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Exotic trees can sustain native birds in urban woodlands

Emily R. Gray[1] **· Yolanda van Heezik**[1]

Abstract Native landscaping has been proposed as a means of increasing native bird diversity and abundance in urban landscapes. However residents' preferences for vegetation are such that exotic plants are often preferred over natives. We investigated the extent to which native birds foraged in three common native and three exotic tree species in mixed urban woodland during four seasons. We predicted that native birds would spend more time foraging in native trees, and that food resources provided by deciduous exotic trees would be more seasonal than those provided by non-deciduous natives. Native birds spent a lot of time foraging in two of the native tree species, but very little time in native red beech (*Nothofagus fusca)*. They used exotic oak (*Quercus robur)* throughout the year, and sycamore (*Acer pseudoplatanus)* seasonally. Oak and European beech (*Fagus sylvatica*) were used by the largest number of species overall, because they attracted both native and exotic birds. With the exception of tree fuchsia (*Fuschia excorticata*), which produces large volumes of nectar followed by fruits, all tree species were sources of invertebrates for insectivorous feeding. Seasonality of use was high only in sycamore, indicating limited support for our second prediction. We show that being native doesn't necessarily entail being a good food source for native birds, and popular landscaping exotic species, such as oak, provide foraging opportunities across all seasons.

Keywords Non-native · Alien · Introduced · Insectivore · Trees · Urban forest · Behavioural flexibility

Introduction

Biotic homogenisation is the process of gradual replacement of native endemic species by widespread exotic species, resulting in high local biodiversity but a loss of regional and global diversity (McKinney and Lockwood 1999). This process is especially evident in urban areas where a high proportion of plant species are exotic (Kowarik 1995; Thompson et al. 2003;

✉ Yolanda van Heezik
Yolanda.vanheezik@otago.ac.nz

[1] Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

McKinney 2006; Loram et al. 2007), and where typically only a small proportion of native birds (5 – 29 %) adapt to urban living (McKinney and Lockwood 1999). Native landscaping has been advocated as a means of improving biodiversity through increased use of native plants (Meurk and Swaffield 2000; Hostetler and Main 2010; Stewart et al. 2010). While there is some debate about the validity of what has been termed a "pro-native tyranny" based on a simplistic "good versus evil paradigm" (Hitchmough 2011), there is evidence of positive associations between native species diversity, and the occurrence and volume of native plants (Mills et al. 1989; Clergeau et al. 1998; Day 1995; Germaine et al. 1998; McIntyre and Hostetler 2001; White et al. 2005; MacGregor-Fors 2008; Burghardt et al. 2009; Pardee and Philpott 2014).

Foraging flexibility and opportunism are traits that are usually associated with success in urban-dwelling exotic bird species (Sax and Brown 2000; Bando 2006; Sol et al. 2012), whereas native species typically have more specialised diets (McLain et al. 1999; Sax and Brown 2000; Sol 2007), selecting native plants for feeding over exotic alternatives (Daniels and Kirkpatrick 2006; Mackenzie et al. 2014). Native plants may provide a more valuable and abundant source of food than similar exotic species for suburban nectarivorous and insectivorous birds (Beissinger and Osborne 1982; French et al. 2005; White et al. 2005; Hodgson et al. 2006; Mackenzie et al. 2014). Native insectivores, nectarivores and frugivores are all more likely to be adversely affected by urbanisation than omnivores and granivores due to limited food availability as a result of the replacement of native with exotic vegetation (Lim and Sodhi 2004; White et al. 2005; Corlett 2005), with insectivorous birds being particularly vulnerable (Beissinger and Osborne 1982; Lim and Sodhi 2004; White et al. 2005; Hodgson et al. 2006). Native plants support more abundant invertebrates for insectivores (Southwood 1961; Bhullar and Majer 2000; McIntyre 2000; Burghardt et al. 2009; Tallamy and Shropshire 2009; Helden et al. 2012). Many species of invertebrate herbivores and insectivores are known to reproduce only on plants with which they have a shared evolutionary history (Bernays and Graham 1988). Consequently, urban landscapes dominated by exotic plants will provide fewer resources for native insectivores (Tallamy and Shropshire 2009; Tallamy et al. 2010).

A number of native bird species do succeed in adapting to urbanisation to varying degrees, resulting in complex ecological relationships between introduced plants and native species (Carlos and Gibson 2010; Aslan and Rejmanek 2010). Although generally highly selective in behaviour, native birds can use exotic-dominated vegetation for foraging and nesting (Fegley 1988; Green et al. 1989; Ellis 1995; Sogge et al. 2008). Exotic plants may offer essential resources replacing those of absent native plants, permitting the persistence of some birds in highly modified areas (Aslan and Rejmanek 2010). They may even act to attract native birds into urban areas (Gleditsch and Carlo 2011). Interactions between birds and non-native plants have important implications for conservation management, but remain poorly understood (Aslan and Rejmanek 2010).

Few studies on bird foraging behaviour in urban areas have distinguished between native and exotic plant and bird species (but see Catterall et al. 1989; Green et al. 1989; Daniels and Kirkpatrick 2006; Mackenzie et al. 2014). Management strategies that focus on the replacement of exotic vegetation with native vegetation are based on the assumption that there will be clear benefits for native birds. However landscaping decisions by urban residents are often motivated by values and preferences that result in low abundance and diversity of native vegetation (Marzluff 2001; Kendal et al. 2012). In Australia some people feel that exotic trees contribute to a sense of place, and native trees are inappropriate in urban areas (Kirkpatrick et al. 2012). Residents may be more amenable to planting for birds if they did not always have to plant native. A better understanding of the interactions between native and exotic species is required in order to proceed towards some kind of reconciliation ecology (Meurk and Swaffield 2000).

In New Zealand there has been substantial removal of the original vegetation and the proportion of exotic vegetation is high compared to other countries (van Heezik et al. 2014; Meurk et al. 2009; Stewart et al. 2010). Native bird diversity in urban areas is rather low: in one city native birds made up 44 % of only 39 species and 47 % of numbers (van Heezik et al. 2008), and the nation-wide garden bird survey found only four native species in the top 10 (by occurrence and abundance) with six more in the top 20 (Spurr 2012). Planting native vegetation is promoted in New Zealand as a way to attract native birds, however many of the native plants are less colourful than exotic species. Spurr (2012) noted that some winter-flowering exotic plants in urban gardens provided a source of food for nectarivorous species at a time when it was not available in native habitats. In this study we evaluate the extent to which common exotic and native trees in mixed woodland in an urban area are used as food resources by native urban birds across all seasons. We predict that native birds will spend more time foraging in, and visit native trees to forage more often than exotic tree species. We also predict that foraging in exotic trees is more seasonal than in native trees, because most exotic trees are deciduous and most native trees are not. These results should better inform advocacy on which tree species should be planted to support native bird populations.

Methods

Selection of tree species

Selected trees were situated in a chain of urban forest fragments within Dunedin, New Zealand (45°52′S 170°30′E). We chose six tree species (three native and three exotic) on the basis of their commonness and their similar canopy height. Kanuka (*Kunzea ericoides*), tree fuchsia (*Fuchsia excorticata*) and red beech (*Nothofagus fusca*) were native and European (common) beech (*Fagus sylvatica*), oak (*Quercus robur*) and sycamore (*Acer pseudoplatanus*) were exotic. Three locations were selected for each tree species, giving a total of 18 spatially independent locations, each containing multiple individuals of one of the six tree species (between 4 and 12 of the focal species) clumped closely together in a stand of not more than 20 m^2. While the surrounding woodland varied with respect to the relative proportions of native and exotic trees, we selected locations for each of the three stands of each tree species so that they were spatially well separated (>1 km) and surrounded by the range of woodland types. Phenological changes were noted throughout the year.

Recording bird behaviour

We recorded feeding behaviour once a month between September 2012 and August 2013, at each location within 2 h after dawn and 2 h before dusk, in the absence of rain or strong winds. There were six recording bouts (three morning, three evening) per location each season, conducted 2 weeks apart, adding to 24 for the year and totalling 72 recordings per tree species. Using focal animal sampling (Martin and Bateson 1993), we recorded all behaviours of as many individual birds as possible for up to five minutes from within the stand of trees during a 30-min period, but focused on feeding behaviours (i.e., time spent searching for, handling and eating food) in this study. We discarded recordings of < 1 min (if the bird left the area). When individuals moved from view, recording was paused and then continued once the individual returned to view, stopped if the individual didn't return or discarded if recording time was insufficient. Recording was only continued when the bird disappeared for a short period of time (i.e., <10 s) and the observer was certain it was the same individual. We recorded the length of time birds spent feeding and the number of feeding visits (i.e., the total number of feeding visits across all individuals, excluding visits that were <1 min). To ensure that the same individual wasn't recorded twice in one recording period, all movement was observed post-recording until the individual had left the site.

Statistical analysis

We compared the amount of time birds spent feeding using GLMs (Generalised Linear Models; R Studio 0.97.246), with a quasi-poisson distribution when testing for the effect of tree species and native/exotic bird status on time birds spent feeding. Initially season and tree species were combined in the same analysis, but when no interactive effects were found we ran separate analyses to facilitate interpretation of the models. "Feeding time" was mean-centred using the total recording times to allow for recordings of varying lengths (ranging from 60 to 300 s). We ran these analyses for each season individually and then again to compare seasons. Silvereyes (*Zosterops lateralis*) comprised a large proportion of the total number of native bird recordings each season and a silvereye bias was observed during the analyses, so most analyses presented do not include silvereye data, which are presented separately. In some instances silvereye data could not be removed because there were too few data remaining for analysis. Silvereyes were the only species showing strong flocking behaviour: when a flock of any species was encountered the behaviour of only one individual in the flock was recorded. Red beech was removed from all analyses (total bird recordings for the year, $n=17$), tree fuchsia from the native bird autumn analysis ($n=2$ recordings) and European beech from the native bird winter analysis ($n=3$ recordings) due to lack of data.

We also used GLM analyses to compare the number of feeding visits (i.e., number of recordings when most time was spent feeding than in other behaviours) made by native and exotic birds between seasons for each of the tree species. Because there were very few visits by exotic birds we combined exotic and native birds in the one analysis.

Results

Nine native and 11 exotic bird species fed in the six tree species throughout the year. Silvereyes were the dominant species recorded in almost all tree species and all seasons. Over the course of the year kanuka was visited by 10 species (eight native and two exotic), tree fuschia by eight species (seven native and one exotic), red beech by five species (four native and one exotic), European beech by 11 species (six native and five exotic), oak by 14 species (six native and eight exotic) and sycamore by eight species (five native and three exotic) (Table 1).

Table 1 Feeding visitations made by bird species each season in three native tree species, kanuka, tree fuchsia, and red beech, and three exotic species, oak, sycamore and European beech

Tree species	Bird species	Spring	Summer	Autumn	Winter
Kanuka	Silvereye	11	9	5	5
	Natives	4 (4)	12 (4)	9 (2)	12 (6)
	Exotics	0	2 (2)	2 (1)	0
Tree fuschia	Silvereye	19	8	1	3
	Natives	17 (3)	9 (4)	0	12
	Exotics	3 (2)	1 (1)	1 (1)	0
Red beech	Silvereye	2	0	0	1
	Natives	5 (2)	0	3 (2)	5 (3)
	Exotics	0 (1)	0	0	0
European beech	Silvereye	11	9	5	4
	Natives	4 (2)	2 (2)	2 (2)	0
	Exotics	11 (3)	4 (3)	3 (2)	0
Oak	Silvereye	10	5	11	10
	Natives	7 (3)	4 (3)	8 (4)	1 (1)
	Exotics	9(3)	5 (4)	14 (5)	12 (3)
Sycamore	Silvereye	16	6	7	7
	Natives	6 (3)	2 (2)	5 (3)	1 (1)
	Exotics	8 (1)	2 (1)	5 (3)	0

Numbers in brackets are the number of species; those for "Natives" exclude silvereyes

Time spent foraging by native birds

In spring, time spent feeding by native birds was longer in tree fuchsia than European beech or oak and almost significantly longer in kanuka than in European Beech, but time spent feeding in sycamore was no different to that in any other tree species (Fig. 1; Table 2). In summer, native birds spent more time feeding in tree fuchsia than in all other tree species (Fig. 1; Table 2). In autumn, time spent feeding was longer in sycamore and oak than in European beech (Fig. 1; Table 2), and in winter longer times were spent feeding in kanuka, tree fuchsia and oak than in sycamore (Fig. 1; Table 2). Because most visits to oak and sycamore were by silvereyes, we could not remove this dominant species from the winter analysis.

When we compared across seasons, the amount of time native birds spent feeding did not differ in kanuka (*p* values: 0.071 – 0.78), tree fuchsia (*p* values: 0.13 – 0.91), European beech (*p* values: 0.083 – 0.66) and oak (*p* values: 0.19 – 0.75). The amount of time native birds spent feeding in sycamore was longer in spring and autumn than in winter (c.f. spring, GLM est. $-0.579 \pm$se 0.228, $t=-2.54$, $p=0.014$; c.f. autumn, GLM est. $-0.841 \pm$se 0.246. $t=-3.41$, $p=0.0011$; Fig. 2). Approximately two-thirds of all native bird feeding visits to European beech, oak and sycamore were by silvereyes and because of this, the seasonal comparative analyses for these tree species included silvereye data.

The amount of time silvereyes spent feeding did not differ across all tree species in spring (*P* values: 0.20 – 0.98), summer (*p* values: 0.11 – 0.99) and autumn (*p* values: 0.096 – 0.82), but they spent longer periods of time feeding in kanuka and oak than in sycamore in winter (Table 1). When we compared across seasons, there was no difference in time spent feeding in

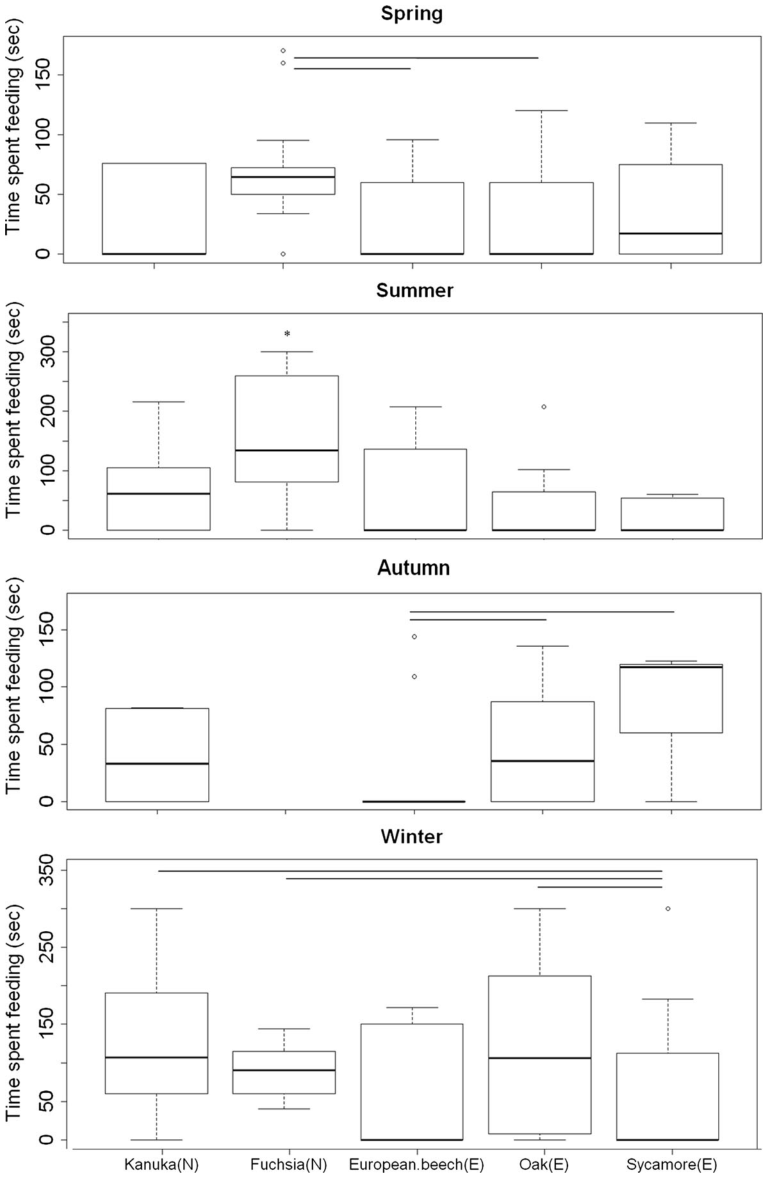

Fig. 1 Time spent feeding (in seconds) by native birds in five tree species (*N* native, *E* exotic) during four seasons (silvereyes excluded from spring, summer and autumn but included in winter due to insufficient data from remaining native species; insufficient data collected from red beech for analysis). Horizontal lines indicate significantly different tree species with respect to feeding time ($P<0.05$); *Asterisk* denotes that time spent feeding in this tree species was significantly longer than in all other tree species ($P<0.05$)

most tree species (kanuka, p values: 0.51 – 0.90; tree fuchsia, P values 0.41 – 0.98, European beech, P values 0.47 – 0.96; oak, P values 0.47 – 0.95), but silvereyes spent longer feeding in sycamore in spring, summer and autumn than in winter (c.f. spring, GLM est. −0.530±se 0.195, $t=-2.71$, $p=0.010$; c.f. summer, GLM est. −0.488±se 0.231, $t=-2.12$, $p=0.041$; c.f. autumn, GLM est. −0.612±se 0.214, $t=-2.86$, $p=0.0069$).

Table 2 Comparison of time spent feeding by native birds (only significant results shown) and silvereyes (same comparisons shown, including significant results) across five tree species (insufficient data collected from red beech for analysis)

Season	Analysis	Time spent feeding by native birds (without silvereyes)				Time spent feeding by silvereyes			
		GLM est.	± SE	*t* value	*P* value	GLM est.	± SE	*t* value	*P* value
Spring	Fuchsia~EB	−1.375	0.500	−2.75	0.0076	−0.06	0.083	−0.76	0.45
	Fuchsia~O	−0.981	0.422	−2.33	0.023	0.002	0.081	0.02	0.98
	Kanuka~EB	0.948	0.492	−1.93	0.058	−0.043	0.086	−0.50	0.62
Summer	Fuchsia~K	−0.803	0.348	−2.31	0.026	−0.612	1.182	−0.52	0.61
	Fuchsia~EB	−1.166	0.552	−2.11	0.040	−0.396	1.218	−1.20	0.24
	Fuchsia~O	−1.304	0.494	−2.64	0.011	−0.482	1.291	−1.37	0.18
	Fuchsia~S	−1.774	0.894	−1.98	0.053	−0.575	1.305	−1.62	0.12
Autumn	Sycamore~EB	−1.269	0.430	−2.95	0.0040	−0.081	0.049	−1.66	0.11
	Oak~EB	−0.897	0.377	−2.38	0.019	−0.027	0.044	−0.61	0.55
Winter	Kanuka~S	−0.689	0.235	−2.93	0.0047	−0.597	0.288	−2.08	0.049
	Fuchsia~S	−0.938	0.295	−3.18	0.0023	–	–	–	–
	Oak~S	−0.551	0.242	−2.28	0.026	−0.602	0.250	−2.41	0.024

For significant results, native birds in tree species written out in full had longer feeding times than those written as acronyms (*K* Kanuka, *EB* European Beech, *O* Oak, *S* Sycamore). Silvereyes included in winter native bird analyses due to insufficient data from remaining native species

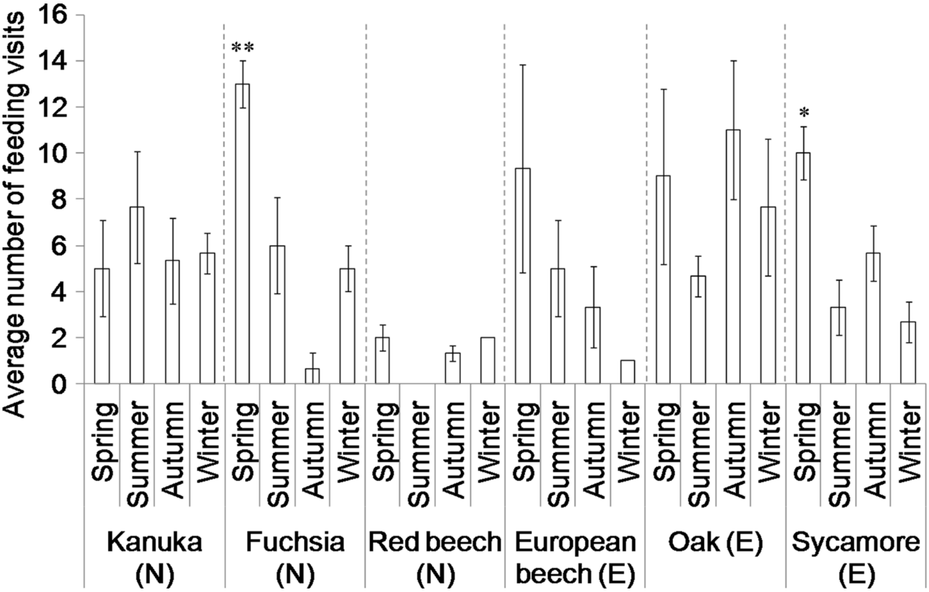

Fig. 2 Avian feeding visits (mean±SE) to the six tree species (*N* native, *E* exotic) each season. Significantly higher number of visits than all other seasons: * $P<0.05$; **<0.1

Number of feeding visits

All birds made more feeding visits to tree fuchsia in spring than in any other season, and fewest in autumn (Fig 2; Table 3). Because exotic birds made very few feeding visits, results were the same when they were removed from analyses. There were more feeding visits to sycamore in spring than in any other season (Fig 2; Table 3). There were more visits to European beech in spring compared to winter (Fig 2; Table 3). The number of feeding visits to kanuka and oak remained consistent throughout the year (kanuka, *p* values: 0.35 – 0.90; oak, *p* values: 0.16 – 0.75).

Discussion

Use of native and exotic trees as food resources by native birds

Native birds in this study were more flexible in their use of the tree species than we predicted: while they spent a lot of time foraging in two of the native tree species (kanuka all year and tree fuchsia late winter-late summer) they spent very little time in red beech, but used exotic oak throughout the year, and exotic sycamore seasonally. Trends in use were unlikely to be due to changing detectability following leaf abscission, as visitations were lowest in winter in deciduous species, when detectability was likely to be highest. Tree species varied considerably both in the extent to which they were visited by birds, and the time birds spent foraging. Only four native and one exotic bird species visited native red beech, whereas native kanuka and tree fuchsia were used by the largest number of native bird species (eight and seven native c.f. two and one exotic species respectively). However, it was the exotic species (oak and European beech) that were used by the largest number of species, because both native and exotic birds used these trees (six native in both and eight and five exotic species respectively). Although the number of species and feeding visits may appear rather low overall, the species recorded in this study (9 native and 11 exotic) represent >80 % of woodland species recorded during monthly counts in a range of woodland patches during a year in the same city

Table 3 Comparison of number of feeding visits for each tree species across four seasons

Tree species	Number of feeding visits				
	Analysis	GLM est.	± SE	*t* value	*P* value
Tree fuchsia	Spring~summer	−7.00	1.841	−3.80	0.0052
	Spring~autumn	−12.33	1.841	−6.70	0.00015
	Spring~winter	−8.00	1.841	−4.35	0.0025
	Summer~autumn	−5.33	1.841	−2.90	0.020
	Winter~autumn	−4.33	1.841	−2.35	0.046
Sycamore	Spring~summer	−6.67	1.581	−4.22	0.0029
	Spring~autumn	−4.33	1.581	−2.74	0.025
	Spring~winter	−7.33	1.581	−4.64	0.0017
European beech	Spring~winter	−8.33	3.712	−2.25	0.055

Only significant results are shown. Seasons written first had more visits than those written second (van Heezik et al. 2008). Native species other than silvereyes occur at very low densities in NZ cities; e.g., between 0.7 and 3.1 /ha (van Heezik and Adams 2014).

Use of trees by birds largely reflected the availability of food resources over the year. Kanuka was visited by insectivorous native birds, including fantails (*Rhipidura fuliginosa*), grey warblers (*Gerygone igata*) and silvereyes, which gleaned trunks and branches year-round. A slight increase in visits in summer was most likely because insectivorous birds were attracted to insect pollinators during the flowering period (Crowe 1992; Fig. 3). Year-round use by several insectivorous native bird species and kanuka's characteristic rough bark (Adams and Morrison 1993; Spurr et al. 2011) suggest this tree harbours a large arthropod biomass. Arthropods are particularly important during breeding, when there is increased insectivorous foraging to feed chicks (Craig et al. 1981; Bergquist 1985; Peach et al. 2008), and during winter, when other resources decline (Gill 1980).

The other well-used native tree species, tree fuchsia, is one of the first to start flowering in late winter, providing early supplies of rich, voluminous nectar and filling the gap between other nectar-producing species such as kowhai (*Sophora microphylla*) and flax (*Phormium tenax*; Baker 2009; Spurr et al. 2011; Fig. 3). Not surprisingly, most visitors to tree fuchsia in this study were nectarivores. Baker (2009) noted that all nectarivorous bird species seem to like it, including exotics such as common starlings (*Sturnus vulgaris*) and crimson rosellas (*Platycercus elegans;* Baker 2009). Visits displayed a "boom and bust" pattern in that most occurred during nectar-production in spring, fewer during fruit-production in summer and then very few until late winter when flowering resumed. Tree fuschia bears fruit early in the season when the general availability of fruit is still quite scarce (Baker 2009), and is one of the few native trees that drop leaves in winter. The almost complete absence of feeding visits in autumn suggests that tree fuchsia is a poor source of arthropods for insectivores relative to what can be found on other species, although other studies have reported that they do support a reasonable abundance of arthropods (Spurr et al. 2011; Barrett 2013).

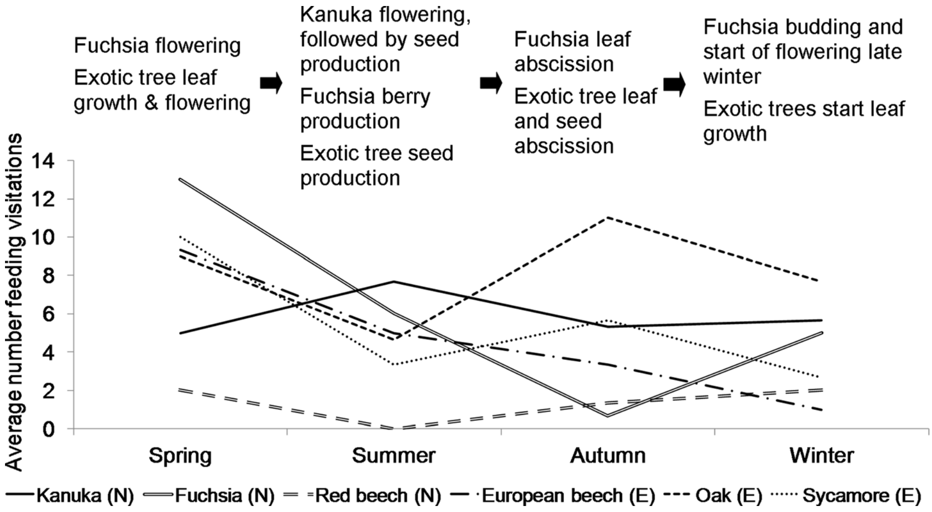

Fig. 3 Phenological changes of the six tree species (*N* native, *E* exotic) and fluctuations in feeding visits throughout the year

We show that being native doesn't necessarily entail being a good food source for native birds. Red beech was seldom visited by any birds throughout the year. Productivity was low, with no perceptible flowers or seeds (Fig. 3). Honeydew is a natural insect-attractant associated with red beech (Murphy and Kelly 2003) but was not present during this study, and may not be present when this species occurs outside its natural range (Tscharntke and Brandl 2004).

We also show that the exotic trees we observed were an important resource for native insectivores. All the exotic tree species were used for foraging, mostly by native birds, and almost entirely for invertebrates. Seasonality of use was high for only one of those species, sycamore, indicating limited support for our second prediction. Sycamore was visited mostly in spring by insectivores, which gleaned branches and foliage. Flowers and fresh leaves may have attracted invertebrates and insectivorous birds at a time when birds were feeding invertebrates to their young (Craig et al. 1981; Bergquist 1985; Peach et al. 2008). In contrast, oak especially and also European beech to a lesser extent were consistently used by native birds throughout the year.

The abundance of invertebrates on trees can vary greatly with seasonal and tree phenological changes, but also between different species (Recher et al. 1996; Helden et al. 2012). Insectivorous birds are known to select between plant species on the basis of arthropod availability (Mackenzie et al. 2014). Oak leaves are most palatable to phytophagous invertebrates in spring (Southwood et al. 2004), leading to a higher invertebrate abundance at this time (Feeny 1970; Waite et al. 2012). However, oak was visited in this study by native birds in all seasons, suggesting arthropod biomass remains relatively high throughout the year, even during leaf abscission, possibly due to the roughness of the bark in comparison to European beech and sycamore. Increased time spent feeding on arthropods in oak in autumn and winter may be due to a reduction in availability of nectar and fruit in other plant species.

In their natural range (Europe), sycamore and oak have more abundant arthropods and leafhoppers than European beech (Claridge and Wilson 1981; Kennedy and Southwood 1984; Rushforth 1999). In New Zealand, little is known about the invertebrate communities on these species, but both kanuka and oak appear to provide year-round invertebrate resources for insectivorous foragers, with oak acting as a good alternative to kanuka in more urbanised areas, such as parks, where oaks are popular for planting. While non-native plants are known to be less palatable to local herbivorous invertebrates than native plants, and support fewer species and lower abundance of insects (Tallamy and Shropshire 2009; Tallamy et al. 2010), seasonal patterns of foraging by birds in this study did not indicate any overall preference for native over exotic tree species. Mackenzie et al. (2014) also found little discrimination between native and non-native trees and shrubs by foraging insectivorous great tits (*Parus major*), in contrast to blue tits (*Cyanistes caeruleus*), which foraged more often in native than exotic plants. The absence of information on arthropod abundance associated with different tree species existing out of their natural range, including in New Zealand, means it is difficult to evaluate whether the varied use of exotic trees reflects arthropod abundance. Some studies have shown that exotic plants are not necessarily invertebrate-poor: exotic-dominated gardens and well-established exotic plants can harbour abundant biomasses of invertebrates (Esler 1990; Smith et al. 2006; Brändle et al. 2008; Waite et al. 2012).

Flexible feeding strategies in native birds

The native bird species we observed typically demonstrate flexibility in their feeding. Bellbird (*Anthornis melanura*) and the native wood pigeon/ kereru (*Hemiphaga novaeseelandiae*) browse on a wide range of plant species (Spurr et al. 2011; McEwen 1978; Baker 1999; Campbell et al. 2008), grey warblers use numerous foraging methods or surfaces (Moon 2009) and fantails forage across various habitat types (Williams and Karl 2002). Some use bird-feeders and garden resources, such as the tui (*Prosthemadera novaeseelandiae*), silvereye and bellbird (Spurr 2012). Species equipped with a variety of foraging strategies can more easily cope with environmental changes than those with narrower, more specialised diets (Walker 2006). The small proportion of native birds that have adapted to urbanisation are most likely those with less specialised foraging habits. Most of the native bird species we observed used both native and exotic tree species. Increasingly more positive associations between native birds and exotic plants are being reported (Buchanan 1989; Corlett 2005; Aslan and Rejmanek 2010). For example, the kereru has incorporated at least 50 exotic plant species into its diet (McEwen 1978; Allen and Lee 1992).

Despite this flexibility, the native bird species we observed exist at much lower densities in the city than exotic species (van Heezik and Seddon 2012), indicating that their populations must be limited by other factors. For example, native birds that are dependent on the presence of trees will be disadvantaged by the low density of trees in private gardens, which cover substantial proportions of city areas (Mathieu et al. 2007, Loram et al. 2007). Native species may also be more susceptible to cat (*Felis catus*) predation (van Heezik *et al*. 2010), competition and aggressive behaviour of other species (Borowske et al. 2012), and less likely to habituate to human activity (Miller et al. 1998).

The silvereye was the most prevalent native species observed, dominating all other species in number of feeding visits in five of six tree species. Silvereyes are self-introduced from Australia in the 1850s and their use of diverse food sources, including a variety of arthropods, fruit, nectar and seeds from a wide range of substrates and native and exotic plants, has facilitated their spread: they are the most common native garden bird in New Zealand (Moeed 1979; Williams and Karl 1996; Spurr 2012). Time spent feeding by silvereyes in all tree species except red beech did not vary across the seasons, except for an increase in insectivorous gleaning behaviour in winter when nectar and fruit were absent, emphasizing their wide foraging abilities and possibly explaining their abundance in cities.

Choosing plants for enhancing urban native birds

The scarcity of native vegetation across urban landscapes means that natural winter food resources, including arthropods, are less abundant in cities (McIntyre 2000; Tallamy et al. 2010). Planting native and exotic species that provide food outside the usual seasonal period may benefit urban birds by extending the availability of food (Williams and Karl 1996; Corlett 2005) and reducing the need for birds to use anthropogenic food sources or feeders, which can alter community composition, spread disease and increase predator/competitor populations (Fuller et al. 2008; Jones and Reynolds 2008). Some ornamental plants have been cultivated to bear flowers and produce nectar prolifically year-round (Beardsell et al. 1993; Sewell and Catterall 1998; Brown et al. 2010) and are exploited by urban native birds (Michelsen-Heath and Sohle 2005; Campbell et al. 2008). Because of these native bird-exotic plant associations, large-scale removal of exotic plants could have detrimental effects on the survival of urban native birds (Ridley 1998; Campbell et al. 2008).

While it is important to keep native forest remnants intact by controlling pest species such as sycamore, which outcompetes native trees through its huge seed set, efficient wind-dispersal and fast seedling growth (Howell 2008), the incorporation of a variety of non-invasive exotic species into gardens and parks could provide alternative food resources and enhance native bird populations (Alvey 2006). Residents' preferences on what to plant in their gardens vary widely, with some people preferring exotic plants over natives (Kendal et al. 2012; Kirkpatrick et al. 2012). Suburban exotic plantings could be used if they do not have negative impacts on native plants in forest remnants and offer resources to native birds. Increasingly non-native species are shown to play an important conservation role in providing resources for maintaining native populations (Schlaepfer et al. 2010; Shackelford et al. 2013). Management practices that incorporate both native and exotic plant diversity have the potential to increase native foraging opportunities and native bird diversity, but need to incorporate both fine-scale (residential gardens) and large-scale (i.e., community-based) actions (Pennington and Blair 2011).

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