Characteristics of the *Psidium cattleianum* invasion of secondary rainforests

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Abstract   Strawberry guava (*Psidium cattleianum*) is a shade-tolerant shrub or small tree invader in tropical and subtropical regions and is considered among the world's top 100 worst invasive species. Studies from affected regions report deleterious effects of strawberry guava invasion on native vegetation. Here we examine the life history demographics and environmental determinants of strawberry guava invasions to inform effective weed management in affected rainforest regions. We surveyed the vegetation of 8 mature rainforest and 33 successional sites at various stages of regeneration in the Australian Wet Tropics and found that strawberry guava invasion was largely restricted to successional forests. Strawberry guava exhibited high stem and seedling densities, represented approximately 8% of all individual stems recorded and 20% of all seedlings recorded. The species also had the highest basal area among all the non-native woody species measured. We compared environmental and community level effects between strawberry guava-invaded and non-invaded sites, and modelled how the species basal area and recruitment patterns respond to these effects. Invaded sites differed from non-invaded sites in several environmental features such as aspect, distance from intact forest blocks, as well as supported higher grass and herb stem densities. Our analysis showed that invasion is currently ongoing in secondary forests, and also that strawberry guava is able to establish and persist under closed canopies. If left unchecked, strawberry guava invasion will have deleterious consequences for native regenerating forest in the Australian Wet Tropics.

Key words: community species diversity, biological invasion, *Psidium cattleianum*, secondary rainforest, shade-tolerant invader, strawberry guava.

INTRODUCTION

Tropical forests are of great importance because of their immense contribution to global biodiversity and carbon budgets, but are experiencing major changes in species composition and richness at local and global scales because of environmental changes caused by anthropogenic activities. A major symptom of this change is the establishment of invasive species in natural environments (Ortega & Pearson 2005; Ditham *et al.* 2007). Once they achieve a certain level of abundance, introduced species may displace native species by competing for resources, such as space, water, nutrients and light (Levine *et al.* 2003; Vila & Weiner 2004). Invasive species can also cause community species shifts by impeding the colonization success of native species (Hager 2004; Yurkonis & Meiners 2004). Invasive species typical impose considerable

propagule pressure and can saturate suitable microsites (Brown & Fridley 2003), reducing the rate of establishment by native species. Where competitive interactions shape community structure, the invasion process may more strongly inhibit colonization of species within the same functional group as the invader (Symstad 2000; Fargione *et al.* 2003). Furthermore, some invasive species can behave like 'ecosystem engineers' and modify important ecological processes such as disturbance regimes and nutrient cycling (Yurkonis *et al.* 2005).

Heywood (1989) argued that invasion of tropical forests follows widespread disruption or conversion of the primary forest to secondary successional communities, and invasive plant species are thought to establish mostly on forest edges and in disturbed closed forest with high light and nutrient availability (Milbau & Nijs 2004; Gilbert & Lechowizc 2005). As a result, closed-canopied vegetation has long been regarded as highly resistant to invasion (Cavers & Harper 1967; Rejmánek 1989; Von Holle *et al.* 2003). However,

evidence is mounting that shade-tolerant invasive plants can invade forests with relatively closed canopies (Murphy *et al.* 2008; Martin *et al.* 2009). There is a need for detailed studies on the effects of such invasive plant species in tropical forests. The susceptibility of a community to invasion of new species can be assessed quantitatively to determine community invasibility (Burke & Grime 1996) – an approach that takes into account ecosystem and native species properties (Lonsdale 1999; Hejda *et al.* 2009). But given the difficulties associated with collecting quantitative data in species-rich tropical forest, such studies are few (e.g. Mullah *et al.* 2014).

Although high species richness has been hypothesized to confer resistance to the invasion of a community (e.g. Elton 1958; Hooper *et al.* 2005), many studies present contrasting results (e.g. Levine & D'Antonio 1999; Shea & Chesson 2002; Hejda *et al.* 2009). It is assumed that higher species richness may repel invasion because species-rich communities exploit available resources more completely and thus leave fewer niches open for colonization (Levine & D'Antonio 1999). However, community vulnerability to invasion may depend on many factors, such as species composition, interactions and successional stage (Shea & Chesson 2002; Hejda *et al.* 2009). Community attributes associated with a healthy ecosystem such as high indigenous species richness and evenness may also potentially facilitate species invasion by conferring protection from pests or predators (Bruno *et al.* 2003; Dunstan & Johnson 2006).

Comprehensive reviews of invasive plant impacts have covered the ecological effects of invaders (Pyšek *et al.* 2012), the modification of nutrient cycles (Ehrenfeld 2003), mechanisms of plant invasion (Levine *et al.* 2003) and competition (Vila & Weiner 2004; Vila *et al.* 2004). Synthesizing accurate predictions of the invasive potential of specific plant taxa was proven difficult, and there is no universal trait that can be applied to predict invasiveness (Rejmanek & Richardson 1996; Hayes & Barry 2008; Thompson & Davis 2011; Morin *et al.* 2013). The few studies that have examined the relationship between invasive species and community properties have shown that impacts on species diversity and composition depend on the individual invader (Hejda & Pyšek 2006; Hulme & Bremner 2006). Similarly, native species also differ in their relationship with the invader, as some are excluded from a community more easily than others (Standish *et al.* 2001). A quantitative way to assess invasibility of a non-native species on a community is to examine how the adults, saplings and seedlings of an invader affect community attributes of the community being invaded.

In Australia the presence of strawberry guava, *Psidium cattleianum* Sabine (Myrtaceae), a shade-tolerant invasive shrub or small tree species, was first documented in the 1940s (Atlas of Living Australia 2014) and has since been recorded from several tropical and subtropical rainforest habitats. *Psidium cattleianum* is able to form monospecific stands and has been implicated in studies from numerous tropical regions to alter habitats (Motley 2005), modify successional trajectories and impede native plant regeneration (Lorence & Sussman 1986; Fleischmann 1997), pose a threat to endangered plant species (Meyer 2004) and interact with other invasive species, hence causing further ecological damage (i.e. pigs: Huenneke & Vitousek 1990). The presence of *P. cattleianum* in tropical and subtropical regions in Australia is therefore a matter of concern. Having been gazetted as a World Heritage Area in 1988 and having relatively long-term and comprehensive records of land use, the Australian Wet Tropics provides an important setting for examining the invasibility of *P. cattleianum*. We (i) characterize the demographics of *P. cattleianum* populations across rainforest sites of different stages of successional development; (ii) compare various community (e.g. species diversity indices and abundance of other species) and site (e.g. soil properties, aspect and slope) attributes between *P. cattleianum*-invaded and non-invaded sites; and (iii) model *P. cattleianum* invasibility in relation to these attributes.

METHODS

Study species and sites

Psidium cattleianum is an evergreen shrub or small tree (2–4 m, occasionally taller) native to the Atlantic forests of Brazil, extending from the Ceará state of Northeast Brazil to Uruguay (Reitz *et al.* 1983; Sobral *et al.* 2013). The species has been cultivated, to a small extent, in various parts of the world for its edible fruits and ornamental value (Patel 2012). The species embodies a wide range of traits that could facilitate its invasibility and affect ecosystems, including: a high relative growth rate (Pattison *et al.* 1998), extremely abundant fruit and seed set (Huenneke & Vitousek 1990), high coppicing and resprouting ability (Huenneke 1989), an ability to form dense thickets (Uowolo & Denslow 2008) and high stemflow that funnels water, to increase water available for transpiration (Safeeq & Fares 2014). As a result of human introductions and interactions with birds or feral mammals (i.e. feral pigs; Diong 1982), *P. cattleianum* has become invasive in at least 31 countries, representing major biogeographical regions in tropical to subtropical zones (Ellshoff *et al.* 1995; Richardson & Rejma'nek 2011). Hence, *P. cattleianum* is listed in the Global Invasive Species Database as being among the world's top 100 worst invasive alien species (Global Invasive Species Database 2014), with the islands of Hawaii (Huenneke & Vitousek 1990), Mauritius (Lorence & Sussman 1986), Réunion (Tassin *et al.* 2006) and Seychelles (Fleischmann 1997; Dietz *et al.* 2004) being especially affected.
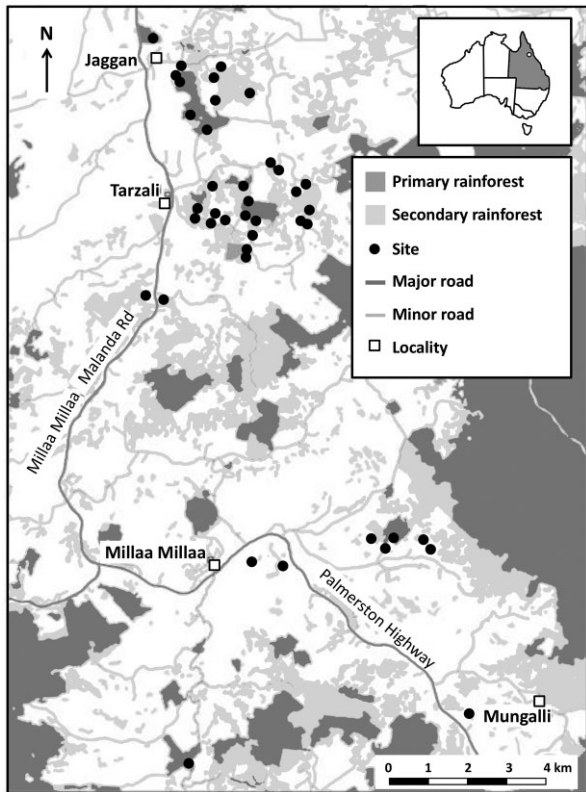
Fig. 1. Locations of sample sites on the Atherton Table-lands, Queensland, Australia.

The form of *P. cattleianum* afflicting Australia is red-fruited, and the earliest known collection in 1945 was from Koah, north Queensland (Atlas of Living Australia 2014). The species was probably introduced for its edible fruits, and is presently classed as a potential environmental weed (Csurhes & Edwards 1998). It is now known to be invasive in various tropical and subtropical locations stretching from north Queensland to northern New South Wales (Downey *et al.* 2010) and also on some offshore islands like Lord Howe (Auld & Hutton 2004) and Norfolk (Mills 2012).

Our study sites are on the Atherton Tablelands (17° 21′ S, 145° 35′ E) in north-eastern Queensland, and ranged in altitude from 700–830 m asl (Fig. 1). Annual rainfall in the study area ranges from 1700 to 2600 mm with a distinct dry season (where mean monthly rainfall is less than 100 mm) from July to September. Mean monthly temperatures range from a minimum of 10°C to 29°C. The vegetation of the study sites comprises upland tropical evergreen rainforest in various stages of recovery from anthropogenic disturbance. Primary rainforests are confined to ranging from 1 to 600 ha (Laurance & Laurance 1999), and secondary rainforests comprises >11 000 ha and distributed into almost 2500 patches (Sloan *et al.* in press).

Survey methods

A total of 33 regrowth rainforest sites on soils derived from granite and basalt were selected along a successional

chronosequence, which ranged in age of abandonment from 3 to 69 years. An additional eight sites representing primary rainforest were sampled for comparison. *Psidium cattleianum* was present at 27 sites, all of which were successional. Adult *P. cattleianum* was present in 19 of these sites. We determined that site ages was using a range of Queensland State Government digital or hardcopy aerial photography (1943–2011), and satellite imagery from Google Earth from 2002 to 2014 (©2014 Google Image, ©2014 DigitalGlobe), and Queensland Globe from 2011 and 2014 (©State of Queensland 2013, ©CNES 2012, Spot Image S.A. France, ©2013 Pitney Bowes). Each image was examined for vegetation cover, using stereo pairs of images where available (1943–1997). Otherwise, aerial photographs were scanned at high resolution and successive pairs of digital images were compared side-by-side on-screen. We determined the age since abandonment to be the mid-point between successive images where pasture had been replaced by another vegetation type (e.g. shrubby weeds, scramblers, shrubs and scattered tree saplings).

At each site, we recorded plant community structure and composition along 50 m transects, using survey methods described in Preece *et al.* (2012). All stems >2.5 m in height and <10 cm dbh were recorded in 3 m belt transects and trees ≥10 cm dbh in 10 m belt transects. At 5 m intervals along the transect we counted seedlings in 1×1 m plots, and estimated canopy cover using a spherical crown densiometer, canopy height and slope using a clinometer, and aspect with a compass.

Distances to continuous rainforest blocks, to remnant primary rainforest, to waterbodies and to the nearest anthropogenic land-use feature (roads, pastures, abandoned fallows, human residences, etc.) and elevation were derived from aerial photography and GIS layers. For each site, we obtained 10 soil samples – one every 5 m along the transect and a single sample 5 m perpendicular to transect. At each sample site, the top 30 cm of the soil layer (after removing the leaf litter) was collected with a hand auger. The 10 soil samples for each site were pooled and sent to a commercial laboratory (Nutrient Advantage – Incitec Pivot, Southbank, Vic., Australia) for analysis. Soil particle analysis (clay, silt and sand percentages) was performed using the hydrometer method, pH was determined using a digital pH metre in a 1:5 soil–water suspension, and cation exchange capacity (CEC = sum of exchangeable cations) was obtained using standard protocols by Rayment and Lyons (2011).

Data analysis

First, we described the population structure of *P. cattleianum* across our study sites. From the 19 sites with *P. cattleianum* adults we grouped individuals (each individual being the sum of all stems or coppice shoots) into six dbh size class categories ranging from 2.5 cm to 17.5 cm dbh. To further determine if duration since site abandonment had an effect on *P. cattleianum* demographics, we plotted *P. cattleianum* size-classes segregated into three categories of forest succession (years since abandonment: <15; 15–29 and; >30 years). A chi-squared test was used to test for homogeneity of size class distribution in the different forest succession categories.

Second, we compared the density of *P. cattleianum* (mean number of individual stems) with that of four common shrub species that occupy the same ecological niche in the study area. This allowed us to examine the relative proportions of the shrub niche occupied by these species in the understorey. We restricted this demographic comparison to individuals within the stem size range of 2.5–10 cm dbh for the shrub species: *Guioa lasioneura*, *Neolitsea dealbata*, *Rhodamnia sessiliflora* and *Rhodomyrtus pervagata*. We used Kruskal–Wallis H test to test for differences in the mean percentage of individuals that formed multi-stemmed plants among the five shrub species.

Third, we examine what environmental parameters best account for *P. cattleianum* basal area and seedling (stems <2.5 cm) density. We used two sets of environmental variables, one pertaining to vegetation community attributes and another to site attributes. Community attributes included Shannon Weiner diversity index, evenness and the densities of grass clumps and tree, shrub, vine, herb, ferns and exotic species seedlings. We also computed and compared the basal area of *G. lasioneura*, *N. dealbata*, *R. sessiliflora* and *R. pervagata* between invaded and non-invaded sites, to examine if these species occupy more niche space in non-invaded secondary forest sites. We calculated the basal area (m^2) of each species as $(dbh/200)^2 \times 3.14$, and in the case of multiple-stemmed individuals, the basal area was the sum of all stems. Site attributes included canopy height, slope, aspect, soil pH and CEC, and fractions of sand and clay. We used Mann–Whitney *U*-tests ($P < 0.05$) to compare these attributes between *P. cattleianum*-invaded ($n = 27$) and non-invaded secondary rainforest sites ($n = 6$). As the differences between primary and secondary forests were largely floristic (see later), we restricted these univariate comparisons between 27 *P. cattleianum*-invaded and the six non-invaded secondary forest sites.

Fourth, we examined how basal areas and seedling densities of *P. cattleianum* varied among communities and correlated with site attributes, using all 41 sites, including sites with and without *P. cattleianum*. Site attributes and community attributes were examined in separate models. For the community attribute models we included gradients in community composition as an additional explanatory variable. To achieve this, we performed non-metric multidimensional scaling (NMDS) ordinations on species presence/absence data (excluding the presence of *P. cattleianum*) using Bray–Curtis similarity. NMDS ordinations were performed using the vegan package (Oksanen *et al*. 2014) in R 2.10.0 (R Development Core Team 2009). The NMDS axes reflect floristic gradients, which are associated with the distribution of mature-phase rainforest species. NMDS axis 1 increases with greater numbers of mature-phase species (Fig. 2). A standard protocol of data exploration was used to determine significantly correlated variables, which were excluded from the models. In the final generalized linear models (GLM) we included nine community attributes (NMDS axis 1; NMDS axis 2; grass clump density; seedling densities of vines, shrubs, trees and other exotic species; and canopy height) and five site attributes (CEC, distance to remnant forest, pH and sand fraction). Because the response variables were zero-inflated, we fitted our GLM models using a Tweedie distribution and log link (Dunn *et al*. 2009). GLM models were fitted in SPSS (IBM Corp 2011).
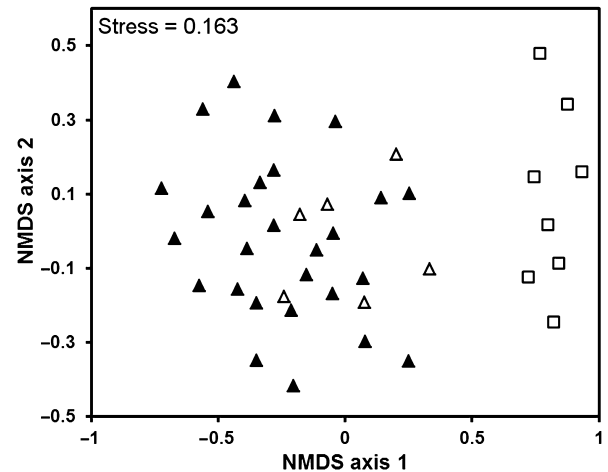

Fig. 2. Ordinations of the floristic composition of species presence–absence (with the site presences of *Psidium cattleianum* omitted) of 41 tropical rainforest sites in the Atherton Tablelands, Australia, using non-metric multidimensional scaling (NMDS). Closed and open symbols respectively represent *P. cattleianum*-invaded and non-invaded sites. Open squares represent primary rainforest sites, and open and closed triangles represent secondary forest sites. The gradients represented are largely floristic. NMDS axis 1 shows no significant correlation with any of the site and community variables measured in the study, and NMDS axis 2 correlated positively only with soil cation exchange capacity ($r = 0.424$, $P = 0.006$).

RESULTS

Psidium cattleianum demographics

Psidium cattleianum was recorded in 27 of the 41 sampled sites, comprising 326 established stems (including all coppice stems) and accounting for 7.9% of all individual stems recorded in the study. We counted 1324 seedlings of *P. cattleianum*, which represents 19.5% of all seedlings recorded and also the highest number of seedlings per species. *Psidium cattleianum* was also the most abundant non-native species encountered across all of our study sites. Among four other woody non-native species with basal area measurements (*Cinnamomum camphora*, *Lantana camara*, *Ligustrum sinense*, *Michelia champaca*), *P. cattleianum* comprised 88.3% of the stems and 49.9% of their total basal area. Among non-native seedlings and herbs (<2.5 cm dbh), *P. cattleianum* comprised 59% of the stems.

The size class distribution of *P. cattleianum* individuals exhibited a consistent reverse J-shaped distribution regardless of the time since forest abandonment (Fig. 3). However, individuals with a dbh size class above 12.5 cm were found only in sites from the recently abandoned category (<15 years) ($\chi^2 = 4.492$, d.f. = 1,
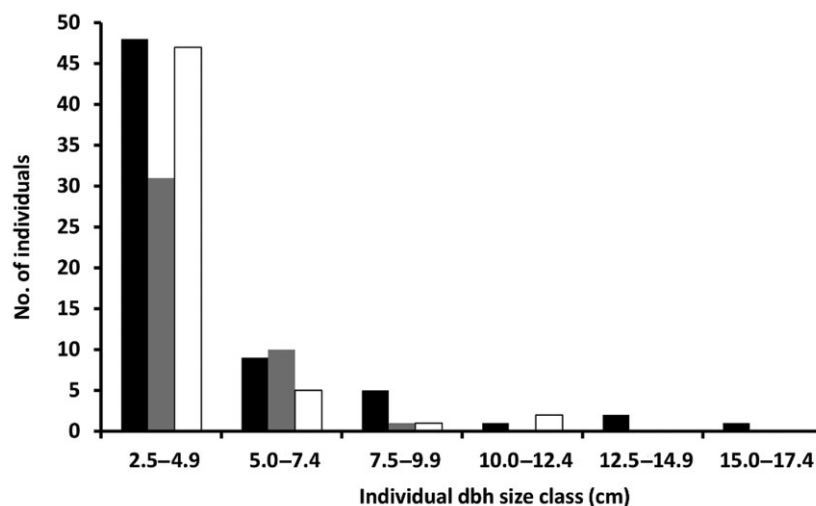
Fig. 3. Size class distributions of *Psidium cattleianum* individuals (i.e. all multistems regardless of number considered part of that individual) from the sites divided into three age classes based on their number of years since abandonment (black: <15 years; grey: 15–29 years; white: >30 years).

$P = 0.034$) – a result that can be attributed to one particularly infested site.

Among the shrub species compared across the 19 sites with established *P. cattleianum* individuals, *P. cattleianum* was the most common shrub species encountered and exhibited the highest mean number of individual stems within the 2.5–10 cm dbh range (Fig. 4a). Although all the four native shrub species formed multi-stemmed plants, none exhibited as high a percentage of multi-stemmed individuals as *P. cattleianum* (Kruskal–Wallis *H*-test: $\chi^2 = 10.8$, d.f. = 4, $P = 0.009$; Fig. 4b). *Psidium cattleianum* also achieved almost four times the stem number of the most abundant native species *R. pervagata* (Fig. 4c).

Environmental correlates of
P. cattleianum invasion

Relative to non-invaded sites, invaded sites tended to be more west facing (higher aspect degrees; $P = 0.011$) and were further away from intact forest blocks ($P = 0.009$). However, invaded and non-invaded sites did not differ in canopy cover ($P > 0.05$). Invaded sites also had higher grass clump densities, higher densities of seedlings of tree species and native groundcover species, but lower densities of seedlings of other exotic species (Table 1). Importantly, the diversity and the basal areas of the four understorey shrub species (*G. lasioneura, N. dealbata, R. pervagata, R. sessiliflora*) did not differ between *P. cattleianum*-invaded and non-invaded sites (all $P > 0.05$).

Community and environmental correlates of
P. cattleianum invasion

For each of the two response variables, *P. cattleianum* basal area and seedling density, we fitted two sets of GLMs – one using community attributes and the other using site attributes. Across the 41 sites, *P. cattleianum* basal area and seedling density increased as forest canopy height declined (Table 2). *Psidium cattleianum* seedling density further exhibited negative relationships with NMDS axis 1 and the seedling densities of other exotic species. No significant relationship with the other predictive variables was detected. Both *P. cattleianum* basal area and seedling density increased with distance to remnant forest, soil pH and a declined with soil CEC. Finally, *P. cattleianum* seedling density associated with soil sand fraction, suggesting seedling recruitment, is higher in sandy soils (Table 3).

DISCUSSION

Our study of secondary forest communities revealed that *P. cattleianum* is now well-established in upland successional forests of the Australian Wet Tropics. Adult stems occurred in 65% of our study sites and seedlings comprised 20% of the 6800 individuals that we identified. Other shade-tolerant understorey weeds in rainforest in the current study include *Ardisia crenata* and *C. camphora*, but none of these achieved stem densities or basal areas as high as *P. cattleianum*. Contrary to expectation the age of secondary forest did not influence the number of *P. cattleianum* individuals or their size, with almost equal numbers
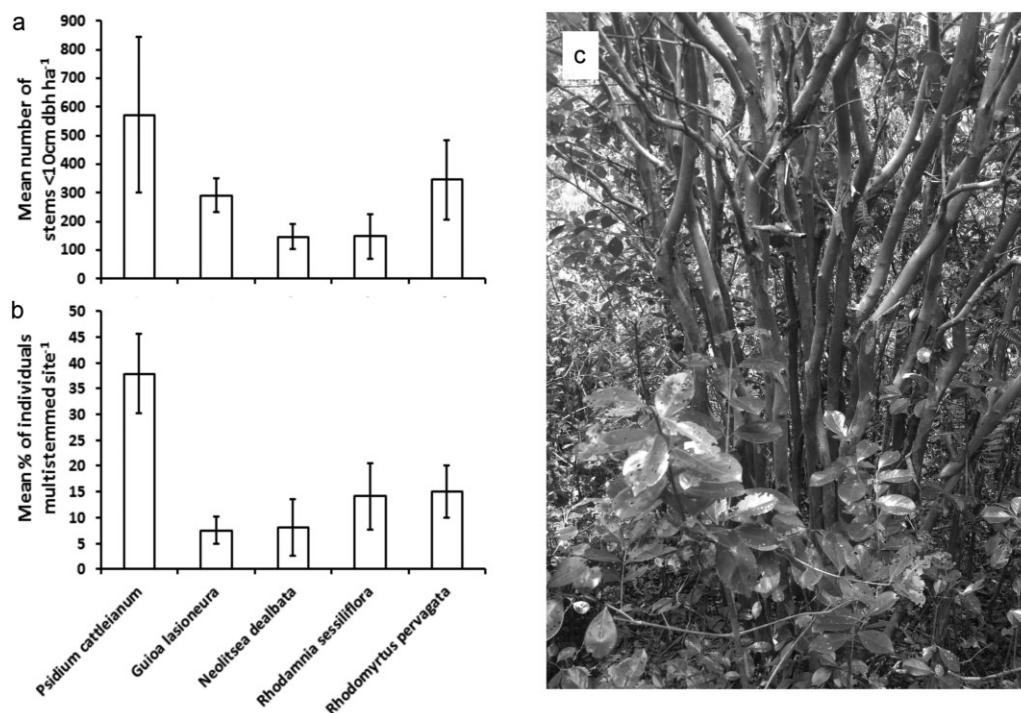
Fig. 4. Comparisons of the mean (±standard errors) of (a) number of stems of the top five most abundant stems-species within the 2.5–10 cm diameter at breast height range, and (b) percentage of individuals with multiple stems. The means of stems per hectare were extrapolated from nineteen 50×3 m transects with *Psidium cattleianum* invasion. Across all woody species, the greatest capacity for forming multiple-stemmed individuals was observed in *P. cattleianum* (c), with up to 21 stems >2.5 cm dbh.

Table 1. Means (±1SD) of significantly different site and community attributes between *Psidium cattleianum*-invaded ($n = 27$) and non-invaded ($n = 6$) secondary rainforest plots (50×10 m). Seedling averages are of 10 quadrats (1×1 m) per plot extrapolated to 500 m². Significance was determined by Mann–Whitney U-tests ($P < 0.05$)

	P. cattleianum-invaded sites ($n = 27$)		Non-invaded sites ($n = 6$)		Mann–Whitney U-tests	
Descriptor	Mean	±SD	Mean	±SD	U-statistic	P
Site attributes						
Aspect (°)	183.41	107.52	159.00	66.02	26	0.011
Distance to intact forest block (m)	2.63	1.21	2.48	0.98	25	0.009
Community attributes						
Grass clump density	687.04	1095.85	33.33	60.55	6	<0.001
Other exotics seedling density	1411.11	2625.59	1533.33	3537.47	27.5	0.013
Tree species seedling density	3642.59	9037.77	1758.33	1225.73	36.5	0.040
Total seedling density of native groundcover	5925.93	9772.97	3700.00	2230.47	27.5	0.013
Total seedling density (excluding *Psidium*)	7338.89	9962.43	5233.33	3867.51	33	0.026

found in young and older forests, and some of the largest stems were found at the youngest sites. However *P. cattleianum* was strongly associated with sites that had low forest canopies and abundant in grass, herbs, which suggests that this species may spread into abandoned lands and secondary rainforest in this region.

Little invasion of *P. cattleianum* into primary rainforest was detected, suggesting that primary rainforest may have some resilience to invasion. Significantly, *P. cattleianum*-invaded sites were further from intact forest blocks, which could be a result of a longer history of disturbance at these invaded sites. Similarly, invasions were more prominent further from primary rainforest fragments. It is unlikely that the lack of *P. cattleianum* in the eight primary rainforest remnants was due to seed limitation as the species produces abundant seed and exerts considerable propagule

Table 2.   Results of generalized linear models (GLM) fitted with community attributes to estimates of *Psidium cattleianum* basal area and seedling density across 41 rainforest sites (8 primary and 33 secondary). NMDS axis 1 is an ordination axis reflecting a floristic gradient that increases with mature-phase rainforest species (See Fig. 2)

	Psidium cattleianum basal area				*Psidium cattleianum* seedling density			
Attribute	Estimate	SE	Walds Chi-Square	P	Estimate	SE	Walds Chi-Square	P
(Intercept)	−1.815	1.614	1.264	0.261[ns]	9.591	1.393	47.426	<0.001***
NMDS axis 1	−1.038	0.732	2.011	0.156[ns]	−1.764	0.631	7.830	0.005**
NMDS axis 2	−0.335	0.755	0.197	0.657[ns]	−.538	0.667	0.650	0.420[ns]
Grass clump density	−0.003	0.019	0.029	0.864[ns]	0.016	0.015	1.129	0.288[ns]
Vine seedling density	−0.050	0.054	0.867	0.352[ns]	−0.068	0.046	2.215	0.137[ns]
Shrub seedling density	0.013	0.029	0.197	0.657[ns]	0.026	0.025	1.100	0.294[ns]
Tree seedling density	−0.002	0.008	0.048	0.826[ns]	−0.001	0.006	0.008	0.928[ns]
Seedling density of other exotic species	−0.013	0.012	1.244	0.265[ns]	−0.023	0.011	4.299	0.038*
Canopy height (m)	−0.204	0.071	8.219	0.004**	−0.207	0.061	11.603	0.001**

Significance levels: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. ns, not significant.

Table 3.   Results of generalized linear model (GLM) fitted with site attributes to estimates of *Psidium cattleianum* basal area and seedling density across 41 rainforest sites (8 primary and 33 secondary)

	Psidium cattleianum basal area				*Psidium cattleianum* seedling density			
Attribute	Estimate	SE	Walds Chi-Square	P	Estimate	SE	Walds Chi-Square	P
(Intercept)	−57.045	13.272	18.474	<0.001***	−62.955	11.900	27.986	<0.001***
Cation exchange capacity	−1.119	0.307	13.315	<0.001***	−0.996	0.299	11.122	0.001**
Distance to remnant forests (m)	1.891	0.598	10.015	0.002**	2.589	0.632	16.788	<0.001***
pH	73.028	19.767	13.649	<0.001***	83.323	17.471	22.745	<0.001***
Sand fraction	2.160	2.446	0.780	0.377[ns]	7.216	2.552	7.997	0.005**

Significance levels: **$P < 0.01$, ***$P < 0.001$. ns, not significant.

pressure wherever found. Taking into account the well-established shade tolerance of the species (Huenneke & Vitousek 1990; Fleischmann 1997), we can only hypothesize that some other undetermined factor reduces seedling recruitment. Soil pathogens, seed or seedling predators, competition with or allelopathy from established tree species or combinations of these factors can all potentially limit recruitment.

Psidium cattleianum was the most common stem (<10 cm dbh) encountered in secondary rainforests and occurred in 82% of these sites. Relative to non-invaded sites, invaded sites were generally abandoned more recently, and associated with a higher abundance of grass and herbs, which suggests that if there is no seed limitation in the area then recruitment is higher in younger rather than older secondary rainforests. Although *P. cattleianum* invasion appeared to be favoured by a number of community and site attributes, in particular, soil structural and chemical attributes, the persistence and demographic structure of

P. cattleianum in these forests suggests that further spread is likely.

Site and community correlates of *P. cattleianum* invasibility

Communities with high species richness are thought to be resistant to invasion (Hooper *et al.* 2005; Martin *et al.* 2009) because local niches are filled by representatives from different functional groups (Zavaleta & Hulvey 2007). We found no direct evidence of this in our analyses. However, we found a negative relationship between *P. cattleianum* seedling density and the gradient of community composition determined in our NMDS ordination, which in general segregated secondary rainforest from primary rainforest (Fig. 2). The primary rainforest in turn had a higher Shannon–Weiner diversity than all secondary forest sites as a group (Mann–Whitney U, $P < 0.001$), so it is plausible

that the floristic composition and higher diversity of the primary rainforests either separately or in combination suppress the establishment of *P. cattleianum* seedlings. Likewise, the negative association of canopy height with density of *P. cattleianum* seedlings is likely to be a function of the generally taller canopy found in primary rainforests. However, it is notable that canopy cover did not have a significant effect on *P. cattleianum* basal areas or seedling densities, reinforcing the broad range of light conditions the species can tolerate.

The invasibility of a community is thought to decrease when the native species matrix includes species of similar functional groups or with traits similar to the invader because such species will fill a greater proportion of potentially available niches (Elton 1958; Gilbert & Lechowizc 2005). Several native understorey shrubs, *G. lasioneura*, *N. dealbata*, *R. pervagata* and *R. sessiliflora* that are shade tolerant, coppice like *P. cattleianum*. These species could be interpreted as belonging to the same functional group but the mean basal areas of these species did not differ in *P. cattleianum*-invaded and non-invaded secondary forest sites. Follow-up studies using functional niche-modelling (e.g. Moles *et al.* 2008) may provide insight on whether *P. cattleianum* is occupying empty niches in these secondary rainforests.

Empirical observations and implications of *P. cattleianum* invasion

The probability plant invasiveness increases if a species reproduces vegetatively and has a history of invasion elsewhere (Kolar & Lodge 2001). *Psidium cattleianum* meets both these criteria – it has the highest number of coppice stems of any woody species examined in the study and has a significant history of invasion in Hawaii and many other tropical regions dating back to the early- to mid-1800s (Lorence & Sussman 1986; Huenneke & Vitousek 1990; Kueffer *et al.* 2008). With prolific seeds and seedling establishment and the ability to survive under a broad range of light conditions (Loh & Daehler 2007), *P. cattleianum* fits the profile of a 'super invader' (Daehler 2003). Given that *P. cattleianum* has established self-sustaining populations in tropical north Queensland, the invasion of more areas is imminent.

The continuing establishment and spread of *P. cattleianum* in Australian rainforest could also be favoured by the apparent lack of natural herbivore enemies. In our study, *P. cattleianum* leaves were observed to be always in a healthy state and with no signs of herbivory. This is consistent with the enemy-release hypothesis of Keane and Crawley (2002), which posits that there is greater impact of natural enemies on natives than on a given exotic species in its introduced range. In Hawaii, Shiels *et al.* (2014) reported experimental findings of *P. cattleianum* seedlings being less susceptible to herbivory than native plant seedlings. Similarly, myrtle rust, which is an exotic rust disease affecting members of the myrtle family (Morin *et al.* 2011), has been observed to affect several native members of the myrtle family in the study sites. In contrast, we have observed no certifiable cases of infection in *P. cattleianum*, even when growing adjacent to myrtle rust-infected native *R. pervagata* and *R. sessiliflora*.

Another set of features that could facilitate the success of *P. cattleianum* is the rapidity with which it attains reproductive maturity, and its dispersal mechanism. We have observed stems below 30 cm in height and less than 2.5 cm in stem diameter in flower. The seedling density of *P. cattleianum* was also the highest among all species encountered, reflecting the copious fruit set from preceding fruiting seasons. *Psidium cattleianum* fruits are eaten by native birds and spectacled flying foxes (Cooper & Cooper 2004), which undoubtedly aids in the spread of the species.

The ability of *P. cattleianum* to persist under shade and to attain high basal areas and stems densities can have serious ecological consequences. *Psidium cattleianum* comprised about 60% of woody basal area and 85% of the seedlings at an extreme site that had been abandoned for 12.5 years. At this stage there is insufficient evidence to conclude whether the species will self-thin and be replaced as the forest matures, although this is unlikely in light of the shade tolerance of the species. For instance, Zimmerman *et al.* (2008) found in lowland Hawaii that the functional and compositional integrity of forests were increasingly compromised by *P. cattleianum* invasion, even though these forests remained at least partially intact in several locations. Likewise, *P. cattleianum* invasion has been implicated in modifying successional trajectories in Mauritius (Lorence & Sussman 1986) and on the Seychelles (Fleischmann 1997). How severely *P. cattleianum* invasion will arrest the succession of rainforest in the region will require monitoring. However, we may speculate that in the absence of *P. cattleianum* invasion, successional trajectories involving the native woody genera *Acacia*, *Alphitonia* or *Rhodomyrtus* (Yeo & Fensham 2014; Goosem *et al.* in review) would proceed.

Although it is arguable that *P. cattleianum* may at least provide some ecosystem services such as habitat and seasonal food resources for native animals, the species has potential to alter ecosystem structure and function in ways that are difficult or impossible to reverse (Gaertner *et al.* 2014). We therefore advocate that *P. cattleianum* be prioritized for control in Australia. The current national and state listings are inadequate for *P. cattleianum*, and a first step could be

to list the species as an environmental weed under the National Environmental Alert List (Department of the Environment 2014). With increased and sufficient public awareness, and given the recent occurrence in Australia relative to other infested tropical regions, controlling *P. cattleianum* invasion may be achievable. However decisive action is required, and control efforts need to be sustained and monitored for efficacy.

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REFERENCES

Atlas of Living Australia. (2014) Psidium cattleianum var. littorale [Cited 29 October 2014.] Available from URL: http://www.ala.org.au

Auld T. D. & Hutton I. (2004) Conservation issues for the vascular flora of Lord Howe Island. *Cunninghamia* **8,** 490–500.

Brown R. L. & Fridley J. D. (2003) Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. *Oikos* **102,** 15–24.

Bruno J. F., Stachowicz J. J. & Bertness M. D. (2003) Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* **18,** 119–25.

Burke M. J. & Grime W. J. P. (1996) An experimental study of plant community invasibility. *Ecology* **77,** 776–90.

Cavers P. B. & Harper J. L. (1967) Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. *J. Ecol.* **55,** 59–71.

Cooper W. T. & Cooper W. (2004) *Fruits of the Australian Tropical Rainforest*. Nokomis Editions, Melbourne.

Csurhes S. & Edwards R. (1998) *Potential Environmental Weeds in Australia*. Queensland Department of Natural Resources, Land Protection, Coorparoo Delivery Centre, Australia.

Daehler C. C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Ann. Rev. Ecol. Syst.* **34,** 183–211.

Department of the Environment. (2014) National Environment Alert List. [Cited 8 December 2014.] Available from URL: http://www.environment.gov.au/biodiversity/invasive/weeds/weeds/lists/alert.html

Dietz H., Wirth L. R. & Buschmann H. (2004) Variation in herbivore damage to invasive and native woody plant species in open forest vegetation on Mahé, Seychelles. *Biol. Invasions* **6,** 511–21.

Diong C. H. (1982) *Population biology and management of the feral pig (*Sus scrofa*) in Kipahulu Valley, Maui* (PhD dissertation). University of Hawaii Manoa, Hawaii.

Ditham R. K., Tylianakis J. M., Gemmel N. J., Rand T. A. & Ewers R. M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22,** 489–96.

Downey P. O., Scanlon T. J. & Hosking J. R. (2010) Prioritizing weed species based on their threat and ability to impact on biodiversity: a case study from New South Wales. *Plant Protect. Quart.* **25,** 111–26.

Dunn P. K., Smyth G. K., Walker N., Saveliev A. A. & Smith G. M. (2009) Series evaluation of Tweedie exponential dispersion model densities. *Stat. Comput.* **15,** 267–80.

Dunstan P. K. & Johnson C. R. (2006) Linking richness, community variability, and invasion resistance with patch size. *Ecology* **87,** 2842–50.

Ehrenfeld J. G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6,** 503–23.

Ellshoff Z. E., Gardner D. E., Wikler C. & Smith C. W. (1995) *Annotated bibliography of the genus* Psidium *with emphasis on* P. cattleianum *(Strawberry guava) and* P. guajava *(common guava), forest weeds in Hawai'i.* Technical Report 95. Department of Botany, Honolulu, Hawai'i.

Elton C. S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

Fargione J., Brown C. S. & Tilman D. (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *PNAS* **100,** 8916–20.

Fleischmann K. (1997) Invasion of alien woody plants on the islands of Mahé and Silhouette, Seychelles. *J. Veg. Sci.* **8,** 5–12.

Gaertner M., Biggs R., Te Beest M., Hui C., Molofsky J. & Richardson D. M. (2014) Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships. *Divers. Distrib.* **20,** 733–44.

Gilbert B. & Lechowizc M. J. (2005) Invasibility and abiotic gradients: the positive correlation between native and exotics plant diversity. *Ecology* **86,** 1848–55.

Global Invasive Species Database. (2014) *Psidium cattleianum*. [Cited 27 September 2014.] Available from URL: http://www.issg.org/database/species/ecology.asp?si=59&fr=1&sts=sss&lang=EN

Goosem M. W., Paz C. P., Fensham R. J., Preece N. D., Goosem S. & Laurance S. G. W. (in review) Delayed recovery of species diversity and community composition in secondary forests in tropical Australia. *J. Veg. Sci.*

Hager H. A. (2004) Competitive effect versus competitive response of invasive and native wetland plant species. *Oecologia* **139,** 140–9.

Hayes K. R. & Barry S. C. (2008) Are there any consistent predictors of invasion success? *Biol. Invasions* **10,** 483–506.

Hejda M. & Pyšek P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol. Conserv.* **132,** 143–52.

Hejda M., Pyšek P. & Jarošík V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J. Ecol.* **97,** 393–403.

Heywood V. H. (1989) Patterns, extents and modes of invasions by terrestrial plants. In: *Biological Invasions: a Global Perspective, SCOPE 37* (eds J. A. Drake, H. A. Mooney, F. di Castri *et al.*) pp. 31–60. John Wiley, New York.

Hooper D. U., Chapin I. I. I. F. S., Ewel J. J. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monographs* **75,** 3–35.

Huenneke L. F. (1989) Contribution of sprouting behavior to population persistence in woody species. *Amer. J. Bot.* **76** (Suppl), 84–5.

Huenneke L. F. & Vitousek P. M. (1990) Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: implications for management of native Hawaiian forests. *Biol. Conserv.* **53,** 199–211.

Hulme P. E. & Bremner E. T. (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J. Appl. Ecol.* **43,** 43–50.

IBM Corp. (2011) *IBM SPSS Statistics for Windows, Version 20.0.* IBM Corp, Armonk, NY.

Keane R. M. & Crawley M. J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17,** 164–70.

Kolar C. S. & Lodge D. M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16,** 199–204.

Kueffer C., Klinger G., Zirfass K., Schumacher E., Edwards P. J. & Güsewell S. (2008) Invasive trees show only weak potential to impact nutrient dynamics in phosphorus-poor tropical forests in the Seychelles. *Funct. Ecol.* **22,** 359–66.

Laurance S. G. W. & Laurance W. F. (1999) Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. *Biol. Conserv.* **91,** 231–9.

Levine J. M. & D'Antonio C. M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87,** 15–26.

Levine J. M., Vila M., D'Antonio C. M., Dukes J. S., Grigulis K. & Lavorel S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc. Biol. Sci.* **270,** 775–81.

Loh R. K. & Daehler C. C. (2007) Influence of invasive tree kill rates on native and invasive plant establishment in a Hawaiian forest. *Restor. Ecol.* **15,** 199–211.

Lonsdale W. M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80,** 1522–36.

Lorence D. H. & Sussman R. W. (1986) Exotic species invasion into Mauritius wet forest remnants. *J. Trop. Ecol.* **2,** 147–62.

Martin P. H., Canham C. D. & Marks P. L. (2009) Why forests appear resistant to exotic plant invasions: intentional introductions stand dynamics and the role of shade tolerance. *Front. Ecol. Environ.* **7,** 142–9.

Meyer J.-Y. (2004) Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia. *Pacific Sci.* **58,** 357–75.

Milbau A. & Nijs I. (2004) The role of species traits (invasiveness) and ecosystem characteristics (invasibility) in grassland invasions: a framework. *Weed Technol.* **18,** 1301–4.

Mills K. (2012) The endemic flora of Norfolk Island: conservation challenges on a remote oceanic island. *Aust. Plant Conserv.* **21,** 19–21.

Moles A. T., Gruber M. A. M. & Bonser S. P. (2008) A new framework for predicting invasive plant species. *J. Ecol.* **96,** 13–17.

Morin L., Aveyard R. & Lidbetter J. (2011) *Myrtle rust: host testing under controlled conditions.* NSW Department of Primary Industries, West Pennant Hills, NSW, Australia.

Morin L., Paini D. R. & Randall R. P. (2013) Can global weed assemblages be used to predict future weeds? *PLoS ONE* **8,** e55547.

Motley T. J. (2005) *Tetraplasandra lydgatei* (Araliaceae): taxonomic recognition of a rare, endemic species from O'ahu, Hawaiian Islands. *Pac. Sci.* **59,** 105–10.

Mullah C. J. A., Klanderud K., Totland Ø. & Odee D. (2014) Community invasibility and invasion by non-native *Fraxinus pennsylvanica* trees in a degraded tropical forest. *Biol. Invasions* **16,** 2747–55.

Murphy H. T., Hardesty B. D., Fletcher C. S., Metcalfe D. J., Westcott D. A. & Brooks S. J. (2008) Predicting dispersal and recruitment of *Miconia calvescens* (Melastomataceae) in Australian tropical rainforests. *Biol. Invasions* **10,** 925–36.

Oksanen J., Blanchet F. G., Kindt R. *et al.* (2014) Package vegan: community ecology package. Available from URL: http://CRAN.R-project.org/package=vegan. [Cited 21 February 2014.].

Ortega Y. K. & Pearson D. E. (2005) Strong versus weak invaders of natural plant communities: distinguishing invasibility from impact. *Ecol. Appl.* **15,** 651–61.

Patel S. (2012) Exotic tropical plant *Psidium cattleianum*: a review on prospects and threats. *Rev. Environ. Sci. Biotech.* **11,** 243–8.

Pattison R. R., Goldstein G. & Ares A. (1998) Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* **117,** 449–59.

Preece N. D., Crowley G. M., Lawes M. J. & Van Oosterzee P. (2012) Comparing above-ground biomass among forest types in the Wet Tropics: small stems and plantation types matter in carbon accounting. *Forest Ecol. Manag.* **264,** 228–37.

Pyšek P., Jarošík V., Hulme P. E. *et al.* (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob. Change Biol.* **18,** 1725–37.

R Development Core Team. (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. [Cited 21 February 2014.] Available from URL: http://www.R-Project.org

Rayment G. E. & Lyons D. J. (2011) *Soil Chemical Methods: Australasia,* Vol. 3. CSIRO publishing, Melbourne.

Reitz P. R., Klein R. M. & Reis A. (1983) Flora Catarinense (*Psidium*). *Sellowia* **35,** 684–715.

Rejmánek M. (1989) Invasibility of plant communities. In: *Biological Invasions. A Global Perspective* (eds J. A. Drake, H. A. Mooney, F. di Castri *et al.*) pp. 369–88. John Wiley & Sons, Chichester.

Rejmanek M. & Richardson D. M. (1996) What attributes make some plant species more invasive? *Ecology* **77,** 1655–61.

Richardson D. M. & Rejma'nek M. (2011) Trees and shrubs as invasive alien species – a global review. *Divers. Distrib.* **17,** 788–809.

Safeeq M. & Fares A. (2014) Interception losses in three non-native Hawaiian forest stands. *Hydrol. Processes* **28,** 237–54.

Shea K. & Chesson P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* **17,** 170–6.

Shiels A. B., Ennis M. K. & Shiels L. (2014) Trait-based plant mortality and preference for native versus non-native seedlings by invasive slug and snail herbivores in Hawaii. *Biol. Invasions* **16,** 1929–40.

Sloan S., Goosem M. W. & Laurance S. G. W. (in press) Tropical forest recovery following land abandonment is driven by primary rainforest distribution in an old pastoral region. *Landscape Ecol.*

Sobral M., Proença C., Souza M., Mazine F. & Lucas E. (2013) Myrtaceae in Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro. [Cited 30 January 2015.] Available from URL: http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB10858

Standish R. J., Robertson A. W. & Williams P. A. (2001) The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. *J. Appl. Ecol.* **38,** 1253–63.

Symstad A. J. (2000) A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* **81,** 99–109.

Tassin J., Riviere J.-N., Cazanove M. & Bruzzese E. (2006) Ranking of invasive woody plant species for management on Réunion Island. *Weed Res.* **46,** 388–403.

Thompson K. & Davis M. A. (2011) Why research on traits of invasive plants tells us very little. *Trends Ecol. Evol.* **26,** 155–6.

Uowolo A. L. & Denslow J. S. (2008) Characteristics of the *Psidium cattleianum* (Myrtaceae) seed bank in Hawaiian lowland wet forests. *Pacific Sci.* **62,** 129–35.

Vila M. & Weiner J. (2004) Are invasive species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* **105,** 229–38.

Vila M., Williamson M. & Lonsdale M. (2004) Competition experiments on alien weeds with crops: lessons for measuring plant invasion impact? *Biol. Invasions* **6,** 59–69.

Von Holle B., Delcourt H. R. & Simberloff D. (2003) The importance of biological inertia in plant community resistance to invasion. *J. Veg. Sci.* **14,** 425–32.

Yeo W. L. J. & Fensham R. J. (2014) Will Acacia secondary forest become rainforest in the Australian Wet Tropics?. *Forest Ecology and Management* **331,** 208–217.

Yurkonis K. A. & Meiners S. J. (2004) Invasion impacts local species turnover in a successional system. *Ecol. Letters* **7,** 764–9.

Yurkonis K. A., Meiners S. J. & Wachholder B. E. (2005) Invasion impacts diversity through altered community dynamics. *J. Ecol.* **93,** 1053–61.

Zavaleta E. S. & Hulvey K. B. (2007) Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecol.* **188,** 39–51.

Zimmerman N., Hughes R. F., Cordell S. *et al.* (2008) Patterns of primary succession of native and introduced plants in lowland wet forests in eastern Hawai'i. *Biotropica* **40,** 277–84.