THRESHOLDS FOR SUSTAINABLE REGENERATION IN URBAN RESTORATION PLANTINGS IN HAMILTON CITY, NEW ZEALAND

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ELIZABETH OVERDYCK

KO TE TANGATA

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

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ABSTRACT

Urban forest patches have unique environmental and landscape characteristics which may influence the restoration of native plant communities. Urbanisation can lead to a drier and warmer climate, a prevalence of exotic seed sources and isolation from remnant native forest seed sources. This research investigates how these factors influence native species presence in different aged urban forest patches and uses life history traits to identify vulnerable species groups which may require active reintroduction. Seed rain, soil seed banks and vegetation composition was recorded within urban forest restoration plantings (10-36 years old) in Hamilton City, New Zealand with comparison to naturally regenerating forest within the city and a nearby rural forest remnant. To address dispersal limitation for several key mid to late successional forest species an experiment was also undertaken to investigate broadcast seeding as a method to reintroduce trees with large seeds and fleshy fruits into established early successional vegetation.

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. A prevalence of exotic species in urban seed rain, however, will allow reinvasion through edge habitat and following any 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.

Urban native seed rain was greater in quantity than exotic seed rain (reflecting immediately surrounding vegetation) although only when native canopy species had been planted suggesting a benefit of initial planting to encourage restoration of native communities. Novel species arriving in the seed rain, but not present in the immediate vegetation, were often not abundant in quantity but represented three quarters of the native species recorded in urban seed rain providing evidence for some long-distance dispersal (particularly for wind-dispersed species) and potential for new species to establish. Urban and rural seed rain contained a similar number of novel native species arriving, although compositionally dissimilar, whereas a greater number of novel exotic species arrived in urban seed rain. Establishment for some native species arriving in urban seed rain was limited, e.g. ferns, indicating a suitable forest microclimate is still to develop.

It was found that the native forest flora in Hamilton City represented just over half (57%) of the species present in forests of the broader Hamilton Ecological District. This suggests limited natural colonisation from beyond the urban area and the absent species are suggested as priorities for urban reintroduction. In turn only 35% of the city forest flora was found to be represented in the seed supply (annual seed rain and soil seed bank) and understorey sampling in urban forest patches. An over representation of trees in the city forest flora may reflect some relictual long-lived species that are surviving but may no longer have viable populations. Forbs and parasitic plants, highly shade tolerant (i.e. late successional) species and those with biotic pollinators were under represented in the seed supply and understorey indicating some limitation for regeneration or colonisation in young urban forests. The richness of bird-dispersed native species in urban forest patches increased with proximity and size of good quality native vegetation but no other effects of dispersal mode on urban native species presence were found.

To facilitate dispersal, broadcast seeding was found to be a viable method of improving regeneration of large-seeded late successional trees and may be a cost-effective alternative to planting saplings. Seedling establishment can be improved with fruit flesh removal and clay ball treatments, especially in the presence of mammalian seed predators.

Keywords Beilschmiedia tawa; clay balls; forest restoration; *Elaeocarpus dentatus*; *Litsea calicaris*; regeneration dynamics; seed dispersal; seed predation; seed rain; soil seed banks; urban ecology

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CO-AUTHORS

Name	Nature of Contribution
Bruce Clarkson	original project design, editing drafts, funding

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Name	Signature	Date
Bruce Clarkson		19/07/13

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Student and Academic Services Division
Wahanga Ratonga Matauranga Akonga
The University of Waikato
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Hamilton 3240, New Zealand
Phone +64 7 858 5096
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CO-AUTHORS

Name	Nature of Contribution
Bruce Clarkson	original design, editing drafts, funding
Daniel Laughlin	editing drafts, statistical assistance
Chrissen Gemmill	editing drafts

Certification by Co-Authors

The undersigned hereby certify that:

- the above statement correctly reflects the nature and extent of the PhD candidate's contribution to this work, and the nature of the contribution of each of the co-authors; and
- in cases where the PhD candidate was the lead author of the work that the candidate wrote the text.

Name	Signature	Date
Bruce Clarkson		19/07/13
Daniel Laughlin		19/07/13
Chrissen Gemmill		22/07/13

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1 INTRODUCTION

1.1 RESEARCH TOPIC

This thesis presents research about regeneration dynamics, seed ecology and the restoration of urban forest patches. The research is focussed on restoration plantings within Hamilton City in the North Island, New Zealand with reference to naturally regenerating lowland mixed podocarp-broadleaf forest in both Hamilton City and the broader Hamilton Ecological District. This thesis investigates whether plant species composition and vegetation succession within forest patches in an urban setting is altered as a result of the highly human-modified environment. Comparison is made of species presence in seed rain, soil seed banks and vegetation from sites of differing ages, sizes and isolation from seed sources in order to test hypotheses of seed dispersal limitation, competition with exotic species and a lack of establishment safe-sites as drivers for alternative species composition. Seed dispersal modes and several other plant life history traits are investigated in order to identify traits which may limit the successful restoration of target forest communities. To address potential dispersal limitation for large-seeded late successional forest species, an additional experimental manipulation investigates a novel seed-sowing enrichment method as an alternative to the planting of nursery-raised saplings.

1.2 BACKGROUND

Ecological restoration has the intention to initiate or accelerate ecosystem recovery from a degraded state with respect to its health, integrity and sustainability (SER 2004). Restoration can take many forms ranging from the creation or reconstruction of habitat, such as the plantings at the focus of this research, or the rehabilitation of existing habitat through amelioration of negative environmental (e.g. altered hydrology) or biological (e.g. pest invasion or local species extinctions) stressors (Hobbs & Norton 1996). Ecological restoration projects are increasing in number throughout New Zealand (Jay 2005) and worldwide (Ruiz-Jaen & Mitchell Aide 2005; Roberts et al. 2009), with particular interest in reversing the huge loss of biodiversity in urban areas (Miller & Hobbs

2002; Clarkson & McQueen 2004; Clarkson & Meurk 2004; Pickett et al. 2008; Williams et al. 2009).

The relatively new field of restoration ecology aims to provide a sound scientific basis for the recovery and production of self-sustaining ecosystems (Jordan et al. 1987). Research is necessary to guide restoration efforts to avoid intervention where natural processes may be adequate to reach the desired outcomes and to decide when intervention is beneficial, or indeed essential to achieve or accelerate ecosystem recovery (Prach & Hobbs 2008; Holl & Aide 2011). Ecological restoration also allows many aspects of ecological theory to be investigated, particularly regarding vegetation succession and community assembly theory, as ecosystems may be manipulated or reconstructed and the outcomes closely monitored (Ormerod 2003; Young et al. 2005). Classical vegetation succession theory suggests an orderly and predictable return of an ecosystem to a pre-determined climax state after disturbance (Clements 1916), while more recently proposed assembly theory suggests that alternative species assemblages, in similar functional roles, may persist at a site due to biotic and/or abiotic restrictions or ‘assembly rules’ (Temperton et al. 2004). The latter theory proposes that the presence of broad functional groups rather than particular species enables many ecosystem processes to occur, although in some cases key species have been identified as driving particular and important processes, such as in pollination or seed dispersal mutualisms (Traveset & Richardson 2006). The study of the ecological function of novel species assemblages through restoration in an urban landscape can contribute to the development of vegetation succession theory in the broader landscape (McDonnell & Pickett 1990) as well as identifying potential limitations on restoration success (Hobbs & Harris 2001).

Within an urban context, habitat composition and ecosystem function studies to guide restoration have been increasing (Kostel-Hughes et al. 1998; Duncan & Young 2000; Drinnan 2005; Gaston et al. 2005; Bornkamm 2007; Thompson & McCarthy 2008; Sullivan et al. 2009; Duncan et al. 2011; MacKay et al. 2011) with relevant conceptual frameworks and theories also emerging (Hobbs et al. 2006; McDonnell & Hahs 2008; Pickett et al. 2008; Prach & Hobbs 2008; Williams et al. 2009). Urbanisation has been suggested by Williams et al. (2009)

to create a series of specific environmental filters: habitat transformation; habitat fragmentation; altered abiotic environment; and human preference (species selection). They suggest these filters together contribute to altering floristic composition and consideration of such a structured framework may improve our understanding of the response of vegetation communities to urbanisation and assist in setting sustainable management targets for restoration which maximise retention of urban biodiversity. Restoration plantings often aim to achieve a ‘natural state’ yet restored forest in an urban environment may only ever achieve the creation of ‘novel ecosystems’ (Hobbs et al. 2006) where human imposed influences, as described above, result in new species combinations, including exotic and native which have not previously occurred naturally (Meurk 2011). To formulate appropriate goals historic knowledge along with data from reference sites is necessary to provide information on environmental conditions and ecosystem structure, composition and function to aim for (SER 2004; Ruiz-Jaen & Mitchell Aide 2005). For urban restoration purposes using reference sites in both urban and non-urban vegetation may highlight any variability between the two and allow realistic urban-based goals to be set. Aiming for a single end point may not be a valid goal as multiple alternative states may be possible from the available species pool (Hobbs & Harris 2001), some of which may be more desirable as goals than others. It is necessary, however, to set clear and meaningful goals to allow success towards the goal to be measured (Hobbs & Harris 2001) while bearing in mind that progress toward the target vegetation succession is not always straight forward and the dynamic nature of ecosystem processes over time and space must always be considered (Jackson & Hobbs 2009).

Hobbs and Norton (1996; 2004) propose the idea of thresholds in restoration where abiotic or biotic factors may prevent restoration from progressing to a desired state. This research investigates whether thresholds exist for regeneration in urban restoration plantings and seeks to identify temporal thresholds i.e. time elapsed since planting (affecting, for example, the fecundity of planted species, suitable habitat for pollination and dispersal vectors and suitable germination and establishment conditions) and spatial thresholds such as the loss of forest patch connectivity (affecting proximity to seed sources and also habitat quality).

Previous studies in New Zealand’s early successional lowland forests (Burrows 1994a; Dungan et al. 2001) and restoration plantings (Reay & Norton 1999; Smale et al. 2001) suggest that native regeneration from seed rain appears adequate for natural vegetation succession to occur where mature forest is in close proximity. However, as soil seed banks tend to be primarily composed of pioneer species (Partridge 1989; Burrows 1994b; Sem & Enright 1996; Moles & Drake 1999; Bossuyt & Honnay 2008) the isolation and fragmentation of urban forest habitat may require some tree species of mature forest to be artificially reintroduced for successful restoration and ecological function to occur (Moles & Drake 1999; Honnay et al. 2002). This may apply particularly to large-seeded species dispersed by wide ranging animals due to reduced animal populations in highly modified landscapes and infrequent occupation of small forest patches (Cramer et al. 2007; Garcia et al. 2010; McConkey et al. 2012). There are several key lowland tree species in New Zealand which rely on few native avian dispersers (Clout & Hay 1989; Kelly et al. 2010) and dispersal limitation for such species may also be compounded by seed predation impacts of small non-native mammals (Chimera & Drake 2011; Wotton & Kelly 2011).

The restoration of lowland forest in Hamilton City and New Zealand’s other urban centres contributes to redressing the extensive loss of this habitat type through historical clearance for agriculture (Ewers et al. 2006; Walker et al. 2008) while also presenting opportunities to bring large numbers of people into contact with nature (Miller 2005; Lawson et al. 2008). This research will contribute to more effective restoration of lowland forest habitats by identification of limitations on regeneration for native forest species in an urban environment and the development of new restoration methods.

1.3 RESEARCH QUESTIONS

This thesis investigates the following questions:

- Is seed dispersal limiting restoration success in the urban environment by preventing recruitment of native forest species and encouraging ongoing re-invasion by exotic species?

- Do sources of regeneration change over time as restoration plantings mature?
- How does canopy composition influence the composition of seed rain?
- Does urbanisation affect plant trait composition within the extant vegetation and seed supply (seed rain and soil seed banks)?
- Are some key large-seeded forest species able to be reintroduced to early successional urban plantings using seed-sowing methods as an alternative to enrichment planting?

1.4 THESIS OBJECTIVES

This thesis aims to:

- Characterise the seed rain and soil seed bank as sources of regeneration within Hamilton City's restoration plantings;
- Investigate whether the seed supply (seed rain and soil seed bank) and recruitment in urban forest patches resembles naturally regenerating reference sites 20 years after establishment;
- Identify whether plant traits (including dispersal mode), patch or landscape characteristics are limiting native species and/or favouring exotic species colonisation of urban forest patches; and
- Assess alternative restoration methods for the enrichment of late to mid successional forest species through a multi-factorial seed-sowing experiment.

1.5 THESIS OVERVIEW

The thesis comprises four main chapters (chapters 2-5) all prepared as manuscripts for publication which have been accepted or are intended to be submitted to international scientific journals including: New Zealand Journal of Ecology (published in New Zealand), Restoration Ecology (United States of America) and Urban Ecosystems (United States of America). As a result of this there may be some slight differences in writing style, grammar or format due to individual journal requirements and there is some inevitable duplication between chapters. Chapter 1 provides an introduction to the thesis topic and chapter 6 presents a synthesis of the research with recommendations for management and further research. The research is all my own work and ideas conducted under the supervision of Professor Bruce D. Clarkson, Dr Chrissen E.C. Gemmill and Dr Daniel. C. Laughlin. Specific contributions are acknowledged in each chapter.

Chapter 2 describes and contrasts the composition of seed rain, soil seed bank and vegetation in restoration plantings, Hamilton City with reference to sampling in naturally regenerating forest in both the urban setting and the nearest intact native lowland forest. Particular emphasis is placed on comparison of native and exotic species richness and abundance, soil seed bank persistence and assessment of temporal progression toward target natural communities with site age. This research is published as: Overdyck E, Clarkson BD 2012. Seed rain and soil seed banks limit native regeneration within urban forest restoration plantings in Hamilton City, New Zealand. New Zealand Journal of Ecology 36: 177-190.

Chapter 3 focuses on the seed rain as a source of new recruits for forest restoration and investigates seed dispersal limitation. Seasonal patterns in seed rain density and richness are presented and a comparison between the seed rain and extant vegetation composition is made. Exotic and native species newly arriving in the seed rain are evaluated by dispersal mode and comparison made between urban and rural forests. This chapter is in preparation for journal submission.

Chapter 4 aims to identify plant traits or physical characteristics of urban forest patches which may limit natural recolonisation of native species in urban restoration plantings. It presents an analysis of plant traits for those native forest species occurring in the broader Hamilton Ecological District, those persisting in Hamilton City and those potentially recolonising in urban seed supply and understorey sampling. Relationships are explored between native richness and forest patch characteristics including patch size, adjacent land use, and proximity to high quality native vegetation. This chapter is in preparation for submission to the Journal of Urban Ecosystems.

Chapter 5 presents an experimental study with practical application to native forest restoration in fragmented landscapes with reduced native seed dispersal. It investigates the feasibility of seed-sowing for mid to late succession species as an alternative to enrichment planting. Three seed treatment methods are tested: caging, fruit flesh removal and clay ball application, in order to assess seed predation, germination and seedling survival rates for three large-seeded lowland forest tree species: *Beilschmiedia tawa, Elaeocarpus dentatus* and *Litsea calicaris*. This research has been published as: Overdyck E, Clarkson BD, Laughlin DC, Gemmill CEC 2013. Testing Broadcast Seeding Methods to Restore Urban Forests in the Presence of Seed Predators. Restoration Ecology 21(6): 763-769.

Chapter 6 presents a synthesis of the research in the context of international literature and discusses implications for urban restoration in Hamilton and broader application to other cities. Recommendations for management and further research ideas stemming from this study are also included.

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2 SEED RAIN AND SOIL SEED BANKS LIMIT NATIVE REGENERATION WITHIN URBAN FOREST RESTORATION PLANTINGS IN HAMILTON CITY, NEW ZEALAND[1]

2.1 ABSTRACT

Restoration of native forest vegetation in urban environments may be limited due to isolation from native seed sources and to prevalence of exotic plant species. To investigate urban seed availability we recorded seed rain, soil seed banks and vegetation composition at native forest restoration plantings up to 36 years old in Hamilton City and compared these with naturally regenerating forest in the same urban area and in a nearby rural, intact native forest. 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 any 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 more than 1 year in the seed bank. Enrichment planting will be required for those native species with limited dispersal or short-lived seeds, thus improving urban native seed availability 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.

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Key words ecological restoration; fern spore bank; fragmentation; seed dispersal; succession; urban ecology

2.2 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 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.

2.3 METHODS

2.3.1 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 (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).[2]

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

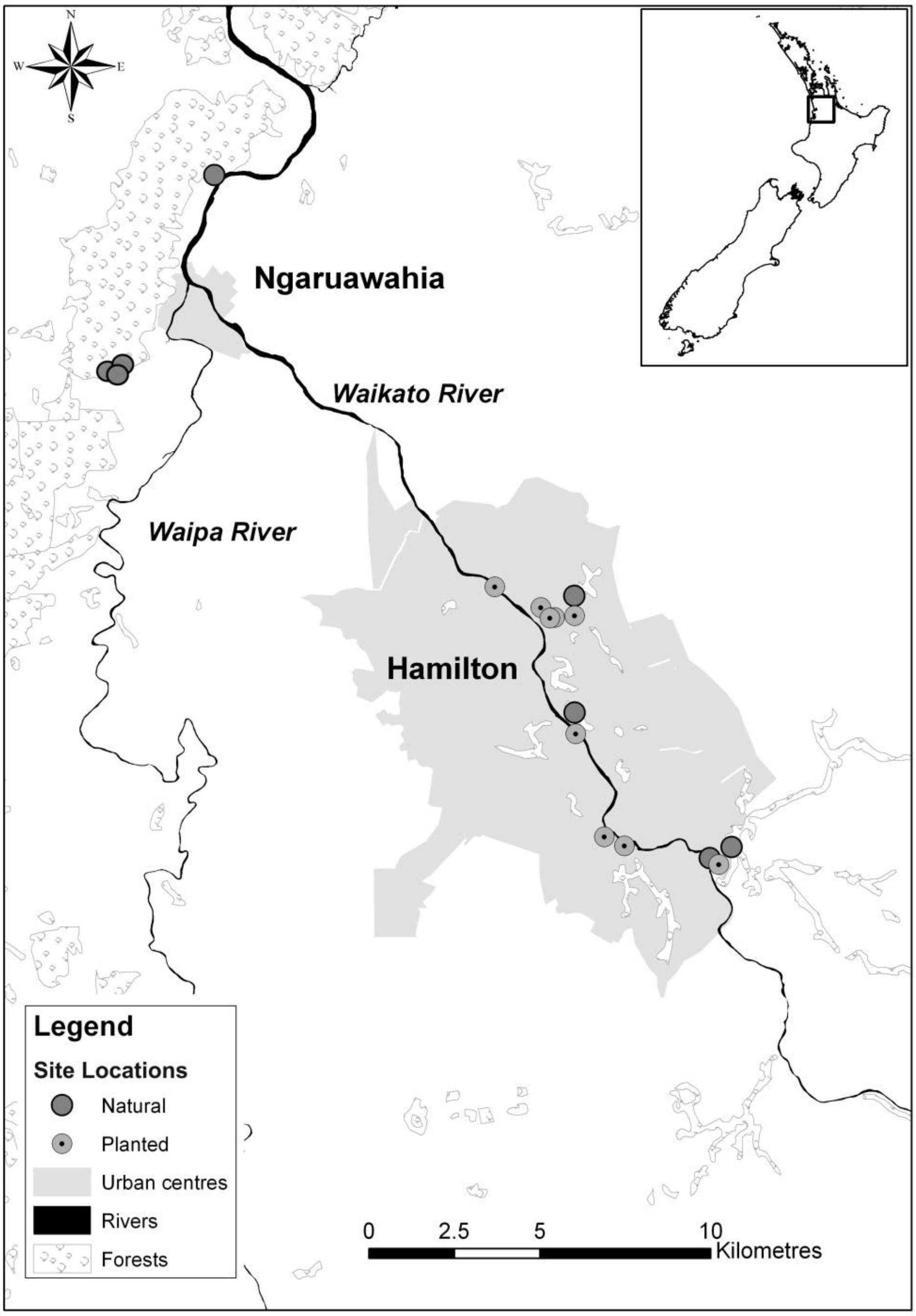


Figure 2.1 Location of study sites (north to south). Urban planted forest (dotted circles) in Hamilton City (*n* = 9): Munro's Esplanade; Tauhara Park (3 sites); Onukutara Gully; Pine Beach; Yendell Park; Dillicar Park; Hammond Park. Urban natural forest (circles) in Hamilton City (*n* = 4): Mangaiti 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).

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 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.

2.3.2 Study design

Sampling effort 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.

Table 2.1 Forest age at sites sampled within Hamilton City (urban planted and urban natural) and Hakarimata Range (rural natural forest).

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

2.3.3 Data collection

2.3.3.1 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.

2.3.3.2 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 m^2) 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 m^2) 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.

2.3.4 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 against assumptions, in STATISTICA 8 (StatSoft, Inc.). Mean seed density and species richness data are presented per site area sampled (0.169 m^2). Canopy (>20 mm dbh) and understorey (>300 mm height, <20 mm dbh) density and species richness data are presented per 100 m^2 to standardise for variable sizes of vegetation plot (range 64–272 m^2). 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 (Dufrêne & Legendre 1997).

2.4 RESULTS

2.4.1 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 2.1). 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 2.1). At urban planted sites the canopy predominantly comprised a mixture of early-successional native trees, while at urban natural sites *Melicytus ramiflorus* and the tree ferns *Dicksonia squarrosa* and *Cyathea* spp. were the main canopy species (Appendix 2.1).

Understorey species richness was significantly higher ($P < 0.05$) at rural compared with urban planted 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 2.1), and was lowest at urban natural sites. Many native species, although particularly mānuka and bracken *(Pteridium esculentum)* (Appendix 2.1), contributed to higher native species density in rural compared with urban understoreys.

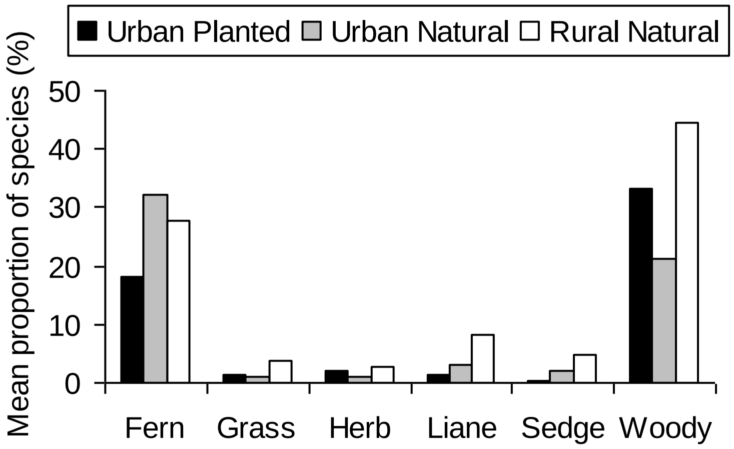
Table 2.2 Mean (± standard error) species richness and density (per 100 m^2) of vegetation canopy (all stems > 20 mm dbh) and understorey (all stems < 20 mm dbh and > 300 mm height) for three forest types: urban planted (*n* = 9), urban natural (*n* = 4) and rural natural (*n* = 4). Bold text indicates 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.

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

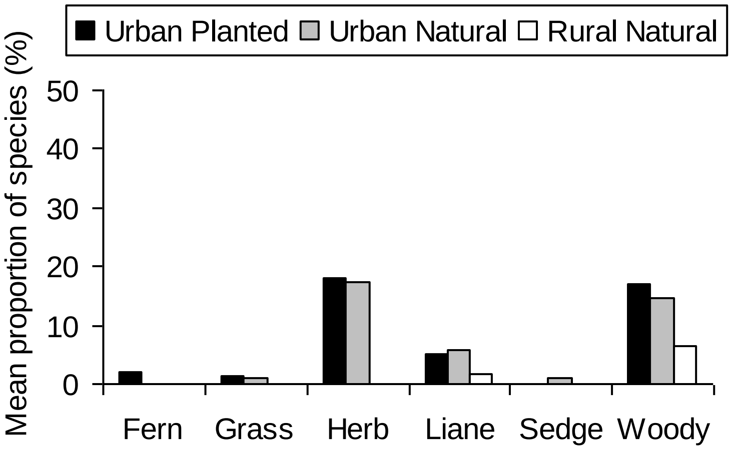
2.4.2 Vegetation growth forms

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.

(a) Native species



(b) Exotic species



Figures 2.2 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.

2.4.3 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 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). 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).

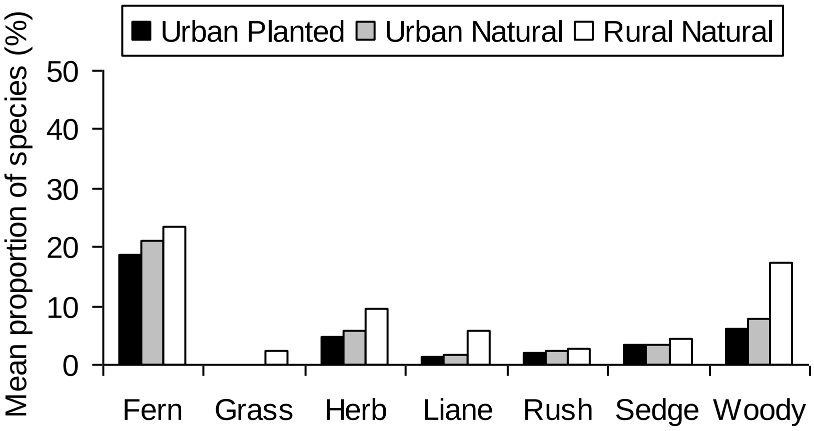
Table 2.3 Mean (± standard error) species richness and density of germinable diaspores (recorded over 18 months) from the soil seed bank and annual seed rain per site (0.169 m^2) for three forest types: urban planted (*n* = 9), urban natural (*n* = 4) and rural natural (*n* = 4). Bold text indicates significant differences between urban and rural treatments: ***P* < 0.01, **P* < 0.05, ANOVA post hoc Tukey's test.

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

2.4.4 Soil seed bank and seed rain growth forms

Soil seed banks of urban planted sites were dominated by exotic herbaceous species (mean 39% of all species), native fern species (19%) and exotic woody species (10%) 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 (23%), native ferns (21%), and exotic woody species (14%), with several exotic rushes (9%) and native woody species (8%). Rural soil seed banks contained predominantly native ferns (24%), exotic herbs (23%), native woody species (17%), and native herbs (10%).

(a) Native species



(b) Exotic species

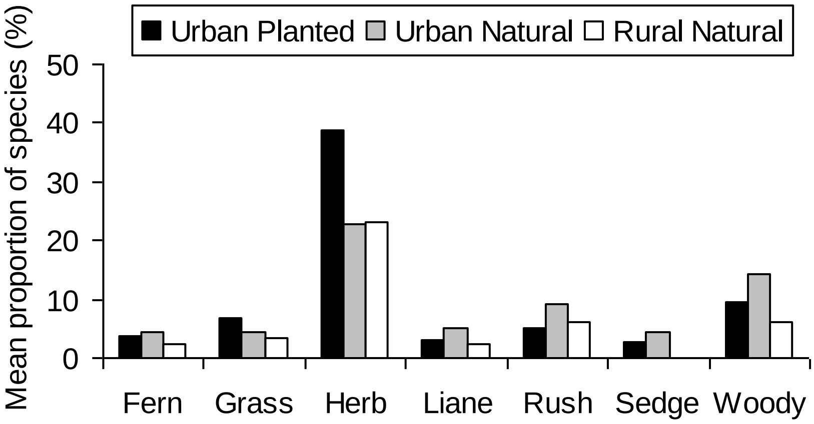
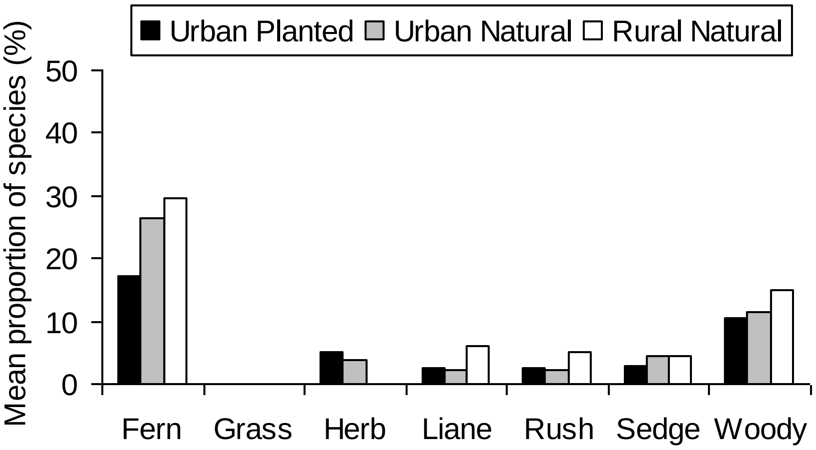


Figure 2.3 Mean percentage of (a) native and (b) exotic species represented by growth form as recorded in the soil seed bank as germinable diaspores for urban planted (*n* = 9), urban natural (*n* = 4) and rural natural (*n* = 4) forests.

Seed rain of urban planted sites was similarly dominated by exotic herbaceous species (31%) and native ferns (17%) but with less exotic (14%) and more native (11%) woody species than in the seed banks (Fig. 4a & b). Seed rain of urban natural sites was predominantly native ferns (26%) and exotic herbs (22%) along with exotic (13%) and native (11%) shrubs and trees. At rural sites native ferns (30%) and exotic herbs (21%) dominated the seed rain, with native shrubs and trees (15%) and exotic rushes (10%) common.

(a) Native species



(b) Exotic species

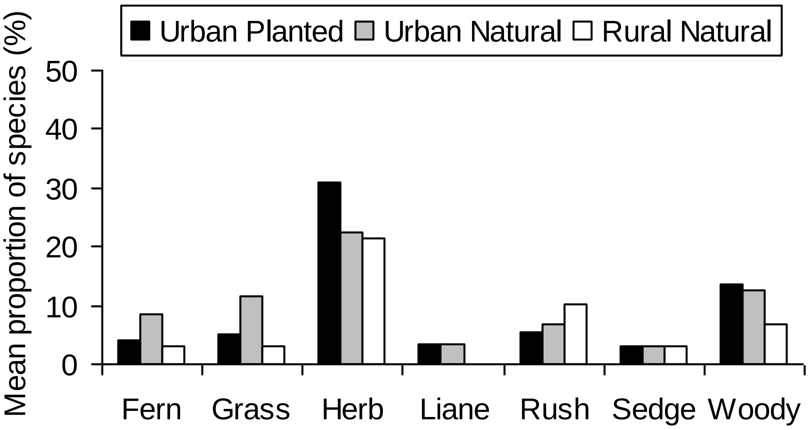


Figure 2.4 Mean percentage of (a) native and (b) exotic species represented by growth form as recorded in the annual seed rain as germinable diaspores for urban planted (n = 9), urban natural (n = 4) and rural natural (n = 4) forests.

2.4.5 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 2.2). 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 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.

2.4.6 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.

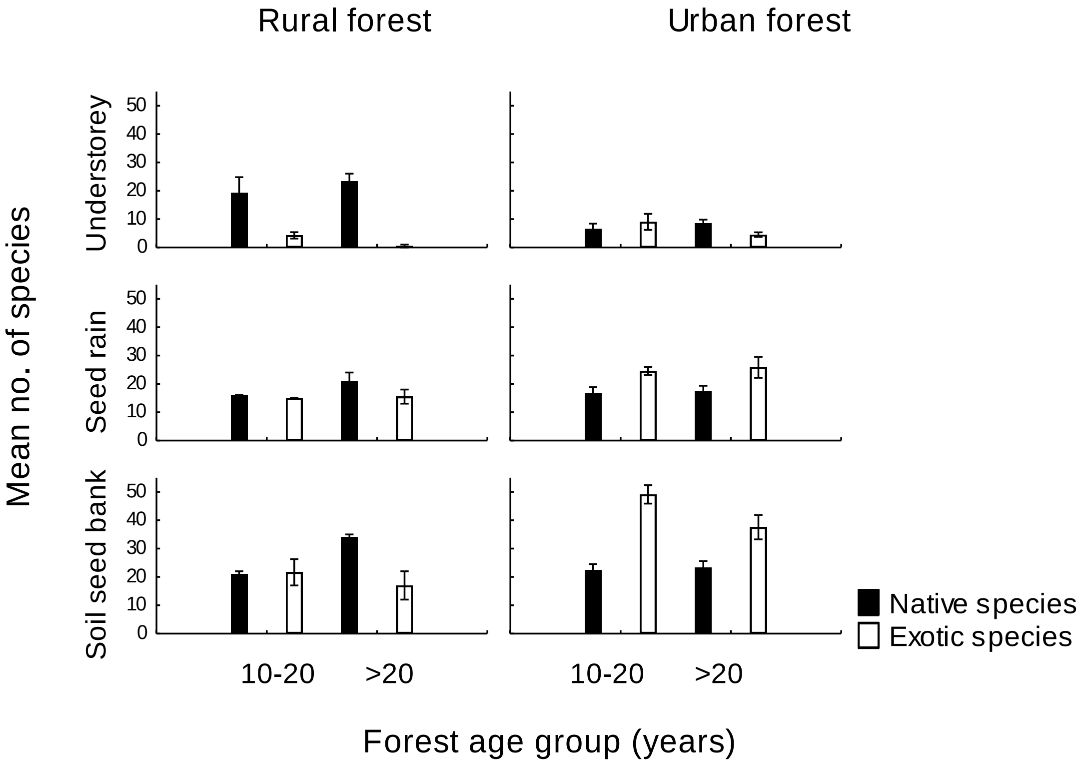


Figure 2.5 Mean (±standard error) native and exotic species richness for understorey vegetation (per 100 m^2), annual seed rain (per 0.169 m^2) and soil seed bank (per 0.169 m^2) for all urban (planted and natural, n = 13) and rural (natural, n = 4) forest sites by vegetation age group: young (10–20 years) and older (>20 years).

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.

Table 2.4 Mean (± standard error) exotic and native density of understorey stems (per 100 m^2) and seed rain and seed bank germinants (per 0.169 m^2) for urban (planted and natural) and rural (natural) forest sites, shown in two site age-groups: young (10–20 years) and older (>20 years).

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

2.4.7 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 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 eugenioides* and *Pseudopanax lessonii* and native ferns *Blechnum filiforme* and *Cyathea medullaris*.

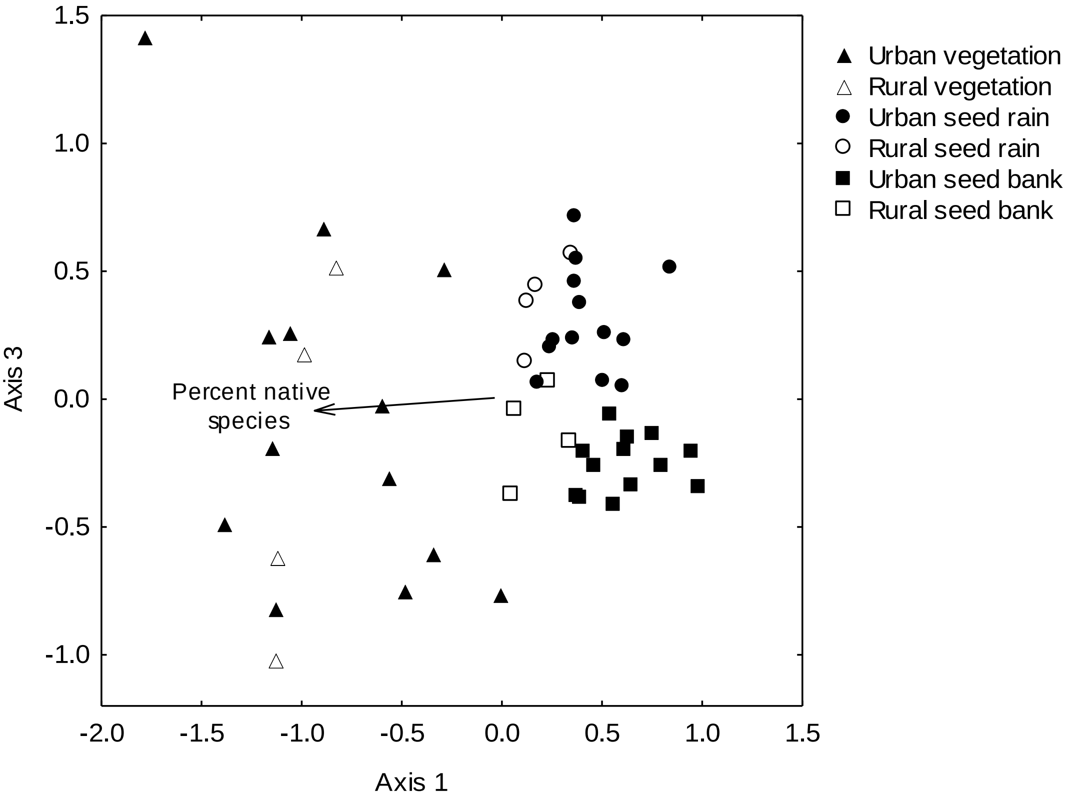


Figure 2.6 NMDS ordination configuration illustrating the compositional difference among vegetation, seed rain and seed bank for all urban (n = 13) and rural (n = 4) forest types. Axes 1 and 3 are shown for simplicity, though a 3-D solution was selected (stress = 12.0, instability < 0.00001, R^2 = 0.90).

2.5 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.

2.5.1 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.).

2.5.2 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 *Dacrycarpus 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).

2.5.3 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).

2.5.4 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 2.1

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
Alnus sp.*	-	7.5	-	-	-	-
Asplenium bulbiferum	-	-	-	-	-	2.2
Beilschmiedia tawa	-	-	1.5	-	-	-
Blechnum novae-zelandiae	-	-	-	-	-	2.4
*Calystegia sepia**	-	1.6	-	-	-	-
*Conyza albida**	-	-	-	-	2.3	-
Coprosma robusta	4.0	-	-	1.6	2.1	-
Cordyline australis	7.4	1.6	-	-	-	-
*Crataegus monogyna**	-	1.3	-	-	-	-
Cyathea dealbata	-	16.1	4.4	2.2	13.9	2.9
Cyathea medullaris	1.4	11.4	2.4	-	-	-
Dacrycarpus dacrydioides	-	1.4	-	-	-	-
Dianella nigra	-	-	-	-	-	2.8
Dicksonia squarrosa	-	29.7	-	-	9.7	-
Diplazium australe	-	-	-	-	2.9	-
Freycinetia banksii	-	1.7	-	-	-	-
Geniostoma rupestre	-	-	4.2	-	-	2.0
*Hedera helix**	1.4	-	-	-	-	-
Hedycarya arborea	-	-	-	-	-	1.2
Hoheria populnea	2.7	-	-	1.3	-	-
Hoheria sexstylosa	1.7	-	-	-	-	-
Jasminum sp.*	4.6	-	-	-	-	-
Juglans sp.*	-	-	-	1.4	-	-
Kunzea ericoides	1.8	-	15.6	-	-	2.9
Leptospermum scoparium	-	-	25.5	-	-	13.7
Leucopogon fasciculatus	-	-	-	-	-	4.4
*Ligustrum lucidum**	-	-	-	1.1	-	-
*Ligustrum sinense**	7.2		-	41.9	29.6	-

*Lonicera japonica**	9.9	5.7	-	1.8	2.0	-
Macropiper excelsum	-	-	-	-	1.4	2.0
Melicytus ramiflorus	11.1	17.4	8.2	34.8	23.4	-
Metrosideros diffusa	-	-	3.4	-	-	-
Microsorum scandens	-	-	-	-	-	1.3
Muehlenbeckia australis	-	2.1	-	-	-	-
Olearia paniculata	1.7	-	-	-	-	-
Phyllocladus trichomanoides		-	-	-	-	2.3
Pittosporum eugenioides	14.5	-	-	-	-	-
Pittosporum tenuifolium	6.2	-	-	-	-	-
Plagianthus regius	1.3	-	-	-	-	-
Podocarpus totara	8.9	-	-	-	-	-
Pteridium esculentum	-	-	-	-	-	13.8
Pteris tremula	-	-	-	1.3	-	-
Rhopalostylis sapida	-	-	-	-	-	1.6
Ripogonum scandens	-	-	12.5	-	-	2.6
*Rubus fruticosus**	-	-	-	4.4	-	-
Schefflera digitata	-	2.2	-	-	-	-
Schoenus tendo	-	-	-	-	-	1.2
Solanum americanum	-	-	-	-	2.6	-
*Solanum chenopodioides**	-	-	-	-	1.1	-
*Ulex europaeus**	-	-	19.5	-	-	26.7
*Zantedeschia aethiopica**	-	-	-	-	1.8	-

APPENDIX 2.2

Species classified as persistent in soil seed banks for either 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
*Actinidia deliciosa**	●	-
*Agrostis stoloniferus**	●	○
*Amaranthus powellii**	●	-
*Anagallis arvensis**	●	○
*Athyrium filix-femina**	●	○
Blechnum novae-zelandiae	●	●
*Briza minor**	●	-
*Buddleja davidii**	●	-
Callicarpa sp.*	●	-
*Callitriche stagnalis**	●	-
Carex sp.	●	-
Carex inversa	●	-
Carex geminata	●	-
Carpodetus serratus	-	●
*Chenopodium album**	●	-
*Cirsium arvensis**	●	○
*Cirsium vulgare**	●	○
Coprosma robusta	●	○
Cordyline australis	●	○
*Crepis setosa**	●	-
Cyathea dealbata	●	●
Cyathea smithii	●	●
Cyathea sp.	●	○
*Cyperus eragrostis**	●	-
Dacrycarpus dacrydioides	●	-
Deparia petersenii	●	○
Dianella nigra	○	●
Dicksonia fibrosa	●	○
Dicksonia squarrosa	●	●
*Digitalis purpurea**	●	○
*Digitaria sanguinalis**	●	-
Diplazium australe	●	-
Doodia australis	●	○
Drosera auriculata	-	●
*Duchesnea indica**	●	-
Hypolepis lactea	●	○
Hypolepis ambigua	●	-
*Idesia polycarpa**	●	○
Isolepis reticularis	●	-
*Isolepis sepulcralis**	●	-
*Juncus acuminatus**	●	-
*Juncus articulatus**	●	-
*Juncus bufonius**	●	●
Juncus planifolius	●	●
*Juncus tenuis**	●	●
Juncus sp.	●	-
Juncus sp.*	●	○
Juncus sp.*	●	○
*Lapsana communis**	●	-
*Lepidium didimum**	●	-
*Leucanthemum vulgare**	●	○
*Leycesteria formosa**	●	○
Lobelia anceps	-	●
*Lotus pedunculatus**	●	●
*Lythrum hyssopifolia**	●	-
*Mimulus moschatus**	●	-
*Modiola caroliniana**	●	-
*Nephrolepis cordifolia**	●	-
Paesia scaberula	●	●
*Paulownia tomentosa**	●	-
*Persicaria maculosa**	●	-
*Phytolacca octandra**	●	●
*Plantago major**	●	○
Pneumatopteris pennigera	●	○
*Poa annua**	●	-
*Portulacca oleracea**	●	-
*Pteris cretica**	●	-
Pteris macilenta	●	-
Pteris tremula	●	○
*Ranunculus repens**	●	-

*Echinochloa crus-galli**	●	-
*Eleusine indica**	●	-
*Epilobium ciliatum**	●	-
*Eragrostis brownii**	●	-
*Erica lusitanica**	○	●
Euchiton involucratus	○	●
*Euphorbia peplus**	●	-
Fuchsia excorticata	●	●
*Fumaria muralis**	●	-
*Gamochaeta coarctata**	●	●
Geniostoma rupestre	○	●
Gonocarpus aggregatus	-	●
Haloragis erecta	●	○
Hebe sp.	●	-
Histiopteris incisa	●	●
*Holcus lanatus**	●	○
*Ranunculus sardous**	●	-
*Rubus fruticosus**	●	○
*Rumex obtusifolius**	●	-
*Sagina procumbens**	●	-
Schoenus apogon	●	-
Schefflera digitata	●	○
*Silene gallica**	●	-
Solanum americanum	●	●
*Solanum chenopodioides**	●	-
*Solanum mauritianum**	●	-
*Solanum nigrum**	●	●
*Sonchus oleraceus**	●	○
*Spergula arvensis**	●	-
*Stachys sylvatica**	●	-
*Ulex europaeus**	●	●
*Verbena bonariensis**	●	-

3 SEED RAIN CONTRIBUTIONS TO URBAN FOREST RESTORATION: SEASONAL PATTERNS AND ORIGINS

3.1 ABSTRACT

Seed rain provides propagules for regeneration and has a major influence on vegetation dynamics and succession. Native forest restoration relies on adequate seed sources and seed rain input to be sustainable in the absence of ongoing species enrichment through planting or seed-sowing. This study investigates seed rain composition and abundance over one year in patches of planted urban forest (10 to 36 years old) with comparison to urban and rural naturally regenerating forest. Strong seasonality in seed rain density was observed but species richness in the seed rain fluctuated little with a small peak in mid-summer. The main quantity of seed rain reflected the immediate vegetation at sites so that the majority of both urban and rural native seed rain (>65% annual germinable propagule rain density) was from species present in the extant vegetation. Exotic seed rain, in contrast, was mostly from vegetation not immediately surrounding seed traps but occurred at lower density than native seed rain for urban planted and rural sites, but not urban natural sites, reflecting the predominance of native canopy vegetation in the former two forest types. In all forest types at least three-quarters of seed rain species recorded did not originate from the immediate vegetation. The number of new native species arriving was not significantly different between urban planted, urban natural and rural seed rain (means of 10, 13 and 11 species per site respectively) while there were significantly more exotic species arriving in urban (20 and 22 species) than rural (15 species) seed rain. Wind or water was the most common dispersal mechanism for species arriving, predominantly native ferns and exotic herbaceous species, and dispersal modes did not differ significantly between urban and rural seed rain. Only half as many native woody species were new arrivals in urban planted compared to rural seed rain over the year (1 species per site compared to 2), in contrast to four new exotic woody species in the seed rain of urban plantings, significantly more than rural seed rain with two new exotic woody species over the year. Animal dispersal was prevalent amongst new native woody species whereas wind or water was more common for exotic woody species. The year round prevalence and high mobility of exotic species in urban seed rain, even for species with apparently unassisted dispersal, suggests that the establishment of exotic species in small urban forest patches poses an ongoing threat to the sustainability of native communities, particularly following any disturbance. The seed rain in urban forest patches was found to be a source of new native propagules, notably ferns, but for woody species was limited to early successional species typical of plantings.

Key words Dispersal limitation; propagule rain; forest succession; seed dispersal

3.2 INTRODUCTION

Seed rain represents the potential species composition at a site (Harper 1977) and the dispersal of propagules in the seed rain is an important factor in the second phase of restoration for the successful establishment of target communities (Bakker et al. 1996). The arrival and establishment of new plant species is necessary to increase compositional diversity following planting of pioneer species and ultimately influences the successional trajectory of a site. Seed rain becomes increasingly important when there is little contribution from soil seed banks (the temporal accumulation of long-lived seed rain species) due to site history or the ecological traits of target species (Bakker et al. 1996; Bossuyt & Honnay 2008). Late successional forest species are not commonly associated with longevity and the formation of soil seed banks (Pickett & McDonnell 1989; Fenner & Thompson 2005; Bossuyt & Honnay 2008); therefore, the long-term sustainability of restoration projects, without ongoing enrichment planting, relies to a great extent on regular dispersal events of desirable native forest seeds or propagules (Prach & Hobbs 2008).

Vegetation regeneration relies not only on successful propagule dispersal but also on the existence of favourable germination niches and establishment conditions (Bakker et al. 1996; Fenner & Thompson 2005). Only a small proportion of the seed rain may germinate and establish successfully on arrival, or become incorporated into the soil seed bank, while the majority suffers mortality pre- or post- germination (Fenner & Thompson 2005). Additionally, considerable seasonality and between year variability in forest seed rain composition and quantity can occur (Beveridge 1964; Burrows 1994a; Sem & Enright 1996) which will affect the species available to regenerate as a niche becomes available (Drake 1998).

Forest seed rain tends to predominantly represent the extant vegetation at a site (Burrows 1994a; Drake 1998), however, longer distance dispersal events are important to move seeds away from parents to suitable establishment sites and advance succession through colonisation of seral vegetation (Dungan et al. 2001). Native regeneration in urban forest patches is more likely to be limited by seed availability due to increased isolation from native seed sources (Moles & Drake 1999; Jacquemyn et al. 2003; White et al. 2004). Seed rain arrives by a variety of seed dispersal mechanisms, sometimes in combination, and the dispersal mode as well as distance of the seed source affects the spatial distribution of seed rain (Harper 1977). In the New Zealand flora the most common dispersal modes, listed in order, use: wind (anemochory); animals internally (endozoochory); water (hydrochory); animals externally (epizoochory) and explosive ejection (ballistic) (Thorsen et al. 2009). Amongst New Zealand’s woody plant species fleshy-fruits are common making frugivorous birds particularly important dispersal agents in forests (Willson et al. 1990; Lord 1999). Wind dispersal may involve the use of external propagule structures to increase air resistance such as wings, plumes or surface sculpting or having minute size, e.g. dust-like seeds of orchids or fern spores. Water dispersal may occur by buoyancy from airspaces or a hydrophobic surface created by marginal filaments or a waxy coating. Seeds or propagules may also attach themselves externally to animals using structural adaptations such as hooks or sticky substances. Explosive or ballistic dispersal is by the plant itself (autochory) allowing only short-distance dispersal and along with barochory, or dispersal by gravity, is also referred to as unassisted dispersal (van der Pijl 1982).

Introduced plants and dispersers have altered the natural balance of seed dispersal (Traveset & Richardson 2006), particularly in more human-modified habitats where many introduced birds and weeds preferentially utilise disturbed forest patch margins over interior forest (Timmins & Williams 1991; Wiser & Allen 2006). In comparison to native birds, introduced birds are more important dispersers of small-fruited exotic plants in New Zealand and utilise disturbed habitats more readily (Williams & Karl 1996) while native birds make greater contribution to native plant dispersal (Kelly et al. 2006). Introduced mammals can also disperse small-fruited exotic weed species, as well as being dispersers and predators of native fleshy-fruited species (Williams et al. 2000). Fragmentation of forest may also increase penetration by wind dispersed plants through disturbed edge habitat (Cadenasso & Pickett 2001) which may increase exotic weed invasion in urban forest (Sullivan et al. 2005).

This study investigates whether new species arriving in the seed rain of urban forest patches can contribute to the successful restoration and ongoing sustainability of native forest habitat. The annual germinable seed rain and extant vegetation composition is quantified and contrasted between urban planted restoration forest sites and urban and rural natural forest to investigate the following questions:

1. How does native and exotic seed rain quantity and composition vary seasonally?
2. What proportion of seed rain is new species arriving at site, i.e. not shared with overhead extant vegetation?
3. Does dispersal mode influence species presence in the arriving seed rain?

3.3 METHOD

3.3.1 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. 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 (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).[3]

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 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, 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.

3.3.2 Study design

Sampling effort focussed on nine urban planted sites where Hamilton City Council had undertaken native forest restoration planting, with comparison to four naturally regenerating forest remnants in the city and four natural forest sites in the Hakarimata Range, site locations and details can be found in Overdyck and Clarkson (2012). Restoration plantings were identified spanning 10–36 years since initial planting date and the sites in natural forest were selected in a similar age group of secondary regenerating forest with one older mature forest site (c. 150 years) included in each of the urban and rural groups. 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.

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

3.3.3 Vegetation and seed rain assessment

Vegetation and seed sampling was undertaken in plots located centrally within each forest patch to reduce any edge effects where possible. Vegetation was assessed using a constant-count plot method (Batcheler & Craib 1985) measuring the 30 nearest canopy tree stems to the plot centre 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, and the understorey was assessed by counting of all stems <20 mm dbh and >300 mm height (including lianes) and presence of ground cover vascular species <300 mm in height were listed.

Four seed rain 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 and spore rain. Four trays (total area 0.169 m^2) 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). 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 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 term seed rain is used for simplicity throughout, although fern spores are included unless otherwise stated.

3.3.4 Data analysis

Data from urban planted and urban natural sites was combined for presentation of seasonal seed rain pattern analysis as the two forest types showed the same trends. For subsequent analysis of total annual seed rain means three treatment groups are retained: urban planted, urban natural and rural natural forest. Compositional similarity between vegetation (canopy, understorey and ground cover), and seed rain was assessed using the Jaccard Coefficient of Community (CC_J) similarity index for species presence/absence data with the formula below; where S_1= species in community 1, S_2= species in community 2 and C= species common to both communities (Brower *et al.* 1990):

$$CC_J = C/\ (S_1+S_2-C)$$

Each species was assigned a primary dispersal mechanism from direct accounts of dispersal where possible or by inference from morphological and ecological characters using published literature (Allan 1961; Esler 1988; Burrows 1994b; Strykstra et al. 2002) and two online databases: New Zealand Plant Conservation Network, www.nzpcn.org.nz, and Landcare Research ecological traits database, www.landcareresearch.co.nz/resources/data/ecological-traits-of-new-zealand-flora. Species were then grouped into three dispersal modes for analysis being either: 1) wind or water (anemochory or hydrochory); 2) animal (endozoochory and epizoochory); or 3) unassisted (ballistic or no apparent specialisation).

Student's two sample t-tests were used to compare native and exotic species means within forest treatment groups (urban planted, urban natural and rural natural). Analysis of variance (ANOVA) was used to test for effects of the three forest treatments on seed rain compostional similarity with extant vegetation and on newly arriving species richness means. Post hoc Tukey HSD pairwise comparisons were used where significant treatment effects were detected. Pearson's chi-squared (χ^2) test was used to determine if representation of the three main dispersal modes was associated with forest treatment. All data analyses were undertaken using the statistical package R version 2.15.2 (The R Foundation for Statistical Computing 2012).

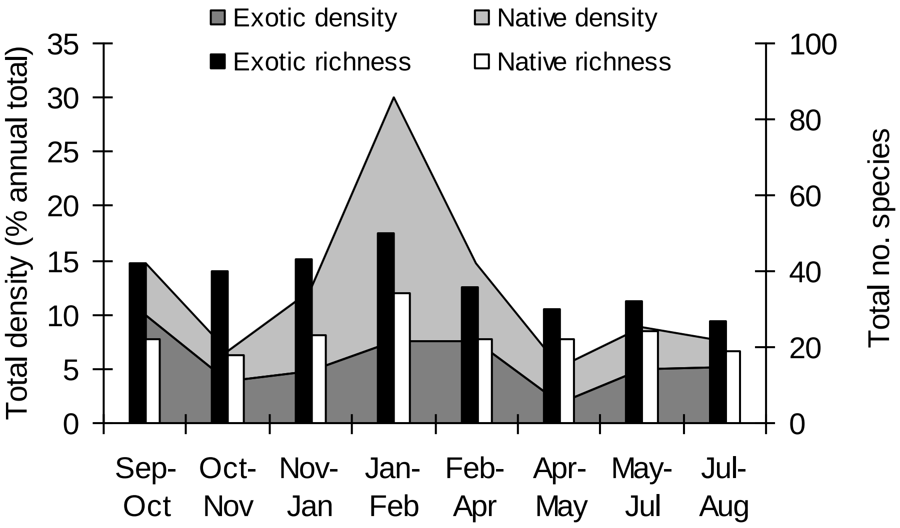
3.4 RESULTS

3.4.1 Seasonal seed rain patterns

Overall, exotic species were more prevalent in urban (both planted and natural) than rural seed rain by both germinable propagule density and richness (Figs. 3.1a & b). Throughout the year species richness at urban sites was dominated by exotic species (range of 57-69% exotic) whereas rural seed rain generally had more native species (27-46% exotic) except in March with 55% exotic species, which was due to a decline in native species present. Native species richness remained greater for urban compared to rural seed rain, particularly due to ferns occurring for a longer season in urban seed rain, although over the whole year native fern richness was similar. Richness of native woody species was also greater in urban than rural seed rain throughout the year with few shared species; seven out of 22 species occurred in both urban and rural seed rain, while 11 and four species were present in only urban and rural seed rain respectively. Notably, all of the native woody species in urban seed rain were potentially from planted sources at or adjacent to sampling sites.

Total density of germinable propagules in the seed rain peaked in January and February for urban planted and natural sites (combined in Fig. 3.1a) contrasting with a peak in June for seed rain at rural natural sites (Fig. 3.1b). The peak in seed rain for urban sites was influenced mainly by a large increase in several native ground ferns (e.g. *Pteris tremula*, *Doodia australis*, *Deparia petersenii*) and exotic herbs (e.g. *Conyza albida*, *Epilobium ciliatum*, *Senecio bipinnatisectus*) (see Appendix 3.1 & 3.2 for all species seasonal occurrence). While at rural sites peak seed rain density was due to increased native woody germinants in June (*Kunzea ericoides* and *Leptospermum scoparium* formed 96% of June seed rain) and there was also a secondary peak from September to November with high numbers of the native ground fern *Blechnum novae-zelandiae* (66% of Sep-Nov seed rain). High species richness in the urban seed rain coincided with peak density in January (bars, Fig. 3.1a) and was due to an increase in native sedge, rush and herbaceous species. Rural sites also peaked in seed rain species richness in January (bars, Fig. 3.2) as with urban sites, which was due to an increase in native fern and rush species present.

(a) Urban planted and natural sites



(b) Rural natural sites

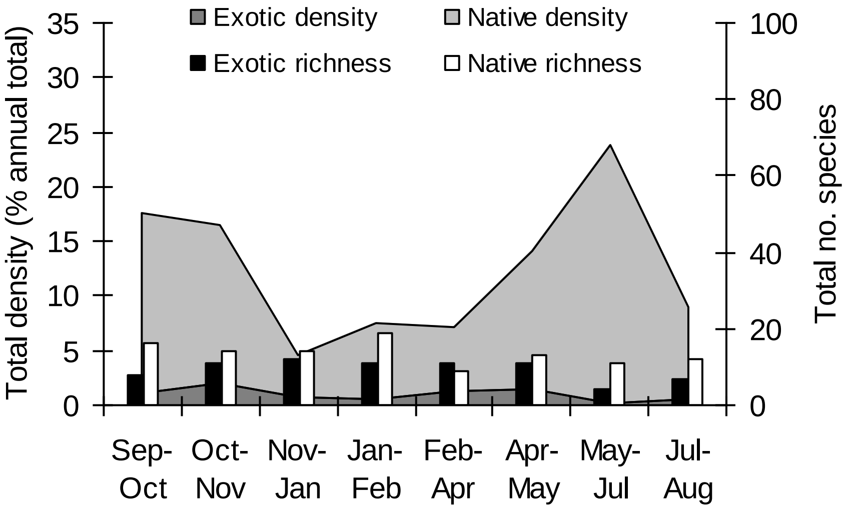


Figure 3.1. Seed rain seasonal germinable propagule density and richness for native and exotic species at 6 weekly intervals, September 2006 to September 2007, for (a) all urban sites combined (urban planted forest n=9, urban natural forest n=4) and (b) rural natural forest sites (n=4).

3.4.2 Extant vegetation and seed rain comparison

Annual seed rain density was found to be highly variable between sites and density of native seed rain was highest for rural forest while exotic seed rain density was higher in both urban forest treatments than in rural forest (Table 3.2). No significant differences in seed rain density were detected between forest treatments or between native and exotic species within treatments. The proportion of annual seed rain from species present in the extant vegetation immediately surrounding seed traps was greater for native than exotic species in all forest types (Table 3.1) and this was significant for urban planted (70% compared to 25%) and rural natural sites (80% compared to 8%) ($p<0.005$, Table 3.1). No significant differences in the proportion of seed rain shared with vegetation were detected between forest treatments.

Table 3.1. Mean ± SD germinable seed rain density (from Chapter 2: Overdyck and Clarkson (2012)) and percentage of seed rain shared with species present in the extant vegetation (<5m from seed traps) for three forest treatments: urban planted, urban natural and rural natural, September 2006-07. *Denotes significantly different means between native and exotic species for Student's two sample t-test, $p<0.05$.

	Seed rain density (count)		**Proportion seed rain density shared with species in vegetation (%)**	
Forest treatment	**Native**	**Exotic**	**Native**	**Exotic**
Urban planted (n=9)	239 ± 151	149 ± 138	70 ± 31	25 ± 23 *
Urban natural (n=4)	182 ± 121	259 ± 302	65 ± 14	36 ± 30
Rural natural (n=4)	756 ± 488	66 ± 15	80 ± 23	8 ± 14 *

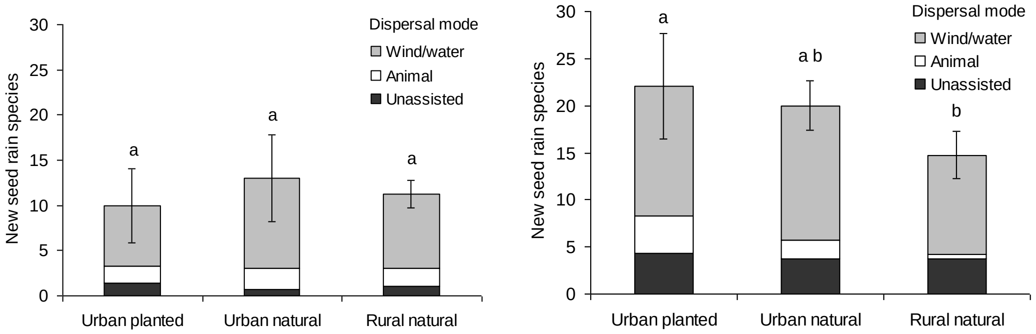
In contrast to density, compositional similarity was low between the extant vegetation and seed rain species (14-18%) for all forest types (Table 3.2). Similarity was greater for native species (20-24%) while fewer exotic species were shared between vegetation and seed rain, this difference was significant for urban planted (10%) and rural sites (3%) ($p<0.005$, Table 3.2).

Table 3.2. Mean ± SD Jaccard Coefficient of Community (CC_J) similarity index (presented as percentage) comparison between species presence in the germinable seed rain and extant vegetation (canopy, understorey and groundcover <5m from seed traps), for three forest treatments: urban planted, urban natural and rural natural, September 2006-07. *Denotes significantly different means between native and exotic species for Students two sample t-test, $p<0.05$.

Forest treatment	**Total species**	**Native**	**Exotic**
Urban planted (n=9)	16 ± 7	25 ± 11	10 ± 7 *
Urban natural (n=4)	18 ± 4	24 ± 5	12 ± 8
Rural natural (n=4)	14 ± 4	20 ± 4	3 ± 4 *

3.4.3 Dispersal modes for new species arriving in seed rain

New species arriving to sites, i.e. not present in the extant vegetation, accounted for between 76% and 78% of species occurring in the annual seed rain at rural and urban (planted and natural) sites. Fewer native species were new in the seed rain (62-65% native species) and more exotic species were new arrivals (85-87% urban and 96% rural exotic species). The average number of new native species arriving in the annual seed rain was not significantly different across forest treatments with 9.9, 13.0 and 11.3 species for urban planted, urban natural and rural treatments respectively (Fig.3.2a). The number of new exotic species was lower in rural natural (14.8 species) than urban natural (20.0 species) seed rain and significantly lower than urban planted seed rain (22.1 species, Tukey's pairwise comparisons $t = 2.693$, $p = 0.0427$, Fig. 3.2b). Wind or water dispersal was most common for new seed rain species arriving, ranging from an average of 6.7 native species in urban planted seed rain to 14.3 exotic species in urban natural seed rain for the year (Figs 3.2a & 3.2b), with no significant difference in dispersal modes between treatments (native species $\chi^2 = 0.4975$, df = 4, p = 0.9737; exotic species $\chi^2 = 2.0947$, df = 4, p = 0.7184). New native species dispersed by wind were predominantly ferns, while exotic species in this dispersal group were predominantly herbaceous species. Native species with unassisted dispersal mode were the least common new arrivals in urban and rural annual seed rain (means <1.4 species) while on average two new native animal-dispersed species arrived in both urban and rural annual seed rain (Fig 3.2a). Exotic species with unassisted dispersal averaged around four new species in urban and rural seed rain (Fig 3.2b), while a higher number of new exotic animal-dispersed species arrived in urban planted (4 species) than urban natural (2 species) or rural natural (0.5 species) seed rain over the year.



(a) all native species (b) all exotic species

(c) native woody species (d) exotic woody species

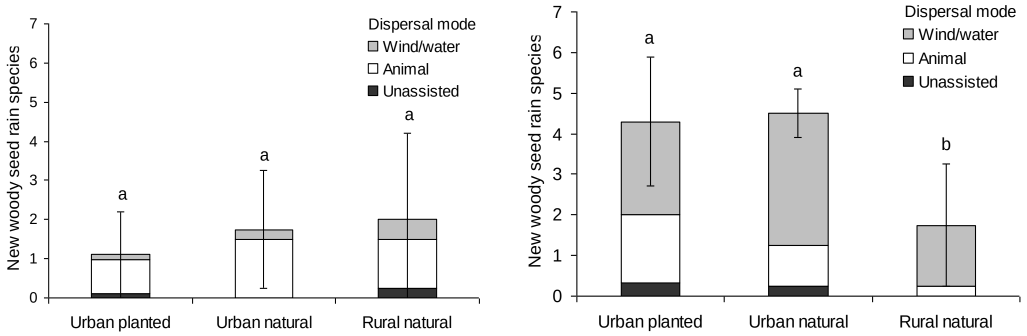


Figure 3.2. Mean (±SD) newly arriving (a) all native species, (b) all exotic species, (c) native woody species, and (d) exotic woody species in the annual germinable seed rain (not present in vegetation at sites) in urban planted (n=9), urban natural (n=4) and rural natural (n=4) treatments, September 2006-07, across three main seed dispersal modes. Different letters denote significant differences between overall treatment means for Tukey's pairwise comparisons, $p<0.05$.

Of the native woody species in the urban planted seed rain one quarter were new arrivals (25% or 1.1 species on average per site) compared to 29% (1.8 species) and 30% (2.0 species) in the urban natural and rural natural seed rain respectively, there was no significant difference in overall means between treatments (ANOVA $F_2 = 0.613$, $p = 0.556$, Fig. 3.2c). There were more exotic woody species arriving with 4.3 and 4.5 species per site in the urban planted and urban natural annual seed rain respectively, which was significantly greater than 1.8 exotic species in the rural seed rain (Tukey's pairwise comparisons: urban planted and rural $t = 3.053$, $p = 0.0217$; and urban natural and rural $t = 2.762$, $p = 0.0376$, Fig. 3.2d). Animal dispersal was most common for newly arriving native woody species in all treatments (Fig 3.2c), whereas wind or water dispersal was more common amongst new exotic woody species (Fig. 3.2d). Dispersal modes were not significantly different between forest treatments for new native woody species ($\chi^2 = 0.3909$, df = 4, p = 0.9832) or exotic woody species ($\chi^2 = 0.7161$, df = 4, p = 0.9493).

3.5 DISCUSSION

Urban native seed rain was greater in quantity than exotic seed rain only when native canopy species had been planted showing a benefit of initial planting to encourage restoration of native communities rather than natural or spontaneous colonisation alone (Bornkamm 2007) which may not be suited to restoration in an urban landscape (Hodge & Harmer 1996; Prach et al. 2001; Prach & Hobbs 2008). The majority of native seed rain was from species present in the immediate vegetation so that novel species arriving in the seed rain were often not abundant in quantity but still three quarters of native species recorded in urban seed rain were novel, providing evidence for some long-distance dispersal (particularly for wind-dispersed species) and potential for new species to establish. However, the greater number of exotic than native species newly arriving in urban seed rain is of concern, though not unexpected given the exotic nature of urban seed sources (Esler & Astridge 1987; Smith et al. 2006; Williams & Cameron 2006). The pervasiveness of exotic vegetation in close proximity to urban plantings and rural forest edges (Timmins & Williams 1991; Sullivan et al. 2005) is also reflected in more exotic than native species newly arriving in rural seed rain, although the actual number and density of exotic species was lower in rural compared to urban seed rain.

Successful forest restoration relies on both propagule dispersal and the availability of suitable establishment niches (Battaglia et al. 2008; White et al. 2009; Bustamante-Sanchez & Armesto 2012) emphasising the importance of regular dispersal events for propagules. The reason that some seed rain species are not currently present in vegetation may be due to the absence or scarcity of suitable germination or establishment conditions, including biotic mycorrhizal associations, as well as niche competition from exotic propagules which may inhibit native regeneration in urban forest patches (Moles & Drake 1999; Smale &

Gardner 1999). Suitable microclimate and establishment niches may develop for forest species as urban native plantings age, although the small size of urban forest patches may limit the ability to create cool, humid conditions typical of mature forest interiors (Young & Mitchell 1994). Ferns can be an important structural component influencing seedling establishment in forests (George & Bazzaz 1999; Gaxiola et al. 2008) and fern spores for many native ferns were identified as large component of the seed rain suggesting no propagule limitation in an urban environment. Although despite presence in the seed rain and given records of fern soil spore bank formation (Dyer & Lindsay 1992; Overdyck & Clarkson 2012) many native forest fern species were not present in urban vegetation. The germination of ferns from propagules in seed rain samples under a regular watering regime suggests that unsuitable dry conditions in urban forest patches (Miller 2011) may be inhibiting their germination or establishment at the present time. Such an absence of ferns in the understorey may contribute to divergent regeneration patterns and successional trajectories for urban forest (Coomes et al. 2005).

Dispersal limitation may also affect the recolonisation of native species and has been identified as a factor in tropical rainforest restoration, in particular the recolonisation of desirable animal-dispersed species can be reduced with increasing distance to a mature forest seed source (Holl et al. 2000; White et al. 2004). This study has found that animal-dispersed woody shrub and tree species were as well represented amongst new arrivals in urban compared to rural seed rain, although these were all small-fruited species able to be dispersed by common introduced birds such as blackbirds (*Turdus merula*), thrushes (*T. philomelos*) and self-introduced silvereyes (*Zosterops lateralis*). These introduced birds also preferentially consume exotic fleshy-fruits (Williams & Karl 1996) which were more abundant in urban than rural seed rain new arrivals. At urban planted sites many more new exotic compared to native fleshy-fruited species arrived in the seed rain (including woody species) suggesting ongoing management of highly mobile weed species will be required to allow native communities to establish given the prevalence of introduced seed dispersers (Williams & Karl 1996; Kelly et al. 2006; Williams 2006). Previous New Zealand seed rain studies in seral vegetation have concluded that observed seed rain was adequate for native regeneration and this was linked to the close proximity of mature forest (Burrows 1994a; Dungan et al. 2001). We found the composition of native woody species in the seed rain of urban planted sites to be restricted to species typical of early successional plantings suggesting seed rain diversity may be limited by the distance to mature forest seed sources. Larger-fruited species can be more vulnerable to dispersal limitation (Wunderle Jr. 1997; Cramer et al. 2007) and post-dispersal predation by small mammals (Holl et al. 2000; Doust 2011; Overdyck et al. 2013). Several native species typical of late successional forest and with large-seeded fleshy fruits (>9 mm diameter) were not recorded in urban seed rain in this study and may be dispersal limited due to reduced numbers of large native frugivorous birds in Hamilton City (Day 1995; Innes et al. 2005; Wotton & Kelly 2011) and distances of at least 10 km to intact remnant forest seed sources.

Because overall seed rain quantities were primarily influenced by the immediately surrounding vegetation this led to high variability between sites and seasonal patterns often reflecting overhead vegetation. Adequate sampling of the seed rain can be problematic not only due to placement of seed traps spatially but also temporal fluctuations in seed production following individual species phenologies. The spatial distribution of seed rain in forests is inherently non-random due to the nature of seed deposition or seed shadows being primarily close to parent plants (Harper 1977; Burrows 1994a), linked to dispersal mode, e.g. clumped beneath bird roosts (Ferguson & Drake 1999; Bustamante-Sanchez & Armesto 2012), and related to seed production at the source which may vary according to factors such as plant age and soil fertility (Dungan *et al.* 2001). Over a year’s sampling this study found that seasonal peaks in seed rain density were influenced to a large extent by wind-dispersed small seeds or spores, e.g. *K. ericoides* dominated vegetation and winter seed rain at the young rural sites and many ferns and annual herbaceous species provided prolific quantities of readily dispersed propagules. As many species have a limited period of seed production the composition of the seed rain also varies seasonally and a small peak in seed rain richness in summer was apparent in this study, as was also found by Sem & Enright (1996) in regenerating lowland forest near Auckland City. However, seed rain species richness showed less seasonal variation than density over one year of sampling with native and exotic propagules available throughout the year. Sampling over more than one year could reveal different results as between year variability in seed production can also affect seed rain density and composition (Beveridge 1964; Burrows 1994a; Sem & Enright 1996). Sem and Enright (1996) found seed rain density varied three-fold and species richness two-fold in two consecutive years of seed rain collections in a similar forest type. Notable between year variability in seed production is found in masting species, such as New Zealand's native podocarps (Beveridge 1964) which were poorly represented in seed rain of this study (only *Dacrycarpus dacrydioides*), with mast years in seed production strongly linked to environmental cues (Schauber et al. 2002). However, it may be expected that such variation in seed rain density from year to year will not necessarily affect the species richness from year to year as long as some seed production occurs in non-masting years (Beveridge 1964). The absence of podocarps and other mid to late successional native forest species in this study is more likely a result of very few urban seed sources, but may also be caused by a lack of overlap between sampling points and favoured bird seed deposition sites (Ferguson & Drake 1999) as many species were also absent from rural seed rain.

In conclusion, novel species arriving in the seed rain were often not abundant in quantity but even rare occurrences can be important in contributing to forest composition at a site if establishment is successful (Fenner & Thompson 2005). Establishment for some native species arriving at urban sites seems to be limited, e.g. ferns, indicating a suitable microclimate is still developing, in some cases 36 years after planting. Management may be required to maximise forest patch size and minimise edge disturbance to improve urban forest habitat for late successional species. Greater replication of collection sites and several years of sampling would be required to make stronger inferences on seed rain composition, however, it appears some native forest species will require active reintroduction to urban forest patches, particularly those with limited urban seed sources and limited dispersal, e.g. late successional and large-seeded species. Reduced dispersal of many target native forest species to young urban forest patches will not only limit vegetation succession but establishment niches are likely be filled by exotic species from the seed rain and soil seed banks (Overdyck & Clarkson 2012). Competition from highly mobile exotic species threatens the structure of urban native plantings and remnant forest patches and the control of weedy exotic propagule sources along with providing native propagule sources is important for their long-term sustainability.

3.6 ACKNOWLEDGEMENTS

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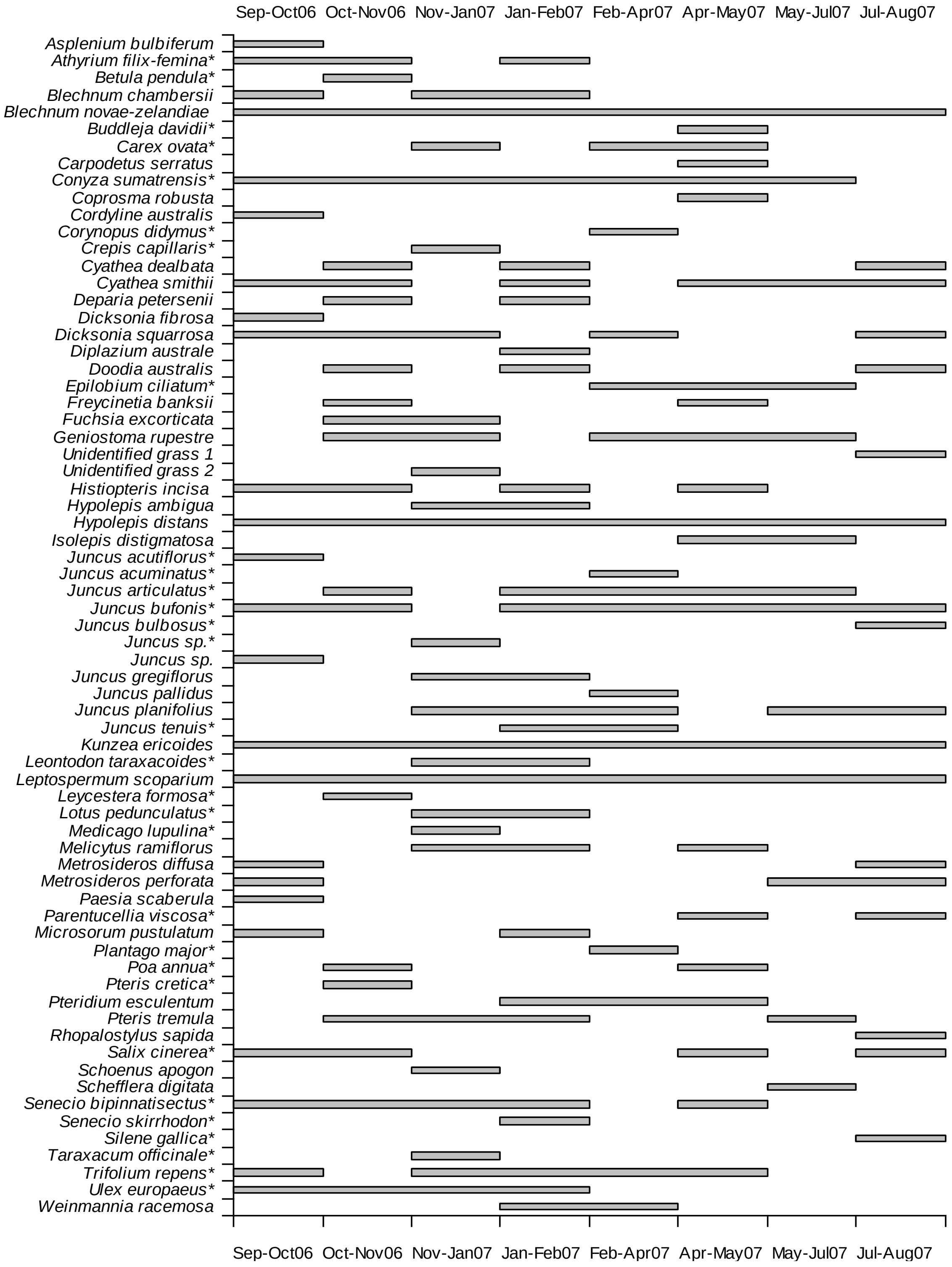
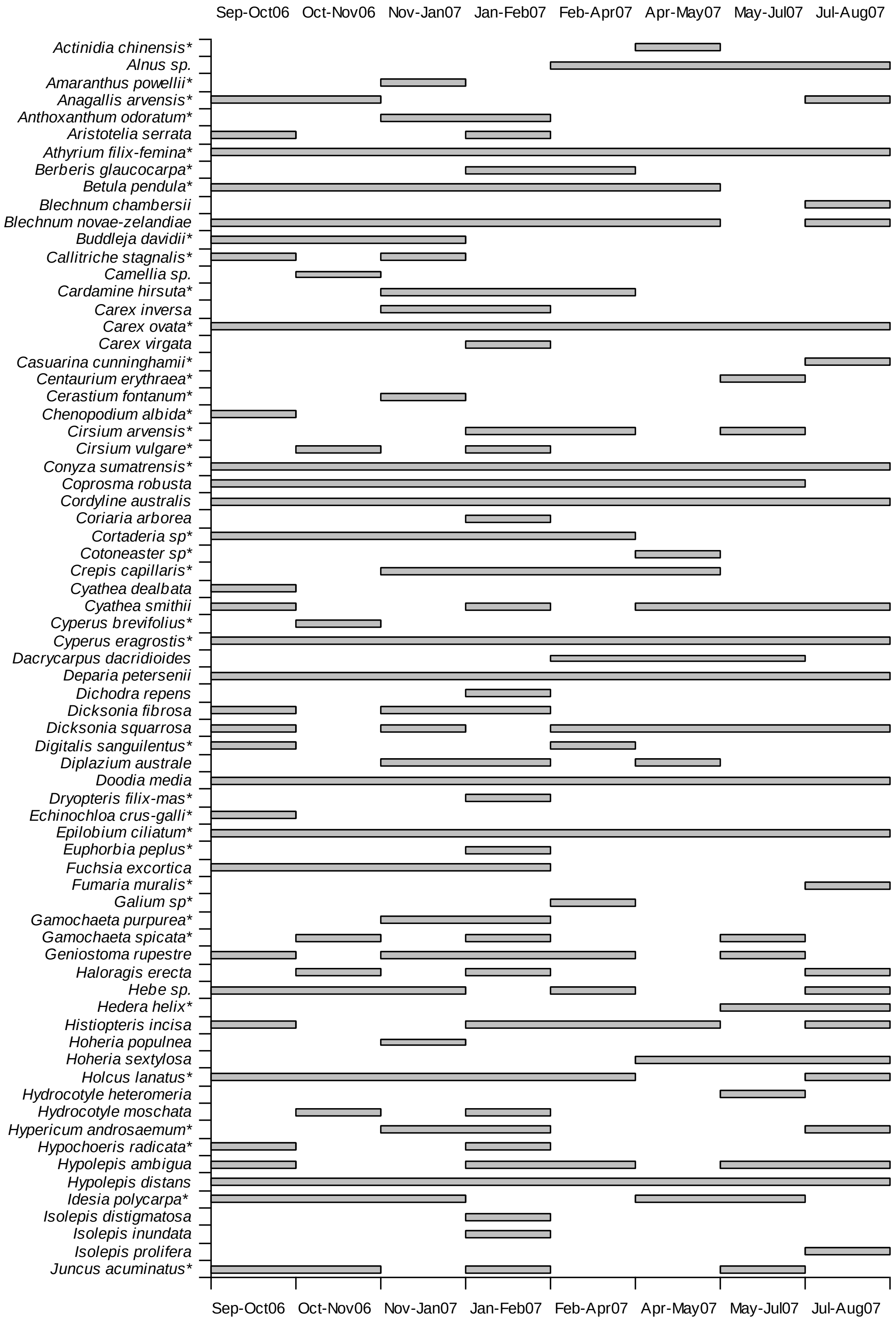
APPENDIX 3.1

Species seasonal occurrence in the seed rain collected at four rural sites in the Hakarimata Range, September 2006 to August 2007, at six-weekly intervals. *Denotes exotic species.

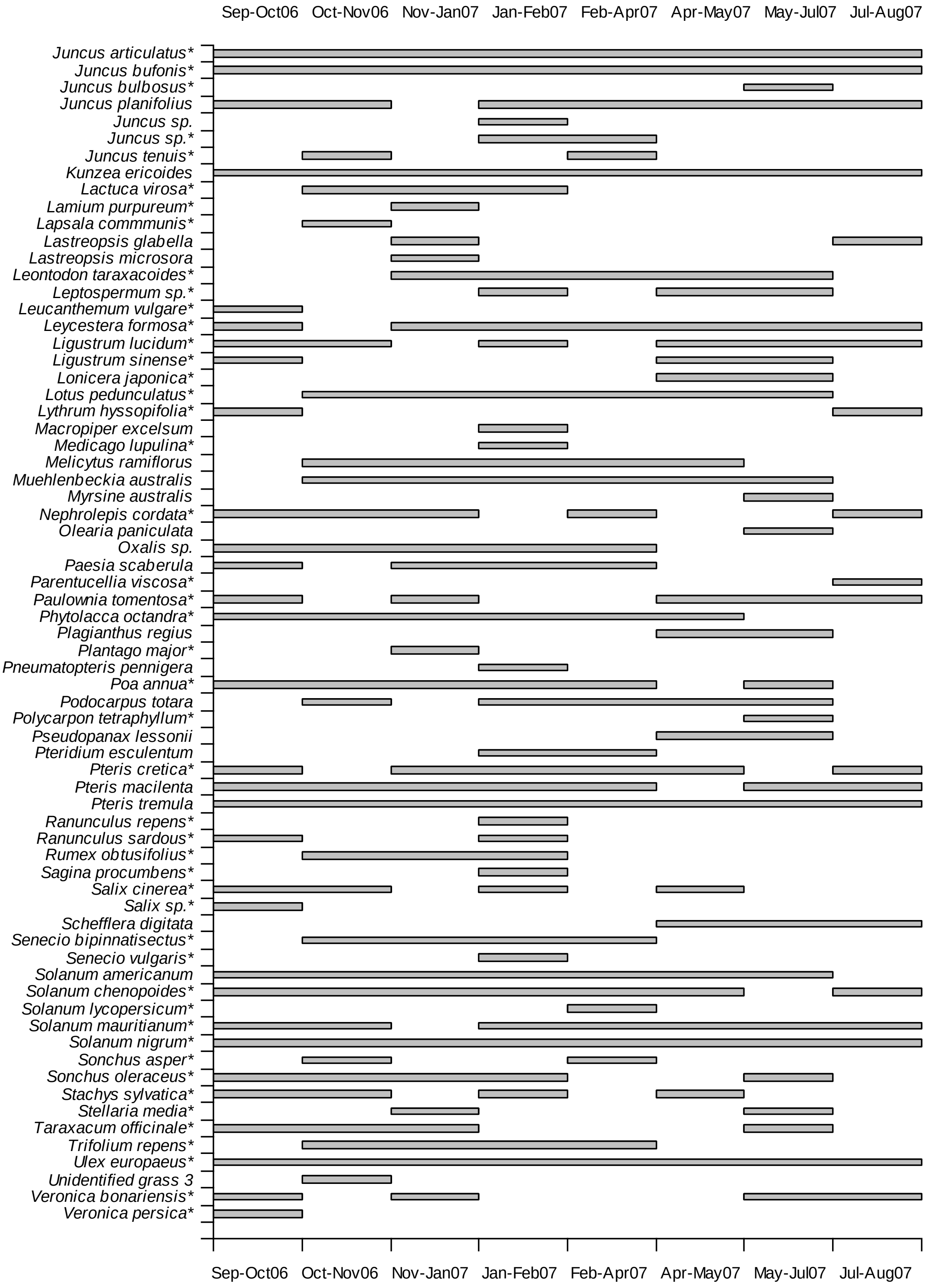


APPENDIX 3.2

Species seasonal occurrence in the seed rain collected at 13 urban sites (9 planted and 4 natural) in Hamilton City, September 2006 to August 2007, at six-weekly intervals. *Denotes exotic species.



APPENDIX 3.2. cont.



4 PLANT LIFE HISTORY TRAITS PARTIALLY EXPLAIN SPECIES ABSENCE FROM URBAN FOREST

4.1 ABSTRACT

Urban forest patches have unique environmental and landscape characteristics which influence their native plant communities. We investigate the response of urban forest patch species richness to local landscape fragmentation factors including patch size and isolation and use plant life history traits to identify vulnerable species groups. We found that the native forest flora in Hamilton City represented just over half (57%) of the species present in forests of the broader Hamilton Ecological District. In turn only 35% of the city species pool was found to be represented in the seed supply (annual seed rain and soil seed bank) and understorey sampling in urban forest patches. Raunkiaer life form was the only trait found to have significant variation between the district and the city, with a disproportionally large number of phanerophytes (tall plants) in the city and a lower representation of hemicryptophytes (including forbs, ferns and graminoids) and geophytes (e.g. orchids) which may reflect some relictual long-lived tree species that are surviving but may no longer have viable populations. Growth form, shade tolerance and pollination vector traits showed some significant variation between the seed supply and understorey of urban forest patches and both the District and City species pools. Forb and parasite growth forms, highly shade tolerant (i.e. late successional) species and those with biotic pollinators were under represented in the seed supply and understorey suggesting limited natural colonisation and regeneration in young urban forests. No effect of dispersal mode or clonality traits was found. Increased proximity and area of good quality native vegetation had a significantly positive effect on zoochorous species richness in urban forest patches. The depauperate nature of the native City forest flora suggests limited natural colonisation from beyond the urban area and offers great opportunity for increased species diversity in plantings and reintroductions in urban forest restoration.

Key words Ecological restoration, forest fragmentation, functional traits, habitat reconstruction

4.2 INTRODUCTION

Ecological restoration aims to increase native species habitat and improve ecosystem function, goods and services, with success often measured by changes in vegetation structure and species diversity towards a reference state (Ruiz-Jaen & Mitchell Aide 2005; Jackson & Hobbs 2009). Forest restoration commonly relies on the process of natural colonisation following the initial planting of early successional tree species, although this may be inadequate to restore entire communities (McClain et al. 2011) with recolonisation of native species found to be greater if restoration is located adjacent to mature forest that serves as a seed source (Reay & Norton 1999; Jacquemyn et al. 2003; MacKay et al. 2011). Natural colonisation rates will also depend on site disturbance and the life history traits of species in addition to the availability of seed sources in the landscape (Wang & Smith 2002). Recent emphasis on the importance of functional diversity in ecosystems (Diaz & Cabido 2001) has led to increased interest in how plant traits influence species distributions (Verheyen et al. 2003; Lindborg et al. 2012). Gathering information on life-history traits for species can provide an insight into the mechanisms driving colonisation and extinction processes and ultimately influencing vegetation community composition (Strykstra et al. 2002; Verheyen et al. 2003; Kolb & Diekmann 2005). Restoration of fragmented forest habitat may benefit particularly from knowledge of plant reproductive traits (e.g. pollination and seed dispersal mechanisms) that could directly limit species distributions and impede natural vegetation recovery and restoration success (Honnay et al. 2002; Aparicio et al. 2008).

Restoration in highly human-modified urban landscapes may be particularly vulnerable to seed or pollen limitations due to increased isolation from intact native forest habitat (Kostel-Hughes et al. 1998; Jacquemyn et al. 2003) and long land use history, such as agricultural development pre-urbanisation (Bastin & Thomas 1999; Bossuyt & Hermy 2001). Altered soils and temperature and moisture regimes are often associated with urban environments and may also influence vegetation composition by favouring species adapted to base-rich soils and warm, dry and unshaded conditions (Whaley et al. 1997; Thompson & McCarthy 2008; Miller 2011). Williams et al. (2009) suggest that urban vegetation composition is altered through a series of four filters created by the urban environment: habitat transformation, habitat fragmentation, altered environmental conditions and human preference. Identifying those plant traits that are affected to a greater or lesser extent by each of these filters can contribute to explaining the success or failure of species in such disturbed habitat (Thompson & McCarthy 2008; Duncan et al. 2011).

The identification of plant traits associated with recolonisation ability in urban habitats has been used for identifying overly successful weed species (Aronson et al. 2007) and in the context of forest restoration may also predict a suite of vulnerable native species which require active restoration. Reproductive traits such as pollination vector, dispersal mode, soil seed bank persistence, seed size and clonality can be important in the recolonisation of species when restoring fragmented forest habitat (Verheyen et al. 2003; White et al. 2004; Kolb & Diekmann 2005; Battaglia et al. 2008) yet in urban habitats such traits have not been shown to have a broad influence on species success (Thompson & McCarthy 2008; Duncan et al. 2011). For particular growth forms, such as woody species, dispersal mode has been suggested to influence urban spread (Aronson et al. 2007; Sullivan et al. 2009) and urban soil seed banks can be limited for native species (Overdyck & Clarkson 2012). Studies have revealed some common traits for those plants which are least successful in urban habitats, such as the combination of short stature and small seeds (Thompson & McCarthy 2008; Duncan et al. 2011). Yet global studies have found inconsistency of traits as predictors between cities and this likely reflects variation in the history and extent of urbanisation (Hahs et al. 2009; Duncan et al. 2011). Hahs et al. (2009) found that the temporal history of urban and/or pre-urban agricultural development and, to a lesser extent, the amount of native vegetation remaining had an influence on urban plant extinction rates. They suggest an extinction debt may occur for decades following urbanisation, particularly for cities without extensive agricultural land transformation prior to urbanisation which initially have high quality vegetation remnants. The temporal delays associated with colonisation and extinction processes (Tilman et al. 1994) may mean that present day trait patterns, particularly in younger cities, are confounded by long-lived relictual species that persist but are destined for extinction as their habitat requirements are no longer met (Vellend et al. 2006; Hahs et al. 2009). In Hamilton City's largest native forest remnant the initial reduction in forest area through milling from 323.7ha to 5.2ha, followed by animal grazing led to many plant species being left with small populations. This resulted in ongoing extinctions decades after grazing ceased, particularly for ground layer shrubs and ferns, as populations were unable to cope with the isolation, desiccation and weed competition associated with fragmentation (Whaley et al. 1997). Thus it is important to additionally investigate morphological traits such as growth form or life form and habitat specialisation (e.g. shade tolerance) which could influence species ability to survive in the urban environment.

Local attributes such as forest patch size, age or edge landuse and the broader landscape configuration operate in tandem with plant traits to filter species composition at a site. Studies of plant traits over larger areas in non-urban forest fragments, with fragments ranging in size from <1ha to >100ha, have suggested that long-distance seed dispersal may be limiting for some groups of forest species, including woody and herbaceous plants with unspecialised or short-distance only dispersal (Herault & Honnay 2005; Aparicio et al. 2008). However, native composition in smaller restored forest patches, those typical of urban areas, may be driven to a greater extent by local factors e.g. increased competition via exotic seed through edge habitat (Cadenasso & Pickett 2001; Devlaeminck et al. 2005) and altered microclimate and seedling establishment conditions (Murcia 1995; White et al. 2009) rather than landscape scale factors (Holl & Crone 2004; Vidra & Shear 2008). The complex urban landscape provides a diversity of native and exotic propagules from residential gardens and park areas (Smith et al. 2006; Vidra & Shear 2008; Kendal et al. 2012). Therefore, determining the importance of distance to and density of desirable native seed sources to maintain native forest regeneration can assist urban restoration efforts (Holl & Crone 2004; Sullivan et al. 2009).

In the present study we aimed to test whether plant traits could predict species groups absent from the Hamilton City urban area and to identify landscape factors within the city associated with increased species richness in forest restoration patches. We assessed which native forest species were currently naturally occurring (not planted) in Hamilton City compared to the wider ecological district species pool, and identified which of these species were arriving (presence in the soil seed bank or annual seed rain) and establishing (presence in understorey vegetation) at urban forest study sites. Species were categorised by a range of life-history traits including morphological (growth form, life form and shade tolerance) and reproductive (pollination vector, dispersal mode and clonality) characteristics. Additionally we investigated whether local landscape factors (patch size, age and adjacent land use and isolation from native seed sources) affected native richness (total and by dispersal mode and pollination vector) and composition of seeds and seedlings in forest patches. We hypothesised firstly that species with unassisted or large animal seed dispersal and shade tolerant late successional species would be limited in the seed supply and understorey of urban study sites and in the Hamilton City species pool; and secondly that larger planting areas, adjacent buffering native vegetation and proximity of native forest remnants would be beneficial for urban native forest species diversity and richness.

4.3 METHODS

4.3.1 Study location

The study was conducted in Hamilton City in the Hamilton Ecological District (McEwen 1987), North Island, New Zealand (Fig. 4.1). The Hamilton Ecological District is an inland basin formed by the historical meanderings of the Waikato River and is surrounded by low sedimentary mountain ranges and several eroded volcanic cones. The natural vegetation of Hamilton Ecological District has been heavily modified by intensive agricultural land use (Nicholls 1976) and currently only 0.2% (368 ha) remains in primary forest cover compared to 12% cover estimated around the time of European settlement in 1840 (Leathwick et al. 1995). Even with the inclusion of secondary and cutover forest still only 1.2% (1,900 ha) of the district is currently forested (Leathwick et al. 1995). Within the Hamilton Ecological District eight forest types have been described, occurring across three main landform units: lowland hill slopes, alluvial plains and gullies (peatlands have been excluded here but would have had forested margins) (Clarkson et al. 2007b). Firstly, the lowland hills and foothills of the surrounding ranges were mainly mixed conifer–hardwood forest, predominantly rimu (*Dacrydium* *cupressinum*[4]) and tawa (*Beilschmiedia tawa*); and some kauri (*Agathis australis*)-hard beech (*Nothofagus truncata*) forest to the north of the district; with pukatea (*Laurelia novae-zealandiae*)-kahikatea (*Dacrycarpus dacrydioides*) forest on poorly drained footslopes of the low hills (no intact remnants remain for the latter type). Secondly, the alluvial plains had kahikatea dominated semi-swamp forest in poorly drained shallow depressions; mixed conifer-hardwood forest on well-drained low mounds; and totara (*Podocarpus totara*)-matai (*Prumnopitys taxifolia*) –kowhai (*Sophora microphylla*) forest on the Waikato river terraces (no intact remnants remain of the latter two types). Thirdly, the gullies had totara-matai-kowhai forest on steep side slopes (no intact remnants remain) and kahikatea-pukatea-swamp maire (*Syzgium maire*) forest on poorly drained gully floors.

Hamilton City is located on the Waikato River in the centre of the Hamilton Ecological District. The city has a population of 203,400 (Statistics New Zealand 2011) and land area of 10,880 ha (Hamilton City Council and Waikato District Council 2005) covering landforms comprised of low hills, alluvial plains, gullies and peatlands (the latter not included in this study) which would have historically been predominantly forested. The city now contains no more than 20 ha of high quality indigenous forest remnants (Clarkson & McQueen 2004), the largest being Claudeland’s Bush a 5.2-ha kahikatea forest (Whaley et al. 1997), with up to 71ha recognised as Key Ecological Sites which are regenerating native vegetation of significant value (Cornes et al. 2012). Urban ecosystem restoration in Hamilton has focused on the numerous, often weed dominated, gully systems (~750ha) that extend from the Waikato River (Downs et al. 2000). 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 restoration plantings established in the urban environment.

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[4] Species nomenclature follows the New Zealand Plant Conservation Network website, accessed February 2013 (www.nzpcn.org.nz).

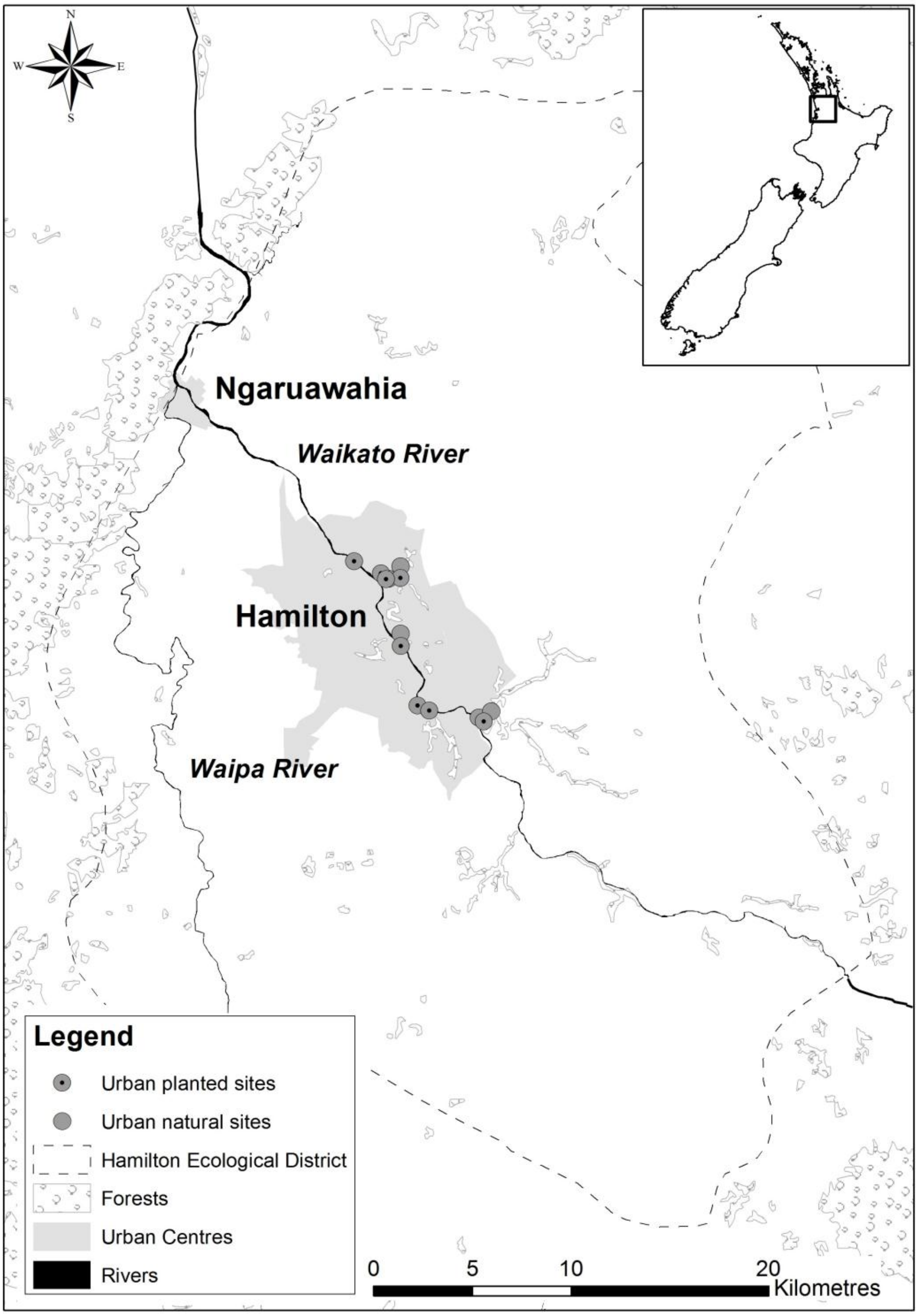


Figure 4.1 Location of Hamilton Ecological District, Hamilton City and urban study sites (north to south). Hamilton City planted forest (dotted circles, *n* = 9): Munro's Esplanade; Tauhara Park (3 sites); Onukutara Gully; Pine Beach; Yendell Park; Dillicar Park; Hammond Park. Hamilton City natural forest (circles, *n* = 4): Mangaiti Gully; Ranfurly Gully; Mangaonua Gully (private); Hammond Park.

4.3.2 Study design

Three species lists were compiled for native forest species, firstly those which occur currently in the Hamilton Ecological District, secondly those which also currently occur within Hamilton City, and thirdly those species that have been recorded in sampling of the soil seed bank, annual seed rain and understorey vegetation of urban forest study sites. The first two lists were compiled from local and regional species lists (de Lange 1996; Whaley et al. 1997; Downs et al. 2000; Clarkson et al. 2002; Clarkson et al. 2007b; Cornes & Clarkson 2010; Cornes et al. 2012) and unpublished data compiled by C. Bryan, F. Clarkson and E. Coleman, University of Waikato. The third list was obtained from field sampling for the present study of both restored and naturally regenerating urban forest patches within Hamilton City. Species were checked against botanical texts and databases to include only records within their naturally occurring range and only species of forest or shrubland habitat were included in analysis (peat bog species were excluded from analysis as this habitat was not sampled in the urban area and has many specialist species not shared with the other main forest types).

Urban forest sampling effort focussed on ten patches of native forest in gullies where Hamilton City Council had undertaken restoration planting with four additional sites in naturally regenerating forest remnants in the city. Restoration plantings were identified that spanned 10–36 years since initial planting date. Restoration sites were chosen for similarity in species composition of initially planted natives, with no remnant native trees and no follow-up enrichment planting. The four sites in natural forest remnants were selected in a similar age group of secondary regenerating forest and with an older mature forest site included (c.120 year old kahikatea dominant patch). All sampling sites were located on gully mid-slopes ranging from 17° to 40°.

4.3.3 Study site vegetation, seed rain and soil seed bank assessment

Vegetation and seed sampling was undertaken in plots located centrally within each forest patch to reduce any edge effects where possible. Vegetation was assessed using a constant-count plot method (Batcheler & Craib 1985) measuring the 30 nearest canopy tree stems to the plot centre 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, and the understorey was assessed by counting of all stems <20 mm dbh and >300 mm height (including lianes) and presence of ground cover vascular species <300 mm in height were listed.

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 and spore rain. Four trays (total area 0.169 m^2) 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 and fern spore bank was sampled to 10 cm depth in September 2006 using the same sized area as the seed rain trays and again at four locations per site (total area 0.169 m^2) 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.

4.3.4 Plant trait classification

Traits were allocated to all species present using categories modified from Aronson et al (2007) and Cornelissen et al. (2003) with the addition of a shade tolerance trait. Species trait information was obtained from published floras and botanical texts (Allan 1961; Moore & Edgar 1976; Brownsey & Smith-Dodsworth 2000; Edgar & Connor 2000; Webb & Simpson 2001; Clarkson et al. 2002) and two online databases: New Zealand Plant Conservation Network, www.nzpcn.org.nz and Landcare Research ecological traits database, www.landcareresearch.co.nz/resources/ data/ ecological-traits-of-new-zealand-flora).

Traits were classified according to the following categories, with only native species of forest habitat included in subsequent analysis:

1. Status (exotic or native)
2. Habitat (forest, shrubland, grassland or wetland)
3. Growth form (forb or herb; fern; graminoid- including grass, sedge and rush; shrub; tree; epiphyte; vine or parasitic)
4. Raunkiaer life form, relating to the position of regenerating tissue or growth buds (phanerophyte >0.5m tall; chamaephyte <0.5m tall; hemicryptophtye with periodic shoot reduction close to ground surface; geophyte with annual reduction below ground; or therophyte with an annual life cycle)
5. Shade tolerance as derived from habitat or successional occurrence (low, moderate or high)
6. Primary pollination vector (abiotic or biotic).
7. Primary seed dispersal mode (unassisted, wind/ water, zoochorous: internal/ external animal or zoochorous+: large internal animal)
8. Clonality or the ability to reproduce vegetatively (non-clonal, clonal aboveground or clonal belowground)

4.3.5 Local landscape factors

GIS mapping and analysis (ARC MAP 10) was used to measure forest patch area, area of contiguous canopy vegetation (adjacent exotic and native vegetation) and edge land use (percentage residential, open parkland, exotic vegetation or native vegetation) for each urban study site. Boundaries and land use types were also verified by ground truthing in the field. To identify areas of native vegetation as seed sources the location of study sites was overlaid with Key Ecological Sites for Hamilton City (Cornes et al. 2012). These key sites are areas of significant natural vegetation comprising predominantly small regenerating forest patches (average size of 0.4ha) along the Waikato River and adjoining gully system and covering 1.5% of the Hamilton City area (excluding peat lake key sites). Two measurements were made using the key sites GIS layer to assess study site isolation. Firstly, the minimum distance from each study site to the nearest key site was measured, and secondly, the proportion of key site area falling within specific radii of the study sites was calculated. Five different sized radii were used initially giving 50m, 100m, 200m, 500m and 1km zones around study sites. The 200m and 500m zones only were retained for further data analysis as the smaller radii did not generally include any key sites and the 1km zone created significant overlap between study sites.

4.3.6 Statistical Analyses

Only native species of forest habitat were included in analyses. Contingency tables and Pearson's chi-squared test were used to determine associations between species' presence at the three locations in all pairwise combinations: Hamilton Ecological District, Hamilton City and study site seed supply and understorey; across six life history traits: growth form, life form, shade tolerance, pollination vector, dispersal mode and clonality. The null hypothesis was that traits would be equally represented at all locations regardless of the number of species present. Bonferroni corrections for significance are indicated with asterisks to adjust for multiple testing within each trait (adjusted P-value 0.05/6 = 0.0083). Linear regression models with stepwise selection were used to investigate relationships between the landscape factors and richness of the urban seed supply (soil seed bank and annual seed rain) and understorey species. To test the effectiveness of animal vector relationships, comparison was also made between the landscape factors and species richness by pollination vector (abiotic and biotic) and also by dispersal mode (unassisted, wind or water, and zoochorous). Permutational multivariate analysis of variance (PERMANOVA) with Sorenson (Bray-Curtis) distances was used to test for relationships between species composition and landscape factors. All data analyses were undertaken using the statistical package R version 2.15.2 (The R Foundation for Statistical Computing 2012).

4.4 RESULTS

4.4.1 Urban representation of district flora

We found that the documented native forest flora of Hamilton City currently represents just over half (57%) the species found in similar habitat types in the broader Hamilton Ecological District (HED) (Table 4.1). Therefore, 148 species potentially found in the urban area prior to human impact are missing. These represent a significant opportunity for greater species diversity in urban forest restoration planting and reintroduction (Appendix 4.1). Within Hamilton City only 68 native forest species in total (35% of the city's forest flora) were assessed as arriving in the seed supply (soil seed bank and annual seed rain) or established in understorey vegetation at ten planted and four natural forest study sites. These species represent only 20% of the HED native forest flora (Table 4.1).

Table 4.1 Native forest species recorded as present in the seed supply (soil seed bank and annual seed rain) or understorey vegetation at all urban study sites (n=14) compared to the total forest flora of Hamilton City and the wider Hamilton Ecological District as assessed from the literature.

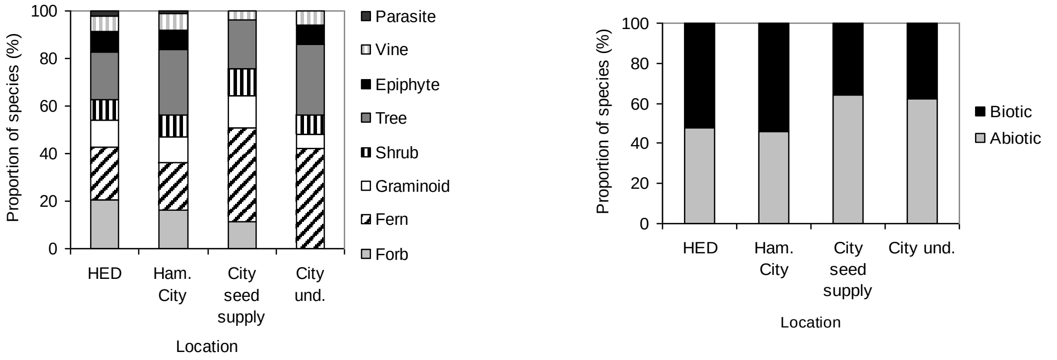
	Location				
	Hamilton Ecological District	Hamilton City	Hamilton study sites		
			Seed supply	Understorey vegetation	Total
No. of Species	343	195	53	50	68
No. of Families	92	74	29	30	36

4.4.2 Plant trait response to fragmentation

Of the six life history traits investigated (Fig. 4.2) growth form, shade tolerance and pollination syndrome were significantly affected by location (Table 4.2, chi-squared $p<0.05$). Life form showed some difference between the HED and Hamilton City, while dispersal and clonality traits were not significantly different between locations.

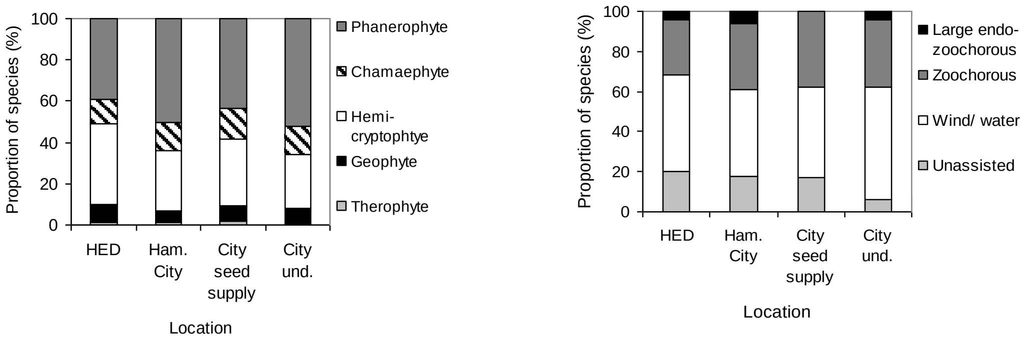
(a) Growth form

(d) Pollination vector



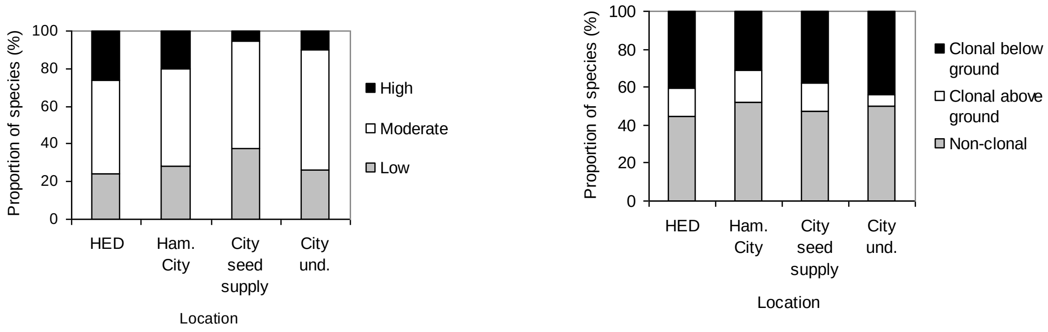
(b) Life form

(e) Dispersal mode



(c) Shade tolerance

(f) Clonality



Figures 4.2. Representation of species (%) amongst six life history traits (a-f) within the native forest flora of Hamilton Ecological District (343 species) and Hamilton City (195 species), and the species present in the seed supply (soil seed bank and annual seed rain) or regenerating in the understorey of Hamilton urban study sites (68 species).

Growth forms were significantly different between the district and the seed supply and understorey of urban study sites (although only the latter group after Bonferroni correction is applied for multiple testing, Table 4.2). The number of forb (herbaceous), epiphyte, vine and parasitic species was disproportionally low in the urban seed supply and understorey compared to the broader district, while ferns were over represented (Fig. 4.2a). A marginally significant difference for growth form between the seed supply and understorey reflects an absence of forbs in the understorey and a greater proportion of tree and fern species, including several epiphytic ferns, compared to the seed supply (Fig. 4.2a). Forb species were also under represented in the whole Hamilton City forest flora (16%) compared with the district (21%) but this was not significant and other growth forms were proportionally represented, except for a greater proportion of trees in the City (27% compared with 20% in the district). Approximately half of the species in the district species pool were classified as having moderate shade tolerance and the remaining species were split evenly as having either low shade tolerance (24%) or high shade tolerance (26%) (Fig. 4.2c). The seed supply particularly but also understorey at study sites showed significant over representation of species with low and moderate shade tolerance when compared to the district and fewer highly shade tolerant species at only 6% for the seed supply and 10% for the understorey (Fig. 4.2c, Table 4.2). The City flora showed the same trend with higher representation of less shade tolerant species (28%) and fewer highly shade tolerant species (20%) but this was not significant. Life form representation was marginally different between Hamilton City and the district (Table 4.2). Phanerophytes (>0.5m tall) formed a larger proportion of the city flora (50%) compared to the district flora (39%) while hemicryptophytes (annual shoot reduction near to the ground surface, e.g. many forbs, ferns and graminoid species) and geophytes (annual reduction to below ground organs, e.g. orchids) had smaller proportions in the city, 29% and 5% respectively, compared to the district, 39% hemicryptophytes and 9% geophytes (Fig. 4.2b).

A higher proportion of abiotic (compared to biotic) pollination vectors were found in the seed supply and understorey (64% and 62% abiotic respectively) of urban study sites compared to both the flora of Hamilton City and the broader district (46% and 47% abiotic respectively) (Fig. 4.2d), although only significant before Bonferroni correction (Table 4.2). Plants with abiotic pollination included all fern and graminoid species while biotic pollinated species included all parasitic species, most forbs and vines, and many trees and shrubs. Although dispersal mode was not found to be significantly affected by location, those species with unassisted dispersal were comparatively underrepresented in the understorey at study sites (6%) compared to the district flora (20%) and the City flora and seed supply (both 17%) (Fig. 4.2e). Wind dispersed species were overly represented in the urban study site seed supply and understorey regeneration particularly, which largely reflects the predominance of fern species. Twelve of fourteen large-seeded (>9mm diameter) endozoochorous (internal animal dispersal) species occurring in the district were represented in the city; however only two of these were recorded as seedlings at study sites (large endozoochorous, Fig. 4.2e). The ability to spread clonally by vegetative reproduction showed no affect of location with 6-17% of species exhibiting above ground clonality and 31-44% with below ground clonality across locations (Fig. 4.2f).

Table 4.2. Pearson's chi-squared test p-values for comparison of trait distributions by location: Hamilton Ecological District (HED), Hamilton City and species present in seed supply and understorey in Hamilton City study sites. Significant p-values<0.05 are indicated in bold type, asterisks indicate significance following Bonferroni correction p<0.0083.

	Morphological traits		
Location	Growth form	Life form	Shade tolerance
HED x Hamilton City x Seed supply x Understorey	**0.0068**	0.3749	**0.0063**
HED x Hamilton City	0.6581	**0.0454**	0.3056
HED x Seed supply	**0.0369**		***0.0030**
HED x Understorey	***0.0024**		**0.0398**
Hamilton City x Seed supply	0.0503		**0.0389**
Hamilton City x Understorey	**0.0131**		0.1847
Seed supply x Understorey	**0.0474**		0.3746

	Reproductive traits		
Location	**Pollination**	**Dispersal**	**Clonality**
HED x Hamilton City x Seed supply x Understorey	**0.0247**	0.1795	0.2005
HED x Hamilton City	0.7652		
HED x Seed supply	**0.0242**		
HED x Understorey	0.0558		
Hamilton City x Seed supply	**0.0169**		
Hamilton City x Understorey	**0.0390**		
Seed supply x Understorey	0.8211		

4.4.3 Local landscape effects on native richness and composition of potentially regenerating species

For the site factors tested (Table 4.3) only site age showed a significant positive linear relationship with the total number of native forest species arriving in the seed supply or establishing in the understorey at study sites (r^2=0.29, $F_{1,12}$=6.297, p=0.0274). This relationship was strongly influenced by a site with c.120 year old naturally regenerating forest which had the highest richness (36 species) while all other sites, less than 36 years old, had a maximum of 31 species. No factors were significant when the oldest site was removed from analysis.

The proportion of Key Ecological Site area within 200m of a site was marginally significant for total native species richness (r^2=0.24, $F_{1,12}$=5.173, p=0.0421). Comparison by dispersal mode revealed that only zoochorous forest species showed a significant increase in richness with a greater proportion of Key Ecological Site area within 200m (r^2=0.58, $F_{1,12}$=18.97, p=0.0009), this was still significant when the older natural site was removed (r^2=0.55, $F_{1,11}$=15.76, p=0.0022). Zoochorous forest species at sites also increased significantly with proximity of the nearest Key Ecological Site (p=0.0415) and with greater adjacent vegetation area (including native and exotic) (p=0.0198), although these factors were not significant when combined in a model with the proportion of Key Ecological Sites within 200m. This suggests correlation of these factors, i.e. canopy vegetation in close proximity to sites is associated with increased nearby Key Ecological Site area. No relationship with site factors was apparent for other dispersal modes or pollination vector. Compared to naturally regenerating sites, the planted sites had lower mean adjacent vegetation area (55,949m^2 compared to 150,490m^2), longer mean distance to key ecological sites (250m compared to 8m) and lower mean proportion of key site area within 200m radius (3% compared to 15%) (Table 4.3).

Table 4.3. Mean and range for species richness variable (richness of native forest species in seed supply and understorey) and local landscape factors tested for 14 urban forest study sites (ten planted and four naturally regenerating).

		Mean	Range
Variables			
	Total species richness	27.6	18 – 37
	Abiotic pollinated species richness	19.9	10 – 30
	Biotic pollinated species richness	6.9	4 – 10
	Unassisted dispersal species richness	1.9	0 – 5
	Wind/ water dispersed species richness	17.9	10 – 26
	Animal dispersed species richness	6.9	5 – 12
Factors			
	Site area (m^2)	2,176.1	216 – 5,155
	Site age (years)	27.4	10 – 120
	Contiguous adjacent vegetation area (m^2)	82,961.0	2,311 – 198,131
	Proportion edge in vegetation (%)	48.9	10 – 90
	Proportion edge in native vegetation (%)	25.0	0 – 80
	Distance to nearest Key ecological site (m)	181.3	0 – 541
	Key ecological site area within 200m (%)	6.3	0 – 23
	Key ecological site area within 500m (%)	3.3	0 – 9

We did not observe any relationship between the local landscape factors measured (Table 4.3) and the composition of native seed supply and understorey species. Species composition was found to be significantly different between urban planted sites and naturally regenerating sites, explaining 14% of variation between sites (PERMANOVA $r^2=0.14$, $F_{1,12}=2.01$, $p=0.042$). However, when the oldest site was removed from analysis the planted or naturally regenerating treatment was no longer significant (PERMANOVA $r^2=0.14$, $F_{1,11}=1.76$, $p=0.069$).

4.5 DISCUSSION

The low representation of the district’s forest flora within Hamilton City indicates that either remaining urban forest habitat is unsuitable for sustaining some species or that species lost through deforestation have been unable to recolonise the urban area. It is likely that both scenarios have contributed to the current depauperate flora of Hamilton City, especially given documented extinctions of species sensitive to the environmental changes associated with forest clearance and urbanisation (Whaley et al. 1997) but also the successful reintroduction of species absent from urban forest patches (Miller 2011). As restoration plantings comprised of early to mid successional canopy species begin to age (10 to 36 years old in this study) it is apparent that natural regeneration, and thus vegetation succession, is currently limited for many native species, including those already present in the urban area. While this study represents a conservative estimate of recolonisation in urban forests it is also likely that a number of long-lived species currently persisting in the urban area will be relictual populations and may be functionally extinct as their habitat requirements for survival are no longer met (Tilman et al. 1994; Vellend et al. 2006; Hahs et al. 2009). In order to support these extant species there is a need to protect and increase the current extent of urban forest and we suggest there is great potential to enhance urban forest composition through trait targeted species reintroductions in restoration projects.

While trait analyses did not support our hypotheses with regard to dispersal mode, the significant discrepancies for several morphological and reproductive traits between the flora of the district and both Hamilton City's flora and species potentially recolonising restored urban forest indicate some groups of species that could be prioritised for restoration. Forb, epiphyte, vine and parasitic species representation was less than expected in the seed supply and understorey at study sites. The latter three groups tend to be associated with late successional forest due to microclimatic preference and host species interactions for structural support or nutrition (Bryan 2011). Forbs were also less frequent in Hamilton City than the district flora. This is consistent with other studies that have found short-statured plants were more likely to go extinct in urban areas (Thompson & McCarthy 2008; Duncan et al. 2011). Studies of larger areas of fragmented forest (Herault & Honnay 2005; Kolb & Diekmann 2005) and a positive relationship reported between plant stature and dispersal ability (Thomson et al. 2011) all suggest that low colonisation ability affects small herbaceous plants following initial forest clearance and fragmentation. Contributing to this there may be a breakdown of urban plant-animal interactions, as pollination and dispersal by animals were common for forbs in this study, and also the altered light, moisture and soil conditions in urban forest habitat (Miller 2011) may favour high-resource demanding exotic forb species rather than native forb groundcover (Herault & Honnay 2005). Trees and phanerophytes, plants over 0.5m tall, as form classes were found to be comparatively well represented in Hamilton City. This could be attributed to longer generation times for taller plants enabling longevity in forest fragments or as isolated specimens even in the absence of regeneration. This notion of relictual populations which may be destined for extinction (Tilman et al. 1994; Vellend et al. 2006) is supported by our finding of only 15 of 53 urban tree species (28%) being recorded as seeds and seedlings in our sampling.

We found that highly shade tolerant or late successional forest species were not well represented at study sites or in Hamilton City and particularly many forb, fern and epiphyte species may require reintroduction through enrichment planting or seed-sowing. Highly shade tolerant species could be described as forest specialists and may be more vulnerable to disturbance, such as fragmentation, than species with more generalist light requirements (Mabry & Fraterrigo 2009). Shade tolerance may also be coupled with a preference for soil and microclimatic conditions typical of mature forest (Herault & Honnay 2005) which may limit successful establishment for these species in the early stages of restoration (McClain et al. 2011). Although, in Hamilton City the initial establishment of late successional species from direct seeding (Overdyck et al. 2013) and planting seedlings (Miller 2011) in relatively young (between 10 and 30 year old) urban forests can be achieved. We also identified several shade intolerant species that no longer occur naturally in Hamilton City and their use in initial restoration plantings could increase diversity through use of a wider range of growth forms besides shrub and tree species and this may help to limit groundcover weed infestations during the early stages of planting (Vidra et al. 2007; Overdyck & Clarkson 2012).

Finding two thirds of the species regenerating at study sites with abiotic pollination vectors compared to only half of the district species could indicate reduced reproductive success for animal-pollinated species in these urban forests. While the floral morphology of many native forest plants suggests insect pollination is common (Newstrom & Robertson 2005), in New Zealand birds may contribute considerably to their pollination as well and are regarded as the primary pollinators for several species with larger flowers (Anderson 2003). Reduced numbers of tui (*Prosthemadera novaeseelandiae*) and only recently reintroduced bellbird (*Anthornis melanura*) in Hamilton City, and the absence of stitchbird (*Notiomystis cincta*), could limit pollination for some long-tubed flowers (e.g. *Sophora microphylla*, *Fuchsia excorticata* and *Rhabdothamnus solandri*) while the more recently self-introduced silvereye (*Zosterops lateralis*) is likely to be the predominant bird pollinator otherwise (Kelly et al. 2006). Common insect visitors to native flowers include Hymenoptera (native bees and introduced honeybees, bumblebees and wasps), Coleoptera (beetles), Diptera (flies) and Lepidoptera (butterflies and moths) with the former two groups being observed to be comparatively more effective pollen bearers for native flowering trees (Anderson 2003; Kelly et al. 2006). The nature of specialisation in insect pollinator relationships with the native flora is poorly understood (Newstrom & Robertson 2005) making the impact of forest fragmentation on pollination rates difficult to ascertain, a knowledge gap of emerging importance for restoration projects worldwide (Dixon 2009). Specialist mutualisms such as pollination by the native bat of the scrambling vine *Freycinetia banksii*, which was not recorded in urban seed supply or understorey (and also the root parasite *Dactylanthus taylorii* now extinct in the district) would limit seed production to small pockets of the urban area where bats are known to occur (Kelly et al. 2006). Our study suggests that animal-plant pollination relationships may suffer some limitations in urban forest patches, such as reduced pollinator diversity, but further investigation is needed.

Seed dispersal mode has not shown a consistent relationship to disturbance or forest fragmentation in previous urban studies (Duncan & Young 2000; Thompson & McCarthy 2008) and no clear trend has emerged in this study either. Herault and Honnay (2005) found the group of forest forbs most affected by fragmentation were perennials exhibiting unassisted dispersal, but the present study found that forbs with wind, water and animal dispersal were just as poorly represented in urban forest. We found little evidence to support the hypothesis of dispersal limitation for species with apparently unassisted seed dispersal. Species with unassisted dispersal were least represented in the understorey sampling but their presence in the seed supply suggests conditions merely may not be favourable currently for germination or establishment in regenerating urban forest. It may be a false assumption to attribute short distance dispersal to these generally small-seeded species, which may form soil seed banks or be transported inadvertently in soil by humans or other animals (Bakker et al. 1996; Fenner & Thompson 2005). Plants with seeds dispersed by animals are proportionally well represented in the urban area compared to the district, although large-seeded fruits were not common at study sites suggesting they may well be limited by the reduced abundance of large native birds in the urban area (Wunderle Jr. 1997; Cramer et al. 2007). Small-fruited plants are likely being dispersed adequately by small introduced birds within the city (Day 1995), although still we have found that 35 zoochorous species were absent from urban forest and their recolonisation from the district may be limited by substantial forest clearance beyond the urban area (Leathwick et al. 1995).

Of the local landscape factors investigated we found some evidence of patch isolation negatively affecting recolonisation for zoochorous species. Increased native vegetation cover within 200m radius, area of adjacent canopy vegetation (native or exotic) and proximity of the nearest Key Ecological Site all positively influenced the arrival and regeneration of zoochorous native species. Other dispersal modes and pollination vector were not significantly affected by landscape factors. This supports the role of native vegetation cover as a corridor for bird and other animal movements (Tremblay & St Clair 2009) and the importance of restoring networks such as the Waikato River gully system both within and beyond the urban area (Clarkson et al. 2007a). The lack of significant influence for other local landscape factors on propagules arriving and regenerating at sites may be due to the young age (<36 years old) of the restoration sites and their comparatively small size (Holl & Crone 2004). In a study of urban forest fragments in Sydney, Australia Drinnan (2005) found that for fragments less than 2ha in size plant species richness declined rapidly, a threshold well above the maximum size of restoration plantings in the present study (0.52ha). Low forest species richness in the present study suggests regeneration in all urban study sites may be limited due to the large (>10km) distance to intact mature forest beyond the urban area. We identified and mapped Key Ecological Sites within the city as sources of propagules for native forest species, yet many of these sites are themselves early successional or small forest remnants (Cornes et al. 2012) and our inability to accurately map all native seed sources in the urban matrix (Bastin & Thomas 1999) could contribute to difficulty in explaining variability in species richness (Holl & Crone 2004). The few older remnant urban forests may retain some species of mature forest but these may take longer than several decades to re-establish at restoration sites following the development of forest soil and microclimate conditions (Herault & Honnay 2005). A significant positive effect of site age in this study was driven by one older naturally regenerating site (~120 year old) that showed notably higher species richness. Thus, time since planting may be an important factor for the re-establishment of many species but on a greater timescale than the chronosequence of restoration sites studied here (Honnay et al. 2002). Similarly to Holl and Crone (2004) we have found that island biogeography theory that predicts increased richness with patch size and age has limited application in the early stages of urban restoration given that patches are not entirely isolated (e.g. species occur elsewhere in the landscape such as parks, gardens) and the low range in size and age for patches. Bastin and Thomas (1999) found that individual species urban distributions could be explained reasonably by habitat age, size and density of available habitat but when analysing total species richness relationships were weakened due to individual species traits.

In conclusion, low representation of the regional native forest species pool within the urban area indicates reduced survival and recolonisation of forest species from beyond the urban area. Absent species, and those present but with little apparent regeneration, are suggested as targets for restoration as an effective way to increase urban forest species diversity and ecosystem function. The identification of life history traits adversely affected by urbanisation and fragmentation of habitat has surprisingly shown little effect of species dispersal ability, although, native richness of animal-dispersed species showed benefits from adjacent vegetated ‘green corridors’ within the city. Many shade tolerant species of late successional forest, including several large-seeded endozoochorous species, will require reintroduction due to absence or reduced regeneration in the urban area. Animal-pollinated species may have reduced regeneration in urban forest and further investigation of specialist pollinator relationships could contribute to the long-term sustainability of restoration efforts. The presence and recolonisation of small herbaceous plants appears to be more negatively affected by forest clearance and urbanisation than that of taller plants. The lack of relationship between current landscape vegetation patterns and species richness may be skewed by lagging present day estimates of species presence in forest patches that do not represent future stable populations. There was also no accounting for the contribution of native species in the urban matrix which were not quantified (e.g. residential gardens). Unfortunately, due to long generation times some trees and long-lived species which currently persist may represent an extinction debt within the city flora that could lead to extinction time lags on the order of decades or even centuries. Optimistically, this time lag also represents an opportunity to prevent extinctions by restoring forest habitat to ameliorate negative environmental affects while enriching species diversity through reintroductions. Management through maintaining the quality of and expanding linkages for existing forest is necessary both within Hamilton City, e.g. the gully system already recognised as important by private and public landowners, and beyond the urban area, e.g. Waiwhakareke Natural Heritage Park restoration on the outskirts on Hamilton City (Clarkson et al. 2012). Along with the reintroduction of absent species, particularly those with vulnerable traits as identified above, active restoration can provide more ecologically functional forest habitat and facilitate future natural recolonisation.

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APPENDIX 4.1

Species of the Hamilton Ecological District absent from Hamilton City, with potential for restoration in Hamilton City forest patches in early successional stages (low shade tolerance) and mid-late successional stages (moderate and high shade tolerance). Dispersal modes are U=unassisted, W/W=wind or water, Z=zoochorous (animal), Z+=large endozoochorous (internal animal, seed >9mm).

Growth form *Species*	**Family**	**Successional stage**	**Pollination vector**	**Dispersal mode**
Forb				
Acaena anserinifolia	Rosaceae	moderate	biotic	U
Acianthus sinclairii	Orchidaceae	high	biotic	W/W
Astelia trinervia	Asteliaceae	high	biotic	Z
Corybas acuminatus	Orchidaceae	high	biotic	W/W
Corybas cheesemanii	Orchidaceae	high	biotic	W/W
Dichondra repens	Convolvulaceae	low	biotic	U
Diplodium alobulum	Orchidaceae	moderate	biotic	W/W
Diplodium trullifolia	Orchidaceae	moderate	biotic	W/W
Galium propinquum	Rubiaceae	moderate	biotic	U
Galium trilobum	Rubiaceae	moderate	biotic	U
Geranium potentilloides	Geraniaceae	low	biotic	U
Hydrocotyle dissecta	Araliaceae	low	biotic	U
Hydrocotyle elongata	Araliaceae	moderate	biotic	U
Hydrocotyle novae-zeelandiae	Araliaceae	moderate	biotic	U
Lagenifera pumila	Asteraceae	moderate	biotic	W/W
Leptinella squalida	Asteraceae	moderate	biotic	W/W
Leptostigma setulosa	Rubiaceae	moderate	abiotic	Z
Libertia grandiflora	Iridaceae	low	biotic	U
Libertia ixioides	Iridaceae	low	biotic	U
Mazus novaezeelandiae	Phrymaceae	low	biotic	U
Microtis parviflora	Orchidaceae	low	biotic	W/W
Nematoceras orbiculatum	Orchidaceae	low	biotic	W/W
Nematoceras rivulare	Orchidaceae	high	biotic	W/W
Nertera ciliata	Rubiaceae	high	biotic	Z
Nertera depressa	Rubiaceae	high	biotic	Z
Nertera dichondrifolia	Rubiaceae	high	biotic	Z

Oxalis magellanica	Oxalidaceae	high	biotic	U
Petalochilus aff. carneus	Orchidaceae	moderate	biotic	W/W
Petalochilus chlorostylus	Orchidaceae	moderate	biotic	W/W
Petalochilus iridescens	Orchidaceae	moderate	biotic	W/W
Pterostylis agathicola	Orchidaceae	high	biotic	W/W
Pterostylis banksii	Orchidaceae	high	biotic	W/W
Pterostylis cardiostigma	Orchidaceae	high	biotic	W/W
Pterostylis foliata	Orchidaceae	moderate	biotic	W/W
Pterostylis graminea	Orchidaceae	high	biotic	W/W
Pterostylis montana	Orchidaceae	high	biotic	W/W
Ranunculus reflexus	Ranunculaceae	high	biotic	U
Stellaria decipiens	Caryophyllaceae	moderate	biotic	U
Wahlenbergia violacea	Campanulaceae	low	biotic	U
Fern				
Abrodictyum elongatum	Hymenophyllaceae	high	abiotic	W/W
Abrodictyum strictum	Hymenophyllaceae	high	abiotic	W/W
Adiantum diaphanum	Pteridaceae	moderate	abiotic	W/W
Adiantum fulvum	Pteridaceae	high	abiotic	W/W
Adiantum viridescens	Pteridaceae	moderate	abiotic	W/W
Anarthropteris lanceolata	Polypodiaceae	high	abiotic	W/W
Asplenium appendiculatum	Aspleniaceae	moderate	abiotic	W/W
Asplenium hookerianum	Aspleniaceae	moderate	abiotic	W/W
Asplenium lamprophyllum	Aspleniaceae	high	abiotic	W/W
Blechnum fraseri	Blechnaceae	moderate	abiotic	W/W
Blechnum nigrum	Blechnaceae	high	abiotic	W/W
Blechnum penna-marina	Blechnaceae	moderate	abiotic	W/W
Blechnum vulcanicum	Blechnaceae	moderate	abiotic	W/W
Botrychium biforme	Ophioglossaceae	high	abiotic	W/W
Cardiomanes reniforme	Hymenophyllaceae	moderate	abiotic	W/W
Doodia mollis	Blechnaceae	moderate	abiotic	W/W

Doodia squarrosa	Blechnaceae	moderate	abiotic	W/W
Gleichenia microphylla	Gleicheniaceae	moderate	abiotic	W/W
Grammitis ciliata	Grammitidaceae	high	abiotic	W/W
Grammitis patagonica	Grammitidaceae	high	abiotic	W/W
Hymenophyllum cupressiforme	Hymenophyllaceae	high	abiotic	W/W
Hypolepis lactea	Dennstaedtiaceae	moderate	abiotic	W/W
Hypolepis rufobarbata	Dennstaedtiaceae	moderate	abiotic	W/W
Lastreopsis velutina	Dryopteridaceae	moderate	abiotic	W/W
Leptolepia novae-zelandiae	Dryopteridaceae	high	abiotic	W/W
Leptopteris hymenophylloides	Osmundaceae	high	abiotic	W/W
Lindsaea linearis	Dennstaedtiaceae	moderate	abiotic	W/W
Lindsaea trichomanoides	Dennstaedtiaceae	high	abiotic	W/W
Lycopodium deuterodensum	Lycopodiaceae	moderate	abiotic	W/W
Lycopodium volubile	Lycopodiaceae	moderate	abiotic	W/W
Polyphlebium endlicherianum	Hymenophyllaceae	high	abiotic	W/W
Polystichum silvaticum	Dryopteridaceae	high	abiotic	W/W
Polystichum wawranum	Dryopteridaceae	moderate	abiotic	W/W
Ptisana salicina	Marattiaceae	high	abiotic	W/W
Sticherus cunninghamii	Gleicheniaceae	moderate	abiotic	W/W
Sticherus flabellatus	Gleicheniaceae	moderate	abiotic	W/W
Graminoid				
Carex dipsacea	Cyperaceae	moderate	abiotic	U
Carex fascicularis	Cyperaceae	moderate	abiotic	U
Carex flagellifera	Cyperaceae	moderate	abiotic	U
Carex forsteri	Cyperaceae	high	abiotic	U
Carex lessoniana	Cyperaceae	moderate	abiotic	U
Carex ochrosaccus	Cyperaceae	moderate	abiotic	U
Carex sinclairii	Cyperaceae	moderate	abiotic	U
Carex testacea	Cyperaceae	moderate	abiotic	U
Gahnia lacera	Cyperaceae	low	abiotic	U
Gahnia pauciflora	Cyperaceae	moderate	abiotic	U

Gahnia setifolia	Cyperaceae	low	abiotic	U
Isolepis pottsii	Cyperaceae	moderate	abiotic	Z
Luzula picta	Juncaceae	low	abiotic	U
Microlaena polynoda	Poaceae	moderate	abiotic	U
Rytidosperma gracile	Poaceae	moderate	abiotic	W/W
Schoenus tendo	Cyperaceae	moderate	abiotic	Z
Tetraria capillaris	Cyperaceae	moderate	abiotic	W/W
Uncinia ferruginea	Cyperaceae	moderate	abiotic	Z
Uncinia laxiflora	Cyperaceae	moderate	abiotic	Z
Shrub				
Coprosma crassifolia	Rubiaceae	moderate	abiotic	Z
Coprosma rigida	Rubiaceae	moderate	abiotic	Z
Gaultheria antipoda	Ericaceae	moderate	biotic	Z
Helichrysum lanceolatum	Asteraceae	low	biotic	U
Olearia furfuracea	Asteraceae	low	biotic	W/W
Olearia virgata	Asteraceae	low	biotic	W/W
Pomaderris kumeraho	Rhamnaceae	low	biotic	U
Pseudowintera axillaris	Winteraceae	high	biotic	Z
Pseudowintera colorata	Winteraceae	moderate	biotic	Z
Raukaua anomalus	Araliaceae	low	biotic	Z
Urtica ferox	Urticaceae	moderate	biotic	U
Tree				
Alseuosmia macrophylla	Alseuosmiaceae	high	biotic	Z
Beilschmiedia tarairi	Lauraceae	high	biotic	Z+
Carmichaelia australis	Fabaceae	low	biotic	U
Coprosma arborea	Rubiaceae	moderate	abiotic	Z
Dysoxylum spectabile	Meliaceae	high	biotic	Z+
Entelea arborescens	Malvaceae	low	biotic	Z
Libocedrus plumosa	Cupressaceae	low	abiotic	W/W
Lophomyrtus obcordata	Myrtaceae	low	biotic	Z
Myrsine salicina	Primulaceae	moderate	biotic	Z
Neomyrtus pedunculata	Myrtaceae	moderate	biotic	Z
Nestegis montana	Oleaceae	moderate	biotic	Z

Nothofagus truncata	Nothofagaceae	moderate	abiotic	W/W
Podocarpus hallii	Podocarpaceae	moderate	abiotic	Z
Raukaua edgerleyi	Araliaceae	moderate	biotic	Z
Toronia toru	Proteaceae	moderate	biotic	Z
Epiphyte				
Brachyglottis kirkii var. kirkii	Asteraceae	high	biotic	W/W
Notogrammitis heterophylla	Grammitidaceae	high	abiotic	W/W
Grammitis billardierei	Grammitidaceae	high	abiotic	W/W
Huperzia varia	Lycopodiaceae	high	abiotic	W/W
Hymenophyllum demissum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum dilatatum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum flexuosum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum multifidum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum rarum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum revolutum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum sanguinolentum	Hymenophyllaceae	high	abiotic	W/W
Hymenophyllum scabrum	Hymenophyllaceae	high	abiotic	W/W
Ichthyostomum pygmaeum	Orchidaceae	moderate	biotic	W/W
Pittosporum cornifolium	Pittosporaceae	low	biotic	Z
Vine				
Clematis cunninghamii	Ranunculaceae	low	biotic	W/W
Clematis foetida	Ranunculaceae	low	biotic	W/W
Clematis forsteri	Ranunculaceae	low	biotic	W/W
Fuchsia perscandens	Onagraceae	moderate	biotic	Z
Lygodium articulatum	Schizaeaceae	moderate	abiotic	W/W
Metrosideros albiflora	Myrtaceae	moderate	biotic	U
Metrosideros carminea	Myrtaceae	moderate	biotic	U

Parsonsia capsularis	Apocynaceae	low	biotic	W/W
Rubus cissoides	Rosaceae	low	biotic	Z
Parasitic				
Danhatchia australis	Orchidaceae	high	biotic	W/W
Gastrodia cunninghamii	Orchidaceae	high	biotic	W/W
Gastrodia minor	Orchidaceae	moderate	biotic	W/W
Ileostylus micranthus	Loranthaceae	low	biotic	Z
Korthalsella salicornioides	Viscaceae	low	biotic	Z

5 TESTING BROADCAST SEEDING METHODS TO RESTORE URBAN FORESTS IN THE PRESENCE OF SEED PREDATORS[5]

5.1 ABSTRACT

Forest restoration in urban areas often occurs in isolation from remnant forest, limiting the chances for recolonization by native species. Plants with bird-dispersed seeds can be particularly vulnerable to dispersal limitation and regeneration can be further impeded by non-native seed predators. We used a factorial experiment to investigate broadcast seeding as a method to reintroduce trees with large seeds and fleshy fruits into early successional forests. We assessed rates of seed and fruit loss, germination and seedling establishment in three seed treatments: 1) caging to exclude introduced mammalian seed predators; 2) removal of fleshy fruit pericarp; and 3) placing seeds in nutritionally enriched clay balls. Across all species (*Beilschmiedia tawa*, *Elaeocarpus dentatus* and *Litsea calicaris*) seeds and fruits accessible to mammalian predators suffered significantly greater loss (58%) than those protected by cages (4%). However, seed and fruit loss in the presence of predators was reduced to only 35% across all species by the treatment combining the removal of fruit flesh and clay ball application to seeds. Establishment of *B. tawa* seedlings after one year was significantly enhanced by the clay ball treatment (12% of seeds sown vs. 6% without clay balls). Very low establishment rates were recorded for *E. dentatus* and *L. calicaris*. Broadcast seeding was found to be a viable method of improving regeneration of large-seeded late successional trees and may be a cost-effective alternative to planting saplings. Seedling establishment can be improved with fruit flesh removal and clay ball treatments, especially in the presence of mammalian seed predators.

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Key words avian seed dispersal, enrichment planting, forest succession, seed balls, small mammal predation, urban restoration

5.2 INTRODUCTION

Extensive forest loss and habitat fragmentation necessitates active restoration to extend existing native forest networks and conserve biodiversity (Honnay et al. 2002; Ewers et al. 2006). Restoring forests in urban areas contributes to redressing forest loss in some of the most intensively developed landscapes (Miller & Hobbs 2002; Clarkson et al. 2007), yet isolation from remnant forest seed sources and the presence of seed predators may limit natural vegetation succession (Doust 2011; McConkey et al. 2012).

Large-seeded species dispersed by animals are particularly vulnerable to dispersal limitation in fragmented forest habitats due to reduced animal populations and movements (Cramer et al. 2007). Island biotas in particular have been impacted by non-native small mammals through nest predation of avian frugivores (Towns et al. 2006; Innes et al. 2010) and also the destruction of seeds (Grant-Hoffman & Barboza 2010). For tree species with large fruits that rely on few avian species for the dispersal of seeds away from parent trees (Meehan et al. 2002; Kelly et al. 2010) seed predation compounds the effect of dispersal limitation on seedling recruitment (Chimera & Drake 2011; Wotton & Kelly 2011). In urban areas, lack of forest habitat and food sources for native birds may result in only seasonal visitation by small numbers of birds and reduced seed dispersal services for large-seeded species (van Heezik et al. 2008; Garcia et al. 2010).

Dispersal limitation necessitates regeneration enrichment for some later successional species to restore native vegetation communities where pioneer species have been planted (McClain et al. 2011). Broadcast seeding, i.e. placing seeds on the surface of the ground, potentially offers a time and cost-effective alternative to enrichment planting on a large scale (Cole et al. 2011) and may be suited to mid- to late-successional forest species once a canopy has established (Bonilla-Moheno & Holl 2010). Simple broadcast seeding methods may be enhanced by treating seeds to mimic animal gut passage, such as removing fruit flesh or scarification of the seed coat to increase germination success (Robertson et al. 2006). Additionally, burying seeds can counter desiccation stress, increase seedling establishment rates and reduce seed predation (Doust et al. 2006; Garcia-Orth & Martínez-Ramos 2008) but considerably increases time and effort. An alternative to seed burial is placing seeds in a small clay and compost ball to provide protection from predators and a nutritious medium for seedling establishment (Fukuoka 1978). The use of dried clay balls in broadcast seeding has potential application in restoration (Clarkson 2005; Lucas 2011), but so far as we are aware has not previously been applied to large seeds.

In this study we simulated broadcast seeding with a field experiment testing whether seedling establishment in three large-seeded native species was enhanced by any combination of three seed treatments: 1) caging to exclude introduced mammalian seed predators; 2) removal of fleshy fruit pericarp; and 3) application of a nutritionally enriched clay ball around individual seeds or fruits. We hypothesized that seedling establishment would be greatest when protected from small mammal predation and when fruits were treated to simulate bird gut passage and burial.

5.3 METHODS

5.3.1 Study sites

Field trials were undertaken at two planted urban restoration sites in Hamilton City, New Zealand (37°47′S, 175°19′E) and two nearby naturally regenerating rural sites. Hamilton City sits in an inland basin surrounded by low sedimentary hills and ranges, up to 500 m elevation, with the Waikato River running centrally through the city. Soils of the Waikato region are variously alluvial, peaty and volcanic, with several eroded andesitic cones (McCraw 2002). Primary forest of the region is mixed conifer-angiosperm forest, mainly *Dacrydium cupressinum-Beilschmiedia tawa* forest on the lowland hills and *Dacrycarpus dacrydioides* conifer forest on poorly drained alluvial sites (Nicholls 1976). The region has a temperate, humid climate, with a mean annual rainfall of 1186 mm (MetService 2011). The two urban study sites were located on moderate slopes in restoration plantings aged 12 and 25 years, within Tauhara Park (planted area 0.23 ha) and Hammond Park (planted area 0.13 ha) respectively. Both parks include approximately 1.5 ha of remnant gully systems containing a mix of original and planted native vegetation, open park areas and unmanaged weed infestations (Clarkson & McQueen 2004). The two rural sites were located in c.30 year old regenerating vegetation adjoining mature forest on the lower slopes of the Hakarimata Range (1811 ha) 10 km northwest of Hamilton City and Mt Maungatautari (3,400 ha) 35 km southeast of the city; the latter site was included as a reference for the caging treatment being in a large fenced enclosure free of mammalian predators (80 ha). The canopy at all sites comprised various mixes of early successional native species.

5.3.2 Study species

We studied three endemic, evergreen angiosperm tree species each with large drupes (single-seeded, fleshy fruits) typically greater than 10 mm diameter (Appendix 5.1). The study species, *B. tawa* (tawa), *Litsea calicaris* (mangeao) and *Elaeocarpus dentatus* (hinau), are found in lowland native forest in the North Island and northern South Island of New Zealand (*L. calicaris* North Island only). Lowland forest has suffered nationwide range contraction due to clearance for agriculture and in the Waikato region is now confined to many small forest remnants and the slopes of several low mountains and ranges (Burns & Smale 2002). Within Hamilton City mature *B. tawa* can be found in several remnant forest patches greater than 1 ha in size, including Hammond Park, while *L. calicaris* and *E. dentatus* now only exist as a few solitary specimens (Downs et al. 2000).

5.3.3 Pre-sowing seed treatments

Ripe fruits were collected from the ground in forest as close to the study sites as possible. A random subset of fruits had the fleshy pericarp removed by soaking them overnight in water then gently rubbing them by hand on a steel mesh sieve. The clay covering comprised a mix of dry red clay, dry commercial organic compost and water at ratio of 5:3:1. The moist clay mix was applied to the outside of a random subset of individual seeds and fruits (2-5 mm deep), and rolled briefly by hand to ensure bonding of the clay. Clay balls were air dried for 24 hrs before being placed out in the field. Fruits and seeds were sown within 7 days of collection (fruits were stored at 4°C) in the order: *B. tawa* February 2008, *E. dentatus* April 2008 and *L. calicaris* December 2008. Cages measuring 0.5 x 0.5

m by 0.2 m height were constructed using 6 x 25 mm green-coated welded steel mesh over a timber frame; a mesh lip extended 0.15 m from the base and was pegged flat to the ground to exclude mammalian seed predators.

5.3.4 Experimental Design

A factorial design was used with all combinations of the three seed treatments: 1) caged versus uncaged; 2) fruit flesh intact versus flesh removed; and 3) clay ball versus no clay ball. At four sites we established three paired replicates of adjacent caged and uncaged treatments. Each of the four fruit flesh and clay ball combinations were laid out systematically in a grid using five, four or two seeds per treatment for *B. tawa*, *E. dentatus* and *L. calicaris* respectively (seed numbers for the latter two were constrained by low availability during collection). Individual seeds and fruits were placed on the litter surface within 50 x 50 x 10 mm height plastic grid squares, which were fixed to the ground to reduce seed loss from rolling and allow tracking of individual seed fates (Appendix 5.2).

5.3.5 Data collection

Seed or fruit presence, predation (assessed as mammalian, insect or other), germination and seedling survival were recorded every 2 to 3 weeks for 2 months after placement in the field and thereafter at 7 to 10 weekly intervals. The experiment proceeded for 57 weeks for *B. tawa*, 50 weeks for *E. dentatus* and 14 weeks for *L. calicaris* (later timing of seed ripening necessitated the shorter time period for the latter two species). Seeds or fruits found outside of the grid were returned to the grid for continued monitoring and any predation was recorded. Germination of *B. tawa* was recorded from May 2008 to March 2009. Seedlings of *E. dentatus* and *L. calicaris* were only observed on a revisit in March 2011, 2 years after the main experiment was completed.

5.3.6 Seed predator presence

Introduced ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*) and brushtail possums (*Trichosurus vulpecula*) are present in forest remnants within Hamilton City and in the surrounding rural area (Morgan et al. 2009). Mice (*Mus musculus*) are also present but they tend to consume only smaller seeds (Williams et al. 2000). No regular predator control had been undertaken at urban Tauhara Park and despite intermittent mammalian predator control at urban Hammond Park and rural Hakarimata predator populations at these sites had reestablished from adjacent areas prior to the study (Appendix 5.3). The rural Maungatautari site was fenced in 2004 (Xcluder Pest Proof Fencing, Rotorua, N.Z.) with the eradication of all mammalian predators completed in 2005.

5.3.7 Statistical analyses

Sample units were defined as the proportion of seeds or fruits within each grid (three replicates/ species/ treatment/ site). Only the three sites with predators present were included in statistical tests and graphs while data from the predator-free site is presented as a best-case reference scenario. Seed loss was used as an index of post-dispersal seed predation and describes those seeds or fruits missing from grids including those found again nearby with mammalian predation damage (rat and possum bite marks). This may slightly overestimate actual predation but is supported in this study by very low seed loss when predators were excluded. Some seeds may have been washed away or become obscured, although no germination occurred in grid cells where seeds had been previously recorded as lost. Seed-hoarding or caching behavior (Vander Wall et al. 2005) has not been documented for possums (Nugent et al. 2000) and although rats may move seeds or fruits to shelter for feeding there is little likelihood of larger seeds removed remaining intact (Williams et al. 2000), in contrast to smaller seeds which may survive gut passage (Shiels & Drake 2011). Seed loss data was analyzed at 16 weeks to include complete datasets for all three study species and 84% of total seed loss (up to 57 weeks) had occurred by this time. Analysis of variance (ANOVA) (Statistica 9, Stat Soft Inc) was used to test for treatment effects on seed loss including five factors and their interactions: species, site (with predators only), caging, flesh removal and clay ball.

Beilschmiedia tawa was the only species that produced enough germinants for further analyses. However, small sample sizes due to the reduced number of uncaged replicates after seed loss limited testing for treatment effects on germination after seed loss and survival of those germinants. We used ANOVA to test treatment effects on *B. tawa* seedling establishment after 12 months as a proportion of all seeds sown. Four factors and their interactions were included:

site (with predators only), caging, flesh removal and clay ball. Post hoc Tukey HSD pairwise comparisons were used where significant treatment effects were detected.

5.4 RESULTS

5.4.1 Seed Loss

In the presence of mammalian seed predators (uncaged treatment) high seed loss was recorded for each species within the first three weeks of the field experiment, ranging from 29 to 37% of seeds and fruits (Fig. 5.1). Uncaged seed loss continued throughout the study, though at a slower rate beyond 16 weeks for *Beilschmiedia tawa* and *Elaeocarpus dentatus*. With no predator access (caged treatment) seed loss was very low, occurring occasionally throughout the experiment (Fig. 5.1).

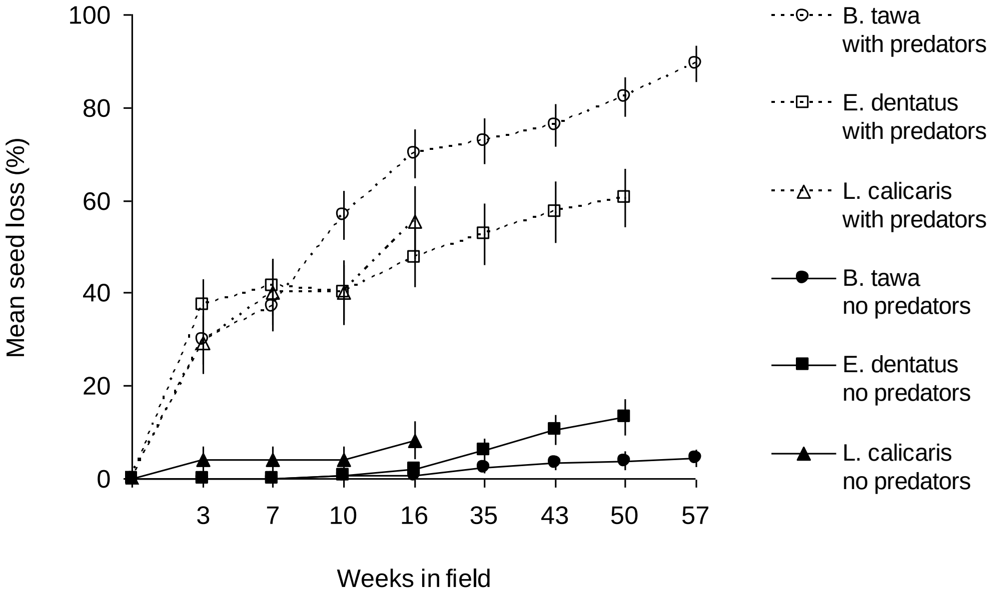

Figure 5.1 Cumulative seed (and fruit) loss including mammalian predation (mean ± SE, *n*=36) for *Beilschmiedia tawa*, *Elaeocarpus dentatus* and *Litsea calicaris*, with predator access (uncaged treatment) and no predator access (caged treatment) at one rural and two urban sites. Species start dates have been standardized to time zero although start dates in the field were staggered due to the timing of seed collection, experiment length was shortened accordingly for the species collected later.

There was no effect of site and a marginal effect of species on mean seed loss by 16 weeks in the field (Table 5.1). Average loss of uncaged seeds and fruits of all species (57.8% ± 3.9; mean ± standard error, hereafter) was significantly greater than that of caged seeds and fruits (3.7% ± 1.5, Table 5.1). Some significant interactions between caging, species and site factors were found reflecting some site specific variation and variable magnitude in the caging effect on seed loss between sites and species (Appendix 5.4).

Table 5.1 ANOVA results reporting the effects of species, site and three seed treatments and their interactions on mean seed loss (including mammalian seed predation) during a 16 week period. Three study species (*Beilschmiedia tawa*, *Elaeocarpus dentatus* and *Litsea calicaris*) have been combined from one rural and two urban sites, all with mammalian predators present. Significant effects are indicated in bold type and only significant interactions are shown.

Predictor	***SS***	***df***	***MS***	r^2	***F***	***p***
Species	4016.9	2	2008.4	0.0071	3.0455	0.0507
Site	2530.8	2	1265.4	0.0045	1.9187	0.1505
Caging	158166.8	1	158166.8	0.2799	239.8317	**<0.0001**
Flesh removal	7061.2	1	7061.2	0.0125	10.7071	**0.0013**
Clay ball	6176.0	1	6176.0	0.0109	9.3649	**0.0026**
Caging*Flesh removal	8127.9	1	8127.9	0.0144	12.3245	**0.0006**
Caging*Species	6361.3	2	3180.7	0.0113	4.8229	**0.0094**
Caging*Site	6211.3	2	3105.7	0.0110	4.7092	**0.0104**
Species*Site	30529.6	4	7632.4	0.0540	11.5732	**<0.0001**
Cage*Site*Species	16340.7	4	4085.2	0.0289	6.1945	**0.0001**
Error	94966.7	144	659.5			

Both flesh removal and clay ball application had significant treatment effects on seed loss by 16 weeks (Table 5.1). The effect of flesh removal treatment was modified by an interaction with caging as only the uncaged treatment had lower seed loss when fruit flesh was removed (45.9% ± 5.3) compared to intact fruits (69.6% ± 5.3). Seed loss was significantly higher without clay ball application 36.1% ± 4.2 compared to 25.4% ± 3.7 with clay balls applied. Hence, seed loss in the presence of mammalian predators was significantly reduced by fruit flesh removal in combination with clay ball application when compared with other treatments (34.8% ± 7.2, Fig. 5.2).

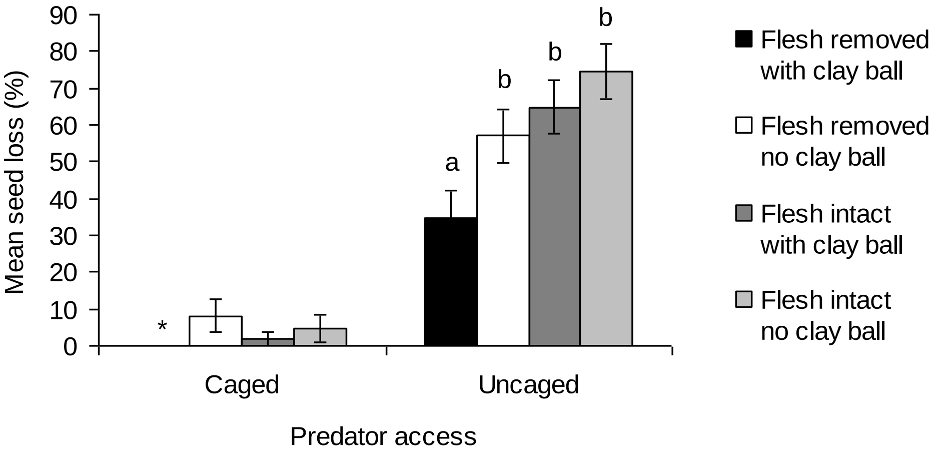

Figure 5.2 Seed (and fruit) loss including mammalian predation (mean ± SE, *n*=27) amongst caging, fruit flesh removal and clay ball treatments. Three species combined (*Beilschmiedia tawa*, *Elaeocarpus dentatus* and *Litsea calicaris*) over a 16 week period at sites with predators present. Tukey HSD post-hoc pairwise comparisons are presented for uncaged treatment only, different letters denote a significant difference in means (p<0.05, df=144, Error between MSE=659.49). * No seed loss occurred in the caged, flesh removed with clay ball treatment.

5.4.2 Germination and seedling establishment

After accounting for seed loss, the germination rate of *B. tawa* was 58.9% ± 5.0 with only 29.8% ± 5.4 of these seedlings alive after one year. As a proportion of seeds sown, *B. tawa* seedling establishment at one year old (8.9% ± 1.7) was significantly improved by caging and clay ball treatments (Table 5.2). Caging significantly increased *B. tawa* establishment from 4.4% ± 1.6 when uncaged to 13.3% ± 2.8 when caged, while the clay ball treatment increased *B. tawa* establishment from 5.6% ± 1.9 without clay balls to 12.2% ± 2.7 when seeds were in clay balls (Table 5.2). A significant interaction showed that only *B. tawa* seeds with fruit flesh intact had greater seedling establishment within clay balls (15.6% ± 3.8) compared to without clay balls (2.2% ± 1.5, Table 5.2). On the other hand, when fruit flesh was removed from *B. tawa* seeds the rate of seedling establishment was the same with or without clay balls (8.9% ± 3.3). Thus, the highest rate of *B. tawa* establishment after one year was with clay ball application and fruit flesh intact when caged from predators (24.4% ± 5.6, Fig. 5.3).

Table 5.2 ANOVA results reporting the effects of site and three seed treatments and their interactions on *Beilschmiedia tawa* seedling establishment after one year, at one rural and two urban sites all with mammalian predators present. Significant effects are indicated in bold type and only significant interactions are shown.

Predictor	***SS***	***df***	***MS***	r^2	***F***	***p***
Site	11.111	2	5.556	0.0006	0.03125	0.9693
Caging	1422.222	1	1422.222	0.0711	8	**0.0068**
Flesh removal	0	1	0	0	0	1
Clay ball	800	1	800	0.0400	4.5	**0.0391**
Flesh removal*Clay ball	800	1	800	0.0400	4.5	**0.0391**
Error	8533.333	48	177.778			

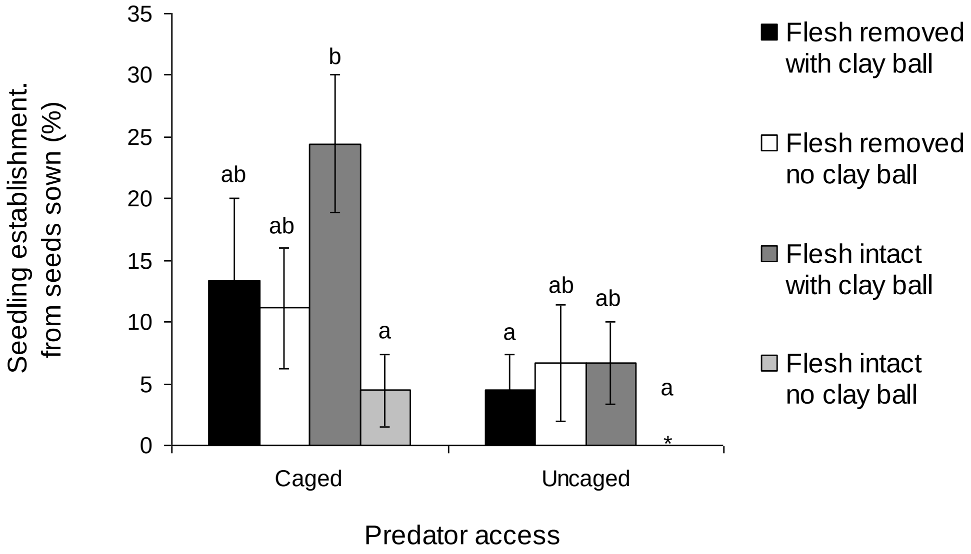

Figure 5.3 *Beilschmiedia tawa* seedling establishment as a proportion of seeds sown (mean ± SE, *n*=9) amongst caging, fruit flesh removal and clay ball treatments at one rural and two urban sites with predators present. Tukey HSD post-hoc pairwise comparisons are presented, different letters denote a significant difference in means ($p<0.05$, df=48, Error between MSE=177.78). * No seedlings established in the uncaged, flesh intact without clay ball treatment.

Results from the reference predator-free site showed the highest rates of *B. tawa* establishment from seeds sown when uncaged (18.3% ± 5.2) and caged (20.0% ± 6.0) across all seed treatments. Establishment at this site was similarly greatest in the clay ball treatment, although particularly with fruit flesh removed (26% ± 8.4);

establishment from clay balls with fruit flesh intact (23.3% ± 9.5) was similar to the caged results from sites with predators.

Twelve seedlings of *L. calicaris* (6.3% of initial seeds) were recorded 2 years 4 months after sowing. These were recorded from all seed treatments but only either in cages or at the predator-free site. Seven *E. dentatus* seedlings (1.8% of initial seeds) had established 3 years after sowing at two of the sites with predators present, from all seed treatments.

5.5 DISCUSSION

Our results strongly suggest that seed loss to predation by introduced mammals will limit the success of broadcast seeding for the restoration of large-seeded, fleshy-fruited trees. However, we found that both pre-sowing seed treatments of fruit flesh removal and clay ball application can significantly reduce seed loss. Given the widespread presence of mammalian predators in New Zealand's forests (Innes et al. 2010) and reports of post-dispersal seed predation limiting tree regeneration elsewhere (Blate et al. 1998; Diaz et al. 1999; Doust 2011) such treatments should be widely applicable to improve seedling establishment from broadcast seeding.

Some variability in seed loss between species and sites may have been due to food availability, specific predator species present or seed and fruit defensive and nutritive properties. Food source familiarity (Beveridge 1964) could contribute to the higher seed loss rate of *B. tawa* since fruit of this species was present in mature forest adjacent to two of the three study sites with predators. Lower seed loss in rural than urban forest for *L. calicaris* may be related to sowing during early summer when other food sources may be preferred in rural forest habitat and when rats typically spend less time foraging on the forest floor than during winter (Beveridge 1964; Daniel 1973). We did not distinguish between rat and possum predation as both animals are usually present in lowland forest, although their comparative densities may have influenced seed predation rates (DeMattia et al. 2004). Large seed size and thin endocarp may have increased vulnerability of *B. tawa* and *L. calicaris* to predation by possums, the largest of the mammalian predators present (Williams et al. 2000). The thick, hard endocarp of *Elaeocarpus* *dentatus* is discarded by possums and only the fruit flesh consumed (Cowan 1990), but seeds of this species are eaten by rats (Daniel 1973). A high proportion of lost uncaged *B. tawa* seeds and fruits were found damaged near grids (49%), but only three *L. calicaris* seeds and one *E. dentatus* seed suffered similar damage. Incomplete predation of *B. tawa* seeds may be due to predators' limited tolerance of defensive toxic compounds (Campbell 1978), but the few damaged seeds that did germinate failed to survive.

The effectiveness of broadcast seeding can be significantly improved using pre-sowing seed treatments. The reduction in total seed loss for seeds with fruit flesh removed compared to intact fruits is consistent with other seed predation studies (Chimera & Drake 2011; Wotton & Kelly 2011). Interestingly, the lowest rate of seed loss occurred when fruit flesh removal was combined with clay ball application suggesting the clay covering further deterred seed predators. Covering fruits or seeds in a clay ball also led to a significant increase in *B. tawa* establishment after one year suggesting that seed burial (Doust et al. 2006; Garcia-Orth & Martínez-Ramos 2008) is not the only seed-sowing method to improve seedling establishment for large recalcitrant seeds. Fruit flesh removal did not improve seedling establishment of *B. tawa* within clay balls and therefore may be a redundant treatment, although without the use of clay balls fruit flesh removal was beneficial, possibly due to the high levels of predation for intact fruits and their vulnerability to pathogens and insect damage (Knowles & Beveridge 1982). High mortality of *B. tawa* during the first year coincided with warmer, drier conditions in early summer that are unfavorable for seedling establishment and may be exacerbated in urban forest patches (Whaley et al. 1997). The small amount of clay and compost mix applied as clay balls possibly benefitted root systems after disintegration by providing a nutritive, water-holding medium. Seeds within a hard endocarp, such as *E. dentatus*, may not require protection from desiccation and roots may not have benefitted from the clay mix due to delayed germination. Further scarification may be necessary to improve germination of species with hard seed coats (Traveset et al. 2008), whereas *L. calicaris* germination may have been affected by the timing of sowing combined with high sensitivity to desiccation.

The reduced investment required per seed makes seeding of late successional species a favorable alternative to planting for accelerating forest succession (Cole et al. 2011). Low seedling establishment rates for broadcast seeding can be countered by the distribution of many seeds, given an abundant seed supply, at a lower cost than planting nursery-raised seedlings. For example, with no predator control and an establishment rate of 6.7% we estimate hand-sowing 15 *B. tawa* seeds with either clay ball or fruit flesh removal treatment (10 minutes preparation @ $NZ15/hr = $2.50 labor) could be less than half the cost of planting one *B. tawa* seedling ($5.20) (W. Bennett 2011, Forest Flora Nursery NZ, personal communication). In this study *B. tawa* showed the most potential for broadcast seeding with the highest rate of seedling establishment from seeds sown, followed by *L. calicaris* and *E. dentatus*. Fortunately *B. tawa* is the dominant species of the most common target ecosystem for lowland forest restoration whereas the other two species naturally occur less frequently (Clarkson et al. 2012). Varying success between species when testing broadcast seeding for regeneration enrichment has also been found previously (Bonilla-Moheno & Holl 2010; Cole et al. 2011) and may be related to seed viability, the timing of sowing and germination, seed and fruit morphology and predator preferences.

We conclude that broadcast seeding in combination with pre-sowing seed treatments can contribute to lowland forest restoration in heavily modified landscapes where avian seed dispersers or seed sources are limited. This may apply to urban forest fragments (Sullivan et al. 2009; MacKay et al. 2011) or forests in agricultural landscapes suffering reduced native bird occupancy and insufficient regeneration of canopy species (Burns et al. 2011). However, we emphasize the importance of controlling non-native mammalian seed predators alongside revegetation efforts to successfully restore native forest habitat.

5.5.1 Implications for Practice

- Control of mammalian seed predators at the time of broadcast seeding will considerably increase the efficacy of the method for large-seeded species.
- Fruit flesh removal and the use of a clay ball can reduce seed predation for large-seeded species.

- Seedling establishment rates for species with recalcitrant seeds can be improved using clay balls applied to fruits, while the removal of fruit flesh may only be beneficial if not using of clay balls.
- For summer ripening fruit it may be beneficial to delay seed collection or sowing as late as possible in the season to ensure maturity of seed collected and avoid long periods of dry weather during field germination.

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APPENDIX 5.1

Reported drupe and seed characteristics for the three study species from: a, Knowles and Beveridge (1982); b, Webb and Simpson (2001); c, Allan (1961); d, Kelly et al. (2010); e, Dijkgraaf (2002); and f, this study.

Species	Common name	Drupe size length (range) [a, b, c] x width (means) [d, e] mm	Seed size (range) length x width [b, c, f] mm	Drupe description [e, b]
Beilschmiedia tawa (A.Cunn.) Benth. & Hook.f. ex Kirk, Lauraceae	tawa	<40 x 15.5, 18.8	22-30 x 12	Dark purple to black with high moisture, sugar-rich flesh and a thin-walled endocarp
Litsea calicaris (Sol. Ex A.Cunn.) Benth. & Hook.f. ex Kirk, Lauraceae	mangeao	15-20 x 12.5	10-13 x 6.5-8	Purplish-black with membranous endocarp
Elaeocarpus dentatus (J.R.Forst. & G.Forst.) Vahl, Elaeocarpaceae	hinau	12-18 x 9.2, 10.9	9-17 x 7-10	Purple with dry and carbohydrate-rich flesh with a thick, hard endocarp

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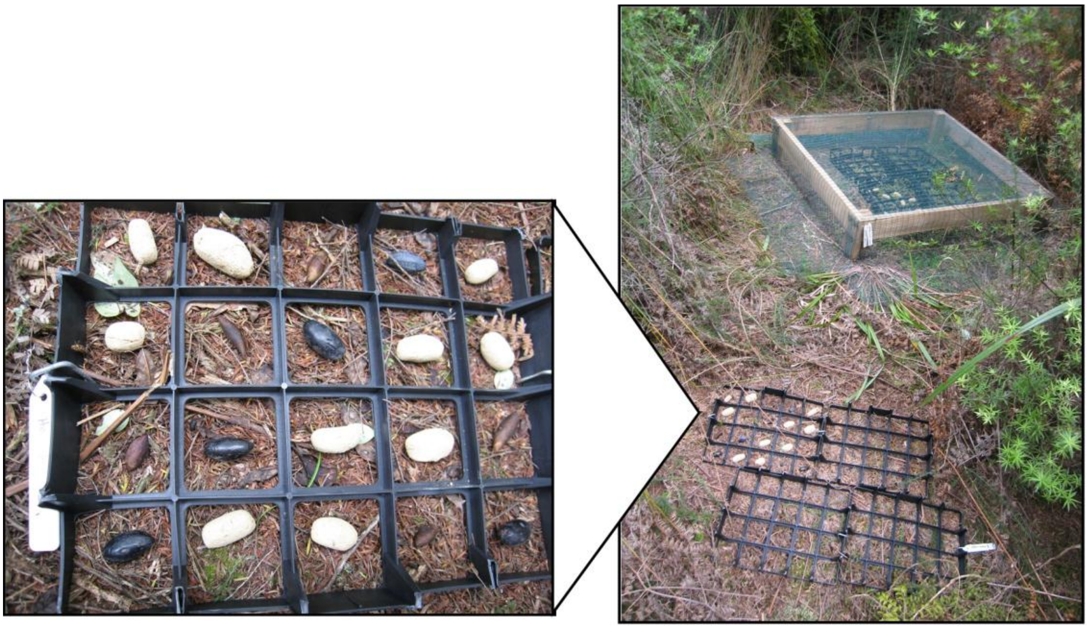
APPENDIX 5.2

Layout of a caged and uncaged replicate (on right) repeated three times at 10-15 m intervals per site, with detail of *Beilschmiedia tawa* (on left) showing seed treatments placed on the ground surface to simulate broadcast seeding. Seed treatments are described from top to bottom for the first column: fruit flesh removed and clay ball; fruit flesh intact and clay ball; fruit flesh removed and no clay ball; fruit flesh intact and no clay ball.



APPENDIX 5.3

Results from mammalian seed predator monitoring undertaken at the four study sites in April 2008. Three tracking tunnels (Black Trakka, Warkworth, N. Z.), baited with peanut butter in the centre of the inkpad, and five wax tags (Pest Control Research, Christchurch, N. Z.) were placed out for two weeks at each site to particularly detect the presence of rats (footprints) and possums (bite marks) respectively. Observations of animal sign including faeces and bite marks on seeds were also recorded throughout the study period. The absence of detection cannot be interpreted as an absence of predators due to the small area and timeframe of monitoring (except at the Maungatautari pest-free enclosure site). Detection method= tracking tunnels (t), wax tags (w) and observation of animal sign (o).

	Urban forest		**Rural forest**	
Predator	Hammond Park	Tauhara Park	Hakarimata ranges	Maungatautari enclosure
Brushtail possum	w, o	w, o	-	-
Rat	t	o	t, w, o	-
Mouse	-	t	t	-

APPENDIX 5.4

Seed loss including mammalian predation amongst species, sites and the caging treatment after 16 weeks (mean ± SE, n=12).

Species	**Site**	**Caged**	**Uncaged**
Beilschmiedia tawa	Hakarimata Ranges	0	93.3 ± 2.8
	Hammond Park	1.7 ± 1.7	73.3 ± 9.0
	Tauhara Park	0	43.3 ± 8.8
Elaeocarpus dentatus	Hakarimata Ranges	0	45.8 ± 10.1
	Hammond Park	0	75.0 ± 9.7
	Tauhara Park	6.3 ± 4.5	22.5 ± 10.0
Litsea calicaris	Hakarimata Ranges	0	25.0 ± 11.5
	Hammond Park	4.2 ± 4.2	58.3 ± 13.5
	Tauhara Park	20.8 ± 11.4	83.3 ± 9.4

6 SYNTHESIS

6.1 DISCUSSION

This thesis contributes to our knowledge of vegetation succession and regeneration dynamics in New Zealand’s lowland forests with practical applications for forest restoration. It has quantified and contrasted both urban and rural seed supply and vegetation composition and investigated changes in species dominance over time (Chapter 2). It has compared the contribution of exotic and native seed rain in relation to seed dispersal modes and the extant vegetation composition (Chapter 3) and identified relationships between native species presence and plant traits, forest patch attributes and connectivity measures in the urban area (Chapter 4). Lastly, it presents an alternative method for species reintroduction into established early successional vegetation using novel seed treatments and broadcast sowing (Chapter 5).

Seed rain and soil seed banks within urban forest patches were found to be dominated by exotic species to a greater extent than the rural forest sampled (Chapter 2) and in comparison to other New Zealand forests (Partridge 1989; Burrows 1994; Sem & Enright 1995, 1996; Moles & Drake 1999; Dungan et al. 2001). This is consistent with other urban soil seed banks (Kostel-Hughes et al. 1998; Fisher et al. 2009) and when coupled with the large proportion of exotic pioneer species identified in the persistent soil seed bank (Chapter 2) suggests reduced potential for native species establishment. Comparison of forest patches by age, however, identified a temporal threshold suggesting urban soil seed banks and understorey vegetation over 20 years old have a reduced exotic component (Chapter 2) indicating that microsites typical of interior forest habitat are developing with canopy closure and favouring native establishment (White et al. 2009) while exotic seed banks are depleting following the initial disturbance from planting.

Urban seed rain quantity was found to be predominantly native for planted sites but not for naturally regenerating sites (Chapter 3), supporting the initial planting of native canopy species versus natural colonisation to encourage the restoration of native vegetation (Prach & Hobbs 2008). Many novel species arrived in seed rain at sites, particularly wind-dispersed species and mostly exotic species which poses an ongoing threat to native regeneration through edge invasion or in the event of forest disturbance. Native woody species arriving in urban seed rain were limited to commonly planted species and numerous native fern species arriving in seed rain (and forming soil seed banks, Chapter 2) had not established in vegetation suggesting niche limitation which may be altering native successional pathways (Coomes et al. 2005).

Nearly half of the native forest species of the wider district were found to be absent from Hamilton City's urban forest flora and these species are suggested as priority targets for urban reintroduction (Chapter 4). Consistent with other urban trait studies (Thompson & McCarthy 2008; Duncan et al. 2011) no significant relationship was evident between species dispersal ability and presence in urban vegetation. This may be influenced by the comparatively young age of Hamilton City (Hahs et al. 2009) leading to some unviable populations of long-lived species remaining, e.g. the over representation of trees in the city flora (Chapter 4), although they may be destined for future extinction in the urban area (Tilman et al. 1994; Vellend et al. 2006). In a trait analysis of the city's flora forb and parasite growth forms, highly shade tolerant (late successional) species and those with biotic pollinators showed limited colonisation and regeneration in urban forest patches. While forbs (Thompson & McCarthy 2008; Duncan et al. 2011; McClain et al. 2011) and late successional species (Mabry & Fraterrigo 2009; McClain et al. 2011) have previously been associated with limited recolonisation ability, native forest pollinator relationships are poorly understood and this is emerging as a knowledge gap for ecological restoration (Dixon 2009). Zoochorous species recolonisation of urban forest patches improved with increased proximity and size of good quality native vegetation, supporting the important role of green corridors for animal movements within cities (Tremblay & St Clair 2009). Evidence for spatial thresholds was inconclusive with little relationship found between patch attributes or forest connectivity and native species richness, which may result from the small size of the patches studied and limited colonisation from beyond the urban area.

This research has found that broadcast seeding in combination with novel pre-sowing seed treatments can contribute to forest restoration in heavily modified environments where avian seed dispersers or seed sources are limited (Chapter 5). This may apply to urban forest fragments (Sullivan et al. 2009; MacKay et al. 2011) or those in agricultural landscapes with insufficient regeneration of canopy species (White et al. 2004; Burns et al. 2011). High rates of seed predation were reduced by the use of pre-sowing seed treatments (Chapter 5) and given reports of post-dispersal seed predation limiting tree regeneration elsewhere (Blate et al. 1998; Diaz et al. 1999; Doust 2011), such treatments should be widely applicable to improve seedling establishment from broadcast seeding. This method potentially offers an efficient and cost-effective alternative to sapling planting or seed burial for forest enrichment with late successional species.

To conclude by applying the theory of Williams et al. (2009) on urban filtering of species composition, this research suggests that fragmentation in the broader landscape plays a significant role in reducing urban native forest species diversity. It has also found that human preference, in the form of exotic species invasion, has a strong influence on species composition, particularly in younger forest vegetation. As vegetation ages conditions become more suited to native species establishing and then the drier, warmer urban environment may play an increased filtering role with species preferring damp, cool microclimate (e.g. ferns) still having limited establishment.

6.2 RECOMMENDATIONS FOR MANAGEMENT

This research has identified the following recommendations for the management of urban forest restoration plantings:

- Urban forest restoration projects need to set clear goals for target species or habitat types with correspondingly appropriate management strategies and monitoring programmes to assess progress towards goals. If native-dominated vegetation with a successional pathway resembling natural forest is desired then intensive management involving exotic species control and native reintroductions will be required. At the other end of the spectrum if no management is undertaken, e.g. following natural or spontaneous colonisation, then mixed native and exotic habitat will result.

- A patch size of at least 0.5 hectares is recommended for restoration projects where creation of interior native forest habitat is the goal. The small size of forest patches in this study (<0.5 ha) appears to allow exotic species to penetrate patches due to high edge to area ratios. For such small patches the management of adjacent exotic seed sources is of increased importance.
- To increase native plant species diversity in Hamilton City's urban forests the species listed in Appendix 4.1 (Chapter 4) are suggested for reintroduction at successional stages appropriate to each species shade tolerance requirements as stated.
- The diversity of urban native forest species in Hamilton City would benefit from greater linkage with forest remnants beyond the urban area. The restoration of river and gully systems extending into the peri-urban zone as well as establishing forest restoration projects within this zone is desirable to facilitate the recolonisation of native species (particularly those relying on native animal vectors) in urban forests.
- Broadcast seeding with pre-sowing seed treatments (Chapter 5) shows potential as a method for the enrichment of established young urban forest with late successional species and would be suitable to trial as a restoration tool where natural colonisation is limited.

6.3 RECOMMENDATIONS FOR FURTHER RESEARCH

This research has identified the following areas of future research:

- Long-term monitoring (5 to 10 yearly) of restoration plantings is essential to continue building on current data, especially with regard to temporal trends and the dynamics between native and exotic species in canopy and understorey vegetation.
- Information on seed traits for many native species is lacking, particularly seed longevity data and germination requirements, which would benefit and assist prioritisation of native reintroductions in restoration.
- Further research on animal-pollinator relationships with native forest plants is needed both in the urban environment and more intact forest remnants in New Zealand. Such information is necessary to understand the

long-term sustainability of fragmented forests and to inform restoration practice.

- Further investigation of the relationship between native species establishment and a greater range in forest patch sizes may help to establish whether urban forest interior conditions improve for native species with increased patch size.
- Broadcast seeding using clay balls and fruit flesh removal treatments needs to be trialled on wider range of late succession native species with large seeds or limited seed sources. This could include forbs and parasitic species which may not otherwise spontaneously colonise restored or fragmented forest patches. Clay balls have been used for sowing small-seeded species in permaculture and grassland restoration overseas and could be more cost-effective than raising and planting nursery seedlings for small-seeded native species, such as forbs. Broadcast seeding could be implemented as an actual restoration enrichment method where seedling establishment can be followed in situ for several years and compared to a sapling planting method.

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