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Impact threshold for an alien plant invader, Lantana camara L., on native plant communities

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Abstract

Alien plant invaders significantly threaten native community diversity, although it is poorly understood whether invasion initiates a linear or non-linear loss of resident species. Where low abundances of an invader have little impact on native species diversity, then a threshold level may exist, above which native communities rapidly decline. Our aim was to assess the broadscale effects of an alien thicket-forming shrub, lantana (Lantana camara L.), on wet sclerophyll forest in southeastern Australia. Vascular plant species richness, abundance and composition were measured and compared along a gradient of lantana invasion. There was a strong negative non-linear relationship between native species richness and lantana cover, indicative of an impact threshold. Native species richness remained stable below 75% lantana cover, but declined rapidly above this threshold level, leading to compositional change. Thus, sparse lantana infestations had evidently little effect on the resident community, with impacts elicited at an advanced stage of invasion. The impact of lantana was pervasive, with all major structural groups (i.e. ferns, herbs, shrubs, trees and vines) exhibiting significant species losses; however, the rate of species loss was relatively greater for tree and shrub species, signalling a shift in vegetation structure from tall open forest to low, dense lantana-dominated shrubland. Potentially, broadscale conservation of species diversity could be achieved by maintaining lantana infestations below the 75% cover impact threshold at sites containing regionally common species that are also widely represented in non-invaded vegetation. This would enable targeted invader eradication at sites of high conservation value (i.e. those containing regionally rare species or endangered ecological communities).

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Impact threshold for an alien plant invader, *Lantana camara* L., on native plant communities

Running Head: Impact threshold for an alien plant invader

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Abstract

Alien plant invaders significantly threaten native community diversity, although it is poorly understood whether invasion initiates a linear or non-linear loss of resident species. Where low abundances of an invader have little impact on native species diversity, then a threshold level may exist, above which native communities rapidly decline. Our aim was to assess the broadscale effects of an alien thicket-forming shrub, lantana (*Lantana camara* L.), on wet sclerophyll forest, southeastern Australia. Vascular plant species richness, abundance and composition were measured and compared along a gradient of lantana invasion. There was a strong negative non-linear relationship between native species richness and lantana cover, indicative of an impact threshold. Native species richness remained stable below 75% lantana cover, but declined rapidly above this threshold level, leading to compositional change. Thus, sparse lantana infestations had evidently little effect on the resident community, with impacts elicited at an advanced stage of invasion. The impact of lantana was pervasive, with all major structural groups (i.e. ferns, herbs, shrubs, trees and vines) exhibiting significant species losses; however, the rate of species loss was relatively greater for tree and shrub species, signalling a shift in vegetation structure from tall open forest to low, dense lantana-dominated shrubland. Potentially, broadscale conservation of species diversity could be achieved by maintaining lantana infestations below the 75% cover impact threshold at sites containing regionally common species that are also widely represented in non-invaded vegetation, enabling targeted invader eradication at sites of high conservation value (i.e. those continaing regionally rare species or endangered ecological communities).

Key words

Lantana, *Lantana camara* L., ecological threshold, plant invasion, species richness, weed impact

Introduction

The invasion of alien species threatens ecosystem processes and species diversity at a global and community scale (Vitousek et al., 1996; Wilcove et al., 1998; Gurevitch and Padilla, 2004). Plant invaders of natural ecosystems, also termed ‘environmental weeds’

(Richardson et al., 2000), have been shown to inhibit the recruitment of resident native species by preventing seedling establishment and growth, and modifying plant-pollinator interactions (Vranjic et al., 2000; Gorchov and Trisel, 2003; Yurkonis et al., 2005; Bjerknes et al., 2007); displace resident species through direct below and above ground competition for resources, such as space, water, nutrients and light (Walck et al., 1999; Vilà and Weiner, 2004); and modify or 'engineer' ecosystem processes and the physical resources of the recipient community, such as sedimentation, nutrient cycling and disturbance regimes (D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998; Lindsay and French, 2004; Minchinton et al., 2006). The cumulative consequences of these effects can be reduced native species richness and abundance, and altered species assemblages (e.g. Bobbink and Willems, 1987; Groves and Willis, 1999; Grice, 2004; Jackson, 2005; Mason and French, 2007; Gerber et al., 2008). However, evidence for impacts of alien plant invaders on native species diversity is scarce relative to the enormity of the threat, which has hampered effective invader management and protection of native species and communities most at risk (Adair and Groves, 1998). Furthermore, there is little scientific understanding of where priorities for weed management should be focused as species losses are only broadly known or assumed (Downey, 2006).

Two aspects are particularly poorly understood. First, it is not understood if the losses to species diversity are linearly related to invasion, such that as the abundance of an invader increases there is a linear loss of native species or individuals from sites (see Groves and Willis, 1999; Panetta and James, 1999; Grice, 2004; 2006 for a related discussion). If responses are not linear then either small quantities of an invader have disproportionately large or small effects on native communities. The effects are thus likely to be great where small levels of invasion impact dramatically on native communities signalling a significant problem in the presence of any level of invasion. Where low levels of an invader have little impact on native species, then a threshold value is likely to exist, above which native communities decline quickly (Panetta and James, 1999; Grice, 2004). Grice (2004) noted that native species are unlikely to decline linearly with increasing invader abundance, and that ‘the impacts of weeds are likely to be greater when weeds are in an advanced stage of invasion’. Such ‘impact thresholds’ for alien plant invaders have rarely been quantified (but see Bobbink and Willems, 1987), yet if thresholds exist, then such information would be useful for management in prioritising sites where biodiversity losses are likely to be greatest.

Second, establishing broad-scale patterns of alien plant invader impacts on species diversity does not necessarily indicate the species most at risk from a particular invader. Individual native species are likely to exhibit varied responses to alien plant invasion; some being displaced, unaffected and others favoured by invasion (Groves and Willis, 1999). For example, Costello et al. (2000) and Mason and French (2007) quantified broad-scale impacts of woody plant invasion on plant species diversity and identified varied responses of individual species to invasion. Knowledge of species or life forms potentially at risk from plant invaders will inform conservation priorities and facilitate effective policy and management strategies for areas of high conservation value (DEC, 2006; Downey, 2006). For instance, congeneric native species may be more impacted by an invader through competition for similar (Elton, 1958; Johansson and Keddy, 1991; Williamson and Fitter, 1996), or respond favourably to conditions also facilitating the invader (Lockwood et al., 2001). Such information will be crucial to develop our understanding about the impacts of alien plant invaders on species diversity in natural communities.

In this study, we assessed the impact of invasion of an alien plant, lantana (*Lantana camara* L.), on vascular plant species diversity in a wet sclerophyll forest community, southeastern Australia. Lantana is a woody thicket-forming shrub native to South America (Swarbrick, 1986), and considered one of the world's worst alien species (IUCN, 2001). Lantana invasion in natural ecosystems is implicated in widespread loss of native plant species diversity via recruitment limitation of native species and altered ecosystem structure and function (Webb et al., 1972; Lamb, 1988; Bhatt et al., 1994; Fensham et al., 1994; Swarbrick et al., 1995; Gentle and Duggin, 1997a; 1998; Sharma et al., 2005; Kohli et al., 2006). However, very little quantitative evidence is available to validate these claims and more information on the patterns of species loss associated with lantana invasion is urgently required to inform management priorities.

Our principal aim was to assess if there was a broad-scale relationship between lantana abundance and native vascular plant species diversity in wet sclerophyll forest communities. We sought to establish what the relationship was like (i.e. if it was linear or non-linear), and thus whether an impact threshold was evident. We also sought to identify whether species losses were associated with particular plant life forms or whether impacts were across many life forms.

Methods

Study area and habitat

The study was conducted in North Coast Wet Sclerophyll Forest (WSF) (sensu Keith, 2004) along the south-east coast ranges of New South Wales, Australia, between April and September 2007. The study area extended approximately 180 km between Barrengarry Nature Reserve (34°40’55.13’ S; 150°31’14.92’’ E) and Wyong State Forest (33°15’01.41’’ S; 151°22’22.48’’ E). North Coast WSF was the most widespread and abundant WSF sub-formation in the study area. Vegetation was characterised by a tall open eucalypt sclerophyllous canopy with a subcanopy of mesophyllous trees and shrubs, and an understorey dominated by ferns and herbs (Keith, 2004). Common species included the sclerophyllous canopy trees *Eucalyptus pilularis*, *E. paniculata* and *Syncarpia glomulifera*; subcanopy trees *Acacia* spp. *Acmena smithii*, *Cryptocarya* spp. and *Pittosporum undulatum*; ferns *Calochlaena dubia*, *Doodia aspera* and *Pteridium esculentum*; and vines *Eustrephus latifolius*, *Marsdenia rostrata*, *Geitonoplesium cymosum* and *Smilax australis*. Lantana formed a dominant component of understorey vegetation and was considered the primary weed threat to WSF in several areas covered by this study (NPWS, 1998; 1999; 2003).

Field methods

Fifty-three sites were haphazardly interspersed throughout the study area across a continuum of lantana invasion, representing non-invaded through to heavily invaded vegetation. At each site, a 20 x 50 m quadrat was established, the size of which was considered a representative measure of community-level vegetation structure and composition (Rice and Westoby, 1985; Mason and French, 2007). Each site was assigned to one of three invasion categories based on the percentage foliage cover of lantana: lantana non-invaded (0-5% lantana cover; n = 19), moderately invaded (6-50% cover; n = 16) and heavily invaded (51-100% cover; n = 18).

Sites were positioned in relatively undisturbed WSF vegetation where the percentage foliage cover of the upper sclerophyllous canopy exceeded 30%. Quadrats were separated by at least 100 m and positioned at least 100 m from a forest edge (including active and abandoned urban and agricultural land, roads and powerline easements) to reduce potential confounding effects of vegetation disturbance on lantana invasion and potential changes to species diversity.

Sampling of biological parameters

The vegetation composition at each site was surveyed in detail using a smaller 20 x 20 m nested quadrat, similar to that used by Mason and French (2007). Within the nested quadrat we recorded the identity, origin (native or alien), growth form (fern, herb, shrub, tree and vine) and abundance of vascular plant species. Species nomenclature followed Harden (1990; 1992; 1993; 2002) and Robinson (2003). Alien or non-indigenous species were considered to be those not native to Australia, as well as native Australian species not indigenous to the study area and present as a consequences of accidental or intentional anthropogenic activity (Richardson et al., 2000). Grasses, sedges, rushes and forbs were recorded as herbs. Ephemeral monocots, such as orchids, were excluded from species records due to the temporal variation in site surveys (i.e. the surveys occurred over six months). Species abundance was measured as percentage foliage cover 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). Additionally, species density (number of individual plants per quadrat) was recorded for all tree and shrub species. The identities of all additional vascular plant species were recorded from the remaining 20 x 30 m of the quadrat; thus species richness at a site was defined as the total number of species recorded in the 20 x 50 m quadrat.

Data analysis

Our analysis of threshold relationships between lantana cover and species richness and density was similar to that used by Drinnan (2005) and Radford et al. (2005). First, individual linear regressions were used to assess the relationship between lantana cover and species richness (total number of native and alien species, as well as native ferns, herbs, shrubs, trees and vines) and density, employing data from the complete set of sites (i.e. n = 53). Second, if negative linear relationships were evident, non-linear cubic models were applied to each relationship to detect the presence of potential impact thresholds (after Panetta and James, 1999). A threshold was defined as the zone or discontinuity where species richness decreased dramatically with increasing lantana cover (sensu Drinnan, 2005). Third, evidence for impact thresholds was further sought by comparing linear and cubic models using the Akaike Information Criterion (AIC). The AIC determines the most parsimonious model (i.e. that which provides the best fit of the data) and was calculated as follows (sensu Quinn and Keough, 2002; Radford et al., 2005): AIC = $n[\ln(SS_{res})] + 2(p + 1) - n\ln(n)$, where n represents the number of sites (n = 53), SS_{res} is the residual sum of squares and p is the number of model predictors (excluding the intercept). For impact thresholds to exist, the cubic model was required to provide the best fit of the data within each set of regression analyses, as indicated by the lowest AIC, residual error (SS_{res}) and P, as well as highest R^2. Finally, significant non-linear relationships were examined visually for thresholds and confirmed by running individual linear regressions below and above the identified threshold level. An impact threshold was evident where a non-significant relationship was detected for values below the threshold level and a strong linear decline in species richness and density was detected with increasing lantana cover above the threshold level.

A two-way crossed analysis of similarity (ANOSIM) was used to assess similarities in species composition between sites among invasion categories and northern and southern regions. Northern and southern sites were those north (n = 21) and south (n = 32) of Sydney, New South Wales (33°52’ S; 151°12’ E). Northern sites were separated from southern sites in this analysis as we were aware that species composition varied with latitude, with a greater range of subtropical species occurring in northern samples. Compositional similarities amongst invasion categories were determined using Bray-Curtis similarity indices calculated on Braun Blanquet cover abundance values (Clarke, 1993; Clarke and Gorley, 2000). Two-dimensional non-metric multidimensional scaling (nMDS) ordination was used to visually compare species compositions. Additionally, similarity percentage (SIMPER) analysis was used to identify species contributing strongly to within-group similarities as well as dissimilarities among invasion categories. Presence/absence data transformations were used to identify species contributing to similarities and dissimilarities based on their occurrence rather than abundance, which was useful for detecting the contributions of rarer or less abundant species to potential differences in composition. Lantana abundance was excluded from analyses as this defined invasion categories.

The impact of lantana on individual species was assessed by analysing changes in native species cover amongst invasion categories using the Kruskal-Wallis non-parametric single-factor analysis of variance by ranks (Zar, 1999). The Kruskal-Wallis test was used instead of Analysis of Variance (ANOVA) since the data did not satisfy assumptions of normality and homogeneity of variance (Zar, 1999). Analyses were undertaken using Braun Blanquet cover abundance indices for species recorded in the 20 x 20 m quadrats as these indices allowed ranking of species abundance below 5% cover, which was necessary for detecting cover changes for less abundant species. Post hoc pair-wise comparisons of species abundance amongst invasion categories were undertaken using the Mann-Whitney test (Zar, 1999). Differences in the number of sites occupied by each species (i.e. occurrence) amongst invasion categories were assessed using the Chi-square analysis using presence/absence data recorded in the 20 x 50 m quadrat. The Yates correction for continuity was used where expected frequencies were lower than five (Zar, 1999). Kruskal-Wallis and Chi-square analyses were undertaken only for species occurring in all three invasion categories and present in at least 10 sites in order to verify species identified from the SIMPER analysis.

Results

In total, 291 vascular plant species were recorded, comprising 261 native and 30 alien species. Species represented 90 families, of which Asteraceae, Fabaceae, Myrtaceae and Poaceae were the most common. Species consisted of 23 ferns, 74 herbs, 39 vines, 70 shrubs and 85 trees. Approximately 55% of species occurred at all stages of lantana invasion; 12% of species, of which most were native, were confined to non-invaded sites.

Species richness

Native species richness declined significantly with increasing lantana cover (Table 1). Each of the five key growth forms showed a significant linear decline in species richness in response to lantana cover. Although linear changes in species richness in response to lantana were consistently detected, non-linear cubic regressions were generally more suitable than linear regressions in explaining changes in species richness, as indicated by the lowest AIC, residual error, *P*-value and highest R^2 (Table 1). Cubic regressions provided the best fit to the data for the total number of native species, as well as native ferns, herbs and vines. Indeed, for cubic regressions, about 58% of the variation in total native species richness was explained by lantana cover. Oppositely, the smallest AIC indicates that linear regressions were most suitable in explaining species loss for native shrub and tree species. This, in turn, indicates that the number of shrub and tree species begins to decline in response to low and moderate levels of lantana invasion, and that no impact threshold exists for these species.

[Insert Table 1]

The non-linear relationship between native species richness and lantana cover indicates potential lantana impact thresholds (Figure 1; Table 2). For total native species richness, as well as native herb and vine species richness, potential lantana impact thresholds were identified between 75% and 80% lantana cover. Native fern species richness exhibited a comparably lower impact threshold at between 25% and 35% lantana cover. In each case, a strong negative linear relationship between species richness and lantana cover was found above the identified threshold zone, yet no change in species richness was evident in response to lantana cover below the threshold zone (Figure 1; Table

2). For example, above 75%, lantana cover predicted about 90% of the variation in total native species richness. Approximately two native species became missing from the wet sclerophyll forest community with every percentage increase in lantana cover over 75%, indicating a rapid decline in species richness once the threshold level is reached. Indeed, above 75% lantana cover, native species richness fell to about 76% of the number of species typical of non-invaded sites. Interestingly, herb species richness appeared to increase moderately in response to lantana cover preceding the identified impact threshold, with the greatest number of herb species found in sites containing between 55% and 60% lantana cover. A similar increase in species richness was evident for vines.

A significant non-linear cubic relationship was detected between alien species richness and lantana cover (Table 1; Figure 2). Alien species richness responded differently to lantana cover at different stages of its invasion, increasing between 0% and 60% lantana cover and rapidly decreasing where lantana cover exceeded 60%. Alien species richness amongst different growth forms was not analysed in relation to lantana cover since most alien species were herbs.

There was a significant negative linear relationship between shrub and tree density and lantana cover (Table 1; Figure 3), similar to the response of shrub and tree species richness to lantana cover. Thus, an impact threshold was not evident in the response of the number of shrub and tree individuals to lantana invasion.

[Insert Table 2]

[Insert Figure 1]

[Insert Figure 2]

[Insert Figure 3]

Species composition

The total species composition varied significantly amongst invasion categories (Global R = 0.162, P = 0.001) and between northern and southern sites (Global R = 0.436, P = 0.001). Alien species composition did not vary amongst invasion categories or northern and southern sites (Table 3). Subsequently, alien species were removed from the ANOSIM to determine compositional changes for native species. Native species composition differed amongst invasion categories and between northern and southern sites (Table 3). Non-invaded and moderately invaded sites had similar native species compositions, with compositional differences occurring between heavily invaded and non-invaded and moderately invaded sites (Table 3; Figure 4). Patterns were similar when presence/absence data were analysed, indicating that differences in composition were largely attributable to changes in species presences rather than abundances.

Native tree species were the most common contributors to average dissimilarities amongst invasion categories. As trees were the most abundant growth form, changes in their abundance greatly influenced the results, potentially masking differences in other growth forms. Thus, each native growth form was analysed separately. Tree and fern species composition were similar between non-invaded and moderately invaded sites, which were both different from heavily invaded sites (Figure 4; Table 3). Conversely, herb, shrub and vine species composition were dissimilar only between non-invaded and heavily invaded sites. Species composition remained distinct between northern and southern sites for all growth forms except ferns.

[Insert Table 3]

[Insert Figure 4]

Species contributing to compositional differences

Kruskal-Wallis and Chi-square tests were undertaken for 98 native species, which were relatively abundant and common across the study region. Many of these species were shown to be good contributors to compositional differences amongst invasion categories based on SIMPER analyses. Of these, 21 species, which were representative of each of the five major growth forms, exhibited significant variations in abundance and/or frequency of occurrence amongst the different lantana invasion categories (Table 4). However, for the vast majority of species examined, there was no evidence for reduced abundance or occurrence with increasing lantana cover (Appendix). Approximately 67% of the 21 affected species showed substantial reductions in their abundance with increasing lantana cover, and many species occupied significantly fewer sites that were heavily invaded by lantana. Most of the affected species showed no difference in abundance and/or occurrence between non-invaded and moderately invaded sites, only declining once lantana cover exceeded 50%, reflecting detected impact thresholds. Furthermore, a few species, including the subcanopy tree *Allocasuarina torulosa* and shrubs *Trochocarpa laurina* and *Zieria smithii*, occurred commonly throughout non-invaded and moderately invaded sites, but were absent from heavily invaded sites. Indeed, *Allocasuarina torulosa* occurred in 42% of non-invaded sites, 50% of moderately invaded sites, but was absent from heavily invaded sites.

Some species, however, showed increases in abundance and/or occurrence in response to moderate lantana invasion. For example, the small herbaceous sedge *Cyperus tetraphyllus* was more abundant in moderately invaded sites than non-invaded sites, both of which were similar to heavily invaded sites. This species also occurred in a similar number of sites amongst invasion categories. The scrambling vine *Cayratia clematidea* occurred more frequently in moderately invaded sites, followed by heavily invaded and non-invaded sites; however, its abundance was similar amongst invasion categories. Importantly, no species were more abundant or occurred more frequently in heavily invaded sites. The small, unequal sample sizes for most species prevented us from detecting stronger responses to lantana invasion. Subsequently, whilst the results from the Kruskal-Wallis tests clearly indicated differences in abundance based on rank, we could not determine the extent or scale of change in species abundance. Relative impacts of lantana amongst individual species were thus difficult to glean, requiring targeted sampling of species to confirm trends (Mason and French, 2007).

[Insert Table 4]

Discussion

Impacts of lantana invasion on species richness

Our results clearly demonstrate a strong negative association between lantana abundance and species richness of the resident native plant community, validating widespread perceptions that lantana invasion in natural ecosystems is detrimental to species diversity (Fensham et al., 1994; Swarbrick et al., 1998; Batianoff and Butler, 2003; Sharma et al., 2005; Gooden et al., 2009). Species richness in each growth form declined significantly with increasing lantana cover, indicating that the threat of lantana is pervasive across all life forms in the recipient community. Similar pervasive losses of plant species across multiple growth forms have been detected elsewhere for lantana (e.g. Gooden et al., 2009), possibly representing a general effect of the invader on native communities.

Historically, lantana impact studies have focussed on altered ecosystem functions, such as nutrient cycling and vegetation structure (e.g. Lamb, 1988; Bhatt et al., 1994; Islam et al., 2001), yet there is very little quantitative evidence of impacts on species diversity. In two examples, Fensham et al. (1994) found a strong negative correlation between plant species richness and lantana density in a dry rainforest site in north Queensland and Gooden et al. (2009) found that lantana-invaded wet sclerophyll forest in south-eastern Australia had substantially fewer plant species than reference non-invaded areas. Our results provide evidence for broadscale patterns of species loss associated with lantana invasion across a much larger scale. Indeed, such patterns are consistent with generalisations that diversity of resident native communities and abundance of a particular plant invader are negatively related in natural ecosystems (see Adair, 1995; Adair and Groves, 1998; Groves and Willis, 1999; Grice, 2004 for related discussions). Negative associations between invader density and resident species diversity have been established for other significant woody weeds including *Chrysanthemoides monilifera* ssp. *rotundata* (bitou bush) (Weiss and Noble, 1984; Mason and French, 2007), *Acacia sophorae* (Costello et al., 2000) and *Cytisus scoparius* (broom) (Prévosto et al., 2006).

Due to the correlative approach used in this study to investigate the impact of lantana on resident plant communities, the results presented do not necessarily indicate causation. Despite our attempts to reduce the influence of forest disturbances, such as fire, historical logging and livestock grazing, on the vegetation composition of survey sites (e.g. by positioning sites within forest interiors away from disturbed edges and widely separating sites over a large spatial scale), it is possible that the strong association between lantana and native species diversity is coincidental. Indeed, lantana invasion is known to be facilitated by the formation of forest openings due to logging, fire and livestock grazing (Fensham et al., 1994; Gentle and Duggin, 1997b; Totland et al., 2005), which may have concurrently led to native species loss and long-term persistence of dense lantana thickets. As with many invasion studies using a multi-site comparison approach to detect weed impacts (e.g. Adair and Groves, 1998; Mason and French, 2007; Turner et al., 2008), pre-invasion site histories were largely unknown and it is possible that lantana invasion was a symptom of native species decline due to forest disturbance, rather than the principal cause of species loss. Thus, in this study, interpretations of patterns of species decline in response to lantana invasion must be made cautiously. Our study is nevertheless important as it is the first to demonstrate a clear negative association between lantana abundance and species diversity at a broad spatial scale, providing patterns of species decline that validate and support existing small-scale empirical studies (e.g. Achhireddy and Singh, 1984; Bhatt et al., 1994; Gentle and Duggin, 1997a; 1998; Saxena, 2000).

Despite the fundamental limitation of our correlative approach to investigating lantana’s impact, our results are consistent with the findings of a previous removal study by Gooden et al. (2009). Gooden et al. (2009) found that lantana-invaded wet sclerophyll forest on the southeastern coast of Australia contained about 50% fewer vascular plant species than intact non-invaded forest, and that removal of dense lantana infestations initiated vigorous species recruitment (i.e. lantana-removed plots had 13 times the number of recruits than invaded plots), substantially increasing the richness and abundance of the resident native vegetation. Forest stands located in their study region were largely products of regeneration following broad scale deforestation, and it was likely that the level of this disturbance was at a scale encompassing both non-invaded and lantana invaded forest plots. In conjunction with their own results and previous evidence, Gooden et al. (2009) suggested that the initial cause of species decline was indeed broadscale vegetation clearance, with lantana becoming established in disturbed forest openings, forming dense monospecific thickets that prevented long-term forest regeneration. Thus, it is clear from the amount of evidence now available that even though lantana may not necessarily initiate species decline in the absence of disturbance, and indeed is poor at invading pristine, intact vegetation with a high cover of native canopy, it significantly impacts native vegetation over large spatial and temporal scales by inhibiting post-disturbance vegetation regeneration.

Impacts of lantana invasion on species composition

Lantana invasion significantly altered native species compositions with heavily invaded sites comprising different species compositions than both non-invaded and moderately-invaded sites. While these compositional changes were exhibited by all growth forms, tree species contributed most to compositional changes, especially between moderately and heavily invaded sites. All tree species contributing to compositional differences had reduced abundance amongst heavily invaded sites, signalling a substantial change in vegetation structure from tall open forest to low, dense lantana-dominated shrubland (Bhatt et al., 1994).

Lantana invasion reduced forest community homogeneity. This contests the widespread view that alien plant invasion increases community homogenisation by replacing both common and endemic components of native communities, in turn leading to reduced spatial biotic diversity (Vitousek et al., 1996; Williamson and Fitter, 1996; McKinney and Lockwood, 1999). Community homogenisation also occurs when rare or locally endemic species are replaced by more common native species that are less susceptible to invader effects (Griffin et al., 1989; McKinney and Lockwood, 1999). Our results indicate that the effects of lantana on native plant species are variable, leading to somewhat inconsistent or unpredictable patterns of species loss in heavily invaded landscapes. This may reflect intraspecific variations in species susceptibility to lantana invasion, depending on species growth stage or density at each site. Indeed, lantana is known to reduce native seedling growth and survivorship but is unlikely to displace adult individuals (Achhireddy and Singh, 1984; Gentle and Duggin, 1997a; 1998; Stock, 2005), and the growth of native seedlings in lantana-invaded vegetation increases with increasing seedling density (Gentle and Duggin, 1997a). For instance, a particular species might resist invasion in one location if adult individuals occur but be displaced in another location if seedlings are the predominant growth stage. Thus, we speculate that natural landscape-scale variation in species growth stage and density may contribute to reduced community homogeneity associated with alien plant invasions, although this must be confirmed by future investigations.

Impact thresholds for lantana invasion on native species

The significant negative relationship between lantana cover and total native species richness was non-linear, with the rate of species loss increasing with lantana invasion. Indeed, species richness showed no response to lantana among non-invaded and moderately invaded sites, but declined rapidly when lantana cover exceeded 75%, strongly indicating a threshold impact of lantana on the resident forest community. Species thresholds have not been described previously for lantana and only very rarely for other plant invaders (Panetta and James, 1999). Thresholds may represent the ‘maximum level of species resilience’ (Adair and Groves, 1998) to lantana, such that invader effects on species richness are negligible at low levels of infestation, becoming greater as the invader gains community dominance.

Tree and shrub species were relatively more impacted than ferns, herbs and vines, exhibiting species losses at all stages of lantana invasion. Restoration of invaded forest should primarily target the reinstatement of native trees and shrubs as these species are likely to be poorly represented in the remnant standing vegetation compared with other growth forms. Fern species richness had an evidently lower potential impact threshold (i.e. 25% lantana cover) than herbs and vines; however, ferns showed considerable site variation in species richness with increasing lantana cover, and it is likely that factors other than the extent of lantana invasion, such as disturbance history and water availability, are important in structuring fern assemblages.

The impact thresholds presented here comprise two distinct functional relationships between lantana and the resident plant community: (1) the maintenance of species richness at low and moderate levels of lantana cover below the threshold zone, and (2) the rapid loss of species once lantana cover exceeds the threshold zone. The first part of the relationship may reflect native vegetation resistance to lantana invasion with increasing species diversity (Elton, 1958; Prieur-Richard and Lavorel, 2000; Prieur-Richard et al., 2000; Brown and Peet, 2003). Increased species richness might confer resistance to lantana invasion through greater community stability, resilience to disturbance and a more complete utilisation of light, space and nutrient resources through niche partitioning (Davis et al., 2000; Ives et al., 2000; Prieur-Richard and Lavorel, 2000; Dukes, 2001; Tilman et al., 2006). This is confirmed by empirical and correlative evidence that lantana invasion is inhibited by intact undisturbed vegetation (Fensham et al., 1994; Duggin and Gentle, 1998; Gentle and Duggin, 1998; Stock, 2005; Totland et al., 2005). The impact threshold signals a subsequent shift in patterns of dependency amongst native species and lantana. Whilst lantana invasion may be initially limited by intact resident vegetation, increased lantana dominance is likely to confer greater adverse impacts on resident species, accounting for the rapid decline in species richness at levels above the threshold (Grice, 2004). This shift may be mediated by disturbance, such as canopy removal, which facilitates lantana invasion and increases its capacity to suppress native species via greater resource acquisition and space utilisation (Duggin and Gentle, 1998; Gentle and Duggin, 1998; Stock, 2005).

Management implications and limitations of invader impact thresholds

In is unlikely that broadscale eradication of lantana will be achievable in the foreseeable future due to its widespread distribution, rapid spread and dominance in natural ecosystems (Swarbrick et al., 1998; Mack et al., 2000; Myers et al., 2000; Mason et al., 2005). Our results for impact thresholds indicate that broadscale conservation of species diversity could be achieved by maintaining lantana cover below 75%, allowing efficient resource allocation in areas with minimal funding for lantana control (Groves and Willis, 1999). Yet, despite this potential use of impact thresholds for the management of lantana, several important limitations must be addressed. First, thresholds do not necessarily indicate single-species responses to weed invasion (Huggett, 2005; Lindenmayer et al., 2006), and species are likely to respond differently to lantana at different stages of its invasion. Indeed, whilst the vast majority of common species tested exhibited no change in abundance in response to lantana cover, many species had lower abundances in heavily-invaded sites. Furthermore, shrubs and trees are evidently more affected by lantana invasion than ferns, herbs and vines. Since our principal measurement of lantana's impact was at the community level, and our analyses of species-specific impacts of lantana were restricted to the most common and abundant species, thresholds are likely to mask the effects of lantana on threatened species and those with low abundances or sporadic, isolated populations occurring within the distribution of the invader. As a result, management programmes that utilise impact thresholds may inadvertently lead to the decline of rare or threatened species that are susceptible to lantana at earlier stages of its invasion. Thus, impact thresholds should only be applied by land managers following rigorous prioritisation of sites for invader control; i.e. invader eradication is preferable for sites containing regionally rare species or endangered ecological communities, and containment of the invader below the threshold level may be viable for sites containing regionally common species that are also widely represented in non-invaded vegetation. This approach may allow more efficient, broadscale conservation of species diversity whilst ensuring targeted invader control to sites of relatively high conservation value.

Lantana impact thresholds presented here represent a 'snap-shot' of community responses to the invader. Time-lag or latency effects of lantana on species richness may occur at earlier stages of its invasion, such that long-term interactions with lantana at cover values below the impact threshold may lead to the decline of some species. Furthermore, impact thresholds for lantana may be confounded in forest remnants due to the concurrent existence of fragmentation thresholds for species diversity (Drinnan, 2005); this may lead to an aggregation of threshold effects which act synchronously on native species (Panetta and James, 1999), leading to an accelerated loss of species at an earlier stage of invasion in fragmented forest landscapes. Thus, different management regimes may be required for lantana infestations in intact, continuous forest than in fragmented forest landscapes. Long-term monitoring of invaded forest by land managers will elucidate whether such time-lag and aggregate threshold effects occur, and ultimately validate the use of impact thresholds as a useful conservation strategy.

Importantly, impact thresholds should only be used for pre-emptive invader control (i.e. containment below the thresholds zone) and cannot necessarily indicate how much of an invader should be removed to initiate native community reinstatement (Adair and Groves, 1998; Panetta and James, 1999). Reducing the cover of lantana to below 75% at a heavily-invaded site is unlikely to reinstate the community due to adverse residual effects of the invader, such as altered soil chemistry and nutrient cycling (Achhireddy and Singh, 1984; Lamb, 1988; Bhatt et al., 1994), as well as differential effects of removal procedure on native species regeneration (Mason and French, 2007). For example, McDonald *et al.* (2002) found that intensive manual woody weed removal from Blue Gum High Forest resulted in lower rates of native plant regeneration than manual weed removal accompanied by burning. Thus, in terms of threshold relationships, early detection and offensive control of lantana will be more effective at conserving species diversity than long-term defensive strategies (Rejmánek, 2000).

Conclusion

This study provides strong evidence for adverse broadscale effects of a significant alien woody plant invader, lantana, on native plant communities. Despite the limitation of our multi-site comparison technique, it is clear that lantana-invaded vegetation comprises substantially fewer native species and subsequently different compositions than reference non-invaded vegetation. Importantly, thresholds were evident in the impact of lantana on native forest, with the number of species declining rapidly only at locations where lantana cover exceeded 75%. Invader control which targets thresholds may enable broadscale conservation of community diversity, allowing limited management resources to be used for invader eradication in areas of relatively high conservation value. Future research will be needed to validate the use of impact thresholds as an effective and efficient conservation strategy for invaded landscapes.

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Appendix: Summary of species with no changes in abundance and frequency of occurrence amongst lantana non-invaded (n = 19), moderately invaded (n = 16) and heavily invaded (n = 18) sites. Species abundance was measured from nested 20 x 20 m quadrat; species occurrence was measured from entire 20 x 50 m quadrat.

Growth form / Species	Test type	Invasion category[a]			χ^2	*P*
		Non-invaded	Moderately invaded	Heavily invaded		
Fern						
Adiantum hispidulum	Abundance	n/a	n/a	n/a	2.653	0.265
	Occurrence	5	8	7	2.089	>0.05
Asplenium flabellifolium	Abundance	n/a	n/a	n/a	1.692	0.429
	Occurrence	7	5	4	0.408	>0.05
Cyathea australis	Abundance	n/a	n/a	n/a	2.327	0.268
	Occurrence	6	3	3	0.542	>0.05
Pellaea falcata	Abundance	n/a	n/a	n/a	1.531	0.465
	Occurrence	7	12	11	5.374	>0.05
Pteridium esculentum	Abundance	n/a	n/a	n/a	0.626	0.731
	Occurrence	9	7	8	0.054	>0.05
Herb						
Aneilema acuminatum	Abundance	n/a	n/a	n/a	3.236	0.198
	Occurrence	9	6	4	2.569	>0.05
Carex appressa	Abundance	n/a	n/a	n/a	0.695	0.706
	Occurrence	11	8	10	0.226	>0.05
Commelina cyanea	Abundance	n/a	n/a	n/a	4.384	0.112
	Occurrence	5	5	8	1.43	>0.05
Desmodium spp. (*gunnii/varians*)	Abundance	n/a	n/a	n/a	4.333	0.115
	Occurrence	4	8	4	2.725	>0.05
Dianella caerulea	Abundance	n/a	n/a	n/a	2.630	0.269
	Occurrence	11	9	8	0.779	>0.05
Dichondra repens	Abundance	n/a	n/a	n/a	0.433	0.805
	Occurrence	8	9	8	0.779	>0.05
Entolasia spp. (*marginata/stricta*)	Abundance	n/a	n/a	n/a	3.541	0.170
	Occurrence	15	15	13	1.387	>0.05
Gahnia melanocarpa	Abundance	n/a	n/a	n/a	2.470	0.291
	Occurrence	8	6	3	3.055	>0.05
Geranium homeanum	Abundance	n/a	n/a	n/a	0.427	0.808
	Occurrence	4	4	6	0.256	>0.05
Gymnostachys anceps	Abundance	n/a	n/a	n/a	4.556	0.103
	Occurrence	12	13	9	3.61	>0.05
Hibbertia scandens	Abundance	n/a	n/a	n/a	1.748	0.417
	Occurrence	10	11	8	2.072	>0.05
Hydrocotyle spp. (*hirta/peduncularis*)	Abundance	n/a	n/a	n/a	0.663	0.718
	Occurrence	11	8	10	0.226	>0.05
Oplismenus spp. (*aemulus/imbecillis*)	Abundance	n/a	n/a	n/a	0.142	0.932
	Occurrence	13	12	15	0.513	>0.05
Oxalis spp. (*chnoodes/rubens*)	Abundance	n/a	n/a	n/a	2.324	0.313
	Occurrence	4	4	3	0.094	>0.05

Panicum spp. (*effusum/simile*)	Abundance	n/a	n/a	n/a	0.973	0.615
	Occurrence	7	6	6	0.077	>0.05
Plectranthus parviflorus	Abundance	n/a	n/a	n/a	1.431	0.489
	Occurrence	7	5	5	0.356	>0.05
Pratia purparescens	Abundance	n/a	n/a	n/a	2.486	0.289
	Occurrence	9	9	5	2.986	>0.05
Sigesbeckia orientalis	Abundance	n/a	n/a	n/a	0.249	0.883
	Occurrence	4	5	7	0.713	>0.05
Stellaria flaccida	Abundance	n/a	n/a	n/a	3.029	0.220
	Occurrence	6	6	2	2.037	>0.05
Veronica plebeia	Abundance	n/a	n/a	n/a	4.465	0.107
	Occurrence	8	5	2	3.012	>0.05
Viola hederacea	Abundance	n/a	n/a	n/a	0.533	0.766
	Occurrence	9	8	8	0.105	>0.05
Shrub						
Breynia oblongifolia	Abundance	n/a	n/a	n/a	3.093	0.213
	Occurrence	12	14	10	4.276	>0.05
Clerodendrum tomentosum	Abundance	n/a	n/a	n/a	3.758	0.153
	Occurrence	12	13	11	1.886	>0.05
Myrsine howittiana	Abundance	n/a	n/a	n/a	4.453	0.108
	Occurrence	8	5	3	1.795	>0.05
Ozothamnus diosmifolius	Abundance	n/a	n/a	n/a	2.020	0.364
	Occurrence	5	4	4	0.07	>0.05
Pittosporum multiflorum	Abundance	n/a	n/a	n/a	3.916	0.141
	Occurrence	11	7	7	1.447	>0.05
Pittosporum revolutum	Abundance	n/a	n/a	n/a	4.041	0.133
	Occurrence	14	14	10	2.855	>0.05
Psychotria loniceroides	Abundance	n/a	n/a	n/a	5.585	0.061
	Occurrence	8	5	2	3.012	>0.05
Rubus moluccanus var. *trilobus*	Abundance	n/a	n/a	n/a	3.674	0.159
	Occurrence	7	9	6	2.098	>0.05
Rubus parvifolius	Abundance	n/a	n/a	n/a	1.974	0.373
	Occurrence	2	5	4	1.214	>0.05
Rubus rosifolius	Abundance	n/a	n/a	n/a	1.936	0.380
	Occurrence	5	5	6	0.047	>0.05
Wilkiea huegeliana	Abundance	n/a	n/a	n/a	1.604	0.448
	Occurrence	8	5	5	0.921	>0.05
Tree						
Acacia binervata	Abundance	n/a	n/a	n/a	2.878	0.372
	Occurrence	9	3	8	3.55	>0.05
Acmena smithii	Abundance	n/a	n/a	n/a	4.540	0.103
	Occurrence	12	9	7	2.292	>0.05
Alphitonia excelsa	Abundance	n/a	n/a	n/a	1.342	0.511
	Occurrence	2	8	6	4.73	>0.05
Angophora costata	Abundance	n/a	n/a	n/a	0.196	0.907
	Occurrence	4	3	3	0.101	>0.05
Angophora floribunda	Abundance	n/a	n/a	n/a	2.227	0.328
	Occurrence	5	4	1	1.687	>0.05
Claoxylon australe	Abundance	n/a	n/a	n/a	1.977	0.372
	Occurrence	6	8	7	1.238	>0.05
Cryptocarya glaucescens	Abundance	n/a	n/a	n/a	2.158	0.340
	Occurrence	9	6	4	2.569	>0.05
Cryptocarya microneura	Abundance	n/a	n/a	n/a	2.172	0.338
	Occurrence	5	8	7	2.089	>0.05
Doryphora sassafras	Abundance	n/a	n/a	n/a	0.105	0.949
	Occurrence	9	4	5	2.403	>0.05

Elaeodendron australe	Abundance	n/a	n/a	n/a	5.09	0.079
	Occurrence	7	6	4	1.216	>0.05
Eucalyptus botryoides	Abundance	n/a	n/a	n/a	0.028	0.986
	Occurrence	4	3	4	0.094	>0.05
Eucalyptus paniculata	Abundance	n/a	n/a	n/a	3.573	0.168
	Occurrence	3	6	3	1.556	>0.05
Eucalyptus pilularis	Abundance	n/a	n/a	n/a	0.349	0.840
	Occurrence	5	6	6	0.518	>0.05
Eupomatia laurina	Abundance	n/a	n/a	n/a	1.160	0.560
	Occurrence	7	6	4	1.216	>0.05
Ficus coronata	Abundance	n/a	n/a	n/a	5.705	0.058
	Occurrence	3	5	3	0.61	>0.05
Glochidion ferdinandi	Abundance	n/a	n/a	n/a	0.520	0.771
	Occurrence	5	6	7	0.779	>0.05
Guioa semiglauca	Abundance	n/a	n/a	n/a	1.723	0.423
	Occurrence	9	7	7	0.272	>0.05
Livistona australis	Abundance	n/a	n/a	n/a	4.902	0.086
	Occurrence	15	14	12	1.105	>0.05
Melicope micrococca	Abundance	n/a	n/a	n/a	5.494	0.064
	Occurrence	5	8	7	2.089	>0.05
Stenocarpus salignus	Abundance	n/a	n/a	n/a	1.470	0.479
	Occurrence	6	3	1	2.66	>0.05
Syncarpia glomulifera	Abundance	n/a	n/a	n/a	5.524	0.063
	Occurrence	9	10	7	1.923	>0.05
Toona ciliata	Abundance	n/a	n/a	n/a	0.747	0.688
	Occurrence	5	4	7	0.346	>0.05
Vine						
Billardiera scandens	Abundance	n/a	n/a	n/a	3.350	0.187
	Occurrence	7	2	4	1.649	>0.05
Cissus antarctica	Abundance	n/a	n/a	n/a	2.530	0.282
	Occurrence	7	9	7	1.557	>0.05
Cissus hypoglauca	Abundance	n/a	n/a	n/a	3.032	0.220
	Occurrence	15	10	9	3.395	>0.05
Clematis aristata	Abundance	n/a	n/a	n/a	1.774	0.412
	Occurrence	9	10	7	1.923	>0.05
Clematis glycinoides	Abundance	n/a	n/a	n/a	3.371	0.185
	Occurrence	4	5	1	2.203	>0.05
Dioscorea transversa	Abundance	n/a	n/a	n/a	4.473	0.107
	Occurrence	5	8	6	2.194	>0.05
Eustrephus latifolius	Abundance	n/a	n/a	n/a	4.689	0.096
	Occurrence	19	16	16	1.117	>0.05
Geitonoplesium cymosum	Abundance	n/a	n/a	n/a	2.398	0.301
	Occurrence	17	16	16	0.468	>0.05
Glycine clandestina	Abundance	n/a	n/a	n/a	0.337	0.845
	Occurrence	5	7	6	1.182	>0.05
Glycine spp. (*microphylla/tabacina*)	Abundance	n/a	n/a	n/a	1.905	0.386
	Occurrence	9	8	4	3.475	>0.05
Kennedia rubicunda	Abundance	n/a	n/a	n/a	0.734	0.693
	Occurrence	6	2	4	0.938	>0.05
Palmeria scandens	Abundance	n/a	n/a	n/a	4.339	0.114
	Occurrence	5	4	1	1.687	>0.05
Pandorea pandorana	Abundance	n/a	n/a	n/a	2.369	0.306
	Occurrence	17	15	15	0.242	>0.05
Parsonsia straminea	Abundance	n/a	n/a	n/a	0.777	0.678
	Occurrence	14	11	9	2.465	>0.05
Rubus nebulosus	Abundance	n/a	n/a	n/a	2.012	0.366

	Occurrence	6	2	3	1.05	>0.05
Sarcopetalum harveyanum	Abundance	n/a	n/a	n/a	2.051	0.359
	Occurrence	4	9	6	4.754	>0.05
Smilax glyciphylla	Abundance	n/a	n/a	n/a	3.235	0.198
	Occurrence	9	4	4	3.209	>0.05
Tylophora barbata	Abundance	n/a	n/a	n/a	0.707	0.702
	Occurrence	13	9	8	2.164	>0.05

[a]Abundance: different letters denote significant differences in rank of species abundance amongst invasion categories (with a ranked greater than b); Occurrence: values presented for chi-square test represent the number of sites occupied by each species within each invasion category.

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Figure captions

Figure 1: Relationships between lantana cover (%) and (a) total native vascular plant species richness, (b) native fern species richness, (c) native herb species richness, (d) native shrubs species richness, (e) native tree species richness and (f) native vine species richness (n = 53). The model type is indicated above each plot. Arrows indicate the location of potential lantana impact thresholds. Note the differences in range of *y*-axes among plots. Species richness was recorded from entire 20 x 50 m quadrat.

Figure 2: Relationship between lantana cover (%) and number of alien vascular plant species (n = 53). Species richness was recorded from entire 20 x 50 m quadrat.

Figure 3: Relationship between lantana cover (%) and native tree and shrub density (n = 53). Shrub and tree density included the three tufted or shrub-like perennial herbs *Gymnostachys anceps*, *Helichrysum elatum* and *Lomandra longifolia*, and the two ferns *Asplenium australasicum* and *Cyathea australis*. Species density was recorded from nested 20 x 20 m quadrat.

Figure 4: Non-metric multi-dimensional ordination scaling) of (a) total native vascular plant species, (b) native ferns, (c) native herbs, (d) native shrubs, (e) native trees and (f) native vines for lantana non-invaded (clear points; n = 19), moderately invaded (grey points; n = 16) and heavily invaded (black points; n = 18) sites between northern (circles) and southern (triangles) regions using species cover abundance values. Points closer together in ordination space represent sites with more similar species compositions. Species abundances were recorded from the nested 20 x 20 m quadrat.

Table 1: Comparison of linear and non-linear cubic regression analyses for native (total, fern, herb, shrub, tree and vine) and alien species richness against percentage lantana foliage cover using the Akaike Information Criterion (AIC) and residual error (n = 53). Species richness was recorded from entire 20 x 50 m quadrat.

Dependent variable		**Model type**	
		Linear	**Cubic**
Number of native species	R^2	0.357	0.582
	P	<0.0001*	<0.0001*
	Residual error	7113.054	**4625.959**
	AIC	263.668	**244.865**
Number of native fern species	R^2	0.192	0.256
	P	0.001*	0.002*
	Residual error	207.998	**191.483**
	AIC	76.464	**76.079**
Number of native herb species	R^2	0.121	0.334
	P	0.011*	0.0002*
	Residual error	1187.847	**900.652**
	AIC	168.809	**158.140**
Number of native shrub species	R^2	0.376	0.421
	P	<0.0001*	<0.0001*
	Residual error	333.181	**309.192**
	AIC	**101.435**	101.475
Number of native tree species	R^2	0.153	0.202
	P	0.004*	0.011*
	Residual error	1312.670	**1236.496**
	AIC	**174.105**	174.936
Number of native vine species	R^2	0.191	0.475
	P	0.001*	<0.0001*
	Residual error	755.494	**490.076**
	AIC	144.825	**125.886**
Number of alien species	R^2	0.054	0.237
	P	0.095	0.004*
	Residual error	38.950	**31.426**
	AIC	-12.324	**-19.701**
Native tree and shrub density	R^2	0.575	0.598
	P	<0.0001*	<0.0001*
	Residual error	319.098	**301.637**
	AIC	**99.146**	100.164

Values in bold denote the lowest AIC and residual error and, thus, the model with the best fit. * denotes statistical significance.

Table 2: Summary of regression analyses for native species richness (total, fern, herb and vine) against percentage lantana foliage cover below and above the potential impact thresholds. Species richness was recorded from entire 20 m x 50 m quadrat.

Dependent variable	**Lantana cover (%)**	**Slope**	**R^2**	***P***
Number of native species	≤75 (n = 45)	0.103	0.06	0.1173
	>75 (n = 8)	2.125	0.90	**0.0003**
Number of native fern species	≤25 (n = 28)	0.054	0.05	0.2423
	>25 (n = 25)	0.056	0.25	**0.0103**
Number of native herb species	≤75 (n = 45)	0.002	0.0002	0.9329
	>75 (n = 8)	0.65	0.70	**0.0091**
Number of native vine species	≤75 (n = 45)	0.001	0.00003	0.9742
	>75 (n = 8)	0.525	0.81	**0.0022**

Values in bold denote statistically significant differences.

Table 3: Two-way crossed ANOSIM pair-wise comparisons of native (total abundance and presence/absence, fern, herb, shrub, tree and vine) and alien species compositions amongst non-invaded (n = 19), moderately invaded (n = 16) and heavily invaded (n = 18) sites (lantana cover excluded). Values in bold denote statistically significant differences. Species abundances were recorded from the nested 20 x 20 m quadrat.

Factor and invasion category comparisons	**Global *R***	***R***	***P***
Total native species			
Location (north vs. south)	0.443		**0.001**
Invasion category	0.16		**0.001**
Non-invaded vs. Moderately invaded		-0.006	0.48
Moderately invaded vs. Heavily invaded		0.15	**0.013**
Non-invaded vs. Heavily invaded		0.269	**0.001**
Total native species (presence/absence)			
Location (north vs. south)	0.421		**0.001**
Invasion category	0.119		**0.004**
Non-invaded vs. Moderately invaded		0.002	0.468
Moderately invaded vs. Heavily invaded		0.091	0.067
Non-invaded vs. Heavily invaded		0.207	**0.003**
Total alien species			
Location (north vs. south)	0.118		0.066
Invasion category	-0.048		0.762
Non-invaded vs. Moderately invaded		-0.059	0.708
Moderately invaded vs. Heavily invaded		-0.008	0.498
Non-invaded vs. Heavily invaded		-0.09	0.823
Native fern species			
Location (north vs. south)	0.099		0.065
Invasion category	0.137		**0.003**
Non-invaded vs. Moderately invaded		0.004	0.444
Moderately invaded vs. Heavily invaded		0.184	**0.021**
Non-invaded vs. Heavily invaded		0.206	**0.005**
Native herb species			
Location (north vs. south)	0.241		**0.002**
Invasion category	0.097		**0.002**
Non-invaded vs. Moderately invaded		0.055	0.206
Moderately invaded vs. Heavily invaded		0.09	0.057
Non-invaded vs. Heavily invaded		0.121	**0.028**
Native shrub species			
Location (north vs. south)	0.202		**0.002**
Invasion category	0.096		**0.024**
Non-invaded vs. Moderately invaded		0.047	0.23
Moderately invaded vs. Heavily invaded		0.036	0.259
Non-invaded vs. Heavily invaded		0.166	**0.003**
Native tree species			
Location (north vs. south)	0.329		**0.001**
Invasion category	0.085		**0.032**
Non-invaded vs. Moderately invaded		-0.066	0.877
Moderately invaded vs. Heavily invaded		0.136	**0.021**

Non-invaded vs. Heavily invaded	0.15	**0.024**
Native vine species		
Location (north vs. south)	0.444	**0.001**
Invasion category	0.113	**0.005**
Non-invaded vs. Moderately invaded	0.007	0.421
Moderately invaded vs. Heavily invaded	0.091	**0.063**
Non-invaded vs. Heavily invaded	0.196	**0.003**

Values in bold denote statistically significant differences.

Table 4: Summary of significant variations in abundance and frequency of occurrence for 21 native species amongst lantana non-invaded (n = 19), moderately invaded (n = 16) and heavily invaded (n = 18) sites. Species abundance was measured from nested 20 x 20 m quadrat; species occurrence was measured from entire 20 x 50 m quadrat.

Impact	**Growth form** / **Species**	**Test type**	**Invasion category**[a]			χ^2	***P***
			Non-invaded	**Moderately invaded**	**Heavily invaded**		
Lower abundance and/or occurrence in heavily invaded sites	**Fern**						
	Blechnum cartilagineum	Abundance	a	a	b	10.357	**0.006**
		Occurrence	14	12	4	13.123	**<0.05**
	Calochlaena dubia	Abundance	a	a	b	9.800	**0.007**
		Occurrence	17	13	6	15.239	**<0.05**
	Doodia aspera	Abundance	a	a	b	10.044	**0.007**
		Occurrence	14	11	6	7.192	**<0.05**
	Herb						
	Hibbertia dentata	Abundance	n/a	n/a	n/a	3.313	0.191
		Occurrence	8	8	2	6.587	**<0.05**
	Lomandra longifolia	Abundance	a	b	b	10.034	**0.007**
		Occurrence	18	13	10	6.084	**<0.05**
	Pseuderanthemum variabile	Abundance	a	a	b	10.675	**0.005**
		Occurrence	19	16	11	11.51	**<0.05**
	Shrub						
	Myrsine variabilis	Abundance	a	a	b	7.718	**0.021**
		Occurrence	7	7	1	5.061	>0.05
	Trees						
	Diospyros australis	Abundance	a	a	b	9.437	**0.009**
		Occurrence	10	8	2	8.249	**<0.05**
	Elaeocarpus reticulatus	Abundance	a	b	ab	6.032	**0.049**
		Occurrence	9	1	3	6.427	**<0.05**
	Notelaea spp. (*longifolia*/*venosa*)	Abundance	a	a	b	7.759	**0.021**
		Occurrence	14	12	9	3.133	>0.05
	Pittosporum undulatum	Abundance	a	a	b	12.285	**0.002**
		Occurrence	15	11	11	0.713	>0.05

	Vine						
	Marsdenia rostrata	Abundance	a	a	b	9.121	**0.011**
		Occurrence	11	12	5	7.885	**<0.05**
	Morinda jasminoides	Abundance	n/a	n/a	n/a	5.806	0.055
		Occurrence	13	14	7	8.939	**<0.05**
	Smilax australis	Abundance	a	a	b	9.982	**0.007**
		Occurrence	17	14	9	7.02	**<0.05**
Higher abundance and/or occurrence in moderately invaded sites	**Herb**						
	Cyperus tetraphyllus	Abundance	b	a	ab	7.888	**0.019**
		Occurrence	2	5	3	1.304	>0.05
	Imperata cylindrica	Abundance	n/a	n/a	n/a	2.140	0.343
		Occurrence	4	9	4	6.153	**<0.05**
	Tree						
	Acacia maidenii	Abundance	ab	a	b	6.161	**0.046**
		Occurrence	11	12	9	2.289	>0.05
	Rhodamnia rubescens	Abundance	ab	a	b	6.614	**0.037**
		Occurrence	6	9	3	5.993	**<0.05**
	Synoum glandulosum	Abundance	ab	a	b	6.874	**0.032**
		Occurrence	14	13	9	4.248	>0.05
	Vine						
	Cayratia clematidea	Abundance	n/a	n/a	n/a	1.489	0.475
		Occurrence	4	10	7	6.243	**<0.05**
	Stephania japonica	Abundance	b	a	ab	6.654	**0.036**
		Occurrence	9	14	14	5.379	>0.05

[a]Abundance: different letters denote significant differences in rank of species abundance amongst invasion categories (with a ranked greater than b), n/a = not applicable; Occurrence: values presented for chi-square test represent the number of sites occupied by each species within each invasion category. Values in bold denote statistically significant differences.

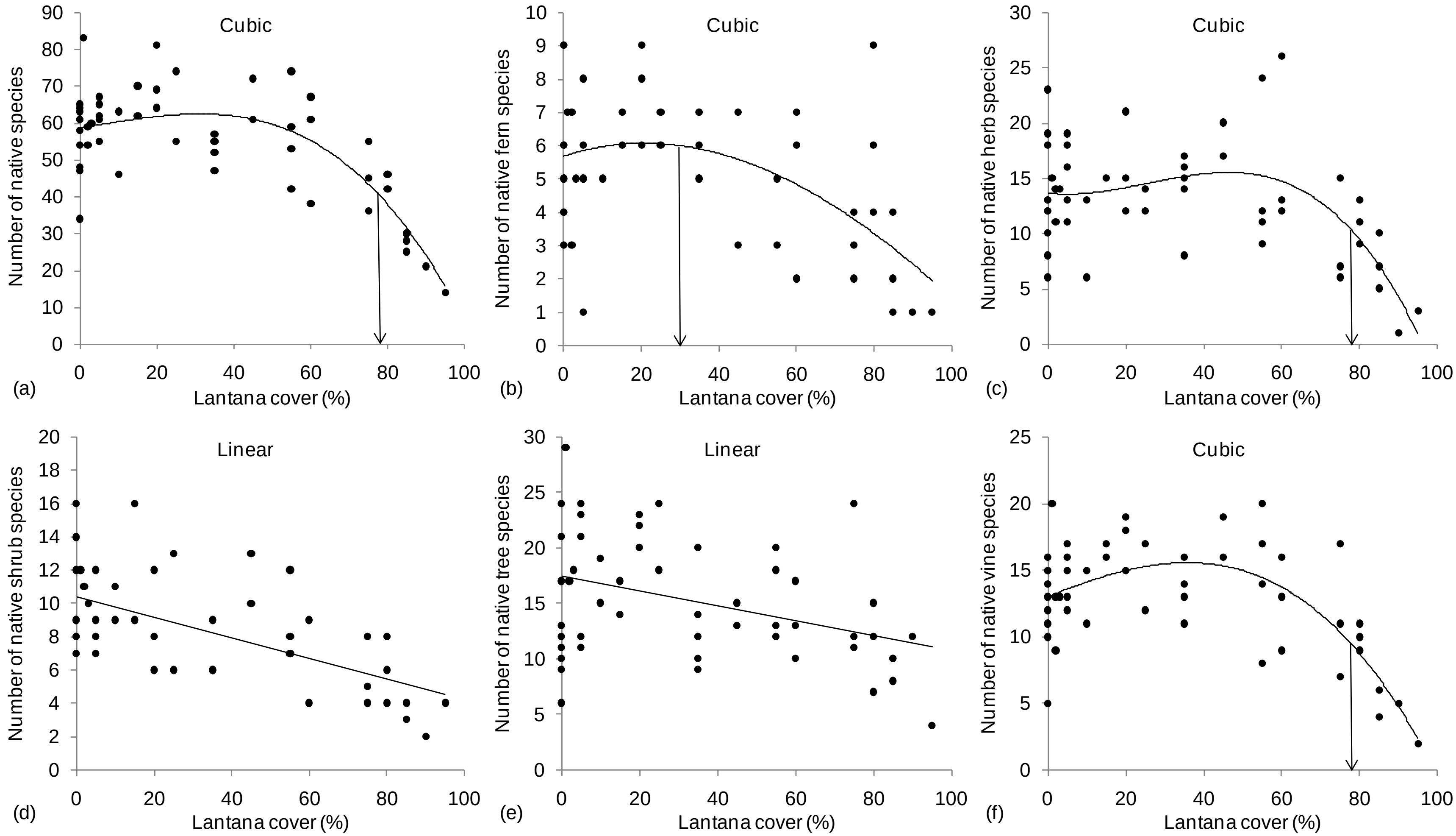
Cubic
Number of native species
Lantana cover (%)
(a)
Cubic
Number of native fern species
Lantana cover (%)
(b)
Cubic
Number of native herb species
Lantana cover (%)
(c)
Linear
Number of native shrub species
Lantana cover (%)
(d)
Linear
Number of native tree species
Lantana cover (%)
(e)
Cubic
Number of native vine species
Lantana cover (%)
(f)

Figure 1

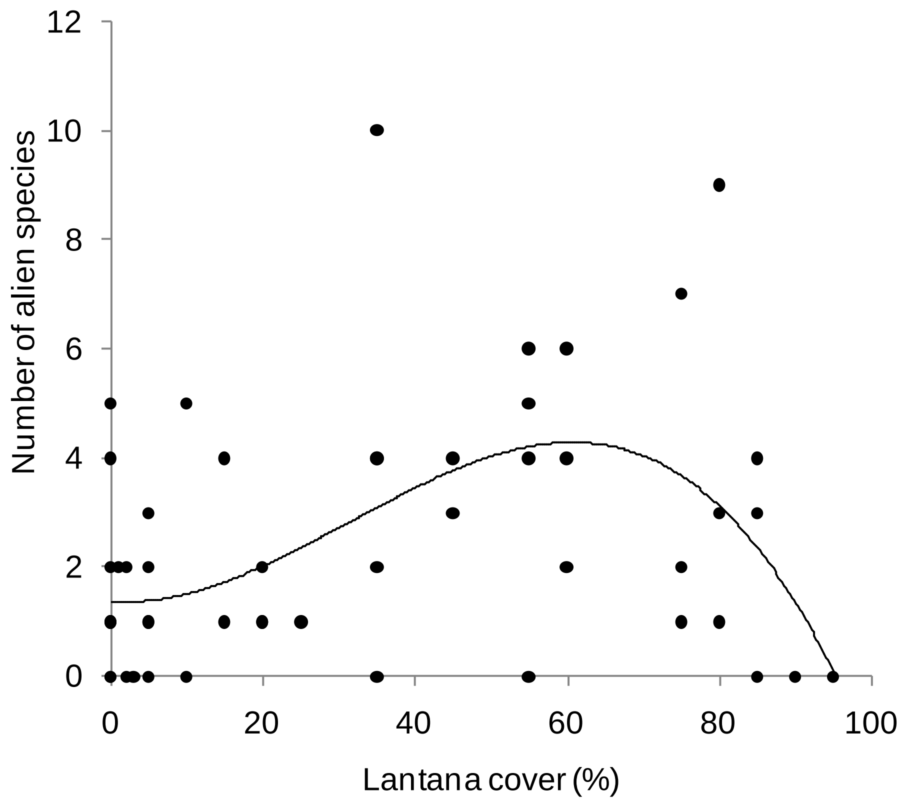
12
10
8
6
4
2
0
Number of alien species
0
20
40
60
80
100
Lantana cover (%)

Figure 2

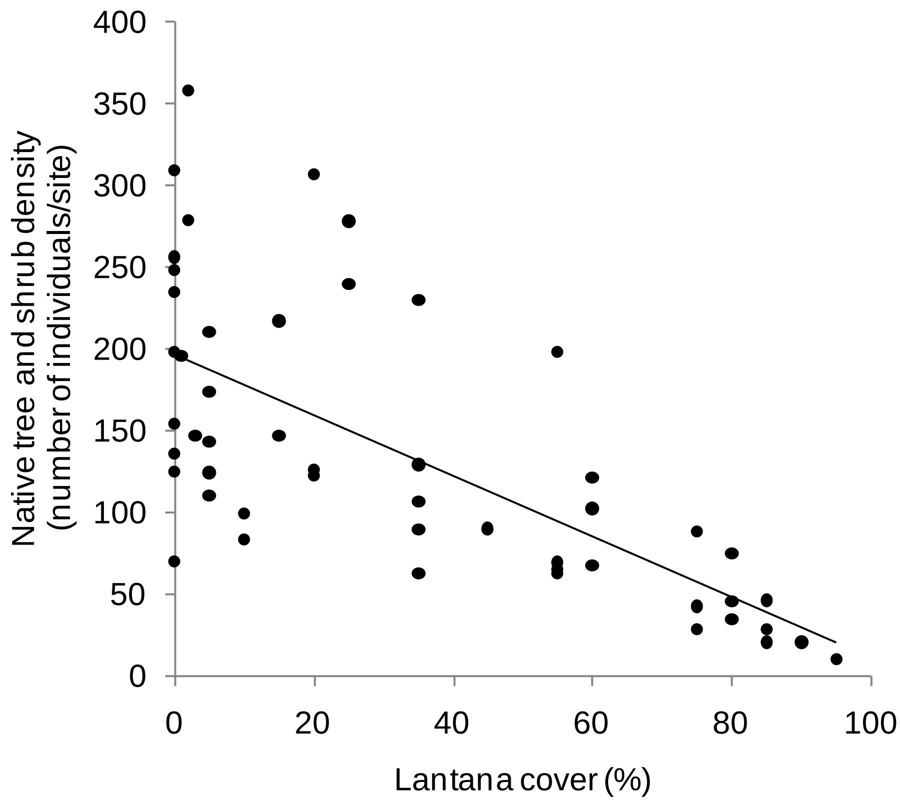
400
350
300
250
200
150
100
50
0
0
20
40
60
80
100
Native tree and shrub density (number of individuals/site)
Lantana cover (%)

Figure 3

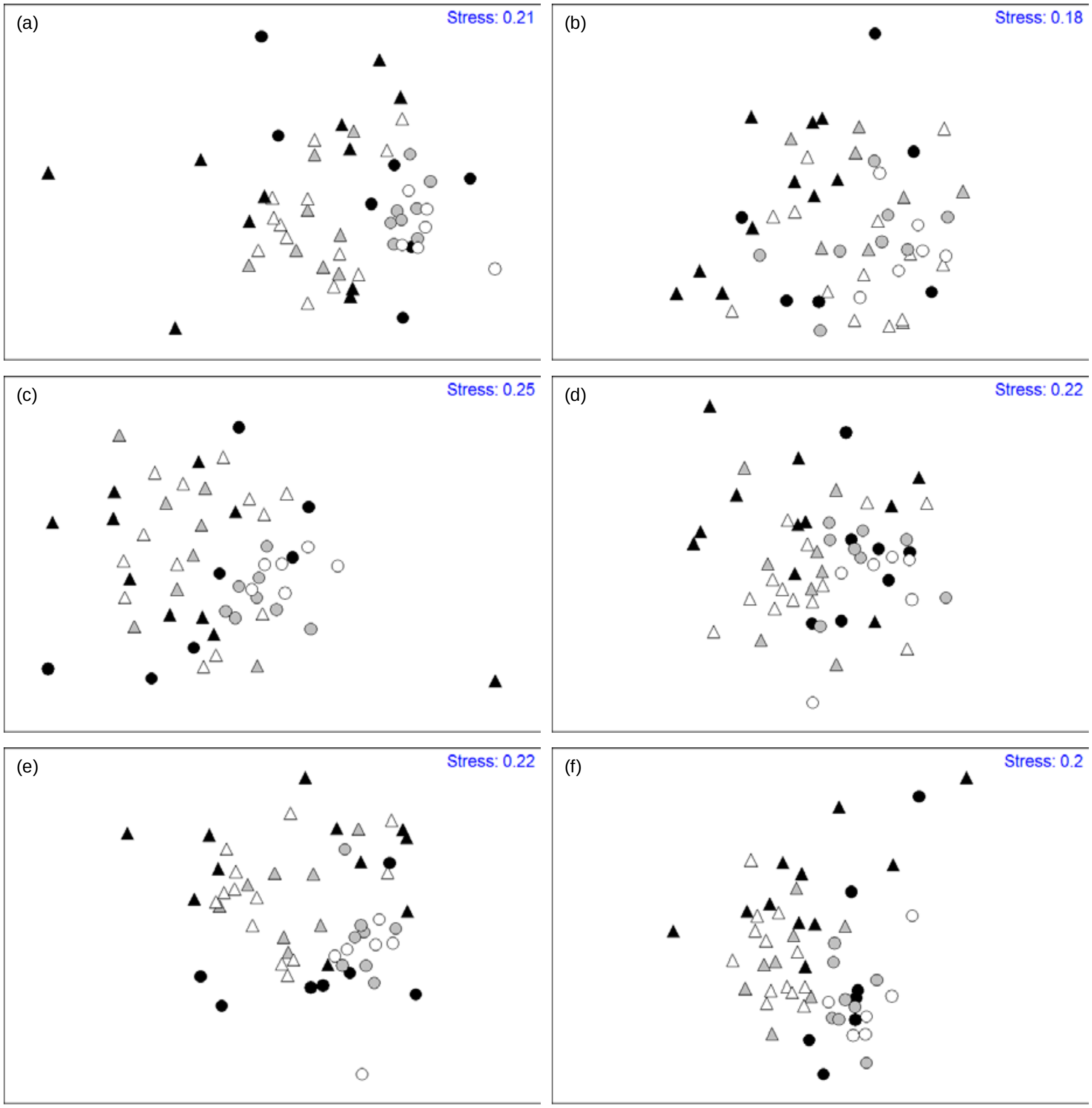
(a)
Stress: 0.21
(b)
Stress: 0.18
(c)
Stress: 0.25
(d)
Stress: 0.22
(e)
Stress: 0.22
(f)
Stress: 0.2

Figure 4