition procedures

(see Adair and Groves (1998) for a related discussion). The multi-site comparison procedure compares resident species diversity values in invaded sites to reference non-invaded sites; however, direct impacts of the weed on species are difficult to establish due to the correlative nature of the procedure (Weiss and Noble, 1984; Adair and Groves, 1998; Gurevitch and Padilla, 2004). Weed removal studies can provide stronger evidence for weed impacts on native species since changes in species diversity and abundance following weed removal can be directly measured (Turner and Virtue, 2006). Weed removal studies can also indicate weed impact mechanisms, such as recruitment limitation, by monitoring demographic changes to resident species populations following weed control (D'Antonio et al., 1998). However, residual invader effects, such as altered soil nutrient compositions and depleted native soil-stored seed banks, as well as differential effects of weed removal regime can influence the response of native species to weed removal (Adair and Groves, 1998; D'Antonio, et al., 1998; Mason and French, 2007; Mason et al., 2007), which limits the utility of this approach.

Weed management programmes can act as surrogates for weed removal studies whereby components of resident species diversity are compared between non-invaded, invaded and managed sites. Weed control aims to improve diversity at the site by mitigating adverse effects of the invader and reducing competitive effects, in turn facilitating native vegetation community regeneration (Davis et al., 2000; Mason and French, 2007). Increased species diversity has been reported following control of the exotic perennial grass *Hyparrhenia hirta* (coolatai grass) (Chejara et al., 2006), and woody exotic shrubs *Mimosa pigra* (Paynter, 2004) and *Chrysanthemoides monilifera* spp. *rotundata* (bitou bush) (Mason and French, 2007). However, the opposite response has been demonstrated for native communities following removal of some weeds, such as *Asparagus asparagoides* (bridal creeper) (Turner and Virtue, 2006), highlighting that removal of the invader alone does not necessarily initiate resident species recovery. Furthermore, weed control itself can significantly disturb natural communities, differentially influencing the composition of

regenerating species and facilitating secondary weed invasion (Yelenik et al., 2004; Turner and Virtue, 2006; Mason and French, 2007). It is therefore necessary to investigate not only the effects of a plant invader, but also the effects of its control on native vegetation. Only then can appropriate and effective management procedures be developed to mitigate the adverse effects of the invader and promote community recovery.

In the current study we investigated the effects of invasion and management (i.e. control) of *Lantana camara* (lantana) on vascular plant species diversity and recruitment in wet sclerophyll forest. *Lantana camara* is a woody thicket-forming shrub widespread throughout wet sclerophyll forest and rainforest margins in eastern Australia (Swarbrick et al., 1998). It dominates understorey vegetation in disturbed areas, often forming dense monospecific thickets, and is implicated in widespread loss of native plant species diversity (Fensham et al., 1994; Duggin and Gentle, 1998; Swarbrick, et al., 1998). Empirical evidence suggests that *L. camara* inhibits native plant species recruitment via allelopathic interference of seed germination, seedling growth and survivorship (Wadhawani and Bhardwaja, 1981; Achhireddy and Singh, 1984; Gentle and Duggin, 1997a); however, quantitative field-based evidence linking reduced species recruitment and diversity is scarce, precluding effective invader management. Furthermore, contrasting results by Fensham et al. (1994) and Webb et al. (1972) in rainforest suggest that further investigation is necessary to elucidate a more general effect. Quantifying the demographic effects of woody plant invaders, such as *L. camara*, on resident plant species would refine our understanding of whether species loss is driven by recruitment limitation or displacement of mature vegetation.

Previous studies have shown that *L. camara* control, which reduces invader abundance, facilitates the regeneration and recovery of invaded plant communities (e.g. Macleay, 2004; Cummings et al., 2007). However, such studies did not compare patterns of vegetation recovery following *L. camara* control with reference non-invaded natural

communities, meaning that there is incomplete evidence for the effects and potential benefits of *L. camara* management.

The study assessed the response of native and exotic vascular plant species to *L. camara* invasion and management. The regeneration of resident species was monitored following removal of *L. camara* after previous control events. The effects of *L. camara* on species recruitment were assessed by comparing juvenile and adult tree densities amongst *L. camara* non-invaded, managed and invaded vegetation. It is predicted that:

1. Native species richness and abundance are higher in non-invaded sites than both managed and invaded sites, leading to divergent species compositions;
2. Invasion of *L. camara* adversely affects native species recruitment such that juvenile density is higher in non-invaded sites than invaded sites;
3. Management of *L. camara* positively affects species recruitment and diversity such that juvenile density and species richness are higher in managed sites than invaded sites.

Methods

Study area and habitat

The study was conducted in June 2007 in Minnamurra Rainforest Reserve on the south-east coast of New South Wales, Australia (34°38'03.83"S; 150°43'31.30"E). The average temperature ranges from 13.6 °C in winter to 23.3 °C in summer and the average annual rainfall is 1600-1800 mm (NPWS, 2006). Native vegetation in the study area is predominantly wet sclerophyll forest, characterised by a tall open sclerophyllous canopy with a dense mesophyllous subcanopy of rainforest trees and shrubs (Keith, 2004). Sclerophyllous canopy species consist mainly of *Eucalyptus quadrangulata* and *E. muelleriana*; common subcanopy species include *Acmena smithii*, *Elaeodendron australe* and *Diospyros australis*;

and understorey vegetation consists of a sparse groundcover of herbs *Pseuderanthemum* *variabile*, *Dichondra repens* and *Viola hederacea* and ferns *Calochlaena dubia*, *Doodia aspera* and *Pellaea falcata*.

Minnamurra Rainforest was reserved for public use in 1896 (NPWS, 1998). Wet sclerophyll forest in the study area was extensively cleared for logging and farming purposes prior to reservation, and current forest stands are a result of widespread natural regeneration (NPWS, 1998). During the period of forest regeneration, *L. camara* invaded and became dominant in isolated forest openings with incomplete canopy cover, forming dense monospecific thickets. The long-term persistence of *L. camara* in these forest openings is thought to have prevented forest regeneration (NPWS, 1998). Furthermore, de Ville (2003) noted that *L. camara* appears capable of invading relatively intact vegetation in the study area.

In May 2001, monitoring and management of *L. camara* infestations within Minnamurra Rainforest commenced as part of a regional integrated weed control and monitoring programme (de Ville, 2004). Infestations of *L. camara* were mapped and control in some areas was conducted during the spring of 2001 (de Ville, 2004). The average percentage foliage cover of *L. camara* ranged from approximately 50% to 100% prior to control implementation (de Ville, 2003). *Lantana camara* was controlled by removing above-ground shoot biomass, either by manually hand-pulling stems or cutting and poisoning stem bases with 100% Roundup® (360 g L⁻¹ glyphosate). Secondary monitoring and manual control of *L. camara* were undertaken annually to prevent reinvasion and facilitate native vegetation regeneration (de Ville, 2004).

Field methods

In 2007, six years after control, ten sites of three *L. camara* invasion categories were surveyed: invaded, managed and non-invaded sites. Sites were 10 x 10 m quadrats, chosen as several managed infestations were this size. Invaded sites were defined as vegetation with $\geq 50\%$ *L. camara* foliage cover with no management history; non-invaded sites comprised intact native vegetation with $\leq 5\%$ *L. camara* foliage cover and no management history; and managed sites comprised $< 20\%$ *L. camara* foliage cover with $\geq 50\%$ cover of *L. camara* removed during the previous control events in 2001. Study sites from each invasion category were haphazardly interspersed across the study area, separated by a minimum of 50 m. All sites were positioned within the forest interior away from adjacent cleared land.

At each site, the percentage *L. camara* foliage cover, percentage sclerophyllous canopy cover, and identity and percentage foliage cover of native and exotic vascular plant species were recorded. Species nomenclature followed Harden (1990; 1992; 1993; 2002) and Robinson (2003). Species percentage foliage cover was measured following a modified Braun Blanquet cover abundance scale (1, $< 5\%$ cover and one or a few individuals; 2, $< 5\%$ cover and uncommon; 3, $< 5\%$ cover and common; 4, $< 5\%$ cover and very abundant; 5, 5-20% cover; 6, 21-50% cover; 7, 51-75% cover and 8, 76-100% cover) (Poore, 1955; Mason and French, 2007). Species were assigned to one of five growth forms: ferns, herbs (including herbaceous monocots), shrubs, trees and vines. Juvenile and adult densities were recorded for canopy and subcanopy tree species as the number of individuals per site. Juveniles and adults were defined as individuals ≤ 1.5 m and > 1.5 m tall, respectively. Shrub density (excluding *L. camara*) was also recorded.

Data analysis

One-way analysis of variance (ANOVA) (JMP version 5.1) assessed differences in species richness and tree (juveniles and adults) and shrub densities amongst invasion categories. Two-way ANOVA assessed differences in species richness within growth forms

amongst invasion categories. Square root data transformations were performed as necessary to satisfy test assumptions of normality and homogeneity of variance. Post hoc comparisons amongst means were performed using the Student-Newman-Kuels (SNK) test. The Kruskal-Wallis non-parametric single-factor analysis of variance by ranks assessed differences in juvenile and adult densities amongst invasion categories for individual tree species (Zar, 1999). The Kruskal-Wallis test was performed only for species occurring in all three invasion categories. Post hoc pair-wise comparisons amongst ranks were undertaken using the Mann-Whitney test (Zar, 1999).

Species composition amongst invasion categories was compared using a multivariate approach, following Clarke (1993) and Clarke and Gorley (2000). Similarities in species composition between invasion categories were assessed using a one-way analysis of similarity (ANOSIM). Species contributing to the within-group similarities as well as differences amongst invasion categories were determined using similarity percentage analysis (SIMPER). ANOSIM and SIMPER utilised species Braun Blanquet cover abundance data as well as species presence/absence. Estimates of compositional similarity amongst invasion categories were determined using a Bray-Curtis similarity matrix (Clarke, 1993; Clarke and Gorley, 2000). Cover of *L. camara* was excluded from composition analyses as this defined each invasion category. Additionally, changes in species composition were assessed visually using two-dimensional non-metric multidimensional scaling ordination (Clarke, 1993) and verified by differences in juvenile and adult densities for the selected tree species.

Results

In total, 157 vascular plant species were recorded, of which 145 were native and only 12 exotic. Altogether, species comprised 15 ferns, 36 herbs, 21 shrubs, 53 trees and 32 vines. Forty-nine species (approximately 31%) occurred in all invasion categories; however, 14

species were only found in non-invaded sites, 49 only in managed sites and 3 only within invaded sites (Appendix).

Effects of L. camara invasion and management on species diversity

The mean native and exotic species richness varied significantly amongst invasion categories (native: $F_{2, 27} = 27.23$, $P < 0.0001$; exotic: $F_{1, 18} = 7.68$, $P = 0.0126$) (Figure 1). Managed sites had significantly more native species than both non-invaded and invaded sites, and invaded sites had the fewest native species overall. Managed sites had significantly more exotic species than invaded sites; no exotic species other than *L. camara* occurred in non-invaded sites.

[insert Figure 1]

The mean native species richness within each growth form responded differently to *L. camara* invasion and management ($F_{8, 135} = 3.3975$, $P < 0.0014$) (Figure 2; Table 1). Non-invaded and managed sites had significantly more fern, herb, tree and vine species than invaded sites. Managed sites had significantly more herb and shrub species than either non-invaded or invaded sites. Shrub species richness was similar between non-invaded and invaded sites. The variation in exotic species richness within growth forms amongst invasion categories was not tested as most species were herbs; no exotic fern or tree species were recorded.

[insert Figure 2]

[insert Table 1]

Invasion categories were compositionally distinct (Global $R = 0.487$, $P = 0.001$) (Table 2). Managed and invaded sites had the most different species compositions (average dissimilarity = 75.39%). Two-dimensional non-metric multidimensional scaling ordination of species cover clearly separated invaded sites from both non-invaded and managed sites (Figure 3a). Invasion categories were also separated when species presence/absence were

analysed (Global $R = 0.433$, $P = 0.001$), indicating that species identity, as well as cover, was a key component of community change (Table 2, Figure 3b). Compositional dissimilarities amongst invasion categories were retained when exotic species were excluded from the ANOSIM (Global $R = 0.49$, $P = 0.001$) (Table 2). As native herb and shrub species richness were significantly higher in managed sites compared with non-invaded and invaded sites, these may have had a greater contribution to compositional differences amongst invasion categories than fern, tree and vine species. However, compositional differences amongst invasion categories still retained significance when herbs and shrubs were removed from the ANOSIM (Global $R = 0.369$, $P = 0.001$), showing that changes in cover of fern, tree and vine species were also key factors of community change (Table 2).

[insert Table 2]

[insert Figure 3]

Native mesophyllous subcanopy trees were the most abundant and common species in the study area, including *Acmena smithii*, *Doryphora sassafras* and *Pittosporum undulatum*. Subcanopy trees contributed strongly to compositional dissimilarities amongst invasion categories (Table 3). The average cover of most species was lower within invaded sites than both non-invaded and managed sites. Two common herbs, *Oplismenus* spp. and *Dichondra repens*, also contributed strongly to compositional differences amongst invasion categories. Both herb species were widespread in managed sites, though found rarely in non-invaded and invaded sites.

[insert Table 3]

Community composition was marginally more homogeneous amongst non-invaded sites (average similarity = 43.74%) compared with managed (average similarity = 39.09%) and invaded (average similarity = 38.76%) sites (Table 4). All species contributing up to 50% of the average similarities between sites within each invasion category were abundant and widespread native species, consisting mainly of subcanopy mesophyllous trees. *Eucalyptus*

quadrangulata was the strongest contributor to similarities in non-invaded and invaded sites, reflecting its dominance in the canopy. Non-invaded sites were also characterised by the herb *Pseuderanthemum variable*. Managed sites were characterised by more vine and herb species than either non-invaded or invaded sites (Table 4). Non-invaded and managed sites became more homogeneous when the total species cover abundance data were presence/absence transformed, as shown by the contraction of sites in ordination space (Figure 3b), indicating that compositional differences amongst non-invaded and managed sites were caused more by altered species cover than occurrence.

[insert Table 4]

Effects of L. camara invasion and management on species recruitment

Total tree juvenile and adult densities as well as shrub density varied significantly amongst invasion categories (tree juvenile: $F_{2, 57} = 30.038$, $P < 0.0001$; tree adult: $F_{2, 57} = 27.3019$, $P < 0.0001$; shrub: $F_{2, 57} = 13.0921$, $P < 0.0001$) (Figure 4). Managed sites had approximately 13 times more tree juveniles than invaded sites and two times more than non-invaded sites. Non-invaded sites had about six times more tree juveniles than invaded sites. There were about two to three times more adult trees in non-invaded sites compared with both managed and invaded sites; adult tree density was similar between managed and invaded sites. Shrub density was 10 to 15 times higher in non-invaded and managed sites compared with invaded sites, and non-invaded and managed sites had similar shrub densities (Figure 4).

[insert Figure 4]

Juvenile and adult densities were compared amongst invasion categories for 11 common native tree species (Table 5). Nine species had significantly higher juvenile densities in both non-invaded and managed sites compared with invaded sites, verifying changes in vegetation composition attributable to these species. There was no significant difference in *Pittosporum undulatum* juvenile density amongst invasion categories. There were no

juveniles of canopy species *Eucalyptus quadrangulata* and *E. muelleriana* found at any site.

Most species had similar adult densities amongst invasion categories; however, three species had higher adult densities in non-invaded sites compared with both managed and invaded sites. Managed and invaded sites exhibited similar adult densities for all species tested.

[insert Table 5]

Discussion

Effects of L. camara invasion and management on species diversity

Our findings demonstrate that the invasion of forest communities by woody plant invaders, in this case *L. camara*, elicits significant adverse effects on native vascular plant species diversity, both in terms of species richness and composition. The results clearly show that fewer species occurred in *L. camara* invaded vegetation than in non-invaded vegetation. While pre-invasion site histories were largely unknown and differences in species composition could have preceded *L. camara* invasion, the *L. camara* invaded areas were at a small scale and well interspersed amongst non-invaded vegetation. Such small-scale differences in species composition caused by disturbance alone are unlikely, since the scale of disturbances in this habitat is known to be larger (i.e. broadscale vegetation clearance). Invasion of *L. camara* is facilitated by habitat disturbance such as canopy removal, fire and livestock grazing (Fensham, et al., 1994; Gentle and Duggin, 1997b; Duggin and Gentle, 1998), which could have simultaneously reduced species richness and altered species compositions, yet over larger areas than the scale of invasion. Minnamurra Rainforest was reserved in 1896 (NPWS, 1998) and extensive regeneration of native vegetation, including non-invaded sites, occurred since this time. Therefore, *L. camara* is the likely cause of long-term native species decline by preventing species regeneration following disturbance in areas where it subsequently established.

The impact of *L. camara* invasion on native vegetation diversity was pervasive, such that ferns, herbs, trees and vines comprised significantly fewer species in *L. camara* invaded vegetation than non-invaded vegetation. Fern species were relatively more affected by *L. camara*, with 70% fewer species in invaded vegetation than non-invaded vegetation. However, shrub species richness was similar between non-invaded and invaded sites, indicating that shrub diversity is resilient to *L. camara* invasion. Some native shrub species, such as *Clerodendrum tomentosum* and *Pittosporum revolutum*, may be favoured by disturbance processes that also facilitate *L. camara* invasion, such as increased light availability. However, shrub density was about 10 times lower within invaded sites than non-invaded sites, indicating that persistent *L. camara* invasion could eventually displace current shrub species.

Management of *L. camara* led to an increase in native species richness. *Lantana camara* managed vegetation comprised 1.2 and 2.5 times more species than non-invaded and invaded vegetation, respectively. All growth forms responded positively to *L. camara* management, but increased species richness was more pronounced for herb and shrub species. Herb and shrub species have been found to dominate regeneration following *L. camara* management in other studies (Macleay, 2004; Cummings, et al., 2007), and may be a function of increased resource availability favouring opportunistic herbaceous or woody colonisers (Davis, et al., 2000; Babaasa et al., 2004). Increased species richness in managed sites suggests that established *L. camara* is a barrier to the recovery of species diversity following vegetation disturbance (Cummings, et al., 2007). Alternatively, increased species richness may relate to management actions rather than the original *L. camara* invasion, such as soil disturbance and increased nutrient availability (D'Antonio, et al., 1998; Davis, et al., 2000).

Lantana camara managed and non-invaded vegetation were compositionally distinct, despite the vigorous increase in native species richness following *L. camara* removal. Management of *L. camara* therefore did not reinstate the original non-invaded vegetation, at least in the short-term. Compositional dissimilarities between non-invaded and managed sites

were caused mainly by a lower cover of subcanopy trees in managed sites. Compositional dissimilarities may therefore reflect differences in the successional stage of *L. camara* managed relative to non-invaded vegetation. Continued recruitment and growth of native tree species following *L. camara* management may lead to long-term reinstatement of the non-invaded vegetation.

Management of *L. camara* led to secondary invasion of some weeds. Managed sites had about 10 times more weed species than invaded sites. Secondary weed invasion may have been facilitated by increased propagule supply during annual monitoring events by weed control officers also operating in adjacent weed-infested areas, as well as by soil disturbance from manual *L. camara* removal (Mason and French, 2007; Theoharides and Dukes, 2007). Alternatively, weed propagule supply to managed areas may have occurred prior to *L. camara* control with *L. camara* inhibiting weed establishment. As with native species, reduced competition and increased resource availability following *L. camara* removal may have facilitated weed recruitment (Davis, et al., 2000). However, weeds contributed very little to overall species diversity and composition in the study area. Nearly all weeds found in managed sites were novel transient annual and biennial herbs, forming incidental components of *L. camara* managed vegetation and likely to confer little impact on regenerating native species. Annual monitoring and non-selective manual weed removal by control officers following initial *L. camara* control may prevent more extensive secondary weed invasion. Continued native species regeneration coupled with removal of incidental weeds may eventually decrease the invasibility of managed vegetation (Elton, 1958; Blumenthal et al., 2003), in turn facilitating long-term community recovery.

Effects of L. camara invasion and management on species recruitment

Invasion of *L. camara* adversely affected tree juvenile density, which was about six times lower in invaded sites than in non-invaded sites. Reduced juvenile densities were found

for most of the common subcanopy tree species. These results indicate that *L. camara* invasion can limit the recruitment of some resident native species, causing reduced species richness, abundance and altered compositions. Native species recruitment limitation is recognised as an important mechanism facilitating woody plant invader establishment and persistence in disturbed communities, as well as a common mechanism of weed impact (Walker and Vitousek, 1991; Standish, et al., 2001; Gorchoff and Trisler, 2003; Yurkonis, et al., 2005).

Lantana camara may limit native tree species recruitment via resource competition and allelopathy (Lamb, 1988; Gentle and Duggin, 1997a). Lamb (1988) suggested that reduced native plant species growth and recruitment are driven by competition with *L. camara* for light and nutrients; however, competition for light is unlikely to be a significant limitation as many subcanopy tree species are presumably adapted to germinate and grow in low-light conditions occurring beneath a dense *L. camara* canopy. Gentle and Duggin (1998) found that seedling biomass of the mesophyllous early forest coloniser *Choricarpia leptopetala* declined substantially in wet sclerophyll forest invaded by *L. camara*. Nutrient addition increased *L. camara* growth and promoted further declines in *C. leptopetala* seedling biomass, yet *C. leptopetala* seedlings grown in non-invaded sites did not respond to increased nutrients. Their study indicated that recruitment limitation was driven by interference rather than exploitative interactions between *L. camara* and *C. leptopetala*, such as allelopathy, which has been indicated elsewhere (Wadhawani and Bhardwaja, 1981; Achhireddy and Singh, 1984; Gentle and Duggin, 1997a).

Overall, adult tree density was significantly lower in invaded sites than in non-invaded sites. However, it is unlikely that *L. camara* actively displaced resident adult individuals (Stock, 2005). Duggin and Gentle (1998) showed that *L. camara* invasion is facilitated by vegetation disturbance, such as livestock grazing, fire and canopy damage, and Stock (2005) showed that the capacity for *L. camara* to displace established intact vegetation is low.

Reduced adult tree density is probably an artefact of the original disturbance that facilitated *L. camara* invasion. *Lantana camara* may occupy gaps between adult individuals, preventing tree re-establishment via recruitment limitation. However, *L. camara* may adversely affect established adult trees by changing nutrient cycling and competing for available nutrients. Bhatt et al. (1994) investigated the replacement of Himalayan *Quercus* forest with *L. camara* shrubland following deforestation. Within invaded areas, *L. camara* comprised 83% of total vegetation. Net primary productivity of the *L. camara* shrubland was equivalent to native forest, but the rate of nutrient uptake and storage was substantially greater for *L. camara* compared with co-occurring native forest species. They found that total soil nutrient content (N, P) was lower in *L. camara* invaded forest than non-invaded forest. Invasion by *L. camara* in wet sclerophyll forest may cause similar functional and structural shifts in resident vegetation. Increased nutrient uptake efficiency by *L. camara* may lead to long-term reductions in soil nutrient availability and a shift in nutrient allocation to the understorey shrub layer. Increased competition between *L. camara* and established adult trees for nutrients may stunt tree growth and affect reproduction, in turn limiting tree recruitment. These potential effects need to be investigated and could be measured by comparing adult tree leaf tissue nitrogen and phosphorus contents and available soil-nutrient pools in managed vegetation compared with non-invaded and invaded vegetation (D'Antonio, et al., 1998).

Conclusion

This study has demonstrated that the invasion of natural forest communities by woody plant invaders, such as *L. camara*, adversely affects vascular plant species diversity by reducing species richness and abundance, in turn altering species compositions. Results indicate that recruitment limitation by *L. camara*, especially of sub-canopy mesophyllous trees, is driving long-term changes in species diversity and community persistence in wet sclerophyll forest. Management of *L. camara* can mitigate such adverse effects by facilitating

native juvenile establishment and increasing species richness. However, management cannot reinstate species compositions, at least in the short-term. Continued monitoring of native forest regeneration following plant invader management will prevent secondary weed invasion and indicate whether long-term community recovery can occur.

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466 **Appendices**

467 *Appendix.* List of vascular plant species found in *L. camara* non-invaded, managed and
 468 invaded sites (n = 10).

Growth form	Family and species	Number of sites occupied ^a		
		C	M	I
Fern	Adiantaceae			
	<i>Adiantum formosum</i> R.Br.	1	2	0
	<i>Adiantum hispidulum</i> Sw.	1	2	0
	<i>Pellaea falcata</i> (R.Br.) Fee	5	5	7
	Aspleniaceae			
	<i>Asplenium australasicum</i> (J.Sm.) Hook.	3	3	0
	<i>Asplenium flabellifolium</i> Cav.	6	3	3
	Blechnaceae			
	<i>Blechnum cartilagineum</i> Sw.	4	0	0
	<i>Blechnum patersonii</i> (R.Br.) Mett.	1	1	0
	<i>Doodia aspera</i> R.Br.	6	4	0
	Cyatheaceae			
	<i>Cyathea australis</i> (R.Br.) Domin	0	1	2
	Davalliaceae			
	<i>Arthropteris tenella</i> (G.Forst.) J.Sm. ex Hook.f.	6	5	0
	Dennstaedtiaceae			
	<i>Hypolepis muelleri</i> N.A.Wakef.	1	2	1
	Dicksoniaceae			
	<i>Calochlaena dubia</i> (R.Br.) M.D.Turner & R.A.White in R.A.White & M.D.Turner	9	3	1
	Dryopteridaceae			
	<i>Lastreopsis decomposita</i> (R.Br.) Tindale	0	2	0
	Polypodiaceae			
	<i>Microsorium scandens</i> (G.Forst.) Tindale	0	1	0
	<i>Platyserium bifurcatum</i> (Cav.) C.Chr.	1	0	0
Herb	Acanthaceae			
	<i>Pseuderanthemum variabile</i> (R.Br.) Radlk.	10	7	2
	Apiaceae			
	<i>Hydrocotyle</i> sp. (<i>peduncularis</i> R.Br. ex A.Rich.)	0	1	0
	Araceae			
	<i>Gymnostachys anceps</i> R.Br.	6	2	0
	Asteraceae			
	<i>Ageratina riparia</i> (Regel) R.M.King & H.Rob.*	0	2	0
	<i>Bidens pilosa</i> L.*	0	1	0
	<i>Cirsium vulgare</i> (Savi) Ten.*	0	2	0
	<i>Conyza bonariensis</i> (L.) Cronquist*	0	3	0
	<i>Sigesbeckia orientalis</i> ssp. <i>orientalis</i> L.	0	3	0
	<i>Sonchus oleraceus</i> L.*	0	2	0
	Caryophyllaceae			
	<i>Stellaria flaccida</i> Hook.	0	5	0
	Commelinaceae			
	<i>Aneilema acuminatum</i> R.Br.	2	3	0
	<i>Commelina cyanea</i> R.Br.	0	2	0
	Convolvulaceae			
	<i>Dichondra repens</i> J.R.Forst. & G.Forst.	0	9	1
	Cyperaceae			
	<i>Carex appressa</i> R.Br.	2	4	0
	<i>Cyperus</i> sp. (<i>laevis</i> R.Br.)	0	4	1
	<i>Cyperus tetraphyllus</i> R.Br.	0	4	0
	<i>Gahnia</i> sp. (<i>melanocarpa</i> R.Br.)	0	1	0
	Dilleniaceae			
	<i>Hibbertia dentata</i> R.Br. ex DC.	2	1	0

	Fabaceae			
	<i>Desmodium varians</i> (Labill.) G.Don	0	2	0
	<i>Glycine tabacina</i> (Labill.) Benth.	0	3	0
	Geraniaceae			
	<i>Geranium homeanum</i> Turcz.	0	1	0
	Lamiaceae			
	<i>Plectranthus parviflorus</i> Willd.	0	1	4
	Lobeliaceae			
	<i>Pratia purpurascens</i> (R.Br.) E.Wimm.	0	1	0
	Lomandraceae			
	<i>Lomandra longifolia</i> Labill.	2	1	1
	Peperomiaceae			
	<i>Peperomia tetraphylla</i> (G.Forst.) Hook. & Arn.	0	1	0
	Phytolaccaceae			
	<i>Phytolacca octandra</i> L.*	0	1	0
	Plantaginaceae			
	<i>Veronica plebeia</i> R.Br.	0	4	0
	Poaceae			
	<i>Entolasia stricta</i> (R.Br.) Hughes	0	1	0
	<i>Oplismenus</i> spp.	4	10	4
	Rosaceae			
	<i>Potentilla indica</i> (Jacks.) Th.Wolf*	0	1	0
	Sapindaceae			
	<i>Alectryon subcinereus</i> (A.Gray) Radlk.	3	4	1
	Solanaceae			
	<i>Solanum nigrum</i> L.*	0	2	0
	<i>Solanum pungetium</i> R.Br.	0	3	0
	Urticaceae			
	<i>Urtica incisa</i> Poir.	0	2	0
	Violaceae			
	<i>Viola hederacea</i> Labill.	0	5	1
	<i>Viola sieberiana</i> Spreng.	0	2	-
Shrub	Asteraceae			
	<i>Cassinia trinerva</i> Wakef.	0	3	1
	<i>Ozothamnus diosmifolius</i> (Vent.) DC.	0	2	0
	Euphorbiaceae			
	<i>Breynia oblongifolia</i> Muell.Arg.	2	1	0
	<i>Phyllanthus gunnii</i> Hook.f.	0	1	0
	Eupomatiaceae			
	<i>Eupomatia laurina</i> R.Br.	4	1	2
	Fabaceae			
	<i>Indigofera australis</i> Willd.	0	1	0
	<i>Senna barclayana</i> (Sweet) Randell	0	2	0
	Lamiaceae			
	<i>Prostanthera incisa</i> R.Br.	1	0	0
	Malvaceae			
	<i>Hibiscus heterophyllus</i> Vent.	0	3	0
	Monimiaceae			
	<i>Wilkiea huegeliana</i> (Tul.) A.DC.	7	5	1
	Pittosporaceae			
	<i>Pittosporum multiflorum</i> (A.Cunn. ex Loudon) L.W.Cayzer et al.	6	6	2
	<i>Pittosporum revolutum</i> Dryand. ex W.T.Aiton	3	6	2
	Rosaceae			
	<i>Rubus moluccanus</i> L.	0	2	0
	<i>Rubus rosifolius</i> Sm.	0	6	3
	Rutaceae			
	<i>Zieria smithii</i> Jacks.	0	3	0
	Solanaceae			
	<i>Physalis peruviana</i> L.*	0	1	0
	<i>Solanum aviculare</i> G.Forst.	0	1	0
	<i>Solanum stelligerum</i> Sm.	0	3	0
	Thymelaeaceae			

	<i>Pimelea ligustrina</i> Labill.	0	1	0
	Ulmaceae			
	<i>Trema tomentosa</i> var. <i>viridis</i> (Planch.) Hewson	0	1	0
	Violaceae			
	<i>Melicytus dentatus</i> (R.Br. ex DC.) Molloy & Mabb.	1	3	1
Tree	Araliaceae			
	<i>Polyscias murrayi</i> (F.Muell.) Harms	0	1	1
	Arecaceae			
	<i>Livistona australis</i> (R.Br.) Mart.	8	9	4
	Boraginaceae			
	<i>Ehretia acuminata</i> var. <i>acuminata</i> R.Br.	1	2	1
	Celastraceae			
	<i>Elaeodendron australe</i> Vent.	8	6	5
	Cunoniaceae			
	<i>Ceratopetalum apetalum</i> D.Don	3	3	0
	<i>Schizomeria ovata</i> D.Don	1	0	0
	Ebenaceae			
	<i>Diospyros australis</i> (R.Br.) Hiern	8	6	2
	Elaeocarpaceae			
	<i>Elaeocarpus reticulatus</i> Sm.	1	0	0
	Ericaceae			
	<i>Trochocarpa laurina</i> R.Br.	0	1	0
	Euphorbiaceae			
	<i>Baloghia inophylla</i> (G.Forst.) P.S.Green	4	3	0
	<i>Claoxylon australe</i> Baill.	1	10	0
	<i>Homalanthus populifolius</i> Graham	0	2	1
	Fabaceae			
	<i>Acacia binervata</i> DC.	3	5	5
	<i>Acacia maidenii</i> F.Muell.	3	2	2
	<i>Acacia mearnsii</i> De Wild.	0	0	1
	<i>Acacia melanoxydon</i> R.Br.	1	0	1
	Lamiaceae			
	<i>Clerodendrum tomentosum</i> R.Br.	7	7	9
	Lauraceae			
	<i>Cinnamomum oliveri</i> F.M.Bailey	6	8	3
	<i>Cryptocarya glaucescens</i> R.Br.	7	6	2
	<i>Cryptocarya microneura</i> Meisn.	1	0	0
	<i>Endiandra sieberi</i> Nees	1	5	0
	Meliaceae			
	<i>Melia azedarach</i> L.	0	6	0
	<i>Synoum glandulosum</i> ssp. <i>glandulosum</i> (Sm.) Juss.	5	5	1
	<i>Toona ciliata</i> M.Roem.	3	7	2
	Monimiaceae			
	<i>Doryphora sassafras</i> Endl.	7	7	3
	<i>Hedycarya angustifolia</i> A.Cunn.	1	0	0
	Moraceae			
	<i>Ficus coronata</i> Spin	3	4	1
	<i>Streblus brunonianus</i> (Endl.) F.Muell.	2	1	0
	Myrsinaceae			
	<i>Myrsine howittiana</i> (F.Muell. ex Mez) Jackes	2	0	0
	<i>Myrsine variabilis</i> R.Br.	2	1	0
	Myrtaceae			
	<i>Acmena smithii</i> (Poir.) Merr. & L.M.Perry	8	8	4
	<i>Backhousia myrtifolia</i> Hook. & Harv.	1	0	0
	<i>Eucalyptus muelleriana</i> A.W.Howitt	1	1	3
	<i>Eucalyptus quadrangulata</i> H.Deane & Maiden	9	6	10
	<i>Rhodamnia rubescens</i> (Benth.) Miq.	3	0	1
	<i>Syzygium australe</i> (J.C.Wendl. ex Link) B.Hyland	1	3	0
	<i>Tristaniaopsis laurina</i> (Sm.) Peter G.Wilson & J.T.Waterh.	0	1	0
	Oleaceae			
	<i>Notelaea venosa</i> F.Muell.	10	8	6
	Pennantiaceae			

	<i>Pennantia cunninghamii</i> Miers	3	0	0
	Pittosporaceae			
	<i>Pittosporum undulatum</i> Vent.	9	10	6
	Polyosmaceae			
	<i>Polyosma cunninghamii</i> Benn.	3	1	0
	Proteaceae			
	<i>Stenocarpus salignus</i> R.Br.	8	8	2
	Rhamnaceae			
	<i>Alphitonia excelsa</i> (Fenzl) Benth.	2	7	2
	Rutaceae			
	<i>Acronychia oblongifolia</i> (A.Cunn. ex Hook.) Endl. ex Heynh.	3	1	0
	<i>Melicope micrococca</i> (F.Muell.) T.G.Hartley	2	3	2
	<i>Sarcomelicope simplicifolia</i> ssp. <i>simplicifolia</i> (Endl.) T.G.Hartley	1	0	0
	Santalaceae			
	<i>Exocarpos cupressiformis</i> Labill.	0	0	1
	Sapindaceae			
	<i>Diploglottis cunninghamii</i> (Hook.) Hook.f. ex Benth.	4	5	0
	<i>Guioa semiglaucula</i> (F.Muell.) Radlk.	4	0	0
	Solanaceae			
	<i>Duboisia myoporoides</i> R.Br.	0	1	0
	Sterculiaceae			
	<i>Brachychiton acerifolius</i> (A.Cunn. ex G.Don) Macarthur & C.Moore	0	2	1
	Urticaceae			
	<i>Dendrocnide excelsa</i> (Wedd.) Chew	0	3	1
	Winteraceae			
	<i>Tasmannia insipida</i> R.Br. ex DC.	5	3	1
Vine	Aphanopetalaceae			
	<i>Aphanopetalum resinosum</i> Endl.	4	1	1
	Apocynaceae			
	<i>Marsdenia flavescens</i> A.Cunn. ex Hook.	2	0	1
	<i>Marsdenia rostrata</i> R.Br.	8	9	2
	<i>Parsonsia straminea</i> (R.Br.) F.Muell.	4	9	2
	<i>Tylophora barbata</i> R.Br.	4	2	8
	Asteraceae			
	<i>Delairea odorata</i> Lem.*	0	4	2
	Bignoniaceae			
	<i>Pandorea pandorana</i> (Andrews) Steenis	8	9	5
	Convolvulaceae			
	<i>Calystegia marginata</i> R.Br.	0	1	0
	<i>Convolvulus erubescens</i> Sims	0	1	0
	<i>Ipomoea indica</i> (Burm.f.) Merr.*	0	2	0
	Fabaceae			
	<i>Glycine clandestina</i> J.C.Wendl.	0	2	0
	<i>Kennedia rubicunda</i> Vent.	0	0	1
	Luzuriagaceae			
	<i>Eustrephus latifolius</i> R.Br. ex Ker Gawl.	9	9	7
	<i>Geitonoplesium cymosum</i> (R.Br.) A.Cunn. ex Hook.	4	8	7
	Menispermaceae			
	<i>Sarcopetalum harveyanum</i> F.Muell.	3	1	0
	<i>Stephania japonica</i> var. <i>discolor</i> (Blume) Forman	1	9	1
	Monimiaceae			
	<i>Palmeria scandens</i> F.Muell.	2	0	0
	Moraceae			
	<i>Maclura cochinchinensis</i> (Lour.) Corner	2	2	1
	<i>Trophis scandens</i> (Lour.) Hook. & Arn.	5	1	0
	Passifloraceae			
	<i>Passiflora herbertiana</i> Ker Gawl.	0	1	0
	<i>Passiflora subpeltata</i> Ortega*	0	1	0
	Piperaceae			
	<i>Piper novae-hollandiae</i> Miq.	3	6	0
	Ranunculaceae			
	<i>Clematis aristata</i> Ker Gawl.	0	3	0

<i>Clematis glycinoides</i> DC.	0	1	1
Ripogonaceae			
<i>Ripogonum album</i> R.Br.	2	0	0
Rosaceae			
<i>Rubus nebulosus</i> A.R.Bean	0	2	1
Rubiaceae			
<i>Morinda jasminoides</i> A.Cunn.	9	9	8
Smilacaceae			
<i>Smilax australis</i> R.Br.	6	3	2
<i>Smilax glyciophylla</i> Sm.	2	2	0
Vitaceae			
<i>Cayratia clematidea</i> (F.Muell.) Domin	3	3	1
<i>Cissus antarctica</i> Vent.	3	6	1
<i>Cissus hypoglauca</i> A.Gray	5	3	2

^aNumber of sites occupied by each species for *L. camara* non-invaded (C), invaded (L) and managed (M) sites.

*Denotes an exotic species.

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Table 1. Results for a two-way analysis of variance for variation in native vascular plant species richness amongst growth forms and invasion categories.

Source	d.f.	Mean square	<i>F</i>	<i>P</i>
Growth form	4	20.9245105	86.9738	<0.001*
Invasion category	2	14.188191	58.974	<0.001*
Growth form x Invasion category	8	0.817376	3.3975	0.0014*
Error	135	0.24058		
Total	149			

*Denotes statistical significance.

Table 2. Results for one-way analyses of similarity pairwise comparisons of vascular plant species composition between *L. camara* invasion categories.

Pairwise comparisons of invasion categories ^a		<i>R</i>	<i>P</i>
Total species (cover)	M vs. L	0.602	0.001*
	M vs. C	0.263	0.001*
	L vs. C	0.645	0.001*
Total species (presence/absence)	M vs. L	0.494	0.001*
	M vs. C	0.394	0.001*
	L vs. C	0.478	0.001*
Native species only (cover)	M vs. L	0.607	0.001*
	M vs. C	0.263	0.001*
	L vs. C	0.646	0.001*
Native fern, tree and vine species only (cover)	M vs. L	0.47	0.001*
	M vs. C	0.115	0.031*
	L vs. C	0.554	0.001*

^aANOSIM were undertaken for all species (cover abundance and presence/absence), native species only and native fern, tree and vine species only amongst *L. camara* non-invaded (C), invaded (L) and managed (M) sites.

*Denotes statistical significance.

Table 3. Results of similarity percentage analysis and cover abundances for vascular plant species with the highest contribution to compositional dissimilarities between *L. camara* invasion categories.

Species ^a	Growth form ^b	Average cover ^c	
Managed/Invaded, average dissimilarity = 75.39%		M	L
<i>Oplismenus</i> spp.	H	3.90	0.70
<i>Livistona australis</i>	ST	3.70	1.30
<i>Doryphora sassafras</i>	ST	3.30	0.70
<i>Eucalyptus quadrangulata</i>	CT	4.00	6.20
<i>Alphitonia excelsa</i>	ST	2.80	1.00
<i>Acmena smithii</i>	ST	3.00	0.40
<i>Pittosporum undulatum</i>	ST	3.70	3.30
<i>Notelaea venosa</i>	ST	3.10	1.10
<i>Dichondra repens</i>	H	2.80	0.20
Managed/Non-invaded, average dissimilarity = 64.46%		M	C
<i>Doryphora sassafras</i>	ST	3.30	3.70
<i>Acmena smithii</i>	ST	3.00	4.70
<i>Elaeodendron australe</i>	ST	1.40	3.90
<i>Eucalyptus quadrangulata</i>	CT	4.00	5.40
<i>Oplismenus</i> spp.	H	3.90	0.80
<i>Dichondra repens</i>	H	2.80	0.00
<i>Alphitonia excelsa</i>	ST	2.80	0.60
<i>Pittosporum undulatum</i>	ST	3.70	4.60
<i>Notelaea venosa</i>	ST	3.10	4.30
<i>Cinnamomum oliveri</i>	ST	3.00	2.20
Invaded/Non-invaded, average dissimilarity = 71.21%		L	C
<i>Acmena smithii</i>	ST	0.40	4.70
<i>Doryphora sassafras</i>	ST	0.70	3.70
<i>Notelaea venosa</i>	ST	1.10	4.30
<i>Elaeodendron australe</i>	ST	1.90	3.90
<i>Pittosporum undulatum</i>	ST	3.30	4.60
<i>Wilkiea huegelliana</i>	S	0.10	2.90

^aSpecies, listed in descending order, contributing up to approximately 20% of the total average dissimilarities (%) between invasion categories.

^bCT = sclerophyllous canopy tree; H = herb; S = shrub; ST = mesophyllous subcanopy tree.

^cAverage species cover abundance based on Braun Blanquet percentage cover abundance indices.

682 Table 4. Vascular plant species composition within each *L. camara* invasion category.

Species ^a	Growth form ^b	Contribution (%)
Non-invaded, average similarity = 43.74%		
<i>Eucalyptus quadrangulata</i>	CT	9.72
<i>Pittosporum undulatum</i>	ST	7.48
<i>Acmena smithii</i>	ST	7.25
<i>Notelaea venosa</i>	ST	6.53
<i>Morinda jasminoides</i>	V	5.89
<i>Pseuderanthemum variabile</i>	H	5.14
<i>Elaeodendron australe</i>	ST	4.94
<i>Doryphora sassafras</i>	ST	4.19
Managed, average similarity = 39.09%		
<i>Oplismenus</i> spp.	H	6.90
<i>Pittosporum undulatum</i>	ST	4.98
<i>Livistona australis</i>	ST	4.86
<i>Morinda jasminoides</i>	V	4.82
<i>Pandorea pandorana</i>	V	4.46
<i>Eucalyptus quadrangulata</i>	CT	4.26
<i>Dichondra repens</i>	H	4.21
<i>Marsdenia rostrata</i>	V	4.07
<i>Doryphora sassafras</i>	ST	3.45
<i>Notelaea venosa</i>	ST	3.38
<i>Parsonsia straminea</i>	V	3.13
<i>Acmena smithii</i>	ST	3.02
Invaded, average similarity = 38.76%		
<i>Eucalyptus quadrangulata</i>	CT	34.57
<i>Clerodendrum tomentosum</i>	S	11.47
<i>Pittosporum undulatum</i>	ST	8.36

^aSpecies, listed in descending order, contributing up to approximately 50% of the total average similarities between sites within each invasion category.

^bCT = sclerophyllous canopy tree; H = herb; S = shrub; ST = mesophyllous subcanopy tree; V = vine.

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Table 5. Results for Kruskal-Wallis tests showing variation in native tree juvenile and adult densities for each *L. camara* invasion category.

Species	Pairwise comparisons ^a			χ^2	<i>P</i>
	C	M	L		
Juveniles					
<i>Acmena smithii</i>	a	a	b	11.1460	0.0038*
<i>Cinnamomum oliveri</i>	a	a	b	8.7773	0.0124*
<i>Cryptocarya glaucescens</i>	a	a	b	10.1012	0.0064*
<i>Diospyros australis</i>	a	a	b	8.8627	0.0119*
<i>Doryphora sassafras</i>	a	a	b	11.2784	0.0036*
<i>Elaeodendron australe</i>	a	a	b	9.6674	0.0080*
<i>Livistona australis</i>	a	a	b	9.9861	0.0068*
<i>Notelaea venosa</i>	a	a	b	6.7498	0.0342*
<i>Pittosporum undulatum</i>	n/a	n/a	n/a	4.8737	0.0874, ns
<i>Stenocarpus salignus</i>	a	a	b	10.5576	0.0051*
Adults					
<i>Acmena smithii</i>	a	b	b	7.7057	0.0212*
<i>Cinnamomum oliveri</i>	n/a	n/a	n/a	3.6865	0.1583, ns
<i>Cryptocarya glaucescens</i>	n/a	n/a	n/a	1.3970	0.4973, ns
<i>Diospyros australis</i>	a	b	b	6.0036	0.0497*
<i>Doryphora sassafras</i>	n/a	n/a	n/a	3.2658	0.1954, ns
<i>Elaeodendron australe</i>	n/a	n/a	n/a	5.5056	0.0638, ns
<i>Eucalyptus</i> spp. ^b	n/a	n/a	n/a	3.7099	0.1565, ns
<i>Livistona australis</i>	n/a	n/a	n/a	0.8077	0.6677, ns
<i>Notelaea venosa</i>	a	b	b	7.4703	0.0239*
<i>Pittosporum undulatum</i>	n/a	n/a	n/a	3.2103	0.2009, ns
<i>Stenocarpus salignus</i>	n/a	n/a	n/a	0.5185	0.7716, ns

^aLower case letters, a and b, denote significant differences amongst ranks ($P \leq 0.05$; Mann-Whitney test; a ranked denser than b) for *L. camara* non-invaded (C), invaded (L) and managed (M) sites.

^bAdult densities for the two dominant canopy species, *Eucalyptus quadrangulata* and *E. muelleriana*, were analysed jointly and are presented as *Eucalyptus* spp.

*Denotes statistical significance; ns = not statistically significant; n/a = not applicable.

Figures

Figure 1. Mean ($\pm$ one standard error) number of native and exotic vascular plant species for *L. camara* non-invaded, managed and invaded sites ($n = 10$). Different letters, a, b and c, denote significant differences amongst means ($P \leq 0.05$; Student-Newman-Kuels test). Separate Student-Newman-Kuels tests were undertaken for native and exotic species. No exotic species were found in non-invaded sites.

Figure 2. Mean ($\pm$ one standard error) number of native vascular plant species within growth forms for *L. camara* non-invaded, managed and invaded sites ($n = 10$). Different letters, a, b and c, denote significant differences amongst means ($P \leq 0.05$; Student-Newman-Kuels test). Separate Student-Newman-Kuels tests were undertaken for each growth form.

Figure 3. Two-dimensional non-metric multidimensional scaling ordination of vascular plant species a) cover abundance (stress = 0.15) and b) presence/absence (stress = 0.17) for *L. camara* managed (M), invaded (L) and non-invaded (C) sites ($n = 10$). Points closer together in ordination space represent sites with more similar species compositions. Cover of *L. camara* was removed from the analyses.

Figure 4. Mean ($\pm$ one standard error) native tree juvenile and adult, and shrub (*L. camara* excluded) densities for *L. camara* non-invaded, managed and invaded sites ($n = 10$). Different letters, a, b and c, denote significant differences amongst means ($P \leq 0.05$; Student-Newman-Kuels test). Separate Student-Newman-Kuels tests were undertaken for each plant type and growth stage.

Fig 1.

Fig. 2.

Fig. 3.

Fig. 4.