Cat's claw creeper vine, *Macfadyena unguis-cati* (Bignoniaceae), invasion impacts: comparative leaf nutrient content and effects on soil physicochemical properties

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Abstract. *Macfadyena unguis-cati* (L.) Gentry (Bignoniaceae) is a major environmental weed in coastal Queensland, Australia. There is a lack of quantitative data on its leaf chemistry and its impact on soil properties. Soils from infested vs uninfested areas, and leaves of *M. unguis-cati* and three co-occurring vine species (one exotic, two native) were collected at six sites (riparian and non-riparian) in south-eastern Queensland. Effects of invasion status, species, site and habitat type were examined using univariate and multivariate analyses. Habitat type had a greater effect on soil nutrients than on leaf chemistry. Invasion effect of *M. unguis-cati* on soil chemistry was more pronounced in non-riparian than in riparian habitat. Significantly higher values were obtained in *M. unguis-cati* infested (vs. uninfested) soils for ~50% of traits. Leaf ion concentrations differed significantly between exotic and native vines. Observed higher leaf-nutrient load (especially nitrogen, phosphorus and potassium) in exotic plants aligns with the preference of invasive plant species for disturbed habitats with higher nutrient input. Higher load of trace elements (aluminium, boron, cadmium and iron) in its leaves suggests that cycling of heavy-metal ions, many of which are potentially toxic at excess level, could be accelerated in soils of *M. unguis-cati*-invaded landscape. Although inferences from the present study are based on correlative data, the consistency of the patterns across many sites suggests that *M. unguis-cati* may improve soil fertility and influence nutrient cycling, perhaps through legacy effects of its own litter input.

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Introduction

Invasive plants can have significant impacts on ecosystem goods and services (e.g. Vitousek *et al*. 1996; Mack *et al*. 2000; Ehrenfeld 2003), including changing soil properties. The literature on plant–soil interactions strongly suggests that the introduction of invasive exotics has the potential to change components of the carbon, nitrogen, water and other cycles of many ecosystems (Ehrenfeld 2003; Dassonville *et al*. 2008). Invasive species can alter the biogeochemical cycling of ecosystems because secondary metabolites released by invasive species play important roles in soil chemistry as well as in plant–plant and plant–microbe interactions (Weidenhamer and Callaway 2010). Recent work and reviews have concluded that, on average, alien invasive plants increase nutrient pools and fluxes in novel ecosystems (e.g. Dassonville *et al*. 2008; Osunkoya and Perrett 2011; Penuelas *et al*. 2010). However, high variability both in the magnitude and direction of the response to invasion has been observed (Ehrenfeld 2003; Liao *et al*. 2008; Osunkoya *et al*. 2011). Thus, the impacts of an invasive species are often context-specific, depending on the invader's characteristics relative to those of the system into which it enters. Factors influencing level impact of include the degree of difference in key traits between the invasive and native species,

and specifics of the landscape setting such as habitat type, initial site condition, soil characteristics and moisture regime (Ehrenfeld 2003; Dassonville *et al*. 2008; Penuelas *et al*. 2010; Osunkoya *et al*. 2011).

A plant community becomes more susceptible to invasion with increasing availability of resources (Davis *et al*. 2000; Osunkoya *et al*. 2010*a*; Penuelas *et al*. 2010). For example, the position of riparian forests as edges between terrestrial and aquatic systems tends to enhance fluxes of energy and species turnover, with a high degree of disturbance as a result of water-level fluctuations (Planty-Tabacchi *et al*. 1996; Naiman and Decamps 1997). Consequently, streams enhance invasion of exotic species in riparian habitats, providing suitable niches and acting as corridors for dispersal and reservoirs of propagules (Parendes and Jones 2000; Vivian-Smith and Panetta 2004). A corollary to this observation is that the magnitude of the invasion effect in riparian habitats may be expected to be significantly higher than that experienced in non-riparian habitats; however, there are few quantitative data to support this.

Macfadyana unguis-cati, a perennial woody climbing vine, native to tropical South America (Downey and Turnbull, 2007), has become a major environmental weed in Australia, especially in coastal Queensland (Qld) and New South Wales

(NSW) where it poses a significant threat to biodiversity in exposed riparian areas, rainforest communities and remnant natural vegetation (Osunkoya *et al.* 2009; Dhileepan 2012). It is also a declared weed of great significance in southern Africa (King and Madire, 2011). Observations suggest that *M. unguis-cati* tolerates a wide range of soils and grows prolifically in fertile, well drained and alluvial soils (Vivian-Smith and Panetta 2004; Raghu *et al.* 2006). Information is scanty on the effects of invasion by *M. unguis-cati* on soil chemical properties and little is known of its leaf chemistry relative to co-occurring vines (but see Osunkoya *et al.* 2010*b*, 2011). Given the extent of *M. unguis-cati* distribution and its abundance in various riparian and non-riparian habitats in Australia, we would expect that the weedy vine will have a profound effect on soil nutrients and fluxes and we hypothesised that this effect may be linked to its leaf nutrient concentration which can be expected to be different from that of its less- or non-invasive (native and exotic) neighbours. The aims of the present paper are to compare across riparian and non-riparian habitats (1) physicochemical properties of *M. unguis-cati*-invaded and non-invaded soils, and (2) leaf nutrient content of exotic vines *M. unguis-cati* and *Passiflora suberosa* and that of co-occurring native vine species *Parsonsia straminea* and *Smilax australis*.

Materials and methods

Study species

Cat's claw creeper vine, *M. unguis-cati* (Bignoniaceae), is a high-climbing woody vine with twining stems that produces horizontal runners and/or adventitious roots which can become tuberous. These subterranean tubers are usually golf-ball size (~25 mm × 7 mm) and are massive in numbers (up to ~1000 per m^3), promoting *M. unguis-cati* persistence and aiding its vegetative propagation (Osunkoya *et al.* 2009). Some of its leaflets are modified to form pronged, claw-like tendrils with deciduous horny hooks, which enable the plant to climb natural and man-made structures. This species can grow successfully in varying light and soil conditions (Raghu *et al.* 2006; Osunkoya *et al.* 2010*a*). In densely infested areas, *M. unguis-cati* covers standing vegetation, including large trees and shrubs, eventually causing canopy collapse. In areas without standing vegetation or other structures (e.g. fences), the vines grow along the forest floor and form dense mats that preclude the recruitment and growth of native vegetation (Osunkoya *et al.* 2009; Dhileepan 2012). The three remaining study species (see below) are the most abundant co-occurring vines with *M. unguis-cati* in both riparian and non-riparian habitats; however, their relative abundances differ across sites (O. O. Osunkoya, pers. obs.).

Corky-stemmed passionflower vine, *Passiflora suberosa* (Passifloraceae), is a fast-growing perennial vine native to South America, now naturalised in eastern Australia, Northern Territory (NT), Cape York Peninsula, north-eastern Qld and southwards as far as coastal central NSW (Auld and Medd 1996). It is also recorded as a weed in several countries throughout the Pacific region. This garden escapee is naturalised in open forest and disturbed land, growing best in the subcanopy layers where it smothers shrubs, small trees and the ground layer. It prefers moist, well drained sandy or limestone soils, and has moderate to low nutrient requirements. Its impact in south-eastern Australia is not as dramatic as that of *M. uniguis-cati* (Batianoff and Butler 2002).

Australian native monkey rope, *Parsonsia straminea* (Apocynaceae), is widespread and common in most types of rainforest and sclerophyll forest in NSW and Qld. This woody vine with leathery leaves and pale yellow flowers climbs with the use of adventitious roots and twining stems. Osunkoya *et al.* (2010*b*) contended that this native vine species has a growth strategy and physiology that match that of the invasive *M. uniguis-cati*, is often over-abundant where it occurs, and needs to be managed in its own right.

Smilax australis (Lawyer vine, wait-a-while, barbwire vine) (Smilacaceae) is a dioecious climber endemic to Australia, with stems up to 8 m long and usually prickly. It is found within an altitudinal range from near sea level to 1300 m in the Australian states of NSW, Qld, Victoria and NT, and is widespread and common in rainforest, sclerophyll forest, woodland and heath, often forming dense thickets (Wrigley and Fagg 1997).

Site description

Six study sites in the Brisbane–Gold Coast region, south-eastern Qld, Australia, were chosen on the basis of known *M. unguis-cati* infestations and where previous work had been undertaken (Fig. 1; see Osunkoya *et al.* 2009, 2011). Distances between the sites range from 10 to 150 km. Average yearly rainfall in this region is 900–2000 mm (depending on topography and distance from the coast), approximately half occurring in the summer months of December to February. Average daily temperatures range from a minimum of 6°C in July, to a maximum of 29.6°C in December. Predominant vegetation types include tall open eucalypt (dry sclerophyll) forest and subtropical (microphyll vine) rainforest. In all chosen sites, *M. unguis-cati* is dominant, covering many of the trees (mainly *Eucalyptus*, *Araucaria* and *Alphitonia* species) and much of the ground. Anecdotal evidence suggests that *M. unguis-cati* has been a major weed at all of the sites for at least 30 years.

Study sites at Oxley (27°60′S, 152°59′E) and Carindale (27°30′S, 152°59′E) are within the Brisbane City Council forest parks. The Ipswich site (27°32′S, 152°42′E) is at Pine Mountain, managed by the Ipswich City Council. These three sites are ~5–10 ha each, existing in remnant natural open-forest vegetation in non-riparian landscapes with gentle undulating topography. The remaining *M. unguis-cati*-infestation sites are in linear riparian habitats (10–30 m wide, but are extensive along the creek, often ~10 ha each in total area) dissecting larger open forest areas. The infestation at Nerang (along Nerang River: 27°60′S, 153°20′E) is located in the Gold Coast hinterland, whereas those of Boonah (along Coulson Creek: 27°60′S, 152°41′E) and Moogerah (along Reynolds Creek: 28°03′S, 152°54′E) are within the Esk Shire and ~120 km west of Brisbane.

Soil sampling

In August 2010, soil samples were collected from the six field sites – three riparian and three non-riparian. Within each site,
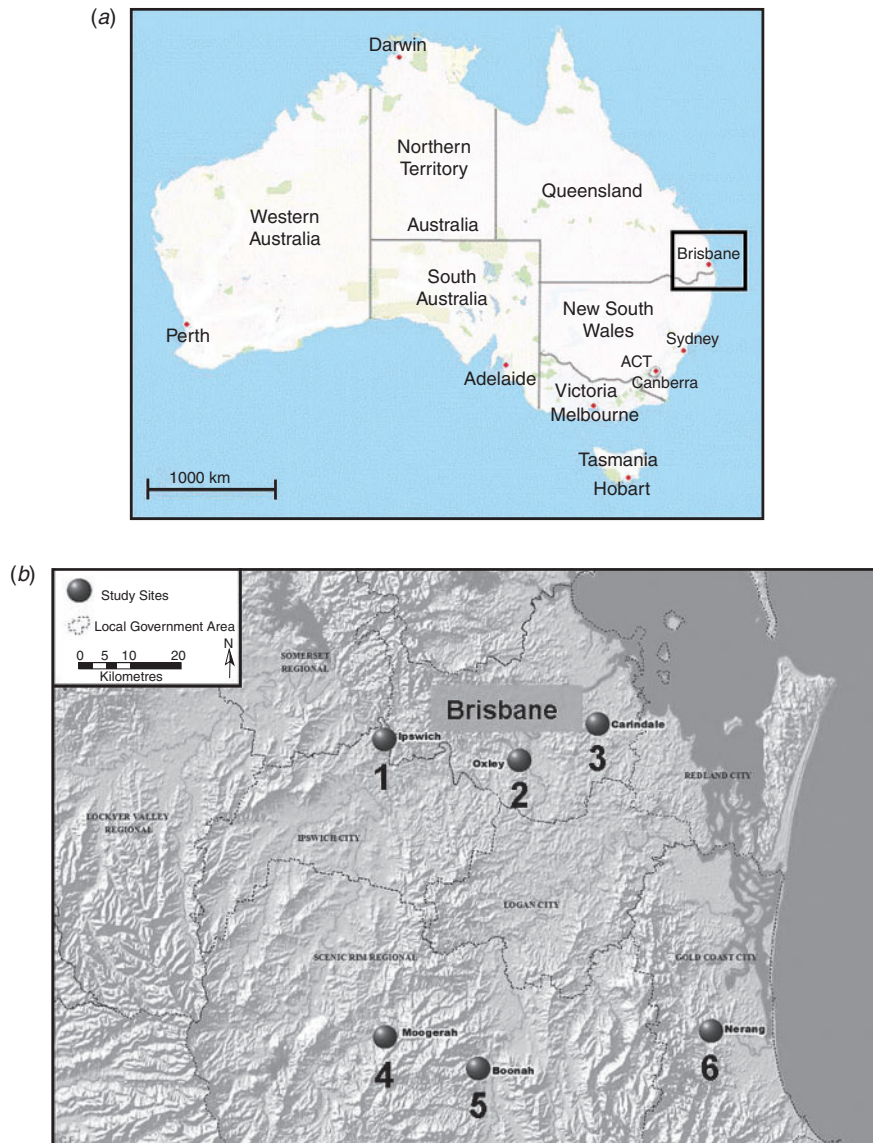
Fig. 1. (*a*) Map of Australia, showing the location of Brisbane, Queensland and (*b*) zoomed-in map of Brisbane and surrounds, showing the location of our six study sites. Numbers on the map represent study locations as follows: 1, Ipswich; 2, Oxley; 3, Carindale (non-riparian sites); 4, Boonah; 5, Moogerah; and 6, Nerang (riparian sites).

five soil collection points within *M. unguis-cati*-infested and five from adjacent uninfested areas (usually within 5–10 m of each other) were taken. At each collection point, leaf litter was cleared and five soil-core samples, 0–10 cm in depth and 6 cm in diameter, were taken using a hand-held soil collector. These soil cores were usually 50 cm to 2 m apart and were bulked to make a composite sample. Soils were transported to the laboratory where they were sieved through <2-mm fine-mesh screen and fine roots and rocks were removed before nutrient analysis.

Leaf sampling

Leaf samples of investigated vines (10–20 leaves from at least three plants per species, each plant ≥5 m apart) were collected from the six field sites. *M. unguis-cati* leaves were collected at

all the six sites, whereas collection sites for the other three species varied depending on availability. Leaves of the exotic vine, *Passiflora suberosa*, were collected from Oxley and Carindale sites only. Leaves of the native vine, *Parsonsia straminea*, were collected from all sites except Moogerah, and those of the second native vine, S*milax australis*, were collected only from the Moogerah and Ipswich sites. Leaves per plant were pooled to make a composite sample (damaged or senescing leaves and vine stems were discarded), samples were washed in the laboratory to remove any surface dirt and dried in an oven at 60°C.

Leaf and soil nutrient analyses

Soil samples were analysed for physical properties (moisture content, sand, slit and clay fractions), pH, organic carbon and

Table 1. Two-way ANOVA summary results of soil physicochemical properties in *Macfadyena unguis-cati*-infested and non-infested patches across six sites in Brisbane–Gold Coast region, south-eastern Australia

Group mean data have been adjusted for site effect. †$P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; n.s., not significant

| Soil trait	Significance (summary ANOVA)			Group mean ±s.e.	
	Site (S)	Invasion (I)	S × I interaction	Infested ($n = 6$ sites)	Uninfested ($n = 6$ sites)
Air dry moisture (%)	***	**	n.s.	3.16 ± 0.28	2.54 ± 0.23
Organic carbon	***	**	n.s.	4.09 ± 0.34	3.48 ± 0.28
Total carbon	***	***	n.s.	4.74 ± 0.36	3.99 ± 0.28
Total nitrogen	***	***	n.s.	0.35 ± 0.03	0.28 ± 0.02
Nitrate nitrogen (mg kg^{-1})	***	n.s.	n.s.	17.71 ± 2.10	15.17 ± 1.30
Ammonia (mg kg^{-1})	***	n.s.	*	3.10 ± 0.50	3.40 ± 0.59
Phosphorus (mg kg^{-1})	***	n.s.	n.s.	29.38 ± 3.77	28.42 ± 5.06
Potassium (meq per 100 g)	***	n.s.	n.s.	0.73 ± 0.07	0.62 ± 0.08
Calcium (meq per 100 g)	***	*	n.s.	15.69 ± 2.04	12.03 ± 1.79
Exchangeable sodium (meq per 100 g)	***	**	n.s.	0.05 ± 0.01	0.09 ± 0.02
Total sodium (meq per 100 g)	***	n.s.	n.s.	0.11 ± 0.02	0.14 ± 0.02
Magnesium (meq per 100 g)	***	†	n.s.	5.55 ± 0.55	4.74 ± 0.59
Copper (mg kg^{-1})	***	n.s.	n.s.	1.29 ± 0.21	1.35 ± 0.23
Iron (mg kg^{-1})	***	*	n.s.	87.10 ± 10.16	109.65 ± 8.57
Manganese (mg kg^{-1})	***	n.s.	n.s.	42.52 ± 7.42	41.46 ± 6.90
Zinc (mg kg^{-1})	**	n.s.	n.s.	4.27 ± 1.05	3.47 ± 1.21
Sulfur (mg kg^{-1})	***	†	n.s.	12.54 ± 1.11	10.62 ± 1.37
pH	***	**	n.s.	6.23 ± 0.14	5.90 ± 0.14
Electrical conductivity (dS m^{-1})	***	***	n.s.	0.10 ± 0.01	0.07 ± 0.01
Chloride (mg kg^{-1})	**	**	†	24.96 ± 0.78	18.60 ± 2.58
Coarse sand	***	n.s.	n.s.	23.83 ± 1.99	24.42 ± 2.41
Fine sand	***	n.s.	n.s.	33.96 ± 2.14	35.58 ± 1.84
Silt	***	n.s.	n.s.	19.50 ± 1.48	20.08 ± 1.75
Clay	***	n.s.	n.s.	25.83 ± 1.68	23.83 ± 1.46

Table 2. ANOVA summary results of soil physicochemical properties in *Macfadyena unguis-cati*-infested and non-infested patches within riparian and non-riparian zones across six sites in Brisbane–Gold Coast region, south-eastern Australia

Values are group means based on 2-way ANOVA of habitat and invasion effects. †$P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; n.s., not significant

Soil trait	Habitat effect (mean)			Invasion effect (mean)					
					Non-riparian			Riparian	
	Non-riparian	Riparian	Significance	Infested	Uninfested	Significance	Infested	Uninfested	Significance
Air dry moisture (%)	2.68	3.03	n.s.	3.11	2.24	n.s.	3.22	2.83	n.s.
Organic carbon	4.81	2.76	***	5.17	4.45	†	3.01	2.51	n.s.
Total carbon	5.46	3.28	***	5.93	4.99	†	3.56	3.00	n.s.
Total nitrogen	0.39	0.24	***	0.44	0.33	n.s.	0.26	0.22	n.s.
Nitrate nitrogen (mg kg^{-1})	18.46	14.42	n.s.	21.33	15.58	n.s.	14.08	14.75	n.s.
Nitrate ammonia (mg kg^{-1})	4.44	2.06	***	5.00	3.88	n.s.	1.21	2.92	n.s.
Phosphorus (mg kg^{-1})	15.46	42.33	***	17.67	13.25	n.s.	41.08	43.58	n.s.
Potassium (meq per 100 g)	0.63	0.72	n.s.	0.66	0.59	n.s.	0.79	0.65	n.s.
Calcium (meg per 100 g)	14.18	13.54	n.s.	16.65	11.71	n.s.	14.72	12.36	n.s.
Exchangeable sodium (meq per 100 g)	0.08	0.06	n.s.	0.06	0.10	**	0.03	0.09	n.s.
Total sodium (meq per 100 g)	0.15	0.10	*	0.15	0.16	n.s.	0.08	0.11	n.s.
Magnesium (meq per 100 g)	4.63	5.65	n.s.	5.30	3.96	n.s.	5.80	5.51	n.s.
Copper (mg kg^{-1})	1.85	0.78	***	1.82	1.89	n.s.	0.76	0.81	n.s.
Iron (mg kg^{-1})	116.03	111.35	n.s.	102.86	129.21	n.s.	101.47	121.23	n.s.
Manganese (mg kg^{-1})	4.63	5.65	n.s.	51.91	51.55	n.s.	33.12	31.37	n.s.
Zinc (mg kg^{-1})	0.66	0.50	*	0.74	0.59	n.s.	0.51	0.49	n.s.
Sulfur (mg kg^{-1})	14.75	8.42	***	15.33	14.17	n.s.	9.75	7.08	n.s.
pH	5.76	6.37	***	5.91	5.61	†	6.54	6.19	n.s.
Electrical conductivity (dS m^{-1})	0.10	0.07	*	0.11	0.08	*	0.09	0.06	*
Chloride (mg kg^{-1})	25.56	18.00	**	26.00	25.12	**	23.92	12.08	n.s.
Coarse sand	20.63	27.63	*	20.75	20.50	n.s.	26.92	28.33	n.s.
Fine sand	30.75	38.79	**	29.58	31.92	n.s.	38.33	39.25	n.s.
Silt	23.25	16.33	**	22.75	23.75	n.s.	16.25	16.42	n.s.
Clay	28.88	20.79	***	30.08	27.67	n.s.	21.58	20.00	n.s.

various exchangeable mineral ions. The leaves were analysed for various macro and micro nutrients. All analyses were carried out in a soil and plant laboratory accredited by the National Association of Testing Authority (NATA), Australia (accredited laboratory number 5072). The soil analytical methods used have been fully described in Osunkoya and Perrett (2011). Total leaf nitrogen and phosphorus concentrations were determined in triplicate on 0.1-g samples per plant by the micro-Kjeldahl method (AOAC 1990). Leaf potassium concentration was determined in triplicate on 1–2-g samples per individual plant by the vanadomolybdic spectrometric and atomic spectrometric methods (Ingle and Crouch 1988). For analyses of other macro- and micro-nutrients (see list below), leaf samples were first solubilised with an acid mixture of HNO_3 (60%) and $HClO_4$ (60%) (2 : 1) in a microwave. Two millilitres of the acidic solution were used per 100 mg of dry biomass of each sample. The digested solutions were thereafter brought to 10 mL of final volume (with 3% of $HClO4$ solution). After digestion, the concentrations of several ions (see below) were analysed using inductively coupled plasma–mass spectroscopy (ICP–MS). With this method, low detection thresholds can be obtained for several elemental ions.

Statistical analysis

The data for each trait were checked for homogeneity and natural log-transformed where appropriate. For soil, data for organic carbon (OC), total carbon (TC), total nitrogen (N), nitrate nitrogen (NO_3^--N), nitrate ammonium (NH_4^+-N), phosphorus (P), potassium (K), calcium (Ca), sodium (Na), magnesium (Mg), copper (Cu), manganese (Mn), sulfur (S) and soil fractions were normally distributed, whereas zinc (Zn) and iron (Fe) were not and hence transformed. For plant leaves, data for Ca, Mg, Cu, Zn, aluminum (Al), boron (Bo) and lead (Pb) were normally distributed, whereas cadmium (Cd), cobalt (Co), molybdenum (Mo), Fe, N, P, K, Mn, Na and S were not, and were hence transformed. Thereafter, data were subjected to nested analysis of variance (ANOVA) using GENSTAT for Windows (11th edn, VSN International Ltd, Hempstead UK). For each soil and plant-trait parameter, effect of site (S: the six study sites), soil infestation (I: *M. unguis-cati* infested *vs* non-infested patches) or species ecological group status (G: exotic *vs* native), habitat type (H: riparian *vs* non-riparian) and two-way interactions between these factors were examined. To examine whether, overall, the physicochemical traits of soils within *M. unguis-cati* infestations were different from those lacking the weed and to explore which of the traits were most influential across sites in driving any separation, data were normalised followed by ordination using principal component analysis (PCA) as implemented with the PRIMER ver. 6.0 statistical package (Clarke and Gorley 2006). PCA was also
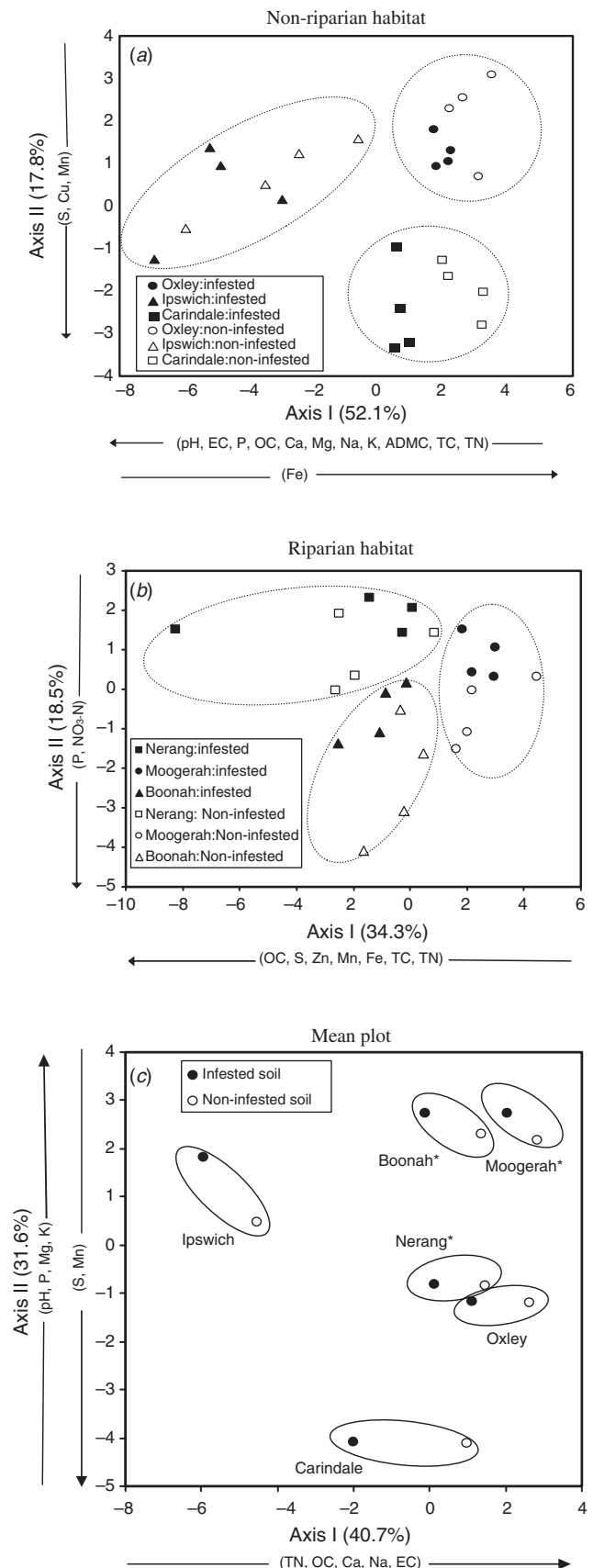
Fig. 2. Ordination of *Macfadyena unguis-cati*-infested (closed symbol) and uninfested (open symbol) soils across (*a*) three non-riparian sites, (*b*) three riparian sites, and (*c*) both habitat types combined in the Brisbane–Gold Coast region, south-eastern Australia. Asterisks indicate riparian sites. Loops indicate individual sites. For *a* and *b*, each data point represents the soil chemistry at a collection spot. Directions of the soil traits driving each axis are indicated.

used to examine overall leaf-trait differences between the invasive *M. unguis-cati* and co-occurring vine species.

Results

Invasion effect on soil properties

All soil properties differed significantly ($P \leq 0.01$) across the six sites (Table 1). There were minimal site × invasion effects, indicating a consistent invasion effect across all sites, except for soil N in form of ammonia ($P \leq 0.05$) and soil chloride (Cl) ($P \leq 0.10$). Differences between *M. unguis-cati*-infested and uninfested soils were significant for ~50% of the soil properties examined. Soils within infested areas had higher air dry-moisture content, higher OC, TC, N, Ca, Mg and S, whereas exchangeable Na and Fe were found to be lower in infested soils. Chemical characteristics pH, electrical conductivity and chloride were also found to be significantly higher in *M. unguis-cati*-infested areas. No significant differences in soil texture were found.

Invasion effect on soil properties in relation to habitat

Soil physicochemical properties in *M. unguis-cati*-infested and adjacent non-infested areas within riparian and non-riparian zones are shown in Table 2 and Fig. 2. A strong habitat effect on soil chemistry exists, with significant differences found between riparian and non-riparian habitats for ~60% of the soil traits tested. OC, TC, TN, NH₄-N, Na, Cu, Zn, S, electrical conductivity (EC), Cl, silt and clay were significantly higher in non-riparian habitats. In contrast, P and pH were significantly elevated in the riparian habitats. Also, and as expected, sand fractions were higher in riparian habitats.

Overall, invasion effect was stronger within non-riparian zones (6 of 24 traits showed a significant invasion effect) than in the riparian zones (only 1 of 24 traits showed a significant

invasion effect), although the directions of differences were the same at both habitats. Within non-riparian zones, OC, TC, pH, EC and Cl were significantly higher in *M. unguis-cati*-infested soils, whereas exchangeable Na was significantly lower. EC was the only significantly higher trait ($P \leq 0.05$) in infested soils in the riparian zones. Consequently, we carried out PCA analyses for soils of these two habitats separately (Fig. 2) in relation to invasion effect of *M. unguis-cati*. The ordination has to be viewed from the perspective of an individual site. For each habitat type, two of three sites (for non-riparian: Oxley and Carindale; for riparian: Moogerah and Boonah) showed clear differences between infested and non-infested soils. Within sites, ANOVA of the vector loadings (scores) of the data points, especially on Axis I (which explained 35–52% of the variation in the dataset) indicated that the soils in infested and non-infested patches differed significantly ($P < 0.05$), except for the Ipswich site (results not shown). The greatest difference within site as a result of the weed invasion appeared to be at the Carindale site, and the least at the Ipswich site. Additionally and overall, the Ipswich site soil chemistry was significantly different from the others and was comparatively aligned more with those of the riparian than the non-riparian habitat (Fig. 2c).

Leaf traits of invasive (exotic) vs non-invasive species

As for the soil data, leaf chemistry of the invasive vines *M. unguis-cati* and *P. suberosa* and native plant species varied more across the six sites investigated than between the two habitat types or as a result of species ecological grouping (Table 3). Nonetheless, following removal of the site or habitat effect using two way-ANOVA, a substantial number of nutrients tested still showed a significant difference in leaf chemistry between the exotic and the native vine species (Table 3, Appendix 1). Leaves of exotic species possessed significantly

Table 3. ANOVA summary results of leaf nutrient contents in exotic/invasive *Macfadyena unguis-cati* and *Passiflora suberosa* vs native *Parsonsia straminea* and *Smilax australis* vines across six sites within riparian and non-riparian habitats in Brisbane–Gold Coast region, south-eastern Australia

†$P \leq 0.10$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$; n.s., not significant

| Leaf trait | Significance (summary ANOVA) | | | | | Ecological-group mean ±s.e. | | Habitat mean ±s.e. | |
| | | Main effect | | Interaction effect | | Exotic | Native | Non-riparian | Riparian |
	Site (S)	Ecological group (G)	Habitat (H)	S*G	H*G	(n = 2 species)	(n = 2 species)	(n = 3 sites)	(n = 3 sites)
Total nitrogen	***	***	n.s.	n.s.	n.s.	2.75 ± 0.09	1.66 ± 0.09	2.53 ± 0.14	2.282 ± 0.15
Total phosphorus	***	*	***	***	***	0.35 ± 0.07	0.10 ± 0.01	0.12 ± 0.01	0.47 ± 0.09
Potassium	***	***	†	***	n.s.	2.54 ± 0.01	1.40 ± 0.04	2.37 ± 0.13	1.97 ± 0.15
Calcium	n.s.	n.s.	n.s.	n.s.	n.s.	2.33 ± 0.21	1.66 ± 0.24	2.14 ± 0.22	2.11 ± 0.22
Magnesium	n.s.	*	n.s.	*	n.s.	0.56 ± 0.07	0.29 ± 0.03	0.52 ± 0.0.07	0.37 ± 0.06
Sodium	***	n.s.	***	*	n.s.	0.04 ± 0.01	0.03 ± 0.01	0.05 ± 0.01	0.02 ± 0.01
Sulfur	**	***	n.s.	*	n.s.	0.23 ± 0.02	0.13 ± 0.01	0.18 ± 0.02	0.21 ± 0.02
Aluminium	*	**	n.s.	n.s.	n.s.	81.70 ± 8.84	37.07 ± 5.79	72.64 ± 9.45	57.71 ± 10.08
Boron	n.s.	†	**	**	*	62.54 ± 5.44	48.12 ± 4.67	54.02 ± 4.11	60.31 ± 7.76
Cadmium	***	**	n.s.	n.s.	n.s.	0.03 ± 0.01	0.01 ± 0.01	0.02 ± 1.23	0.03 ± 0.01
Cobalt	***	n.s.	n.s.	***	n.s.	0.20 ± 0.02	0.17 ± 0.05	0.19 ± 1.12	0.19 ± 0.04
Copper	***	n.s.	*	*	n.s.	14.71 ± 1.19	14.45 ± 1.82	16.83 ± 1.43	12.10 ± 0.99
Iron	***	***	n.s.	n.s.	n.s.	106.29 ± 10.07	63.83 ± 12.15	98.78 ± 11.55	105.78 ± 11.86
Manganese	***	***	n.s.	***	n.s.	73.01 ± 5.48	369.49 ± 19.4	279.99 ± 86.23	411.26 ± 185.61
Molybdenum	***	**	***	***	***	1.08 ± 0.32	0.10 ± 0.01	0.13 ± 0.02	1.68 ± 0.49
Lead	n.s.	n.s.	n.s.	n.s.	n.s.	0.54 ± 0.02	0.53 ± 0.03	0.56 ± 0.03	0.50 ± 0.00
Zinc	n.s.	*	*	n.s.	†	39.10 ± 2.35	30.63 ± 1.93	38.73 ± 2.78	31.98 ± 1.05
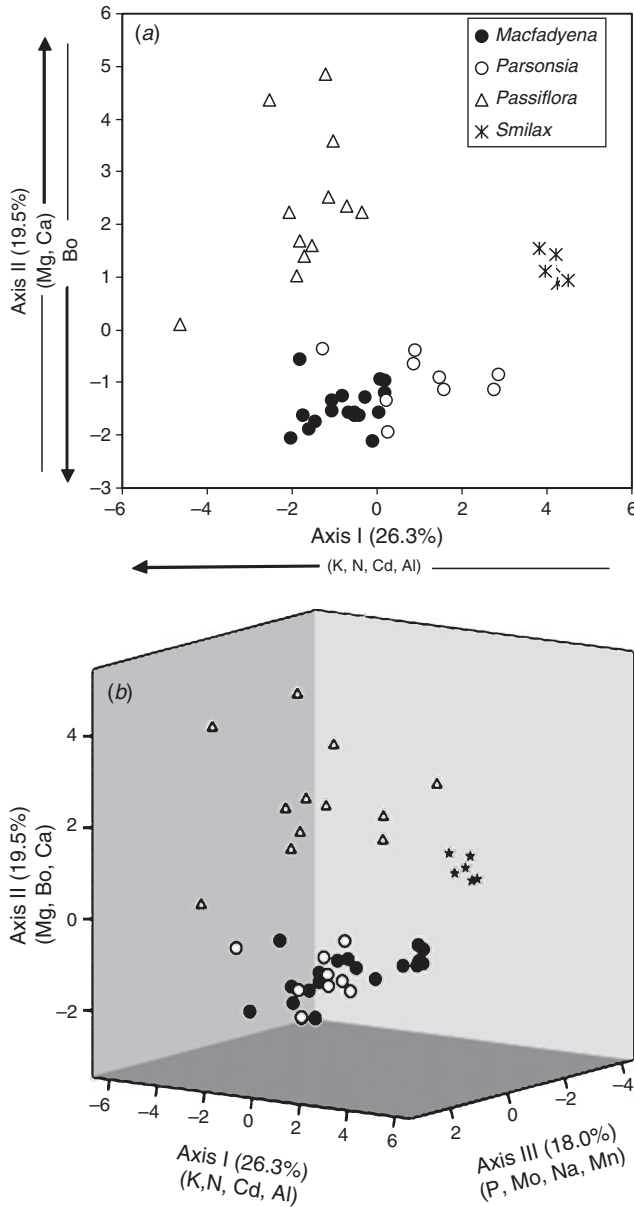
Fig. 3. Ordination on first (*a*) two and (*b*) three principal axes of four vine species (*Macfadyena unguis-cati*, *Passiflora suberosa*, *Parsonsia straminea* and *Smilax australis*) across six sites and spanning riparian and non-riparian habitats in the Brisbane–Gold Coast region, south-eastern Australia. Each data point represents the leaf chemistry of an individual plant. Influential leaf traits driving each axis are indicated.

($P < 0.05$) more N, P, K, Al, Bo, Cd, Co, Fe, Mo and Zn and significantly less Mn than did those of the native vines.

PCA ordination indicated that the exotic separated from the native species, especially on Axis I (Fig. 3*a*). However, Axes I–III (with 26%, 20% and 18% explanatory powers, respectively) are needed to adequately explain differences in leaf chemistry of the investigated species (Fig. 3*b*). Both exotics showed greater plasticity in their leaf-nutrient traits than that exhibited by the natives. Overall, the leaf chemistry of the exotic invasive *M. unguis-cati* was significantly different from two (i.e.

Passiflora suberosa and *Smilax australis*) of three co-occurring vines. Interestingly, leaf chemistry of the native *Parsonsia straminea* is the closest to the invasive *M. unguis-cati* of all species tested.

Discussion

Higher loads of nutrients (especially of N, P, and K) in response to effluents from upstream and up-slopes were to be expected in riparian zone soils because of the peculiarity of such a habitat as a transitional zone in the landscape (Naiman and Decamps 1997; Bruland and Richardson 2004). However, this expected trend is observed only for P both in the soil and leaves sampled (Tables 2, 3), perhaps because in riparian habitats (1) other nutrients are easily leached in the clay-poor substratum, and (2) P binds more to other ions and/or is immobilised more in sandy than in clayey soils (Bruland and Richardson 2004). In general, the observed higher nutrient concentrations in the non-riparian habitat (a reflection of greater negatively charged clay content which can hold greater concentrations of nutrients, notably C and N) might suggest that invasion level and hence differences between invaded and non-invaded plots will be greater here (Davis *et al*. 2000; Burns 2006). This trend is partially observed in the present study as the soil chemistry of invaded vs non-invaded plots differed more in non-riparian sites than in riparian sites (see Fig. 2, Table 2). Our results, however, are not in agreement with the notion that large positive impacts are often found at sites with lower pools of nutrients (as in riparian sites, where only 1 of 20 nutrients showed an invasion effect) compared with those with higher pools (non-riparian, in which 6 of 20 nutrients showed an invasion effect) (Dassonville *et al*. 2008). Perhaps such a generalisation applies to dynamics within similar habitat types rather than between highly diverse ones such as the riparian vs non-riparian habitats that we have contrasted in the present work.

PCA analysis showed that soils are segregated according to habitat type and invasion status (Fig. 2*c*), with the exception of the Ipswich site. The soil chemistry of the non-riparian Ipswich site appears to be more closely related to that of the riparian sites Boonah and Moogerah. This anomaly could be explained by the physical aspects of the site; it has a dry gully dissecting its landscape, which tends to flood in high rainfall events, thus behaving at times like a riparian habitat. It is also possible that invasion at this site is a much more recent event and hence differences between invaded and non-invaded plots will be negligible; however, we lack real data on history of our investigated sites and thus cannot explore this line of argument further.

As in many previous studies (e.g. Ehrenfeld 2003; Marchante *et al*. 2008; Rodgers *et al*. 2008; Osunkoya *et al*. 2011), we found higher concentrations of major nutrients (C, N, Ca and Mg) in *M. unguis-cati*-invaded soils (Table 1). Differences in nutrient concentrations between *M. unguis-cati*-infested and uninfested soil patches were also similar to differences found in areas of *Lantana camara* invasion in the same region (Osunkoya and Perrett 2011). *M. unguis-cati*, like many invasive plants, may change soil nutrient availability in such a way as to create a positive feedback between site occupancy and continued proliferation

of the weed (Dassonville *et al.* 2008; Rodgers *et al.* 2008). The increased nutrient concentrations mediated by *M. unguis-cati* may be a straightforward consequence of increased fluxes of C and N in its nutrient-rich litter return and/or due to its higher net primary productivity (Dassonville *et al.* 2008; Osunkoya *et al.* 2010*b*). Indeed, we know that *M. unguis-cati* forms masses of subterranean tuberous roots and soil surface-running inter-twining stems with accompanying N-rich leaves which, on senescence, tend to create deep litter layers (at times up to 20 cm thick) (see Osunkoya *et al.* 2009, 2011). Decomposition of such nutrient-rich litter may create a higher nutrient load in soils invaded by the weed. An alternative explanation could be that the observed trend may simply be a consequence of the invader itself preferentially colonising richer soil patches.

Higher soil pH in *M. unguis-cati*-infested soils is in line with results reported for other invasive plants (garlic mustard, *Allaria petiolata* – Rodgers *et al.* 2008; Japanese stiltgrass, *Microstegium vimineum* – McGrath and Binkley 2009; *Lantana camara* – Sharma and Raghubanshi 2009; Osunkoya and Perrett 2011). However, both increases and decreases in pH following plant invasion have been equally reported in the literature (Ehrenfeld 2003). Increases in pH may reflect the preferential uptake of ammonium rather than nitrate as N source (as reflected in a significant negative correlation between the soil pH and ammonium; $r = -0.72$, $n = 24$, $P = 0.001$ in invaded soils only) or increased base-cation concentrations in the litter of *M. unguis-cati* (Weidenhamer and Callaway 2010).

Exchangeable Na and Fe, which can be toxic to plant growth if present in excess levels, were at significantly lower concentrations in soils supporting *M. unguis-cati* than in soils lacking the weedy vine (Table 1). Similar results were found for another weed in the region, *Lantana camara* (Osunkoya and Perrett 2011). Fe, which is linked to plant photosynthetic capacity, plays a key role in ecosystem biogeochemical cycling through its interactions with C and P. Liptzin and Silver (2009) found that Fe reduction was generally greater in soils with higher C additions. Higher amounts of leaf litter in *M. unguis-cati*-infested areas and therefore higher C additions to soil could increase Fe reduction in infested soils, as was found in the present study. McGrath and Binkley (2009) found lower aluminum concentrations in soil under dense invasive *Microstegium vimineum* growth than in soil under the surrounding uninvaded understorey. *M. unguis-cati* leaves also had higher concentrations of potentially toxic ions (Al, Cd, Co and Cu) than the concentrations present in leaves of non-invasive species (Table 3), indicating that *M. unguis-cati* may more readily take up metal contaminants from the soil than do native species. Penuelas *et al.* (2010), in a general survey of leaf economics of invasives and biogeochemical niche, alluded to the relatively higher abundance of these potentially toxic trace elements in many invasive plant organs and suggested that the cycling of these elements could be accelerated in invasive alien-dominated ecosystems. However, the influence of *M. unguis-cati* in altering the soil's biogeochemical cycle appeared not to be as dramatic as that of *Lantana camara*, known to decrease the concentrations of a greater number of heavy and/or toxic metals such as Fe, Cu, Mn and S (see Osunkoya and Perrett 2011).

Species identity (native or exotic) had a greater influence on leaf nutrients than did habitat type (Table 3). The trend of higher leaf-nutrient load (especially N, P and K) in exotic vines *M. unguis-cati* and *P. suberosa* (Table 3) is linked to the preference of invasive plant species for disturbed habitats commonly associated with high pulses of nutrient input (Davis *et al.* 2000). As in our study, Penuelas *et al.* (2010) found that several invasive species had enhanced capacities in terms of productivity and nutrient capture both of macro- (N, P, K) and micro elements (Fe, Ni, Cu and Zn) and suggested that potential increases in soil nutrient availability might favour further success of invasive plants.

Exotic species separated from natives in the PCA analysis of plant-leaf nutrients (Fig. 3). Interestingly, of the two native species examined, the overall leaf chemistry of the native *Parsonsia straminea* aligned more closely to that of the invasive species *M. unguis-cati*. A similar finding using leaf physiological traits was also reported by Osunkoya *et al.* (2010*a*). This buttressed the suggestion that *P. straminea* may possess traits of an invader and is in line with the often-observed over-abundance of this native vine in remnant vegetation of eastern Australia and, thus, the need for managing this species in its own right (see Osunkoya *et al.* 2010*a*).

Conclusions

Macfadyena unguis-cati is a major exotic environmental weed in coastal Qld and NSW, Australia. Apart from the recent work of Osunkoya *et al.* (2011) on soil-ant assemblages, there is a lack of quantitative data on the impact of the weed on soil ecosystem properties. To address this, we have compared soil physicochemical properties of paired invaded and non-invaded soils as well, as the leaf nutrient content of the invader and another exotic, *P. suberosa*, with those of two native vines across six study sites and two habitat types. In all, 50% of soil traits examined varied in relation to invasion status; invaded soils had greater OC, TC, TN, moisture, pH, EC, Ca, Mg and S and lower concentrations of Fe and exchangeable Na. Invasive *M. unguis-cati* and *P. suberosa* had higher concentrations of leaf nutrients N, P, K, Fe, Al, Bo, Co, Cu and Mo and lower concentrations of Mn than did native vines. Comparisons between invaded and uninvaded areas after invasion cannot rule out the possibility that initial differences between areas are the causes rather than the results of patterns of invasion impact observed. However, consistency in the direction of differences in nutrient concentrations within and just adjacent to patches of *M. unguis-cati*, and spanning many sites, offer strong circumstantial evidence that this invader species can change soil conditions. Additionally, our findings aligned with those of many previous studies (e.g. Ehrenfeld 2003; Marchante *et al.* 2008; Rodgers *et al.* 2008; Weidenhamer and Callaway 2010; Osunkoya *et al.* 2011). Thus, *M. unguis-cati* may improve soil fertility, decrease (albeit to a limited extent) concentrations of potentially toxic elements, and positively influence nutrient cycling and rhizosphere quality to create, through legacy effects of its own litter input, a positive feedback between site occupancy and its continued proliferation (see also Meisner *et al.* 2012). Further studies are required to ascertain the extent of such hypothesised

litter legacy effect on the growth performance of the exotic invasive relative to that of co-occurring native species.

Acknowledgements

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Appendix 1.　Average nutrient concentrations in leaves of two exotic/invasive (*Macfadyena unguis-cati* and *Passiflora suberosa*) and two native (*Parsonsia straminea* and *Smilax australis*) vine species.
Summary results of one-way ANOVA of test of significance differences between the species are also given for each habitat type and for the pooled data

Habitat and test species	Macronutrients (%)							Mean leaf nutrient concentration				Micronutrients (mg/kg)					
	N	P	K	Ca	Mg	Na	S	Al	Bo	Cd	Co	Cu	Fe	Mn	Mo	Pb	Zn
Riparian																	
Macfadyena (MU)	2.69	0.62	2.34	1.87	0.25	0.03	0.20	74.78	95.32	0.05	0.22	11.44	109.65	75.86	1.20	0.50	31.88
Passiflora (A)	2.34	0.88	2.34	3.70	0.90	0.01	0.41	85.00	29.40	0.03	0.13	9.83	104.71	57.54	1.02	0.50	33.77
Parsonsia (B)	1.86	0.13	1.32	2.16	0.23	0.04	0.15	38.33	46.83	0.05	0.56	20.00	125.89	2041.74	0.10	0.50	35.77
Smilax (C)	1.26	0.13	1.10	0.93	0.22	0.01	0.16	15.67	34.67	0.01	0.08	7.77	38.90	79.43	0.10	0.50	26.63
Prob (sig level) 1: MU, A vs B, C	***	**	***	†	NS	NS	**	*	*	*	NS	NS	†	**	**	NS	NS
Prob (sig level) 2: MU vs B, C	***	**	***	NS	NS	NS	***	*	***	NS	NS	NS	NS	NS	NS	NS	NS
Prob (sig level) 3: MU vs A	NS	NS	NS	***	***	NS	***	NS	***	NS	NS	NS	NS	NS	NS	NS	NS
Non-Riparian																	
Macfadyena (MU)	3.02	0.14	2.51	1.50	0.27	0.03	0.17	87.44	70.99	0.03	0.28	20.93	120.23	67.61	0.14	0.56	34.98
Passiflora (A)	2.69	0.12	2.88	3.40	1.03	0.11	0.32	81.78	32.37	0.03	0.14	13.38	91.20	83.18	0.13	0.57	52.22
Parsonsia (B)	1.95	0.08	2.04	2.01	0.37	0.06	0.09	57.17	63.57	0.02	0.19	18.25	72.44	891.25	0.10	0.58	29.08
Smilax (C)	1.45	0.11	0.89	1.21	0.26	0.02	0.17	17.00	31.97	0.01	0.09	7.97	40.74	52.48	0.10	0.50	32.60
Prob (sig level) 1: MU, A vs B, C	***	**	***	NS	*	NS	***	*	NS	†	NS	NS	**	***	NS	NS	*
Prob (sig level) 2: MU vs B, C	***	**	NS	NS	NS	NS	NS	*	*	NS	NS	†	***	NS	NS	NS	NS
Prob (sig level) 3: MU vs A	NS	NS	NS	***	***	***	***	NS	***	NS	NS	*	NS	NS	NS	NS	**
Overall																	
Macfadyena (MU)	2.88	0.38	2.40	1.69	0.26	0.03	0.19	81.11	83.16	0.03	0.27	16.18	114.82	70.79	0.42	0.53	33.43
Passiflora (A)	2.63	0.31	2.75	3.54	1.00	0.05	0.34	82.58	31.63	0.03	0.14	11.61	93.33	75.86	0.22	0.55	47.61
Parsonsia (B)	1.91	0.1	1.78	2.08	0.33	0.06	0.11	50.89	57.99	0.01	0.25	19.12	87.10	1174.90	0.10	0.56	31.31
Smilax (C)	1.35	0.12	0.98	1.07	0.24	0.01	0.17	16.33	33.32	0.04	0.08	7.87	39.81	64.57	0.10	0.50	29.62
Prob (sig level) 1: MU, A vs B, C	***	***	***	*	*	NS	***	**	*	**	NS	NS	***	***	**	NS	*
Prob (sig level) 2: MU vs B, C	***	*	***	NS	NS	***	NS	***	***	***	***	**	***	***	NS	NS	NS
Prob (sig level) 3: MU vs A	NS	NS	NS	***	***	NS	***	NS	***	NS	***	NS	NS	***	***	NS	***

NS, not significant; † $P \leq 0.10$; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.