

Seed rain and soil seed banks limit native regeneration within urban forest restoration plantings in Hamilton City, New Zealand

Elizabeth Overdyck* and Bruce D. Clarkson

Centre for Biodiversity and Ecology Research, Department of Biological Sciences, University of Waikato, Private Bag 3105, Hamilton 3240, New Zealand

*Author for correspondence (Email: eg3@waikato.ac.nz)

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Abstract: Restoration of native forest vegetation in urban environments may be limited due to isolation from native seed sources and to the prevalence of exotic plant species. To investigate urban seed availability we recorded the composition of seed rain, soil seed banks and vegetation at native forest restoration plantings up to 36 years old in Hamilton City and compared these with naturally regenerating forest within the city and in a nearby rural native forest remnant. Seed rain, soil seed banks (fern spores inclusive) and understorey vegetation in urban forest were found to have higher exotic species richness and lower native species density and richness than rural forest. Both understorey vegetation and soil seed banks of urban sites >20 years old had lower exotic species richness than younger (10–20 years) sites, indicating a developmental threshold that provided some resistance to exotic species establishment. However, the prevalence of exotic species in urban seed rain will allow reinvasion through edge habitat and following disturbance to canopy vegetation. Persistent soil seed banks from both urban and rural sites were dominated by exotic herbaceous species and native fern species, while few other native forest species were found to persist for >1 year in the seed bank. Enrichment planting will be required for those native species with limited dispersal or short-lived seeds, thus improving native seed availability in urban forests as more planted species mature reproductively. Further research into species seed traits and seedling establishment is needed to refine effective management strategies for successful restoration of urban native forests.

Keywords: ecological restoration; fern spore bank; fragmentation; seed dispersal; succession; urban ecology

Introduction

Native forest is characteristically scarce in urban areas and constantly under threat from surrounding development, invasion by exotic pest plants and animals, and disturbance from human activities (McDonnell 2007). High rates of reinvasion by exotic plant species coupled with a potentially reduced input of seeds from native species may necessitate greater management of urban forest patches if the desire is to restore similar successional pathways to those in intact native forests (Norton 2009). The urban landscape provides a diverse and abundant source of non-native plant propagules (Esler 1987; Thompson et al. 2003; Sullivan et al. 2005) and urban forest patches are often isolated from mature native forest as a seed source for regeneration (Sullivan et al. 2009), which can lead to reduced seed rain and soil seed banks for native species (Kostel-Hughes et al. 1998; Moles & Drake 1999).

There has been much recent interest in the ecology of urban natural spaces, both in New Zealand (e.g. Clarkson & McQueen 2004; Clarkson & Meurk 2004; Stewart et al. 2004; Meurk & Hall 2006; Sullivan et al. 2009) and elsewhere (McDonnell & Pickett 1990; Crane & Kinzig 2005; Pickett et al. 2008). Restoring native forest in an urban setting improves public access to and appreciation of native flora and fauna (Miller & Hobbs 2002; Miller 2005, 2006; Meurk & Swaffield 2007; Pickett & Cadenasso 2008) and in New Zealand contributes to redressing the wider extensive loss of native forest habitat in lowlands, where all urban centres are located (Leathwick et al. 2003; Clarkson et al. 2007a; Walker et al. 2008). Many native species are declining due to the impacts of human

activities (de Lange et al. 2009) and the increasing number of naturalised exotic species also can be closely related to human population pressure (Esler & Astridge 1987; Atkinson & Cameron 1993; Williams & Cameron 2006), such that exotic species have become well established among native species in urban ecosystems (Meurk 2011).

Some native forest species in New Zealand regenerate well in urban environments (Smale & Gardner 1999; Stewart et al. 2004), but the loss of other less adaptable species (Esler 1991; Whaley et al. 1997; Duncan & Young 2000) is of concern for restoration and conservation of biodiversity. Hobbs and Norton (2004) propose the concept of thresholds in ecosystem restoration where abiotic or biotic factors may prevent a restoration from progressing toward desired goals. While abiotic conditions in urban forest (e.g. elevated temperature and high vapour pressure deficit) may place some constraints on species composition (Miller 2011), our study considers whether biotic thresholds related to seed availability are operating in urban environments. Seed source, dispersal mode and persistence of seed banks could all represent significant thresholds at various stages in forest restoration, influencing the establishment success of either native or exotic species, with respectively positive or negative consequences for progressing restoration (Holl et al. 2000; Zimmerman et al. 2000; Hooper et al. 2005; Bossuyt & Honnay 2008; White et al. 2009). Vegetation assessments of restoration planting in native forests in urban (Sullivan et al. 2009; MacKay et al. 2011) and rural (Reay & Norton 1999; Smale et al. 2001) New Zealand indicate that native seed input from adjacent intact forest is important for regeneration. However, the

comparative roles of dispersed seed and that inherited from seed banks or extant vegetation have not been established. Many native forest species in New Zealand appear to have short-lived seeds that are not likely to form persistent soil seed banks (Burrows 1994b; Sem & Enright 1996; Rowarth et al. 2007) therefore depending on dispersal in seed rain to seral communities (Partridge 1989; Burrows 1994a; Moles & Drake 1999; Dungan et al. 2001). If thresholds in seed availability are acting in the urban environment as species ‘filters’ (*sensu* Williams et al. 2009) then urban forest vegetation will be distinct from that in more intact native forest. This offers opportunities to study new species assemblages in ‘novel’ (Hobbs et al. 2006) or ‘recombinant’ (Meurk 2011) ecosystems and contribute to vegetation succession theory in the broader landscape (McDonnell & Pickett 1990), as well as identifying potential limitations on restoration success.

This study investigates whether seed availability limits natural succession in urban forest patches (including those restored by planting and those naturally regenerating) by measuring seed rain, soil seed banks and vegetation composition. We hypothesise that there will be relatively fewer native forest species in the seed supply (seed rain and soil seed

banks) of urban forest and that there will be increased seed available from exotic species in comparison with intact rural forest. In addition, we investigate whether there is an increased range and diversity of native forest species present as urban forest ages through improved native seed supply and more suitable microsites for the establishment of late-successional forest species.

Methods

Study location

The study was conducted in Hamilton City and the Hakarimata Range Scenic Reserve (1811 ha), 14 km north of the city, in the Hamilton Ecological District (McEwen 1987), North Island, New Zealand (Fig. 1). The natural vegetation of Hamilton Ecological District has been heavily modified by Polynesian burning and more recently by intensive agricultural land use since European settlement (Nicholls 1976). Predominant vegetation c. 1840 was secondary scrub (56%), wetland (32%) and primary forest (12%); currently only 0.2% (368 ha) of the Hamilton Ecological District is in primary forest cover

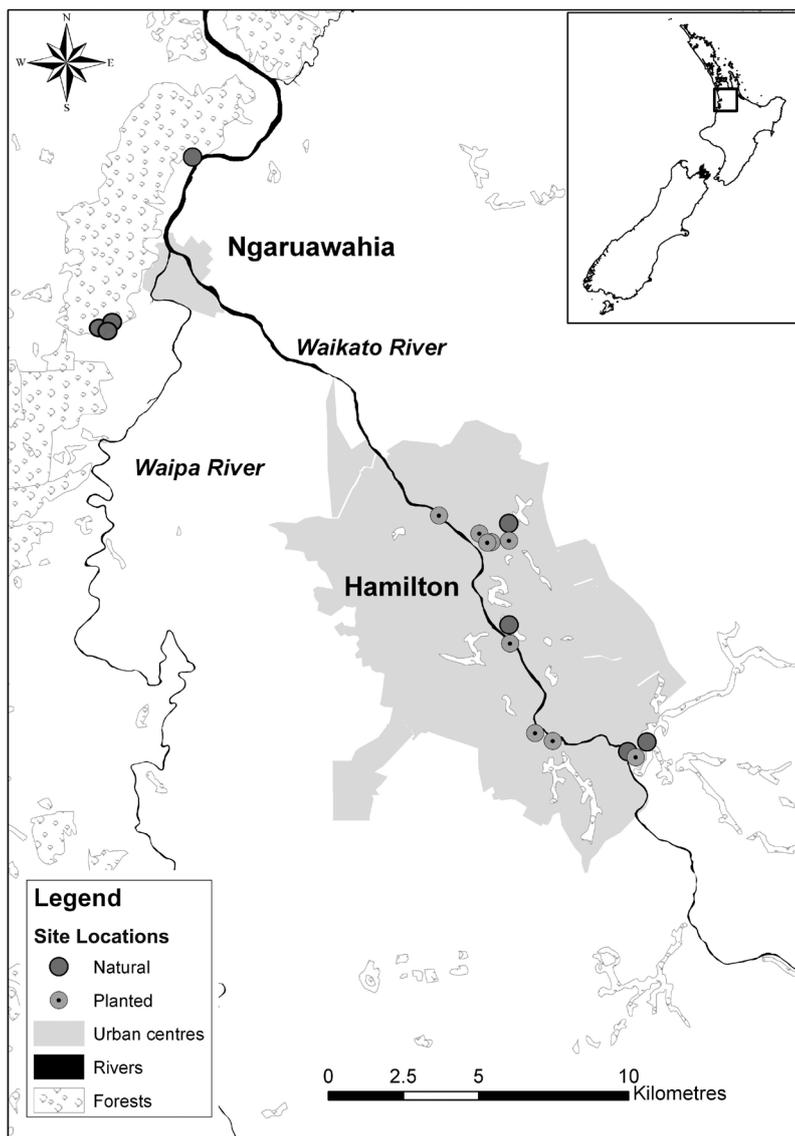


Figure 1. Location of study sites (north to south). Urban planted forest (dotted circles) in Hamilton City ($n = 9$): Munro’s Esplanade; Tauhara Park (3 sites); Onukutara Gully; Pine Beach; Yendell Park; Dillicar Park; Hammond Park. Urban natural forest (circles) in Hamilton City ($n = 4$): Mangaiti Gully; Ranfurly Gully; Mangaonua Gully (private); Hammond Park. Rural natural forest (circles) in the Hakarimata Range to the north ($n = 4$): private property and DOC Scenic Reserve (3 sites).

(Leathwick et al. 1995). Primary forest of the district is mixed conifer–hardwood forest, consisting mainly of *Dacrydium cupressinum* and *Beilschmiedia tawa* on the lowlands and emergent *Metrosideros robusta* on the lowland hills, with *Dacrycarpus dacrydioides* dominant in conifer forest on poorly drained alluvial sites (Nicholls 1976; Clarkson et al. 2007b).¹

Hamilton City – population 136 600 (Statistics New Zealand 2008) and land area 9860 ha (Hamilton City Council 2008) – contains no more than 20 ha of indigenous forest remnants (Clarkson & McQueen 2004), the largest a 5.2-ha kahikatea forest reserve (Whaley et al. 1997). Urban ecosystem restoration in Hamilton has focused on the numerous gully systems that extend from the Waikato River, which runs centrally through the city. These suburban gullies occupy a substantial 750 ha (Downs et al. 2000) and are generally in a degraded state, overrun by invasive weeds, with few examples of remnant indigenous vegetation and many gully heads infilled for urban development. Hamilton City Council has undertaken planting of native trees in gullies since the mid-1970s, with a more ecologically guided approach from the early 1990s (MacKay 2006; MacKay et al. 2011), providing an approximately 35-year span of patches of restoration planting established in the urban environment.

Study design

We compared patches of native forest where Hamilton City Council had undertaken restoration planting (9 urban sites) with naturally regenerating forest remnants in the city (4 sites) and natural forest in the Hakarimata Range (4 sites) as reference sites (Fig. 1). Restoration plantings were identified spanning 10–36 years since initial planting date so that sites could be categorised into two age groups for analyses: 10–20 years and >20 years (Table 1). Reference sites in natural forest were selected in similar age groups of secondary regenerating forest and with an older mature forest (c. 150 years) included. Restoration sites were chosen for similarity in species composition of initially planted natives, with no remnant native trees and no follow-up enrichment planting. All sampling sites were located on gully mid-slopes ranging from 17° to 40° within the altitudinal range 20–80 m above sea level.

Data collection

Vegetation assessment

Sampling of the composition and structure of extant vegetation was undertaken with plots located centrally within each forest patch to reduce any edge effects where possible. A variable-area or constant-count plot method (Jane 1982; Batcheler & Craib 1985) was used where the 30 nearest tree stems to the plot

centre were measured in an outward spiralling sequence. Plot diameter was measured through the plot centre to the widest point of the spiral and again perpendicular to this, allowing calculation of plot area. Within this circular plot all tree stems >20 mm in diameter at breast height (dbh), 1.35 m, were measured and recorded, all stems <20 mm dbh and >300 mm height (including lianes) were counted and recorded, and ground cover vascular species <300 mm in height were listed.

Seed rain and soil seed bank assessment

Four seed sampling points were systematically placed halfway along four fixed-bearing radii (at 90° angles) extending from the centre of the vegetation sampling plot to the plot perimeter at each site. Plastic seed-raising trays (325 × 130 mm) containing seed-raising mix (300–400 m deep) were used to collect seed rain. Four trays (total area 0.169 m²) per site were replaced at 6-weekly intervals for one year (September 2006 to August 2007) and returned to glasshouses for germination to assess the annual germinable seed and fern spore rain after predation losses, following Enright & Cameron (1988) and Sem & Enright (1996). The soil seed bank was sampled in September 2006 to 10 cm depth, using the same sized area as the seed rain trays, at four locations (total area 0.169 m²) per site adjacent to seed rain collections. Soil samples were returned to glasshouses and spread onto plastic seed-raising trays (350 × 295 mm) to a depth of approximately 30 mm, over a base of seed-raising mix 10 mm deep. All trays were regularly watered and glasshouse air temperatures ranged daily from 19 to 26°C in summer and 12 to 20°C in winter. Several trays of seed-raising mix only were placed among samples as a control to identify germination of any airborne glasshouse contaminants. As seedlings and fern sporophytes emerged in trays they were identified to species level where possible, counted and removed; sometimes this required retention and potting of plants for later identification. All vascular plants, including ferns, were recorded. Germination was allowed to proceed for 18 months following each soil seed bank and seed rain collection; the only disturbance to soil in trays over this period was the regular removal of germinants once identified. Very few germinants still occurred at 18 months. The terms soil seed bank and seed rain are used for simplicity throughout, although fern spores are included unless otherwise stated.

Data analysis

Mean density and species richness were tested for significant differences between forest types (urban planted, urban natural and rural natural), using GLM factorial analysis of variance (ANOVA) and post hoc Tukey's tests, after data were checked

Table 1. Forest age at sites sampled within Hamilton City (urban planted and urban natural) and Hakarimata Range (rural natural forest).

Forest type	Vegetation	Forest vegetation age group (years)			Total sites
		10–20	20–36	100+ (mature forest)	
Urban planted	Restoration planting	4	5	-	9
Urban natural	Natural regeneration	2	1	1	4
Rural natural	Natural regeneration	2	1	1	4

¹Plant scientific names follow the New Zealand Plant Names Database of Landcare Research accessed Dec. 2010 (<http://nzflora.landcareresearch.co.nz/>)

against assumptions, in STATISTICA 8 (StatSoft, Inc.). Mean seed density and species richness data are presented per site area sampled (0.169 m²). Canopy (>20 mm dbh) and understorey (>300 mm height, <20 mm dbh) density and species richness data are presented per 100 m² to standardise for variable sizes of vegetation plot (range 64–272 m²). Persistent species, as opposed to transients that persist for less than 1 year (Thompson 1993), were calculated as being those species that occurred in greater quantities (>10 individuals) in the soil seed bank than in the total annual seed rain at one site or more. Urban planted and urban natural forest treatments were combined for age-group comparisons as they followed the same trend. Non-metric multidimensional scaling (NMDS) was used to illustrate compositional differences among vegetation, seed bank and seed rain species, using PC-ORD Version 6 (McCune & Mefford 2011). The Sorenson (Bray–Curtis) dissimilarity measure was chosen to quantify compositional differences among plots. We used a maximum number of 500 iterations to achieve a stable solution with an instability criterion of 0.0000001. We evaluated 250 runs with real data and used 250 runs with permuted data to evaluate the strength of six dimensions. Permutational multivariate analysis of variance (PERMANOVA) with Sorenson (Bray–Curtis) distances was used to test for compositional differences among groups using site/plot as a blocking variable (Anderson 2001). Indicator Species Analysis (ISA) was used to identify species with high relative abundances and frequencies in vegetation, seed bank and seed rain groups (Dufrene & Legendre 1997).

Results

Canopy and understorey species richness and density

There was no significant difference in total canopy species richness or density between urban and rural sites, although mean native density was significantly higher ($P < 0.05$) at rural than at urban planted sites (Table 2). This is attributable to the abundance of kānuka (*Kunzea ericoides*), mānuka (*Leptospermum scoparium*) and *Ripogonum scandens* at rural sites (Appendix 1). High exotic density in canopy vegetation (Table 2) is explained by a dense stand of gorse (*Ulex europaeus*) at a young rural site, while urban sites commonly contained several exotic tree or liane species in the canopy (Appendix 1). At urban planted sites the canopy predominantly comprised

a mixture of early-successional native trees, while at urban natural sites *Melicactus ramiflorus* and the tree ferns *Dicksonia squarrosa* and *Cyathea* spp. were the main canopy species (Appendix 1).

Understorey species richness was significantly higher ($P < 0.05$) at rural compared with urban sites (Table 2). This was largely a function of high native species richness at rural sites compared with urban planted and urban natural sites ($P < 0.01$). Native understorey species richness at urban natural sites was also significantly ($P < 0.05$) higher compared with urban planted sites (Table 2). Understorey exotic species richness was greater at urban sites, particularly urban natural sites, compared with rural sites but not significantly so (Table 2). Density was highly variable between sites but exotic density was similar between urban planted and rural understoreys (Table 2), due mainly to abundant *Ligustrum sinense* and gorse respectively (Appendix 1), and was lowest at urban natural sites. Many native species, although particularly mānuka and bracken (*Pteridium esculentum*) (Appendix 1), contributed to higher native species density in rural compared with urban understoreys.

Vegetation growth forms

The floristic composition (canopy, understorey and groundcover vegetation) of urban planted sites comprised predominantly native woody shrubs and trees (mean 33% of all species) and almost equal amounts of native fern (18%), exotic herbaceous (18%) and exotic woody species (17%) (Fig. 2a & b). Native ferns (32%) dominated at urban natural sites followed by native woody species (21%) and exotic herbs (17%) and woody species (15%). Rural sites had numerous native species, particularly woody trees and shrubs (44%) and ferns (28%), with the only exotic growth forms recorded being woody trees and shrubs, and one liane.

Soil seed bank and seed rain species richness and density

Total species richness recorded from the soil seed bank ($n = 17$ sites) was 247 species (including 33 fern species) and seed and fern spore germinants numbered 60 988 (of which 36 828 were ferns). From the annual seed rain at all sites, 160 species (including 25 fern species) were recorded; with 8549 seedlings (3348 were ferns) germinating.

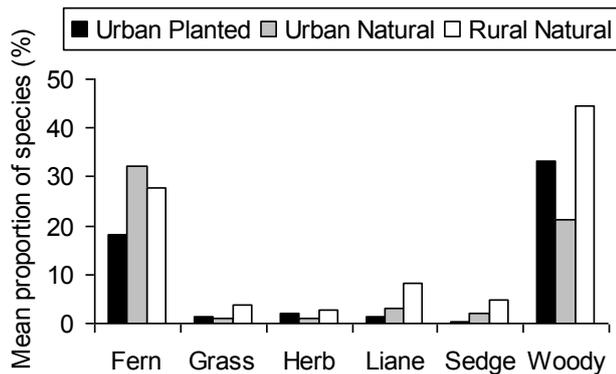
Mean species richness of soil seed banks was significantly ($P < 0.05$) greater in urban planted than rural sites, due to high exotic species richness ($P < 0.01$) (Table 3). Native species

Table 2. Mean (\pm standard error) species richness and density (per 100 m²) of vegetation canopy (all stems > 20 mm dbh) and understorey (all stems < 20 mm dbh and > 300 mm height) for three forest types: urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$). Bold text indicates significant difference between urban and rural treatments: ** $P < 0.01$, * $P < 0.05$, and between urban treatments: # $P < 0.05$, ANOVA post hoc Tukey's test.

Species	Forest type	Canopy		Understorey	
		Species richness	Density	Species richness	Density
Total	Urban planted	4.2 \pm 0.6	18.1 \pm 2.3	*12.3 \pm 2.0	122.2 \pm 41.6
	Urban natural	4.5 \pm 0.4	26.7 \pm 4.6	21.7 \pm 5.0	85.7 \pm 12.0
	Rural natural	3.6 \pm 1.1	45.7 \pm 18.1	*26.7 \pm 2.4	260.9 \pm 107.9
Exotic	Urban planted	0.6 \pm 0.2	2.1 \pm 1.4	6.0 \pm 1.3	67.3 \pm 32.6
	Urban natural	0.6 \pm 0.4	2.8 \pm 2.1	9.8 \pm 4.6	34.4 \pm 18.2
	Rural natural	0.4 \pm 0.4	10.8 \pm 10.8	2.9 \pm 1.4	70.9 \pm 51.6
Native	Urban planted	3.6 \pm 0.5	*16.1 \pm 2.1	**#6.3 \pm 1.1	54.9 \pm 29.5
	Urban natural	3.8 \pm 0.1	23.9 \pm 4.7	**#11.9 \pm 1.1	51.3 \pm 7.7
	Rural natural	3.2 \pm 1.2	*34.9 \pm 7.6	**23.8 \pm 2.0	190.0 \pm 62.1

richness in soil seed banks was greater at rural sites than at urban planted or urban natural sites, but this was not statistically significant. Annual seed rain showed the same trend as the soil seed banks, with higher total and exotic species richness and lower native species richness for urban planted and natural sites, but with no statistically significant differences (Table 3).

(a) native



(b) exotic

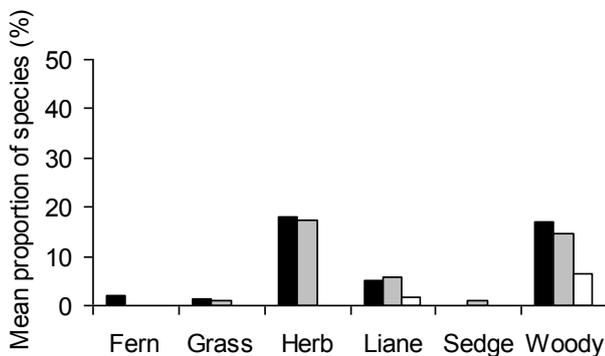


Figure 2. Mean percentage of (a) native and (b) exotic species represented by growth form as recorded in the extant vegetation (canopy, understorey and groundcover) for urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$) forests.

Density of germinable diaspores in soil seed banks and seed rain similarly showed increased presence of exotic species at urban compared with rural sites, with no statistical significance and high variability between sites (Table 3). Native species mean density in soil seed banks and seed rain was greater at rural sites; this was significant for seed rain ($P < 0.05$) between rural and both urban planted and urban natural sites (Table 3).

Soil seed bank and seed rain growth forms

Soil seed banks of urban planted sites were dominated by exotic herbaceous species (mean 37% of all species), native fern species (18%) and exotic woody species (9%) with only 6% native woody species, including two cultivated varieties (Fig. 3a & b). At urban natural sites seed banks were similarly dominated by exotic herbs (21%), native ferns (20%), and exotic woody species (7%), with several exotic rushes (9%) and native woody species (7%). Rural soil seed banks contained predominantly native ferns (22%), exotic herbs (21%), native woody species (16%), and native herbs (9%).

Seed rain of urban planted sites was similarly dominated by exotic herbaceous species (29%) and native ferns (16%) but with less exotic (13%) and more native (10%) woody species than in the seed banks (Fig. 4a & b). Seed rain of urban natural sites was predominantly native ferns (22%) and exotic herbs (19%) along with exotic (11%) and native (10%) shrubs and trees. At rural sites native ferns (28%) and exotic herbs (20%) dominated the seed rain, with native shrubs and trees (14%) and exotic rushes (10%) common.

Persistent soil seed bank composition

In total 65 exotic and 39 native species were present at greater density (>10 individuals) in the soil seed bank than in the annual seed rain input, suggesting that for these species some seeds persist in the soil from year to year (Appendix 2). These persistent seed bank species accounted for 34% of all exotic and 26% of all native species recorded as present or as germinants in this study. Of all native species present, herbaceous species were most likely to be persistent (54% of species) while native tree and shrub species were least likely to form persistent seed banks (15%). For exotics, the most species present classified as persistent were rushes (55%) and the least were trees and shrubs (18%). Overall, exotic herbs and native ferns had the most numerous persistent species at both urban and rural sites. Sixty-four per cent of native and 46% of exotic persistent species were common to both rural

Table 3. Mean (\pm standard error) species richness and density of germinable diaspores (recorded over 18 months) from the soil seed bank and annual seed rain per site (0.169 m^2) for three forest types: urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$). Bold text indicates significant differences between urban and rural treatments: ****** $P < 0.01$, ***** $P < 0.05$, ANOVA post hoc Tukey's test.

Species	Forest type	Soil seed bank		Seed rain	
		Species richness	Density	Species richness	Density
Total	Urban planted	*69.2 \pm 5.4	3879.2 \pm 396.7	41.2 \pm 4.0	388.2 \pm 76.2
	Urban natural	61.3 \pm 8.0	3664.3 \pm 731.3	44.3 \pm 4.9	441.5 \pm 166.3
	Rural natural	*44.5 \pm 4.6	2854.5 \pm 532.6	34.5 \pm 3.2	822.3 \pm 245.3
Exotic	Urban planted	**46.4 \pm 1.9	1344.1 \pm 360.5	25.8 \pm 2.8	148.9 \pm 46.0
	Urban natural	36.3 \pm 3.6	1121.0 \pm 243.5	24.0 \pm 2.7	259.3 \pm 150.9
	Rural natural	**17.3 \pm 4.0	219.5 \pm 120.5	15.3 \pm 1.0	65.5 \pm 7.2
Native	Urban planted	22.0 \pm 3.5	2527.9 \pm 361.9	15.3 \pm 1.5	*238.6 \pm 50.3
	Urban natural	24.5 \pm 6.5	2542.5 \pm 523.6	19.8 \pm 2.6	*181.8 \pm 60.3
	Rural natural	27.3 \pm 2.5	2635.0 \pm 588.5	18.5 \pm 1.9	*756.0 \pm 243.5

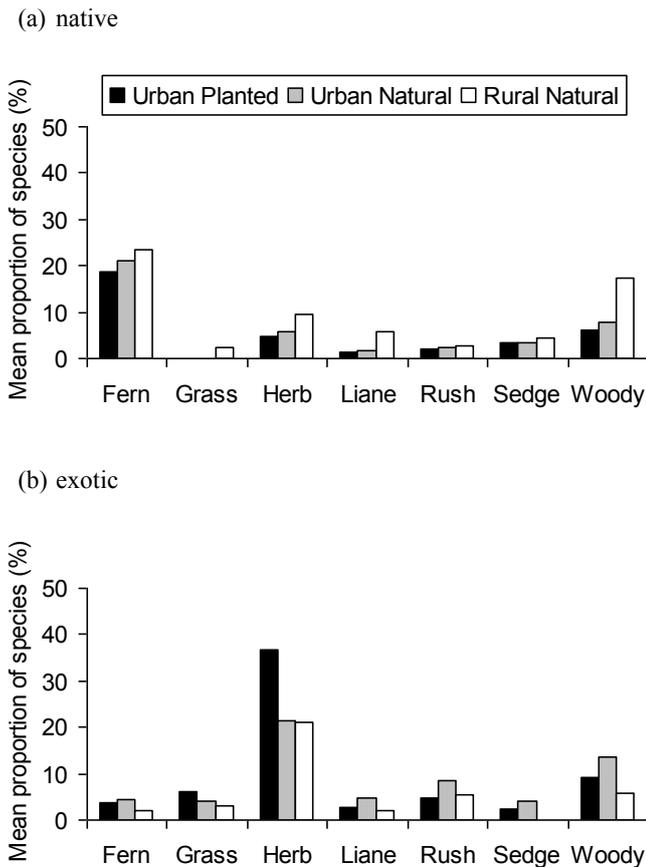


Figure 3. Mean percentage of (a) native and (b) exotic species represented by growth form as recorded in the soil seed bank as germinable diaspores for urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$) forests.

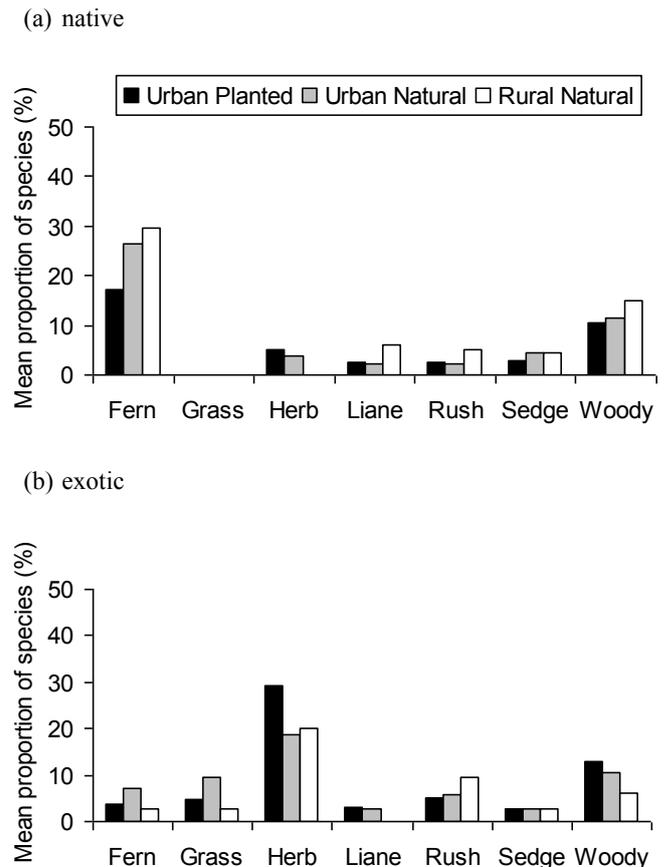


Figure 4. Mean percentage of (a) native and (b) exotic species represented by growth form as recorded in the annual seed rain as germinable diaspores for urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$) forests.

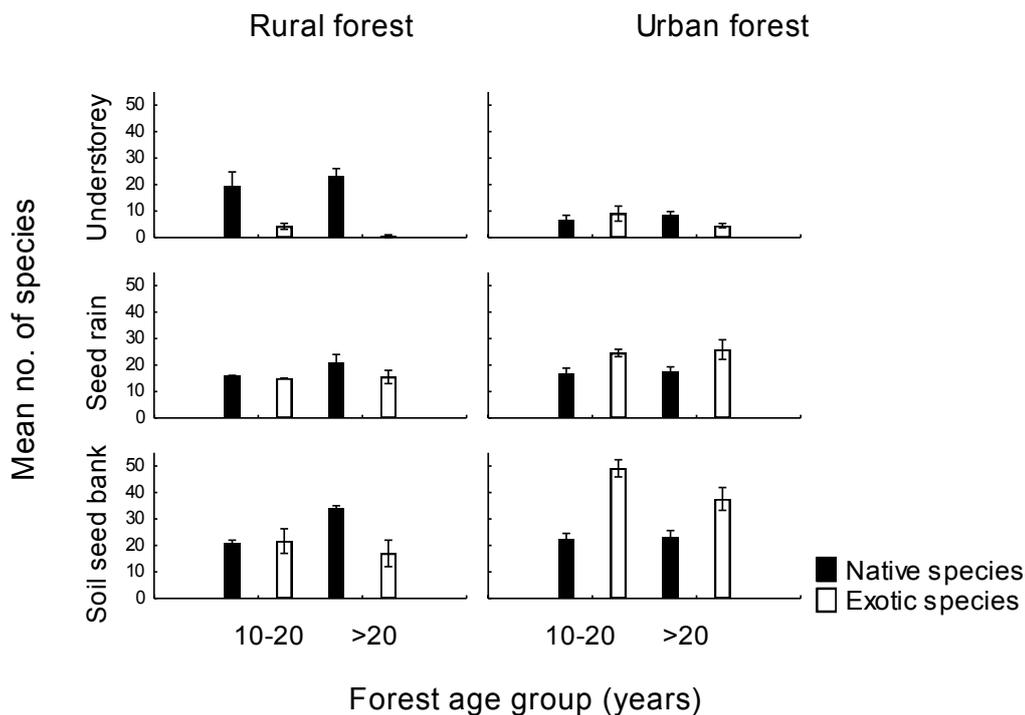


Figure 5. Mean (\pm standard error) native and exotic species richness for understorey vegetation (per 100 m²), annual seed rain (per 0.169 m²) and soil seed bank (per 0.169 m²) for all urban (planted and natural, $n = 13$) and rural (natural, $n = 4$) forest sites by vegetation age group: young (10–20 years) and older (>20 years).

Table 4. Mean (\pm standard error) exotic and native density of understorey stems (per 100 m²) and seed rain and seed bank germinants (per 0.169 m²) for urban (planted and natural) and rural (natural) forest sites, shown in two site age-groups: young (10–20 years) and older (>20 years).

	Forest type	Age group (<i>n</i>)	Understorey	Seed rain	Seed bank
Exotic species	All urban (planted and natural)	Young (6)	28 \pm 9	214 \pm 101	1521 \pm 184
		Older (7)	82 \pm 41	156 \pm 58	1065 \pm 450
	Rural natural	Young (2)	142 \pm 77	75 \pm 5	151 \pm 82
		Older (2)	0	57 \pm 12	289 \pm 267
Native species	All urban (planted and natural)	Young (6)	32 \pm 10	234 \pm 70	2241 \pm 467
		Older (7)	72 \pm 36	210 \pm 46	2782 \pm 353
	Rural natural	Young (2)	295 \pm 7	1124 \pm 171	2022 \pm 149
		Older (2)	85 \pm 33	388 \pm 236	3249 \pm 1142

and urban sites. Five and seven native persistent species were found exclusively in rural and urban seed banks respectively, while many exotic persistent species (41 species) were found only in urban seed banks.

Forest patch age and regeneration potential

Native species richness in the understorey showed little difference between the two age groups (10–20 years and >20 years) for rural and urban sites, and was always at least three-fold higher at rural sites (Fig. 5). Native species richness of soil seed banks and seed rain was similar at rural and urban sites in the young age group (10–20 years) but for the older age group (>20 years) was higher at rural sites. Exotic species richness was consistently higher at urban than rural sites for seed banks, seed rain and understorey in both age groups (Fig. 5). Exotic species richness in the understorey and seed bank was lower for older compared with younger sites for both urban and rural forests, while exotic seed rain showed little change in richness between age groups.

High variability in densities among sites for understorey stems and soil seed bank and seed rain germinants was

particularly influenced by high densities of kānuka, mānuka and gorse at young rural sites. Notably, urban sites had less dense native understorey at young sites (10–20 years) but were similar to rural sites in the older age group (>20 years) (Table 4). Exotic species were not recorded in the understorey at older rural sites, but older urban sites had high exotic density in the understorey. Density of native species in the seed rain was lower at urban than rural sites (especially in younger forest) with little difference between the two age groups in urban forest (Table 4). For soil seed banks, density of native species was greater at older sites, particularly for rural sites (Table 4). Density of exotic germinants in seed rain and soil seed banks was highest at young urban sites and despite being reduced at older urban sites was still higher than rural sites, by around three-fold.

Comparative species composition

Composition differed significantly among vegetation, soil seed banks and seed rain (PERMANOVA, $F = 14.830$, $P = 0.0002$) with site taken into account as a significant blocking variable ($F = 2.7591$, $P = 0.0002$). Post hoc pairwise comparisons

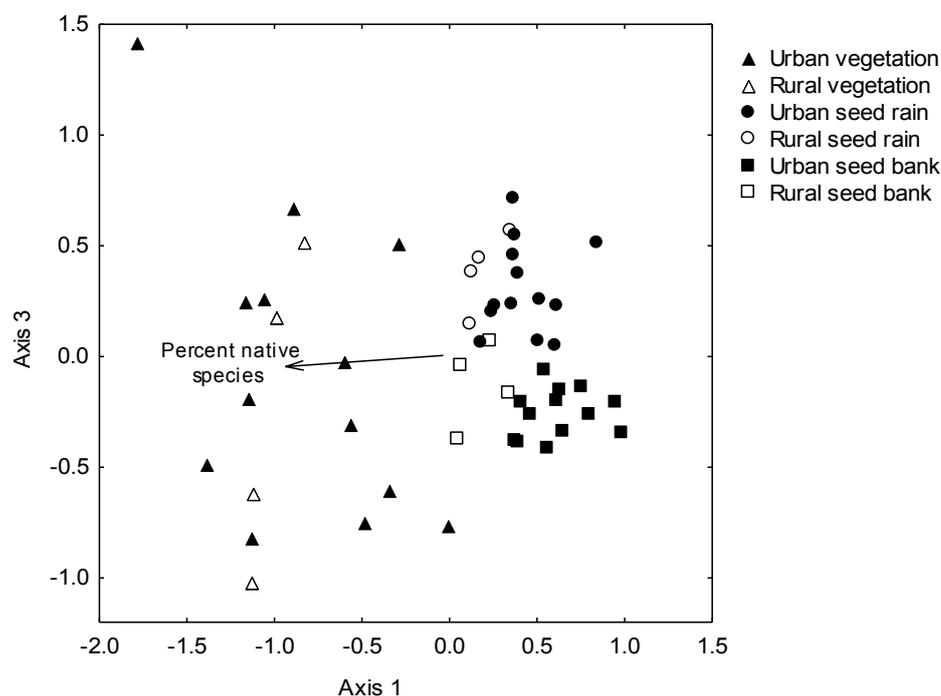


Figure 6. NMDS ordination configuration illustrating the compositional difference among vegetation, seed rain and seed bank for all urban ($n = 13$) and rural ($n = 4$) forest types. Axes 1 and 3 are shown for simplicity, though a 3-D solution was selected (stress = 12.0, instability < 0.00001, $R^2 = 0.90$).

indicated that each of the three groups differed significantly from each other (all P -values < 0.001). A three-dimensional NMDS ordination configuration that accounted for 90% of the compositional dissimilarities illustrates the strong compositional differentiation among groups (Fig. 6). Axis 1 was highly negatively correlated with the proportion of native species in plots ($r^2 = 0.69$) indicating the percentage of native species was lowest for urban seed rain and seed banks and highest for vegetation and rural seed rain and seed banks. Although composition of the seed bank and seed rain overlapped along axis 2 (not illustrated in Fig. 6), seed bank composition was clearly differentiated from the seed rain along axis 3. Indicator species analysis found the composition of soil seed banks driven by numerous exotic herbaceous species notably *Anagallis arvensis*, *Cirsium vulgare*, *Phytolacca octandra* and *Oxalis* spp. along with the native ferns *Cyathea smithii*, *Histiopteris incisa* and *Paesia scaberula*; and the exotic tree *Idesia polycarpa* (all Indicator Values > 50 ; Monte Carlo test, $P < 0.01$). Seed rain composition was distinguished particularly by the exotic trees *Betula pendula* and *Salix cinerea* and groundcover species *Carex ovata* and *Juncus* spp. as well as the native fern *Hypolepis distans*. Strong indicator species for vegetation composition were the native trees *Pittosporum eugenoides* and *Pseudopanax lessonii* and native ferns *Blechnum filiforme* and *Cyathea medullaris*.

Discussion

Seed rain and soil seed banks within Hamilton City's restored native forest patches were more species rich than those of intact native forest in the region, despite similar richness in the extant forest canopy. However, the dominance of exotic species in the seed rain and in persistent soil seed banks of urban forest patches, together with reduced native seed inputs, suggests that the regeneration and succession of native vegetation could be negatively affected in the long term. High species richness recorded in the seed supply of urban forests exceeded not only that in rural forest in this study but also seed rain and seed bank levels for other forests in New Zealand (Partridge 1989; Burrows 1994a; Sem & Enright 1995, 1996; Moles & Drake 1999; Dungan et al. 2001) due to the number of exotic species present.

These results are consistent with other studies of urban soil seed banks (Kostel-Hughes et al. 1998; Fisher et al. 2009) and may be explained in part by the typically large number of naturalised exotic plants in urban environments (Esler 1987) and the proximity of domestic gardens as a diverse source of exotic seed and propagules (Thompson et al. 2003; Sullivan et al. 2005). The typically small size of urban forest patches in this study may also contribute to high species richness in soil seed banks due to a large proportion of edge habitat (Sem & Enright 1995; Devlaeminck et al. 2005); while sparse urban-understorey vegetation, notably the low richness and density of native species (being less than one-third of rural forest, Table 2), could also increase the flow of seeds into forest patches (Cadenasso & Pickett 2001). High inputs of seeds might be expected to result in dense vegetation but we found urban seed rain and soil seed banks to be dominated by exotic herbaceous species (Figs 3b & 4b), which could be contributing to reduced establishment of woody species by the formation of dense groundcover mats (Standish et al. 2001). Additionally in younger urban patches, where understorey

native density and richness were lowest (Table 4, Fig. 5), suitable microclimate and microsites are not likely to have yet developed for the recruitment of native woody seedlings (Young & Mitchell 1994; Davies-Colley et al. 2000; White et al. 2009). Some human disturbance of vegetation through trampling in urban forest patches was noted and may also be a factor in locally sparse understorey vegetation.

Comparative species composition

The significant dissimilarity in species composition between extant vegetation and seed supply for urban and intact rural forest (Fig. 6) indicates some long-distance dispersal in the seed rain and long-term persistence in soil seed banks. Such disparity in species composition between extant forest vegetation and soil seed banks is not uncommon (Enright & Cameron 1988; Pickett & McDonnell 1989; Sem & Enright 1995; Drake 1998; Moles & Drake 1999) with soil seed banks in early-successional vegetation showing greater compositional similarity with extant vegetation due to the predominance of pioneer species in soil seed banks (Partridge 1989; Hopfensperger 2007; Zobel et al. 2007). Despite the early-successional stage of most forest patches in this study, such similarity was not evident; presumably for planted sites this can be attributed to the manipulated nature of the canopy vegetation, i.e. planting of native tree species, while the seed supply from soil seed banks and the seed rain of the surrounding urban matrix maintains a substantial exotic component. At rural forest sites exotic species richness was also greater in the seed supply than the extant vegetation, but there was still a higher proportion of native species, suggesting that seed rain and soil seed banks here will contribute to native vegetation succession.

Diversity of native species in the seed supply, along with the presence of mature forest species, is important in facilitating vegetation succession (Reay & Norton 1999; Smale et al. 2001; Sullivan et al. 2009; MacKay et al. 2011) even if seed rain density predominantly reflects the overhead vegetation (Burrows 1994a; Dungan et al. 2001). We found the seed supply of planted urban sites to be lacking in native species diversity (Table 3), despite older urban sites attaining native richness 68% of that in seed banks and 81% of that in the seed rain of rural forest sites (Fig. 5). The diversity of mature forest species occurring in Hamilton's urban forest patches may be limited by a lack of seed source due to deforestation in surrounding areas (Leathwick et al. 1995) and a low abundance of native seed dispersers and pollinators (Day 1995; Kelly et al. 2006, 2010).

Planted sites in this study did not have any additional enrichment planting and it is apparent that native forest species with short-lived seeds or those with limited dispersal range will need to be artificially introduced as urban forest restoration patches mature to encourage the development of self-sustaining native forest ecosystems. Urban native seed sources will be enhanced as planted species mature and produce seed themselves (MacKay et al. 2011), although this has been found to take 20 years or longer for some lowland forest species in Hamilton gully sites, e.g. *Beilschmiedia tawa*, *Litsea calicaris* and the podocarps *Prumnopitys ferrugineus*, *Podocarpus totara* and *Dacrydium cupressinum* (D. Lee, 2010, pers. comm.).

Soil seed bank persistence

Less than one-third of all species recorded in this forest study appear to persist in soil seed banks for over one year. Unfortunately, a large proportion of persistent species were

exotic (Appendix 2), with only one-quarter of all native species recorded being found to persist in soil seed banks. Native germinable diaspores from the soil seed bank were mainly ferns, including tree ferns, which play an important role in lowland forest succession by providing understorey shading and seedling establishment sites (Wardle 1991; George & Bazzaz 1999; Gaxiola et al. 2008). Native woody species found persisting in urban soil seed banks included *Coprosma robusta*, *Cordyline australis*, and *Dacrydium dacrydioides*, all of which also having effective diaspore dispersal over a distance by producing many small, fleshy fruits. A high number of native species occurred in soil seed banks of older rural forest (Fig. 5), but at low densities, and therefore were likely to have been transients rather than persistent seed bank species. Species of mature forest habitat are recognised as being less likely to form persistent soil seed banks due to the stable and shady environment where large seeds are beneficial to establish (Fenner & Thompson 2005) and alternative strategies such as canopy seed banks (Burrows 1994b) or suppressed seedling banks (Moles & Drake 1999) may be favoured. Such large seeds do not easily penetrate down into the soil, thus the finding of predominantly small-seeded herbaceous species forming seed banks is in keeping with limited data on persistence available for the New Zealand flora (Moles et al. 2000). The lack of formation of soil seed banks for many native forest species found in this study and suggested by others (Partridge 1989; Burrows 1994b; Sem & Enright 1996; Moles & Drake 1999) has implications for reforestation and restoration projects in New Zealand. There will be limited opportunity for soil seed banks to inherit many late-successional forest species, as has been similarly identified in the restoration of ancient forest vegetation in Europe (Bossuyt & Hermy 2001; Bossuyt & Honnay 2008).

Long-term threats of exotic species

Despite exotic richness remaining high in urban seed rain, reduced exotic richness in soil seed banks and understorey vegetation at older (>20 years) urban sites (Fig. 5) is encouraging for native restoration. Initial planting disturbance and a high-light environment favour the establishment of exotic species, which in turn contributes to sustaining the exotic seed bank, whereas unplanted (and undisturbed), naturally regenerating sites in urban areas had greater native species richness in the understorey and soil seed bank, despite similar exotic species composition in the seed rain. Exotic species present in initial seed banks after planting may be depleted over time through germination and loss of viability, while canopy closure appears to offer some resilience against exotic species establishing in older urban and rural sites. Lower light transmittance and nutrient levels in older forests (Miller 2011) may deter the establishment of early-successional exotic species, and as planted vegetation ages, a greater range of microsites become available for the germination and establishment of mid- to late-successional species (White et al. 2009).

In urban forest, however, there is still a high risk of exotic species establishing from seed rain and persistent seed banks following disturbance to vegetation cover. This is an ongoing concern for management not only due to many light-demanding herbaceous species in seed banks that could impair native seedling establishment, but also to a number of exotic woody and liane species in the seed rain that may be more of a long-term threat to native forest structure (Wiser & Allen 2006). Invasive woody species present in seed rain

(such as shade-tolerant *Ligustrum lucidum* and *L. sinense* that formed a dense understorey in some older plantings) are capable of displacing native canopy species (Smale & Gardner 1999; Vidra et al. 2007). The smothering lianes *Lonicera japonica* and *Hedera helix* were widespread in seed rain, while *Leycesteria formosa*, *Rubus fruticosus* and *Actinidia deliciosa* were found to form persistent soil seed banks – the former two able to produce dense stands impenetrable to native species (McQueen 1993) and the latter able to invade closed-canopy forest (Sullivan et al. 2007). *Tradescantia fluminensis* was the dominant groundcover in several restoration forest patches, and although spread by vegetative growth rather than seed, this weed species colonised several seed-rain trays during this study, displaying an ability to quickly form a mat capable of suppressing the establishment of native seedlings (Whaley et al. 1997; Standish et al. 2001).

Conclusion

An important species filter (*sensu* Williams et al. 2009) – for which seed traits are in part responsible – may be considered to be influencing processes of urban vegetation succession in Hamilton City. Without management intervention for at least the first 20 years it is likely that the vegetation communities would become dominated by exotic species from the seed rain and persistent soil seed banks at urban restoration sites. In sites over 20 years old there was a decline in the exotic soil seed bank and fewer exotic species establishing in the understorey. While reduced availability of native seed in urban forests is at least partly responsible for the observed depauperate native regeneration, environmental factors including microclimate, smothering semi-shade-tolerant groundcover weeds, and human disturbance may limit establishment for some native species regardless of whether seed is available. Some native forest species, such as those with diminished dispersal and no persistent seed bank, will have to be artificially introduced as urban restoration plantings mature, to counter the disparity in native seed supply between urban and rural forest. Urban restoration requires management goals that reflect the surrounding landscape and recognise these forests as novel ecosystems comprised of native and exotic components. Further research into species' seed traits, including dispersal mode and germination requirements, would help refine management strategies for successful native species introductions and exotic weed control in different stages of urban forest restoration.

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Appendix 1. Percentage of total density for common species (>1%) occurring in the canopy and understorey for three forest types: urban planted ($n = 9$), urban natural ($n = 4$) and rural natural ($n = 4$). * Denotes exotic species.

Species	Canopy			Understorey		
	Urban planted	Urban natural	Rural natural	Urban planted	Urban natural	Rural natural
<i>Alnus</i> sp.*	-	7.5	-	-	-	-
<i>Asplenium bulbiferum</i>	-	-	-	-	-	2.2
<i>Beilschmiedia tawa</i>	-	-	1.5	-	-	-
<i>Blechnum novae-zelandiae</i>	-	-	-	-	-	2.4
<i>Calystegia sepia</i> *	-	1.6	-	-	-	-
<i>Conyza albida</i> *	-	-	-	-	2.3	-
<i>Coprosma robusta</i>	4.0	-	-	1.6	2.1	-
<i>Cordyline australis</i>	7.4	1.6	-	-	-	-
<i>Crataegus monogyna</i> *	-	1.3	-	-	-	-
<i>Cyathea dealbata</i>	-	16.1	4.4	2.2	13.9	2.9
<i>Cyathea medullaris</i>	1.4	11.4	2.4	-	-	-
<i>Dacrycarpus dacrydioides</i>	-	1.4	-	-	-	-
<i>Dianella nigra</i>	-	-	-	-	-	2.8
<i>Dicksonia squarrosa</i>	-	29.7	-	-	9.7	-
<i>Diplazium australe</i>	-	-	-	-	2.9	-
<i>Freycinetia banksii</i>	-	1.7	-	-	-	-
<i>Geniostoma rupestre</i>	-	-	4.2	-	-	2.0
<i>Hedera helix</i> *	1.4	-	-	-	-	-
<i>Hedycarya arborea</i>	-	-	-	-	-	1.2
<i>Hoheria populnea</i>	2.7	-	-	1.3	-	-
<i>Hoheria sexstylosa</i>	1.7	-	-	-	-	-
<i>Jasminum</i> sp.*	4.6	-	-	-	-	-
<i>Juglans</i> sp.*	-	-	-	1.4	-	-
<i>Kunzea ericoides</i>	1.8	-	15.6	-	-	2.9
<i>Leptospermum scoparium</i>	-	-	25.5	-	-	13.7
<i>Leucopogon fasciculatus</i>	-	-	-	-	-	4.4
<i>Ligustrum lucidum</i> *	-	-	-	1.1	-	-
<i>Ligustrum sinense</i> *	7.2	-	-	41.9	29.6	-
<i>Lonicera japonica</i> *	9.9	5.7	-	1.8	2.0	-
<i>Macropiper excelsum</i>	-	-	-	-	1.4	2.0
<i>Melicytus ramiflorus</i>	11.1	17.4	8.2	34.8	23.4	-
<i>Metrosideros diffusa</i>	-	-	3.4	-	-	-
<i>Microsorium scandens</i>	-	-	-	-	-	1.3
<i>Muehlenbeckia australis</i>	-	2.1	-	-	-	-
<i>Olearia paniculata</i>	1.7	-	-	-	-	-
<i>Phyllocladus trichomanoides</i>	-	-	-	-	-	2.3
<i>Pittosporum eugenioides</i>	14.5	-	-	-	-	-
<i>Pittosporum tenuifolium</i>	6.2	-	-	-	-	-
<i>Plagianthus regius</i>	1.3	-	-	-	-	-
<i>Podocarpus totara</i>	8.9	-	-	-	-	-
<i>Pteridium esculentum</i>	-	-	-	-	-	13.8
<i>Pteris tremula</i>	-	-	-	1.3	-	-
<i>Rhopalostylis sapida</i>	-	-	-	-	-	1.6
<i>Ripogonum scandens</i>	-	-	12.5	-	-	2.6
<i>Rubus fruticosus</i> *	-	-	-	4.4	-	-
<i>Schefflera digitata</i>	-	2.2	-	-	-	-
<i>Schoenus tendo</i>	-	-	-	-	-	1.2
<i>Solanum americanum</i>	-	-	-	-	2.6	-
<i>Solanum chenopodioides</i> *	-	-	-	-	1.1	-
<i>Ulex europaeus</i> *	-	-	19.5	-	-	26.7
<i>Zantedeschia aethiopica</i> *	-	-	-	-	1.8	-

Appendix 2. Species classified as persistent in soil seed banks for urban (planted and natural, $n = 13$) or rural (natural, $n = 4$) forest types: closed circle (●) persistent >10 seeds difference in soil seed bank than annual seed rain, at one or more sites; open circle (○) not persistent but occurred in soil seed banks <10 seeds; dash (–) did not occur in soil seed bank. *Denotes exotic species.

Species	Urban	Rural	Species	Urban	Rural
<i>Actinidia chinensis</i> *	●	–	<i>Hypolepis lactea</i>	●	○
<i>Agrostis stolonifera</i> *	●	○	<i>Hypolepis ambigua</i>	●	–
<i>Amaranthus powellii</i> *	●	–	<i>Idesia polycarpa</i> *	●	○
<i>Anagallis arvensis</i> *	●	○	<i>Isolepis reticularis</i>	●	–
<i>Athyrium filix-femina</i> *	●	○	<i>Isolepis sepulcralis</i> *	●	–
<i>Blechnum novae-zelandiae</i>	●	●	<i>Juncus acuminatus</i> *	●	–
<i>Briza minor</i> *	●	–	<i>Juncus articulatus</i> *	●	–
<i>Buddleja davidii</i> *	●	–	<i>Juncus bufonius</i> *	●	●
<i>Callicarpa</i> sp.*	●	–	<i>Juncus planifolius</i>	●	●
<i>Callitriche stagnalis</i>	●	–	<i>Juncus tenuis</i> *	●	●
<i>Carex</i> sp.	●	–	<i>Juncus</i> sp.	●	–
<i>Carex inversa</i>	●	–	<i>Juncus</i> sp.*	●	○
<i>Carex geminata</i>	●	–	<i>Juncus</i> sp.*	●	○
<i>Carpodetus serratus</i>	–	●	<i>Lapsana communis</i> *	●	–
<i>Chenopodium album</i> *	●	–	<i>Lepidium didimum</i> *	●	–
<i>Cirsium arvensis</i> *	●	○	<i>Leucanthemum vulgare</i> *	●	○
<i>Cirsium vulgare</i> *	●	○	<i>Leycesteria formosa</i> *	●	○
<i>Coprosma robusta</i>	●	○	<i>Lobelia anceps</i>	–	●
<i>Cordyline australis</i>	●	○	<i>Lotus pedunculatus</i> *	●	●
<i>Crepis setosa</i> *	●	–	<i>Lythrum hyssopifolia</i> *	●	–
<i>Cyathea dealbata</i>	●	●	<i>Mimulus moschatus</i> *	●	–
<i>Cyathea smithii</i>	●	●	<i>Modiola caroliniana</i> *	●	–
<i>Cyathea</i> sp.	●	○	<i>Nephrolepis cordifolia</i> *	●	–
<i>Cyperus eragrostis</i> *	●	–	<i>Paesia scaberula</i>	●	●
<i>Dacrycarpus dacrydioides</i>	●	–	<i>Paulownia tomentosa</i> *	●	–
<i>Deparia petersenii</i>	●	○	<i>Persicaria maculosa</i> *	●	–
<i>Dianella nigra</i>	○	●	<i>Phytolacca octandra</i> *	●	●
<i>Dicksonia fibrosa</i>	●	○	<i>Plantago major</i> *	●	○
<i>Dicksonia squarrosa</i>	●	●	<i>Pneumatopteris pennigera</i>	●	○
<i>Digitalis purpurea</i> *	●	○	<i>Poa annua</i> *	●	–
<i>Digitaria sanguinalis</i> *	●	–	<i>Portulacca oleracea</i> *	●	–
<i>Diplazium australe</i>	●	–	<i>Pteris cretica</i> *	●	–
<i>Doodia australis</i>	●	○	<i>Pteris macilentia</i>	●	–
<i>Drosera auriculata</i>	–	●	<i>Pteris tremula</i>	●	○
<i>Duchesnea indica</i> *	●	–	<i>Ranunculus repens</i> *	●	–
<i>Echinochloa crus-galli</i> *	●	–	<i>Ranunculus sardous</i> *	●	–
<i>Eleusine indica</i> *	●	–	<i>Rubus fruticosus</i> *	●	○
<i>Epilobium ciliatum</i> *	●	–	<i>Rumex obtusifolius</i> *	●	–
<i>Eragrostis brownii</i> *	●	–	<i>Sagina procumbens</i> *	●	–
<i>Erica lusitanica</i> *	○	●	<i>Schoenus apogon</i>	●	–
<i>Euchiton involucratus</i>	○	●	<i>Schefflera digitata</i>	●	○
<i>Euphorbia peplus</i> *	●	–	<i>Silene gallica</i> *	●	–
<i>Fuchsia excorticata</i>	●	●	<i>Solanum americanum</i>	●	●
<i>Fumaria muralis</i> *	●	–	<i>Solanum chenopodioides</i> *	●	–
<i>Gamochaeta coarctata</i> *	●	●	<i>Solanum mauritianum</i> *	●	–
<i>Geniostoma rupestre</i>	○	●	<i>Solanum nigrum</i> *	●	●
<i>Gonocarpus aggregatus</i>	–	●	<i>Sonchus oleraceus</i> *	●	○
<i>Haloragis erecta</i>	●	○	<i>Spergula arvensis</i> *	●	–
<i>Hebe</i> sp.	●	–	<i>Stachys sylvatica</i> *	●	–
<i>Histiopteris incisa</i>	●	●	<i>Ulex europaeus</i> *	●	●
<i>Holcus lanatus</i> *	●	○	<i>Verbena bonariensis</i> *	●	–