



## Spatial patterns of presence, abundance, and richness of invasive woody plants in relation to urbanization in a tropical island setting

Brenda J. Lowry<sup>a,1,\*</sup>, John H. Lowry<sup>a,b</sup>, Karl J. Jarvis<sup>c</sup>, Gunnar Keppel<sup>d,e</sup>, R.Randolph Thaman<sup>a</sup>, Hans Juergen Boehmer<sup>a</sup>

<sup>a</sup> School of Geography, Earth Science and Environment, Faculty of Science, Technology and Environment, The University of the South Pacific (USP), Suva, Fiji

<sup>b</sup> School of People, Environment and Planning, College of Humanities and Social Sciences, Massey University, Palmerston North, New Zealand

<sup>c</sup> Department of Biology, Southern Utah University, Cedar City, Utah, USA

<sup>d</sup> School of Natural and Built Environments, University of South Australia, Mawson Lakes Campus, Adelaide, SA, Australia

<sup>e</sup> Biodiversity, Macroecology and Biogeography Group, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

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### ABSTRACT

Tropical Pacific island countries, many of which are less-developed, are experiencing invasions of alien plant species at rates faster than areas of comparable size elsewhere. In this paper we examine the relationship between the presence, abundance, and richness of 14 invasive woody plant (IWP) species and level of urbanization and road type in the Greater Suva Urban Area (GSUA), Fiji. One hundred and fifty-four sample locations within a 29 km transect traversing urban, peri-urban and rural land sectors on local, collector and arterial roads were surveyed. We analyzed the 14 species for frequency of occurrence across the urban-rural gradient and found spatial patterns of IWP presence differed by species. We analyzed the abundance of seven species using multi-variable regression and found abundance was more often influenced by urban-rural sector than road type, though road type had a significant effect for some species. We conclude by offering plausible explanations for differences attributed to modes of dispersal, introduction history and human activities. We include supplementary material providing detailed characterization of biology, ecology, and history of the 14 target species. These findings are expected to help inform risk assessments and management of IWP in other tropical urban-rural gradients, and especially small island developing states.

### 1. Introduction

The number of naturalized alien plant species in Pacific Island Countries (PICs) is increasing at a rate faster than other areas of similar size (van Kleunen et al., 2015). Many small island developing states in the Pacific are not equipped to cope with introduced species and the potential harm they present (Keppel et al., 2014). Isolation of the islands, relatively small island size, a lack of management infrastructure, lack of communication (Wittenberg and Cock, 2001), and limited financial, material and human resources (Tye, 2009) make the challenge of dealing with invasive species in Pacific island countries problematic (Lenz et al., 2019 in press).

The link between human activity and the establishment, propagation and spread of invasive species is well known (Heger and Boehmer, 2005; Kowarik and von der Lippe, 2006; Tye, 2009; van Kleunen et al.,

2015). Urban areas are commonly the foci of non-native plant and animal species naturalization due to varied human activities that occur through the urbanization process (McKinney, 2002; Noble, 1989; Pauchard et al., 2006; Puth and Burns, 2009). Non-native plants are commonly introduced for ornamental, agricultural, or forestry purposes (Essl et al., 2010; Lambdon et al., 2008) and may escape and become naturalized in the new environment. Species' biology and ecology are influential in the success of invasive plants, but there is also ample evidence that human resources and preferences are significant drivers of plant species presence and diversity in urban/peri-urban areas (Boone et al., 2010; Gulezian and Nyberberg, 2010; Hope et al., 2003; Kinzig et al., 2005; Luz de la Maza et al., 2002; Pauchard et al., 2006; Staudhammer et al., 2015). Socioeconomic factors, such as financial and educational resources as well as cultural biases, play an important role in the introduction of non-native species and composition of urban

\* Corresponding author at: 5 Tingey Place, Awapuni, Palmerston North, 4412 New Zealand.

E-mail addresses: [B.Lowry@massey.ac.nz](mailto:B.Lowry@massey.ac.nz) (B.J. Lowry), [J.Lowry@massey.ac.nz](mailto:J.Lowry@massey.ac.nz) (J.H. Lowry), [karljarvis@suu.edu](mailto:karljarvis@suu.edu) (K.J. Jarvis), [gunnar.keppel@unisa.edu.au](mailto:gunnar.keppel@unisa.edu.au) (G. Keppel), [randolph.thaman@usp.ac.fj](mailto:randolph.thaman@usp.ac.fj) (R.R. Thaman), [juergen.boehmer@usp.ac.fj](mailto:juergen.boehmer@usp.ac.fj) (H.J. Boehmer).

<sup>1</sup> School of Agriculture and Environment, College of Science, Massey University, Palmerston North, New Zealand.

vegetation (Gulezian and Nyberberg, 2010; Hard, 1998; Hope et al., 2003; Lowry et al., 2012).

Urban landscapes can have higher overall species richness than areas outside of cities (Kuehn et al., 2004; Wania et al., 2006), partly due to multiple introductions, both unintentional and intentional (Kowarik, 2003). Across the gradient from a built urban core to semi-natural rural areas, plant richness has been noted to vary with highest amounts in moderately urbanized areas (McKinney, 2008). Cusack and McCleery (2014) found, however, that species diversity in forest understorey was highest under rural native canopies compared to urban forest canopies. To better understand the effects of anthropogenic influences on invasive plants in urban environments, many studies have employed an urban-to-rural gradient (hereafter urban-rural) framework (Boone et al., 2010; Burton et al., 2005; Gulezian and Nyberberg, 2010; Cusack and McCleery, 2014; Pauchard et al., 2006).

A key structural component of urban environments and urban-rural gradients is transportation corridors, especially roads. Roadsides and other ruderal and disturbed sites are more likely to be invaded by non-native plant species than other habitats (Hansen and Cleverger, 2005; Stajerova et al., 2017), and roadside exotic species can spread into adjacent natural or agricultural areas (Joly, Bertrand, Gbangou, White, Dubé, & Lavoie, 2011; Kowarik and von der Lippe, 2006; Padmanaba and Sheil, 2014; Pauchard and Alaback, 2004). Vehicles are major vectors of non-native species dispersal as roads with higher traffic density and larger margins can harbor more exotic plant species and aid alien invasion (Joly et al., 2011; Vakhlamova et al., 2016; Cusack and McCleery, 2014), most commonly as exports from urban areas to rural areas (von der Lippe and Kowarik, 2008). In some environments, however, little if any relationship between road type and exotic plant richness or abundance exists (Craig et al., 2010; Sharma and Raghubanshi, 2009) and species richness of exotic plants can be greater on local, unpaved roads than on paved roads (Kalwij et al., 2008).

Most urban-rural gradient studies of invasive plants have been carried out in developed countries within temperate climates (Burton et al., 2005; Gavier-Pizarro et al., 2010; Gulezian and Nyberberg, 2010; Hope et al., 2003; Kowarik, 1995; McKinney, 2008; Pauchard et al., 2006). From the present to 2050 the largest proportion of global population growth is expected to occur in the cities of less developed countries (UNDESA, 2012). There have been few urban-rural gradient studies in developing countries (Pauchard et al., 2006), or in tropical environments (Cusack and McCleery, 2014), and none that we know of focused on plant invasions in the Pacific islands. Given rapid changes expected in Pacific country urban areas over the next decades there is a critical need to fill this gap (Asian Development Bank, 2012).

The aim of this research was to understand how the presence, abundance, and richness of invasive woody plants (IWP) is associated with different levels of urbanization and different road types in a tropical urban environment of a small developing country in the South Pacific. The Suva, Fiji urban area is used as a case study. This fills a critical gap in the scientific literature as there have been no studies heretofore aimed specifically at examining and comparing the characteristics of several IWPs in a single tropical island urban area in the South Pacific region. The research addresses two important needs: 1) to empirically examine the relationship between levels of urbanization and the pattern of IWPs in tropical South Pacific urban environments, and 2) to provide relevant foundational data leading to a better understanding of the biology, ecology, and historical background of key IWP species in small tropical Pacific island countries. These findings will help inform risk assessments and management of invasive alien species in small island developing states.

## 2. Methods

### 2.1. Study area

Approximately 56% of Fiji's nearly 900,000 residents live in urban

areas (Fiji Bureau of Statistics, 2018). With a population of approximately 300,000 the Greater Suva Urban Area (GSUA) is Fiji's largest and fastest growing urban area, growing at an estimated annual rate of 1.7% (UN-Habitat, 2012). The GSUA extends from Lami Town west of Suva City, to Nausori Town 20 km northeast of Suva (Fig. 1). Suva City's central business district (CBD) is a major commercial and industrial complex with higher density residential neighborhoods, including informal settlements of poor rural and outer island migrants. One major arterial road (King's Highway) passes through Suva to Nausori and beyond. Extending from Suva toward Nausori lies an urban to rural transition of relatively high-density residential housing with occasional commercial, institutional or light industrial centers to lower density urban and peri-urban neighborhoods. Built areas not directly on the King's Highway are peri-urban residential areas and informal settlements, interspersed with undeveloped areas which are often under traditional shifting agriculture. There is significant dependence on urban food gardening in domestic gardens and on otherwise unused land in Suva urban and peri-urban areas (Thaman, 1987, 1995; personal observation, B.J.L.). The less built peri-urban areas are dominated by farms, as are the rural areas outside of Nausori. Pasture for livestock is occasional in these areas as well.

Suva has a tropical rainforest climate. Average annual rainfall is 2000–3000 mm, with average temperatures ranging from a low of 20 °C in July to a high of 32 °C in February (Mataki et al., 2006). The natural vegetation of southeastern Viti Levu is lowland rainforest of a relatively species rich and heterogeneous composition (Ash, 1992; Kirkpatrick and Hassall, 1985; Mueller-Dombois and Fosberg, 1998). Natural vegetation in and around the GSUA is highly fragmented, with only about 30% of Viti Levu's land covered by dense, closed forests (both primary and secondary) (S. Pene, personal communication, 6 June 2019). Elevational changes within the region range from sea-level to approximately 160 m in the hills above the Rewa River floodplain (Barker and Price, 2012).

### 2.2. Selection of target species

An initial list of 50 potential woody and semi-woody target invasive species was compiled from the literature (Daehler et al., 2004; Keppel and Watling, 2011; Meyer, 2000, 2014; Mune and Parham, 1967; Parham, 1972; Smith, 1979–1996; Thaman, 1974, 2009, 2011; US Forest Service, 2015; Whistler, 1983, 1995). The list was narrowed to 21 species through administration of a questionnaire to local experts (3 academic, 2 forestry authorities, 5 landowners and farmers) and subsequently reduced to 14 species that were easily identifiable in the field (Table 1).

The Hawaii-Pacific Weed Risk Assessment System (HPWRA) (Daehler et al., 2004), a tool designed to assess invasive plant risk in the Pacific region, was used to confirm that the selection of 14 target plants were considered high risk for ecological and/or socio-economic impact. Thirteen of the 14 target IWP scored as high risk by the HPWRA. The 14<sup>th</sup> species, *Ipomoea cairica*, was not listed in the HPWRA, but using the HPWRA assessment sheet (Gordon et al., 2010) it also scored in the high-risk category.

Of the final 14 target species, ten of which were likely introduced for ornamental or food purposes, all but *Coccinea grandis*, *Ipomoea cairica*, *Schefflera actinophylla*, and *Spathodea campanulata* were well established in Fiji by the 1940s (see Supplementary Material). *Merremia peltata* is the sole species that is considered native, and is therefore, by most definitions, not invasive, but rather a problematic native species (Tye, 2009). *Merremia peltata* and *Leucaena leucocephala*—which was introduced as a nitrogen-fixing browse plant—were the two target species expected to be most common in the rural area. Of the 14 species, only *S. campanulata*, *I. cairica* and *Mikania micrantha* are predominantly wind-dispersed. *Clerodendron chinense* and *L. leucocephala* may have limited dispersal distances due to predominantly reproducing asexually (Liogier, 1995) and having gravity-dispersed seeds,

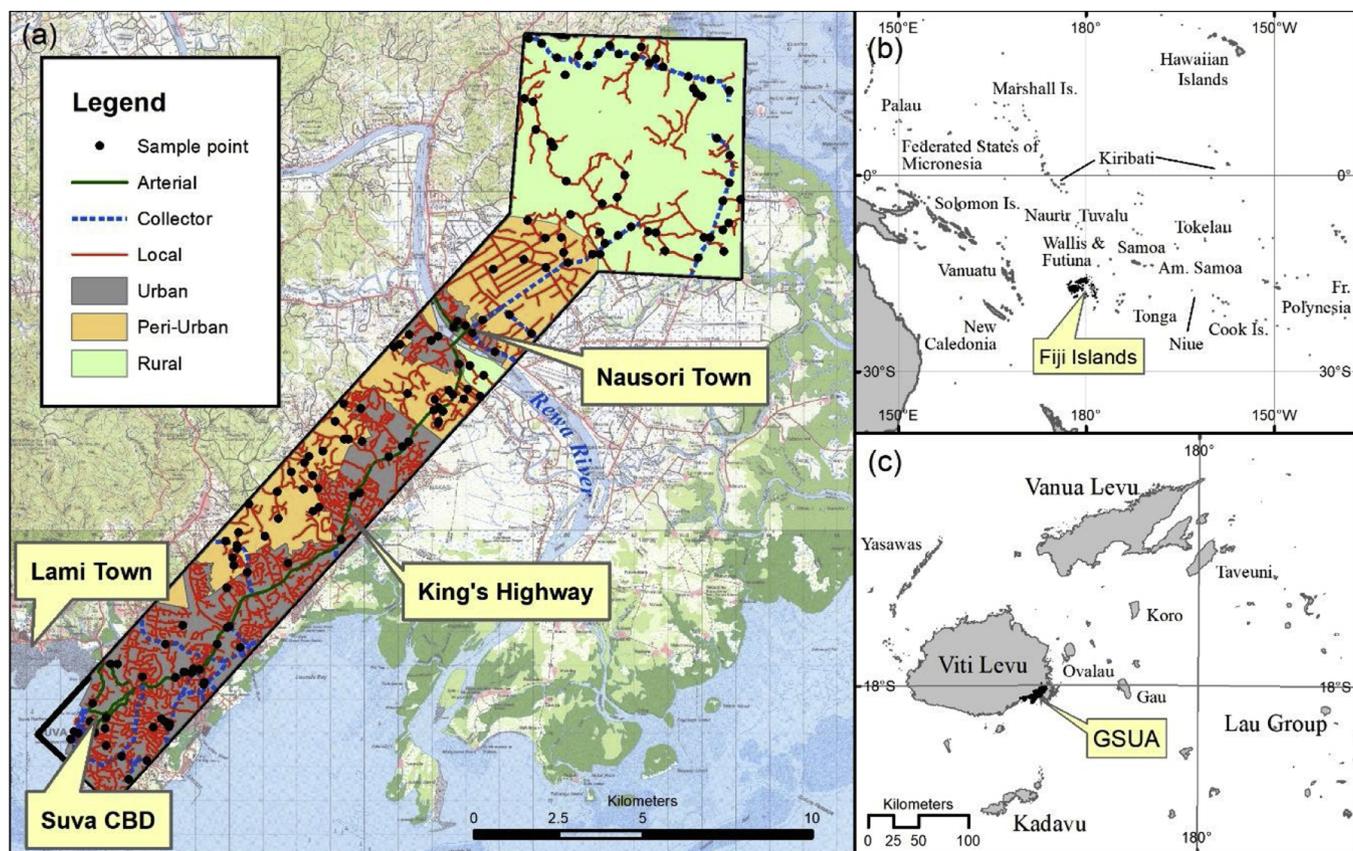


Fig. 1. Urban-rural gradient sample frame with randomly placed sites in urban, peri-urban and rural sectors of the Greater Suva Urban Area (a). The Fiji Islands within context of Pacific islands (b). Greater Suva Urban Area (GSUA) within the Fiji Islands (c).

respectively (Raghu et al., 2005). Thirteen of the 14 species form dense stands, or have a smothering habit; twelve species produce very high seed numbers, and/or produce year-round, and reproduce vegetatively as well; two species reproduce mainly by vigorously suckering or creeping (Table 1).

### 2.3. Geospatial data

Geospatial data identifying urban, peri-urban, and rural sectors were obtained from the 2007 Census (Bainimarama, 2008) and roads data were obtained from Fiji Roads Authority (Fiji Roads Authority, 2014a) (Table 2).

Table 1

Fourteen invasive woody plant (IWP) target species examined in this study. Abbreviations conform to United States Department of Agriculture (USDA) Plant Database (<http://plants.usda.gov/java/>).

Abbrev	Species	Common Name	Form
CISP3	<i>Citharexylum spinosum</i> L.	fiddlewood	Tree
PSGU	<i>Psidium guajava</i> L.	guava	Tree
SCAC2	<i>Schefflera actinophylla</i> (Endl.) Harms	Queensland umbrella	Tree
SPCA2	<i>Spathodea campanulata</i> P.Beauv.	African tulip	Tree
CLCH4	<i>Clerodendrum chinense</i> (Osbeck) Mabb.	Chinese glory bower	Shrub
CLHI3	<i>Clidemia hirta</i> (L.) D.Don	Koster's curse	Shrub
LCAC2	<i>Lantana camara</i> L.	lantana	Shrub
LELE10	<i>Leucaena leucocephala</i> (Lam.) de Wit.	leucaena	Shrub
PIAD	<i>Piper aduncum</i> L.	spiked pepper bush	Shrub
SOTO4	<i>Solanum torvum</i> Sw.	prickly solanum	Shrub
COGR9	<i>Coccinia grandis</i> (L.) Voigt	ivy gourd	Vine
IPCA	<i>Ipomoea cairica</i> (L.) Sweet	Cairo morning glory	Vine
MEPEM10	<i>Merremia peltata</i> (L.) Merr.	merremia	Vine
MIMI5	<i>Mikania micrantha</i> Kunth	mile-a-minute	Vine

### 2.4. Sample frame and field data collection

A sample frame was created by buffering (2 km on each side) a line transect starting from Suva CBD extending northeast along the King's Highway approximately 29 km, through other urban and peri-urban sectors and across the Rewa River to rural zones beyond Nausori. Using a geographical information system (ArcGIS 10.1) approximately 50 sample locations (hereafter sites) were randomly generated along accessible roads within the urban, peri-urban, and rural sectors. Because the rural sector had fewer roads, the northeast end of the sample frame was enlarged by approximately 24 km<sup>2</sup> to allow for a proportional number of sites (i.e. roughly 50) in each sector (Fig. 1).

Sampling was carried out from July to September 2014 as follows: 1) Navigate to site using handheld GPS, 2) flip a coin to determine which direction to walk from the navigation point (forward or backward from the direction of travel getting to the site), 3) record general plant community type and land use at the location (plant community and land use data were found to be highly correlated to urbanization sector, and were thus not used in the analyses), 4) walk 70 m along one side of road while cataloging all visible target species present—the number of individual plants or estimated number based on area covered, depending on species type—between the road and 10 m from it (visibility was occasionally impeded by walls, hedges, or other obstacles), 5) return to the starting point cataloging the same information on the opposite side of the road. The aim of this method was to avoid selection bias while surveying a consistent area at each sample site.

Nine of the target species grow as distinct individuals and were easily counted. Because growth habits of five species make it difficult to easily distinguish individuals, their abundances were estimated for an area of coverage (class 1: < 4 m<sup>2</sup> = 2 individuals, class 2: 4–16 m<sup>2</sup> = 10 individuals, class 3: > 16 m<sup>2</sup> = 80 individuals).

**Table 2**

Descriptions of GIS data for sectors and roads, as defined by Fiji Bureau of Statistics (P. Naimila, personal communication, 2 September 2014) and Fiji Roads Authority (Fiji Roads Authority, 2014a).

Sector	Description
Urban	Census Enumeration Areas with 200+ persons/km <sup>2</sup> ; continuous "built up area"; max. 200 m between developments; majority labor force in non-agriculture employment; center for commerce, industry, administration or utility services.
Peri-Urban	Enumeration Areas outside urban sector, but majority of population in urban employment; regular travel to urban sector for most economic activities and health care.
Rural	All Enumeration Areas outside urban and peri-urban sectors.
Road type	Description
Arterial	Major roads and highways connecting municipalities; traffic volume over 10,000 vehicles/day.
Collector	Arterial-feeding streets and side roads; traffic volume approx. 6000 vehicles/day.
Local	Less movement; lower traffic volume; many unpaved.

### 2.5. Descriptive and univariate analysis

Field data were compiled into a spread sheet and summarized as bar-plots, showing species presence by sector, and box-plots, showing species richness and abundance. A one-way Chi-square test was used to test whether observed frequency of individual species' presence by urban-rural sector was equal across sectors. The data were checked for normality using Shapiro-Wilks test and data for several species found to be non-normal. The Wilcoxon rank sum test (two-tailed) was used to test for differences of medians for invasive species richness and overall abundance by sector and road type. All descriptive and univariate statistics were performed using R v 3.1.

### 2.6. Cartographic visualization

Cartographic visualizations of the spatial pattern and abundance of target species were created by mapping the total number of individuals at each site using graduated symbols. Classification breaks for three classes plus a class for zero individuals were defined using quantiles to assure uniform classification breaks for species abundance.

### 2.7. Multivariable regression and interaction plots

A generalized linear regression model (glm) was used to test for a relationship between plant abundance (response variable) and sector and road type (explanatory variables). The *urban* category was set as the reference for the sector variable, and *local roads* set as the reference for road type. Response data were counts of individual plants in each sample site. A negative binomial (NB) regression form of glm was used because the data were not normally distributed and were overdispersed (Ver Hoef and Boveng, 2007) (R v3.3, MASS package). Spatial autocorrelation in the data was not found to be significant based on a Moran's I test ( $\alpha = 0.05$ ). Of the 14 total target species, it was possible to fit a NB glm for seven. There were too few data for the remaining seven species.

An important aim of the multivariable regression models was to evaluate and disentangle the relationship of levels of urbanization (sector) and road type to plant abundance. For NB models the influence of explanatory variables on the response variable is measured using an Incidence Rate Ratio (IRR) (an exponentiated transformation of model coefficients in log form (Hoffman, 2016)). As a ratio the IRR measures change in the response variable due to an explanatory variable while adjusting for other explanatory variables. An IRR greater than 1.0 suggests the response variable increases with a change in the explanatory variable, and an IRR less than 1.0 suggests a decrease. Interpreting the coefficients of linear models (or transformations thereof) with factors can be challenging, particularly when there are interaction effects (Faraway, 2005). Therefore, to describe the relationship between the response and explanatory variables, plots of predictions based on estimated marginal means were created (Hoffman, 2016; Lenth, 2016) (R v 3.3.4, emmeans package).

## 3. Results

### 3.1. Spatial patterns: frequency of occurrence by sector—species presence

The number of sites where a species was found present provides a measure of how common it is within the sector (Fig. 2). For the 14 target species, four general spatial patterns emerged:

- 1 no differences among sectors (NDS)
- 2 not common in any sector (NCS)
- 3 common toward urban sector (CUB)
- 4 common toward rural sector (CRL)

Differences in the frequency of occurrence in each sector were tested using a Chi-square test for observed frequency ( $\alpha = 0.05$ ) and graphed (Fig. 2). Of the 14 target species, three species (*Mikania micrantha* (MIMI5), *Spathodea campanulata* (SPCA2), and *Psidium guajava* (PSGU)) were observed to have no difference in frequency by urban-rural sector and were designated NDS. These species were also the most commonly encountered in the entire sample (MIMI5 130 total sites, SPCA2 113 total sites, and PSGU 85 total sites).

Based on a frequency threshold of 10% (i.e. proportion of sites with species present less than 0.1) four species (*Citharexylum spinosum*, *Clerodendrum chinense*, *Ipomoea cairica* and *Lantana camara*) were not common in any sector (NCS). These ranged from 4 total sites with species present (*L. camara*) to 15 total sites (*C. chinense*) (Fig. 2).

Three species (*Coccinia grandis*, *Leucaena leucocephala*, and *Schefflera actinophylla*) were more common toward the urban or peri-urban sectors (CUB) and occurred in no more than one-third of the total study area sites. *Schefflera actinophylla* was common in the urban sector (20 sites), more common in the peri-urban sector (27 sites), but quite rare in the rural sector (4 sites). The frequency of *C. grandis*'s decreased dramatically from the urban sector (30 sites) to the peri-urban sector (12 sites), and was entirely absent in the rural sector (Fig. 2). *Leucaena leucocephala* was represented in more than twice the number of urban sites than rural sites (21 urban vs. 9 rural).

Four species (*Clidemia hirta*, *Merremia peltata*, *Piper aduncum*, and *Solanum torvum*) were more common toward the rural sector (CRL). While *C. hirta* occurred in fewer than 20% of the study sites (Fig. 2) it exhibited a distinct pattern of greater frequency toward the rural sector, as did *P. aduncum* and *M. peltata*. *S. torvum* was found in more than 50% of the study sites, with significantly greater frequency in the peri-urban and rural sectors (Fig. 2).

### 3.2. Multivariable regression of species abundance by sector and road type

A species may be more common in the urban sector (e.g. see LELE10 in Fig. 2), but may not be very abundant in the sites where it is present. One aim of the regression models was to examine abundance of individuals by sector and road type. Sufficient data on species abundance were available to fit regression models for seven of the 14 target

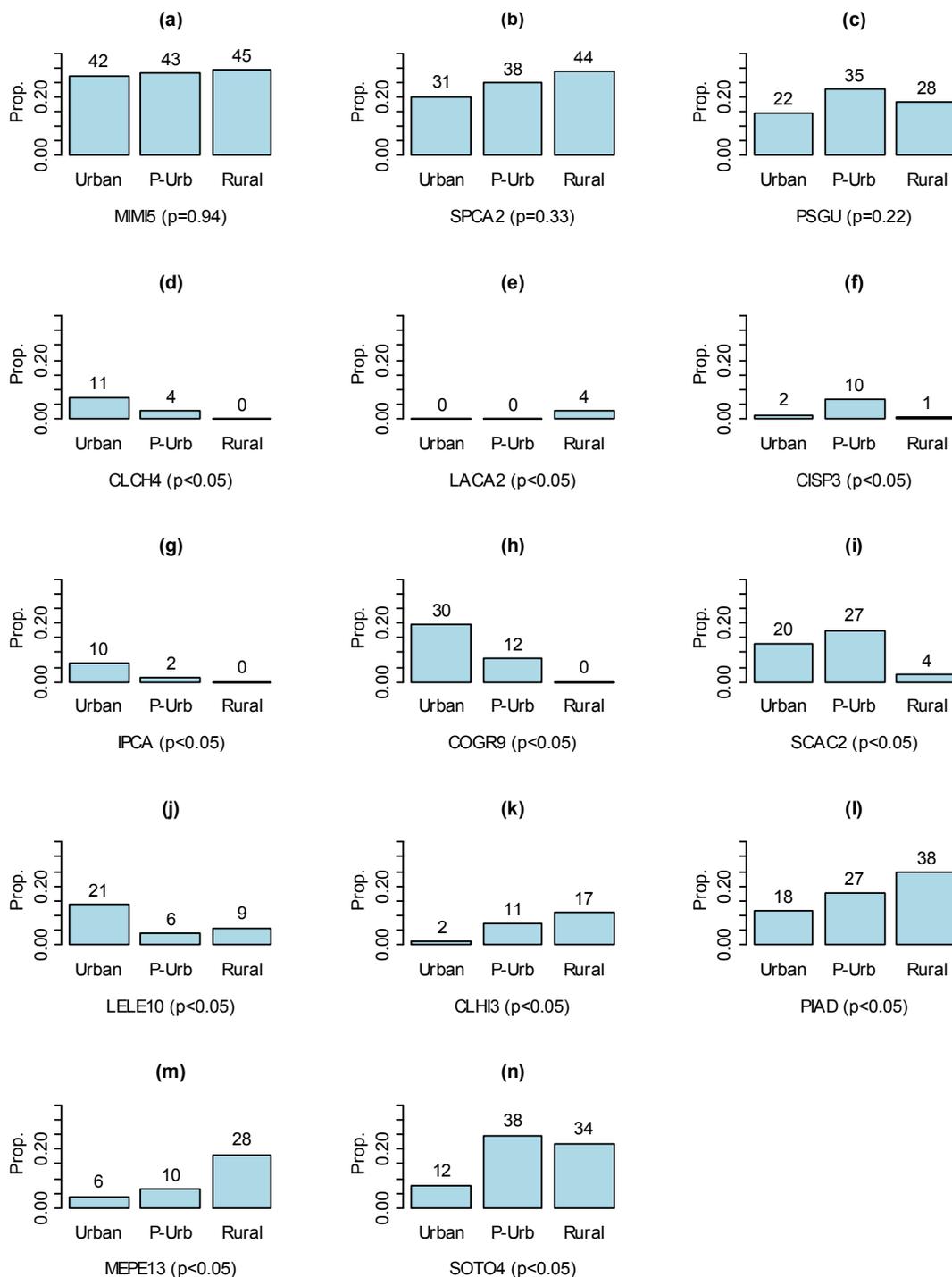


Fig. 2. Frequency of sites where species were present by sector (number of sites indicated above bar; y-axis indicates proportion of all sites N = 154) with p-values for one-way Chi-square test that observed frequencies are equal across sectors. Plots a–c = pattern **NDS** (no difference among sectors), plots d–g = pattern **NCS** (not common in any sector) plots h–j = pattern **CUB** (common toward urban sector), and plots k–n = pattern **CRL** (common toward rural sector).

species. Generally, the results suggest that road type by itself is not as influential in explaining plant abundance as is sector. The IRR for sectors (Peri-urban or urban) are statistically significant ( $\alpha = 0.05$ ) for all seven species, whereas for road types IRR are statistically significant for three species (Table 3). To interpret road type and sector interaction effects it is helpful to examine plots of predicted abundances based on estimated marginal means (Fig. 3).

To illustrate the value of examining abundances as well as frequency of occurrence (presence) we look at a few examples. The plot of predicted abundance for *L. leucocephala* (LELE10) shows a very high

abundance for sites on collector roads in the rural sector, yet low abundance in the urban sector for all road types (Fig. 3). This is an example where a species is common (i.e. found in many sites) in a sector, but is not necessarily highly abundant where it is found (not abundant in the urban sector, but very abundant in the rural sector). *Spathodea campanulata* (SPCA2) is common in all three sectors (Fig. 2), but is more abundant in the peri-urban sector on collector and arterial roads, and most abundant in rural sector on collector roads (Fig. 3). In some cases the abundance of a species resembles its frequency of occurrence. For example, *C. hirta* abundance is highest on local and

**Table 3**

Results of negative binomial (NB) regression models with local roads and urban sector as reference categories for seven of the 14 species. Incidence Rate Ratios (IRR) with p-value < 0.05 in bold. 'NA' denotes no samples in this category.

Target Species	Road Type		Sector		Road Type * Sector Interactions			
	Collector	Arterial	Peri-urban	Rural	Collector*PU	Arterial*PU	Collector*R	Arterial*R
<i>Spathodea campanulata</i> (SPCA2)	0.25	0.50	3.65	13.07	0.19	2.36	6.16	NA
<i>Schefflera actinophylla</i> (SCAC2)	0.76	2.45	3.12	0.14	0.97	0.24	1.78	NA
<i>Piper aduncum</i> (PIAD)	0.79	26.19	5.62	13.54	9.36	0.04	1.07	NA
<i>Leucaena leucocephala</i> (LELE10)	2.10	0.58	0.12	2.75	0.67	20.05	4.44	NA
<i>Solanum torvum</i> (SOTO4)	0.06	0.57	9.13	3.37	9.47	0.07	28.15	NA
<i>Psidium guajava</i> (PSGU)	0.60	1.14	4.08	4.61	2.95	0.78	1.04	NA
<i>Clidemia hirta</i> (L.) D. Don (CLHI3)	2.70	NA	38.74	106.7	0.00	NA	0.47	NA

collector roads in the rural sector, while higher than the urban sector on local roads (Fig. 3). This is similar to its pattern of frequency of occurrence (Fig. 2).

### 3.3. Cartographic visualization

An effective way to illustrate both frequency and abundance of each species is with a map. Fig. 4 shows four species, representative of the four observed spatial patterns of presence (NDS, NCS, CUB and CRL), across the urban-rural gradient and indicates abundance of individuals at each site by symbol size.

### 3.4. Species richness and overall abundance by sector and road type

Overall invasive target species richness was significantly lower in the urban sector than peri-urban and rural sectors ( $\alpha = 0.05$ ); with no significant difference in richness between peri-urban and rural sectors (Fig. 5a). Target species abundance (total number of individuals across all 14 species) increases along the gradient, with significant differences between all sectors (Fig. 5b).

There are fewer significant differences in target species richness and abundance among the different road types than among sectors. Target species richness is significantly lower on collector roads than on local roads (Fig. 5c). Overall target species abundance is higher on local roads than on arterial roads, but is not significantly different between other road types (Fig. 5d).

## 4. Discussion

### 4.1. Spatial patterns of frequency, abundance and richness

Anthropogenic influence on the distribution of invasive plants in urban, peri-urban and rural environments can be, in part, attributed to the physical structure of the landscape. For example, moderately built environments in developed countries have been shown to have greater plant diversity due to a more heterogeneous landscape (Kowarik, 1995; Kühn, Brandl & Klotz, 2004; McKinney, 2008). Urban core areas and heavily built environments have fewer habitat niches to support the diversity and abundance observed in other areas. Our results are consistent with this observation with richness of target species and overall abundance significantly lower in the urban sector (Fig. 4). The physical structure of urban-rural environments, however, only explains part of the observed patterns. Other potentially important factors include mechanisms of dispersal, histories of introduction, and current and past human preferences and uses (Dolan et al., 2017; Gulezian and Nyberberg, 2010; Hard, 1998; Hope et al., 2003; Lowry et al., 2012; McKinney, 2002). The remainder of this section discusses plausible explanations for spatial patterns of presence and abundance of the species observed in this study.

#### 4.1.1. Spatial frequency pattern – no difference among sectors (NDS)

The intentional cultivation of all NDS target species is currently common in the GSUA which is likely a contributing factor to the spatial pattern they exhibit. *Psidium guajava* is intentionally planted for its fruit (although not commercially), *M. micrantha* is left uncontrolled, because of its usefulness as a medicinal herb, and *S. campanulata* is unintentionally encouraged when cut and used as fence posts, which resprout and grow into new trees. We observed the practice of using *S. campanulata* as fence posts to be more common in settlements and agricultural zones toward the rural end of the gradient and this is supported by the data.

*Mikania micrantha* and *S. campanulata* are the most common and most abundant target IWP in the study area. Although introduced 50–70 years before the other two NDS species, *P. guajava* has a far lower presence. This may be partly explained by the fact that *M. micrantha* and *S. campanulata* seeds are wind-dispersed, whereas *P. guajava* seeds are dispersed by birds and bats (US Forest Service, 2015). It is possible that *M. micrantha* abundance is being curbed by biocontrol rust agent, *Puccinia spegazzinii*, introduced into the rural areas of the study area in 2009 (A. Tunabula-Buli, personal communication, 19 June 2015), and thus the lack of significant differences in abundance between sectors. Although *P. guajava* is reputed as a nuisance in agricultural and pastoral land, its numbers in the peri-urban and rural sectors were moderate, and it may be reasonable to assume that its presence and abundance are partly curtailed by selective control by farmers, and also by sooty mold that commonly attacks it and reduces its ability to photosynthesize and produce fruit (personal observation, B.J.L.).

#### 4.1.2. Spatial frequency pattern – not common in any sector (NCS)

Possible explanations for the low frequency of occurrence of NCS species could be that they are not as invasive in roadside habitats as our consulting experts assumed, or the species may require more time to become invasively successful (Crooks, 2005). In the case of *L. camara*, the leaf mining beetle, *Uroplata girardi*, introduced as a biocontrol agent in 1969, and reported to be moderately successful, may be contributing to its low presence (Broughton, 2000). *Clerodendrum chinense*'s low presence is likely due to its primary mode of reproduction (suckering), which limits its dispersal to spreading from intentional garden plantings (US Forest Service, 2015). According to Smith (1979)-96, it is common to see *C. chinense* naturalized in agricultural settings and near roadsides, and Thaman (2011) claims it is problematic along streams and in taro farming areas. Thus, although *C. chinense* may not currently be a major concern in the GSUA, it apparently is an IWP of concern in other parts of Fiji.

#### 4.1.3. Spatial frequency pattern – common toward urban sector (CUB)

As both *C. grandis* and *S. actinophylla* were introduced in the 1940s, it is plausible that they are still expanding outward from their urban point of origin, and simply have not reached their full potential in the rural sector. However, Smith (1979) 96 suggests that *C. grandis* is common in cane fields, as well as roadsides and waste places, and

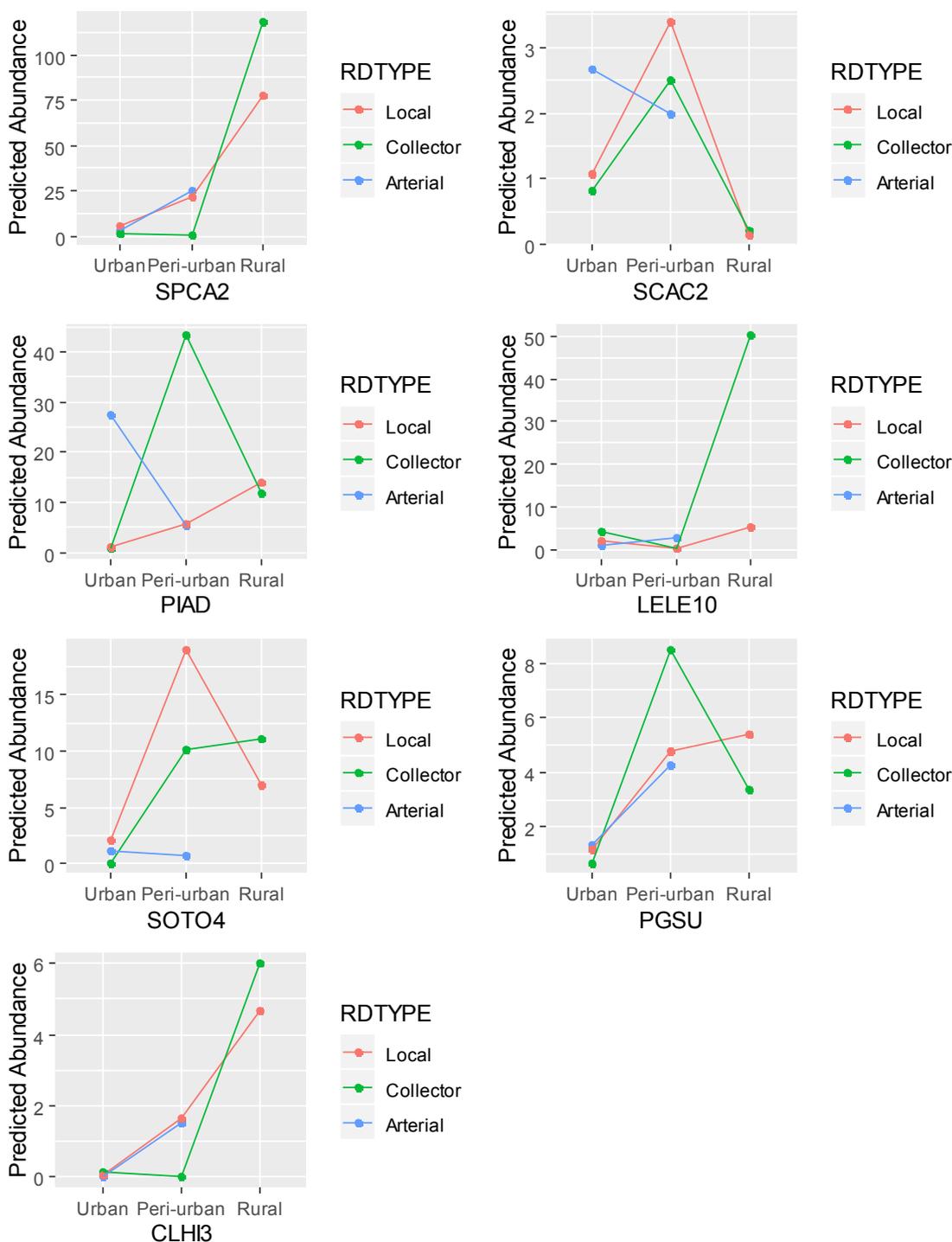


Fig. 3. Interaction plots using estimated marginal means showing predicted abundances from NB regression models for seven of the 14 target species. Note: y-axis is predicted abundance and number range is not the same for all plots.

therefore may be more widespread in Fiji outside of the study area. *Leucaena leucocephala* was the sole target species known to have been a rural introduction, as a high protein browse plant for livestock. The introduction occurred before 1860 (Smith, 1979-96), and the plant is now widespread around the Fiji Islands, most commonly in dry, rocky habitats. *Leucaena leucocephala*'s strong representation in urban sites may be due to its preference for dry, exposed environments, which—in the tropical rainforest climate of the GSUA—are more prevalent in the urban built areas than the rural agricultural and forested areas.

4.1.4. Spatial frequency pattern – common toward rural sector (CRL)

*Merremia peltata* is considered a native species. It is known to grow best when climbing and covering other vegetation, which is more abundant in the rural sector. Our results support this, showing *M. peltata* occurs in increasingly more sites toward the rural sector (6 urban, 10 peri-urban, 28 rural) (Fig. 2). This seems to contradict the reason for *M. peltata*'s selection as a target species, which was its apparent encroachment onto newly cleared land for development. The other three CRL species were introduced in the late 1800s or early 1900s (Evenhuis, 2014; Smith, 1979-1996). *Clidemia hirta* was an accidental introduction (Evenhuis, 2014), and the reasons for the introductions of *P. aduncum*

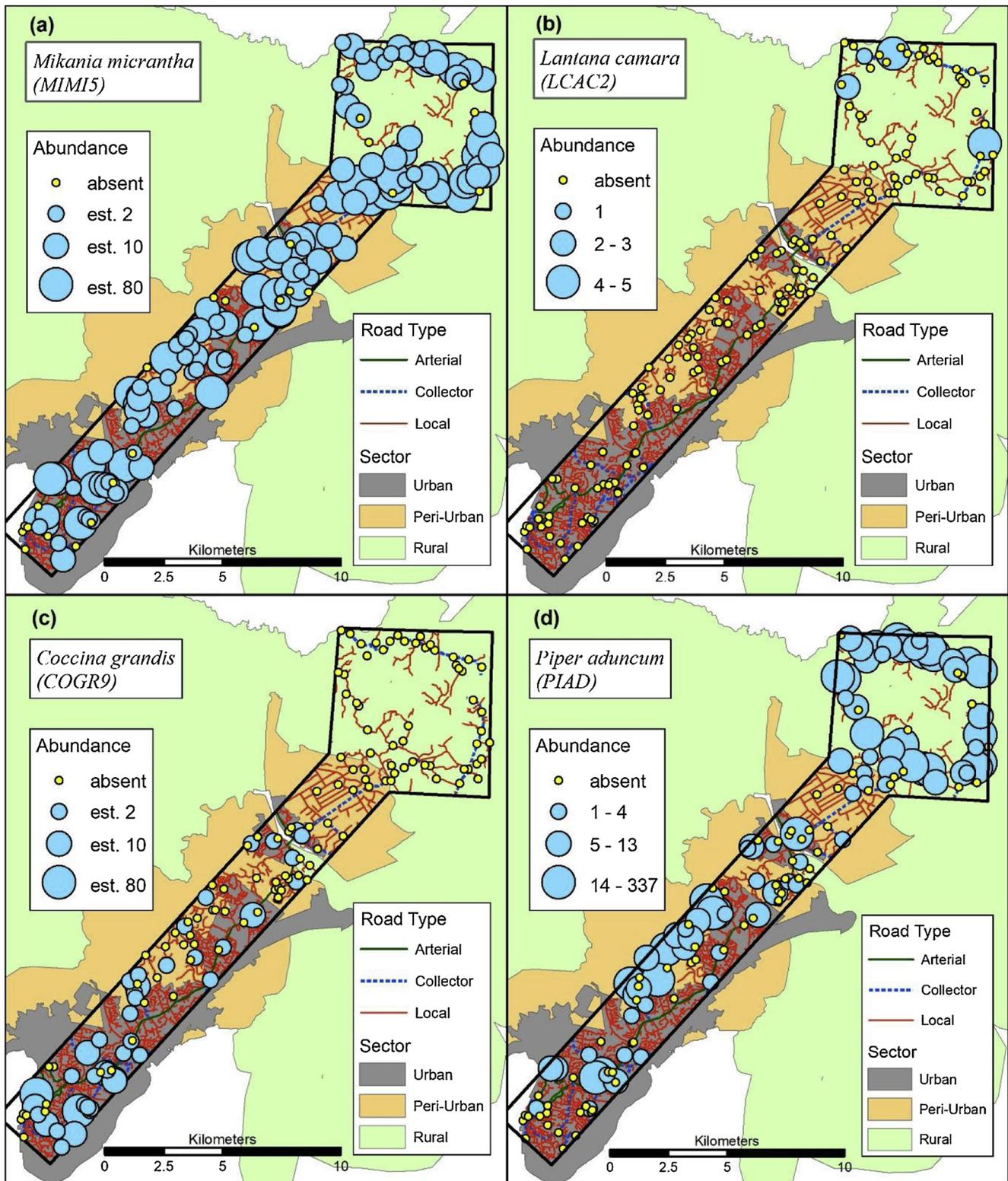


Fig. 4. Maps representing the four patterns of species presence and abundance. Map (a) an example of pattern **NDS** (no difference among sectors), map (b) an example of **NCS** (not common in any sector), map (c) an example of **CUB** (common toward urban sector), and map (d) an example of **CRL** (common toward rural sector). Note species abundance for MIMI5 and COGR9 was estimated in the field (see section 2.4).

and *S. torvum* are unclear. None of the CRL species are cultivated at present, which may help explain their relative scarcity in the urban environment, as well as the fact that the highly paved urban sector offers fewer opportunities for colonization. *Clidemia hirta*, was a problematic, widespread and highly invasive plant until a thrips species (*Liothrips urichi*) was introduced for its biological control in 1930

(Simmonds, 1933). *L. urichi* reduced its spread and vigor, except in shaded areas (Julien, 1982). *Clidemia hirta* was most plentiful in the undergrowth of trees of the rural sector, which is consistent with previous research on the success of its biocontrol (Julien, 1982).

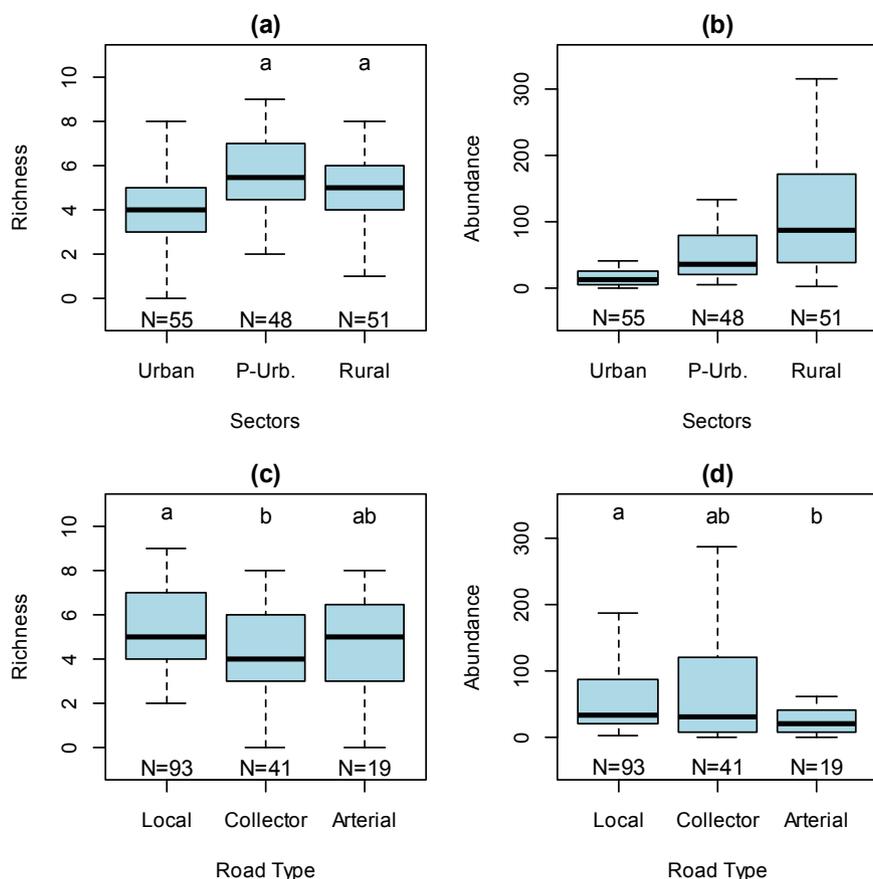


Fig. 5. Species richness and abundance for all species taken together by sector (P-Urb. = Peri-Urban) and road type. Letters above groups indicate significance of difference; i.e. groups with shared letters are not significantly different ( $p$ -value > 0.05) using pairwise Wilcoxon rank sum test.

#### 4.2. IWP abundance and richness by road type

Multivariable regression analysis indicates that road type in conjunction with sector was important in explaining plant abundance for three species (*S. campanulata*, *P. aduncum*, and *S. torvum*) (Table 3; Fig. 3). For two species (*S. campanulata* and *S. torvum*) abundance was greater on collector roads in the rural sector, and for *P. aduncum* abundance was greater on collector roads in the peri-urban sector (Table 3; Fig. 3). These results are similar to other studies that found exotic species in higher abundance on paved roads with higher traffic density and larger margins than on unpaved roads (Joly et al., 2011; Vakhlamova et al., 2016).

However, for most of the remaining species, and through an examination of all species collectively, the Wilcoxon test suggests greater overall abundance and greater richness on local roads compared to collector roads (Fig. 4). This is consistent with the findings of Kalwij et al. (2008) who found in South Africa higher non-native plant richness along unpaved roads than paved roads. Many of the local roads (urban, peri-urban and rural) in the GSUA are unpaved. One potential explanation for the higher abundance and richness of IWP (collectively) on local roads—which generally have lower vehicle traffic—could be that only about a third of all journeys within the Greater Suva Area involve private vehicles (Fiji Roads Authority, 2014b), and there is consequently a large amount of foot traffic on local road margins, which increases the disturbance level of the roadsides. Thus, pedestrians may be acting as dispersal vectors as well.

#### 4.3. Implications for IWP management in small island developing states

As in most developing nations, Fiji has limited financial and infrastructural resources to dedicate to the prevention or control of invasive

plants. Due in part to funding shortages, there is a lack of scientific knowledge about invasive plants, and a low priority for control or collaboration, at local and political levels (Keppel et al., 2014). Farmers, gardeners and landowners find it difficult to continually pay for chemical control. In addition, some of the common types of control used by locals, such as cutting and burning, are ineffective alone. Lack of education about the harm caused by a perceived beneficial or harmless species is also an issue, as is the case with the cultivated IWP (e.g. *C. spinosum*, *C. chinense*, *C. grandis*, *I. cairica*, *L. camara*, *P. guajava*, *S. actinophylla*) and *S. campanulata*, which is used for fence posts and other structural purposes.

One potentially effective approach to IWP control in small developing countries is that of biocontrol. While not specifically studied in this research we found spatial patterns of presence and abundance that could be explained by the effects of biocontrol measures (e.g. *M. micrantha* controlled by *P. spegazzinii* rust agent, *L. camara* controlled by *U. girardi* leaf miner, and *C. hirta* controlled by thrips *L. urichi*). Further research into the effectiveness of these agents is warranted.

An important contribution of this research is the provision of comparative empirical data and information about the spatial distribution within urban-rural gradients of some of the most problematic IWPs in South Pacific small island developing states. Meyer (2014) has stated “Prioritization of the worst invaders is a necessity, especially in small Pacific Islands where funding resources are often limited, data are limited and local capacity and political will to address invasive plants are relatively low.” Native, protected and multiple use forests cover approximately 51% of the land on the island of Viti Levu (S. Pene, personal communication, 6 June 2019). Shade-tolerant trees and species that reproduce vegetatively, such as *S. campanulata* and *S. actinophylla* can invade forests, and should be prioritized for control (Meyer, 2014). Another 30% of the island is agricultural (Fiji Department of

Agriculture, 2009). Some IWP (*C. grandis*, *P. guajava*, *S. torvum*) are hosts to agricultural pests and diseases that could threaten some agricultural crops (US Forest Service, 2015). Of the target species examined in this study, based on their frequency of occurrence and abundance, as well as their ecological traits that favor invasibility, we believe the most problematic target species in the GSUA are *M. micrantha* and *S. campanulata*, and to a lesser degree *M. peltata*, *P. guajava*, *P. aduncum* and *S. torvum*.

#### 4.4. Limitations

Sample sites along roadsides are by their nature highly disturbed, and provide habitats that are different from those not near roads. In the urban and peri-urban sectors, cataloguing target species a full 10 m from the road was occasionally impeded by the presence of walls, fencing, hedges, and buildings. Also, we can only infer from this research about how widespread and abundant the target IWP are along roads within the sample transect, but not how far the IWP have penetrated past the roadsides. However, research has shown that roadsides provide opportunistic non-native species with favorable habitats for invasion, and that roadside exotic species can act as a source of invasion into nearby natural areas (Hansen and Clevenger, 2005; Joly et al., 2011; Kowarik and von der Lippe, 2006; Pauchard and Alaback, 2004; Stajerova et al., 2017).

#### 5. Conclusion

An island ecosystem, the presence of informal urban and peri-urban settlements on unsuitable land, heavy rainfall, and the relatively large presence of urban agriculture, all distinguish the GSUA from temperate counterparts. However, this research indicates that the relationship between levels of urbanization and presence and abundance of invasive plants in tropical, developing countries resembles that of temperate, developed countries. Spatial patterns of IWP species vary across the urban-rural gradient and plausible explanations for these patterns can be attributed to historical introductions and present human activities in addition to species biology and ecology. In terms of the relationship between road type and IWP richness and abundance, our findings are similar to those of previous research—greater invasive plant species abundance and diversity is found on roads with high levels of disturbance.

The most important distinctions between developed and developing countries with regards to IWP control are educational and financial, namely the knowledge and resources available to confront the issue. Educational and economic constraints in Fiji could allow invasive species to become a much larger problem than they now are (Lenz et al., 2019 in press), which is a serious matter of concern, considering the rapid rate of exotic species accumulation in the Pacific islands (van Kleunen et al., 2015). Fiji has had some success with relatively inexpensive biological control for a limited number of invasive species (Day and Winston, 2016). When developing a list for prioritization the species' potential as a target for biological control as well as its harmfulness should be considered. Our study has identified 14 of the most problematic IWP in the GSUA based on expert opinion and provided important baseline information about their distribution and growth habits along the urban to rural continuum. To our knowledge this study is unique in its comparative examination of the spatial patterns of multiple IWP in an urban area of a small tropical island in the South Pacific. A compendium summarizing the origin, introduction history, biological, and ecological traits of the 14 IWP is provided in the Supplementary Material for this article. We anticipate these findings will provide valuable information for risk assessment of invasive plants in other South Pacific island countries, and particularly small island developing states.

#### 6. Author contributions

**B. J. Lowry:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review and editing. **J. H. Lowry:** Visualization, Formal analysis, Writing – review and editing. **K. J. Jarvis:** Formal analysis, Writing – review and editing. **G. Keppel:** Writing – review and editing. **R. R. Thaman:** Conceptualization, Supervision. **H. J. Boehmer:** Conceptualization, Supervision, Writing – review and editing.

#### CRediT authorship contribution statement

**Brenda J. Lowry:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **John H. Lowry:** Visualization, Formal analysis, Writing - review & editing. **Karl J. Jarvis:** Formal analysis, Writing - review & editing. **Gunnar Keppel:** Writing - review & editing. **R.Randolph Thaman:** Conceptualization, Supervision. **Hans Juergen Boehmer:** Conceptualization, Supervision, Writing - review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ufug.2019.126516>.

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