

REVIEW ARTICLE

Seed dispersal of fleshy-fruited environmental weeds in New Zealand

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Published online: 26 March 2015

Abstract: Fruit-eating animals play a key role in spreading non-native environmental weeds, via seed ingestion and subsequent dispersal. We reviewed available information on dispersal of fleshy-fruited environmental weeds in New Zealand. We found almost a third (32.9%) of 295 environmental weed species in New Zealand have fleshy fruits adapted for internal dispersal by animals. Fruiting phenology differs between weeds and native plants, with many weed species fruiting from late autumn until early spring (May to September) when native fruits are scarce. Weed fruiting duration does not differ from natives. Eight birds and two mammals are the main dispersers of weed seeds in New Zealand: blackbirds (*Turdus merula*), silvereyes (*Zosterops lateralis*), starlings (*Sturnus vulgaris*), kereru (New Zealand pigeons, *Hemiphaga novaeseelandiae*), song thrushes (*Turdus philomelos*), tui (*Prosthemadera novaeseelandiae*), bellbirds (*Anthornis melanura*), mynas (*Acridotheres tristis*), brushtail possums (*Trichosurus vulpecula*) and feral pigs (*Sus scrofa*). All 10 species include significant quantities of fruit in their diet annually or seasonally and are widespread in New Zealand. The bird dispersers rarely damage ingested seeds. Possums and pigs destroy some seeds, but possums in particular are likely to disperse several smaller-seeded weeds. Blackbirds, silvereyes and starlings are probably the most important dispersers; they are the most widespread birds, and all disperse more than 20 weed species. Starlings pose additional risks because they disperse seeds long distances to roost sites, including offshore islands. The kereru is a significant disperser of weed seeds also, and the key disperser for three species with large, single-seeded fruits. Most seeds are likely to be dispersed less than 100 m by birds, with some dispersed hundreds of metres or even several kilometres (by birds and mammals). Reducing the spread of fleshy-fruited weeds via animal ingestion is challenging. Potential management tools include reducing invasive mammal abundance and seed availability using traditional or biological control (particularly in populations that are major seed sources for dispersal to high value sites), providing alternative native food sources by planting natives that fruit at peak weed fruiting times, and targeting favoured roost sites for surveillance and control.

Keywords: biological invasions; conservation; dispersal distance; endozoochory; frugivory; germination; invasive plants; mutualisms; phenology; vertebrate dispersal

Introduction

Environmental weeds are one of the greatest threats to native biodiversity in New Zealand (Williams & West 2000). Environmental weeds (sensu Falk-Petersen et al. 2006) are non-native plant taxa that invade natural ecosystems and have the potential to affect native biodiversity or ecosystem function (hereafter referred to as 'weeds'). New Zealand has a large naturalised flora (2390 species; Howell & Sawyer 2006), of which 328 species (13.7%) were classified as environmental weeds in 2008 (Howell 2008). No doubt this list will expand over time, as more species become invasive. Many weeds have fleshy fruits eaten by animals, which disperse ingested seeds by defecating or regurgitating them away from the parent plant (Gosper et al. 2005). Understanding frugivore-mediated seed dispersal is essential for effectively managing the spread of established weeds in New Zealand, predicting how far newly naturalised species will spread, and assessing the feasibility of successful eradication.

Recent reviews have highlighted the importance of fruit-eating animals in facilitating weed spread (Richardson et al.

2000; Gosper et al. 2005; Buckley et al. 2006; McConkey et al. 2012). Weeds may be more likely to be animal-dispersed and have more frugivores and seed dispersers than non-invasive naturalised species (Lloret et al. 2004; Gosper & Vivian-Smith 2009b; Heleno et al. 2013b). Because animal-dispersed seeds can move long distances (e.g. Holbrook et al. 2002), there is considerable scope for the spread of vertebrate-dispersed weeds, especially to isolated high-value conservation sites such as offshore islands. Long-distance dispersal by vertebrate frugivores may also play a key role in achieving or maintaining large geographical ranges (Clark et al. 1998). For example, New Zealand native trees with a wide latitudinal range are nearly twice as likely as narrow range trees to have fleshy fruits (McGlone et al. 2010).

Fruit traits, disperser attributes, and local habitat and landscape features may influence invasion patterns of fleshy-fruited weeds (Gosper et al. 2005). Fruit size, number of seeds, and the timing of fruit production can influence fruit consumption and seed dispersal patterns (Howe & Vande Kerckhove 1981; Wheelwright 1985; Kitamura et al. 2002). Frugivore traits that contribute to weed invasions include diet

composition, gape size, fruit handling techniques, seed retention time (time from fruit ingestion to defecation or regurgitation of seed), and movements (Gosper et al. 2005). For example, avian frugivores are limited by their gape width in the maximum size of fruits they can swallow, especially for single-seeded fruits that usually have to be swallowed whole to be dispersed (Wheelwright 1985). Frugivores can also affect germination by removing fruit pulp from the seed and scarifying the seed coat (Robertson et al. 2006) or by damaging seeds.

Although many weed species in New Zealand have fleshy fruits (Timmins & Williams 1987), information on their dispersal by animals is scattered throughout the literature. This paper reviews available information on vertebrate dispersal of fleshy-fruited weeds in New Zealand. Specifically, we addressed the following questions: (1) What proportion of the New Zealand weed flora has fleshy fruits adapted for vertebrate dispersal? (2) Does fruit size limit dispersal of any weeds? (3) Does fruiting phenology or duration differ between weeds and natives? and (4) Which animal species are the main dispersers of fleshy-fruited weeds?

We reviewed only adaptive seed dispersal mechanisms, focusing on internal dispersal of fleshy fruits by animals. Many weeds spread primarily via dispersal of vegetative fragments and human activities such as dumping of garden refuse (Sullivan et al. 2005; Butcher & Kelly 2011). However, these dispersal mechanisms are likely to produce different patterns of spread (Gosper et al. 2005) and are beyond the scope of this paper. We excluded invertebrate species (e.g. ants and weta) from this review as little information is currently available on seed dispersal by these vectors in New Zealand. We also discuss management implications for the spread of fleshy-fruited weeds via seed dispersal.

Methods

Weed traits

We reviewed the literature to determine which species have fleshy fruits dispersed internally by vertebrates for each of 295 weeds. We used Howell's (2008) list of 328 environmental weeds in New Zealand. This national list includes all naturalised vascular plant species on land administered by the Department of Conservation either being controlled or having a damaging effect on biodiversity on conservation land (Howell 2008). We excluded three native species (two of which have fleshy fruits) that are weedy outside their natural range (*Muehlenbeckia australis*, *Pittosporum crassifolium* and *Metrosideros excelsa*), six ferns or fern allies (which lack seeds), and 24 aquatic species that were in Howell's (2008) list.

We determined seed dispersal mechanisms using published reports of dispersal in that species (or a congener with similar morphology) in New Zealand. We used overseas accounts of dispersal where no information was available from New Zealand. When no published information was available for that species or a congener, we assigned the dispersal mechanism on the basis of seed or fruit morphology. Species with fleshy fruits (berries, drupes, compound drupelets, arillate fruits, or other fleshy appendages attractive to vertebrates) were assumed to be dispersed internally by frugivorous animals. For some species, the primary dispersal mechanism assigned differed among authors. In these cases, to attribute dispersal mechanisms we used evidence in the following order of decreasing priority: (1) direct observation or experimentation, (2) dispersal unit

morphology, and (3) the method used was not reported.

For fleshy-fruited weeds we compiled information on fruit width, seed width, seed mass, number of seeds per fruit, and fruiting phenology. We used data from New Zealand where possible, and also from overseas. We included measurements for the dispersal unit. For example, for dehiscent capsules containing seeds with fleshy arils, we used the width of the arillate seed rather than the capsule width. For compound fruits (e.g. *Rubus fruticosus*), we used the width of the whole fruiting structure. For globose fruits, we considered fruit width to be equal to fruit length where only length was reported. For each weed species, we used the smallest reported fruit width as an estimate of which disperser species could potentially swallow fruits whole.

Where ripe fruit availability was determined using Northern Hemisphere data, we adjusted fruiting times to the corresponding season in New Zealand. For example, a weed fruiting in September in the Northern Hemisphere was recorded as fruiting in March in New Zealand. We compared the timing and duration of fruit availability for 59 weed species (where monthly fruiting data were available) with 59 native fleshy-fruited species (Webb et al. 1988) selected at random from a pool of 349 species (Thorsen et al. 2009). We used a chi-square test to determine whether the number of species fruiting in each month was independent of species status (i.e. native or weed). We used non-parametric bootstrap resampling to determine whether mean number of months fruiting (fruiting duration) was the same for natives and weeds. Data were resampled with replacement with 1000 bootstrap iterations using the *boot* package in R 2.15.3. (R Core Team 2013).

Frugivore traits

We collated from the literature, and unpublished sources, New Zealand records of vertebrates feeding on weed fruits or defecating weed seeds. We grouped observations into the following categories, in decreasing order of potential dispersal effectiveness: (1) viable seeds found in droppings; (2) intact seeds found in droppings; (3) observed feeding on fruits.

We used available information to assess the importance of each frugivore. We included data on consumption and dispersal of native fruits where relevant. Plant species referred to in this paper are non-native, unless otherwise specified.

We defined major dispersers as animals that eat significant quantities of fruit either seasonally or year-round (>5% of annual diet), are relatively widespread (occurring in > 25% of New Zealand map grids; King 2005; Robertson et al. 2007), and pass a significant proportion ($\geq 20\%$) of ingested seeds intact. For major dispersers we collated information (from the New Zealand literature where possible, and also from overseas) on maximum gape size (for birds), maximum size of fruits swallowed, percentage fruit in diet, daily distances moved, time spent in fruiting trees after feeding (residence time, for birds), and seed retention time. We defined minor seed dispersers as those that are range-restricted (in <10% of New Zealand map grids; King 2005; Robertson et al. 2007), eat fruit only occasionally, or destroy most (>95%) seeds ingested.

The distance that fruit-eating animals disperse seeds is a function of seed retention times and daily movement patterns. We used modelled estimates of seed dispersal distance for endemic kererū (New Zealand pigeon, *Hemiphaga novaeseelandiae*) and tūi (*Prosthemadera novaeseelandiae*). For non-native song thrushes (*Turdus philomelos*), blackbirds (*T. merula*), mynas (*Acridotheres tristis*) and brushtail possums (*Trichosurus vulpecula*), and endemic bellbirds (*Anthornis*

melanura), we estimated mean daily distance moved by converting territory or home range size (m²) to linear metres on the basis of the length of one side of a square (after Williams 2006). We were unable to find home range sizes or daily distances moved for native silvereyes (*Zosterops lateralis*) so lack dispersal distance estimates for this species. For non-native starlings (*Sturnus vulgaris*) we used daily flight distance to overnight roosts to estimate maximum seed dispersal distance. We used home range length (McIlroy 1989) to estimate daily movements of the non-native pig (*Sus scrofa*). Seed retention times were unavailable for bellbirds and mynas and were therefore estimated on the basis of body mass (Higgins et al. 2001, 2006), which is strongly correlated with seed retention time (Herrera 1984; Wotton & Kelly 2012).

Results

Weed traits

Of the 295 weeds in our review, 97 (32.9%) have fleshy fruits adapted to vertebrate dispersal (Appendix S1). This excludes species with fleshy fruits in their native range that do not fruit in New Zealand. Even if the 24 aquatic species are included, 30.4% of weeds are vertebrate dispersed. To date, vertebrate

frugivory or seed dispersal has been observed for only 53 (54.6%) of these fleshy-fruited weeds (Appendix S2).

Weed fruits ranged from 2 mm (*Gunnera tinctoria*) to 80 mm wide (*Prunus persica*, peach) (Appendix S1). Mean fruit width across all species for which data were available was 13.88 mm (± 12.30 SD, n = 87), although data were left-skewed (median 9 mm; Fig. 1). Single-seeded fruits were smaller, with a mean fruit width of 12.03 ± 11.22 mm (median 8 mm, n = 29). Minimum fruit width in single-seeded fruits averaged 9.01 ± 6.80 mm (n = 32). Most (71.9%) single-seeded weed species have at least some small fruits (< 10 mm minimum width) that can be swallowed whole by all major dispersers (Fig. 1, Table 1). Of the 32 single-seeded weed species where data were available, only three (9.4%) had fruits 10–15 mm wide, which are too large to be swallowed by silvereyes, bellbirds and possums (Table 1, Fig. 1).

The kererū is the key disperser for three single-seeded species with large fruits (>15 mm; Table 1, Fig. 1): *Eriobotrya japonica*, *Prunus cerasifera*, and *P. ×domestica*. Feral pigs could potentially disperse these species also, if seeds survive ingestion. Other birds have been reported feeding on *Prunus cerasifera* and *P. ×domestica* fruits (Appendix S2). *Eriobotrya japonica* fruits in New Zealand are up to 35 mm wide (Webb et al. 1988) and even the average fruit width (24.5 mm in Australia; Gosper & Vivian-Smith 2010) is at the upper limit of kererū swallowing capacity (Gibb 1970) and well beyond the limit of other birds (Table 1). Several multi-seeded weeds (e.g. *Ficus macrophylla*, *Opuntia monacantha*, *Passiflora caerulea*, *P. edulis*, *P. tarminiana*, and *Psidium guajava*) also have fruits too large for dispersers other than kererū to swallow whole. However, smaller bird and mammal species can eat multi-seeded fruits in pieces and disperse seeds. *Prunus persica* is the only single-seeded weed in New Zealand lacking potential seed dispersers because its fruits are too large to swallow whole.

Fruiting phenology differed between natives and weeds ($\chi^2 = 54.2359$, d.f. = 11, $P < 0.0001$). Native species had a

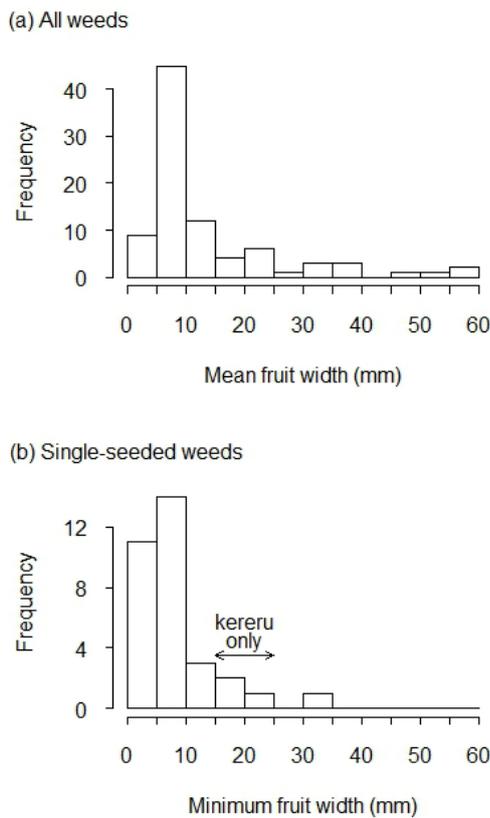


Figure 1. Fruit width of fleshy-fruited environmental weeds in New Zealand. (a) Mean fruit width of all weed species for which data were available (n = 87). (b) Minimum fruit width of single-seeded weed species in New Zealand (n = 32). The arrow indicates weed species where even the smallest fruits are too large for dispersers other than kererū to swallow whole. Fruits smaller than 15 mm can potentially be swallowed by a range of dispersers. The upper gape limit of kererū is around 25 mm (Gibb 1970). Only one single-seeded species (*Prunus persica*) is too large for kererū to swallow.

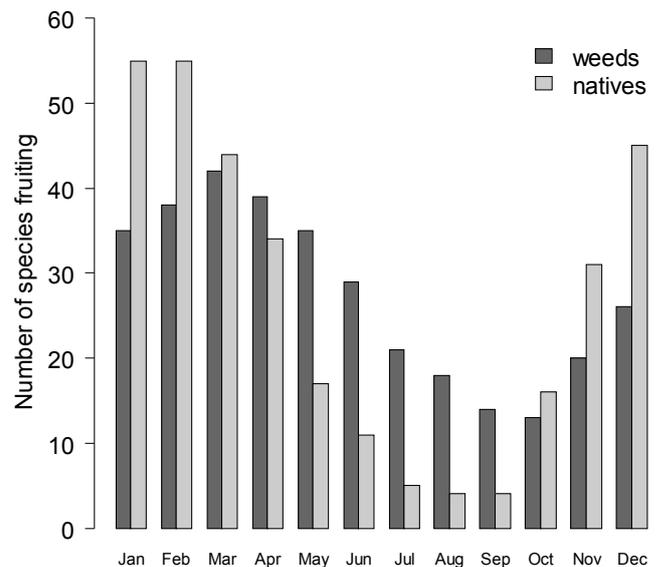


Figure 2. Seasonal fruit availability of 59 environmental weed species and 59 randomly selected native fleshy-fruited species in New Zealand. Fruiting phenology differed between weeds and natives ($\chi^2 = 54.2359$, d.f. = 11, $P < 0.0001$).

Table 1. Attributes of major vertebrate seed dispersers in New Zealand and recorded number of weed species dispersed. Fruit size = maximum width of fruits reported swallowed, with maximum gape width for birds in brackets (Williams et al. 2000; Kelly et al. 2010). Data are presented as means, with range or maximum and number of populations or studies where greater than one in parentheses where applicable. For studies with seed retention times for more than one plant species, retention times were averaged across plant species. See Appendix S2 for details of weed frugivory and seed dispersal records.

Disperser	No. weeds dispersed	Fruit size (mm)	% fruit in diet	Dispersal distance (m)	Daily movement (m)	Residence time (min)	Seed retention time (min)	References
Birds								
Blackbird (<i>Turdus merula</i>)	26	13.0 (13.0)	25.5	–	75 (1600, 2)	1.2	26.7 (6.5–73.7, 2)	Gurr 1954; Bull 1958; Herrera & Jordano 1981; Sorensen 1984; Barnea et al. 1991; O'Donnell & Dilks 1994; Williams 2006
Silvereye (<i>Zosterops lateralis</i>)	24	9.9 (6.3)	10.5	–	–	1	20.4 (6–57, 2)	French et al. 1992; O'Donnell & Dilks 1994; French 1996; Stanley & Lill 2002
Starling (<i>Sturnus vulgaris</i>)	21	(12.7)	6.3	–	– (30 000)	–	38 (15–50, 2)	Coleman 1977; Karasov & Levey 1990; Heather & Robertson 2005; LaFleur et al. 2009
Kererū (<i>Hemiphaga novaeseelandiae</i>)	17	25.0 (14.0)	69.7 (31.2–89.9, 6)	85 (1500, 2)	77 (33 000)	27 (1–315, 2)	111 (19–330, 3)	Clout & Tilley 1992; O'Donnell & Dilks 1994; Trass 2000; Dijkgraaf 2002; Wotton et al. 2008; Emeny et al. 2009; Powlesland et al. 2011; Wotton & Kelly 2012; Powlesland et al. unpubl. data
Tūi (<i>Prothemadera novaeseelandiae</i>)	12	(11.0)	12.7 (5.9–21.7, 5)	223 (2168)	78 (>10 000)	10.8 (>60)	35.5 (9–91, 2)	Gravatt 1971; Bergquist 1985a; Stewart & Craig 1985; O'Donnell & Dilks 1994; Trass 2000; O'Connor 2006; Powlesland et al. unpubl. data
Song thrush (<i>Turdus philomelos</i>)	9	(14.6)	–	–	105 [#] 182 [*]	–	43	Herrera 1984; Williams & Karl 1996; Peach et al. 2004
Bellbird (<i>Anthornis melanura</i>)	9	9.7 (8.5)	7.8 (4.9–15.7, 4)	–	33.6 (3)	–	22.9 ⁺	Gravatt 1971; Craig & Douglas 1986; O'Donnell & Dilks 1994; Murphy & Kelly 2001; Brunton et al. 2008
Myna (<i>Acridotheres tristis</i>)	3	(14.5)	–	–	91.1 (100–700) [#] 120.8 (12 000) [*]	3	40.2 ⁺	Wilson 1971; Counsilman 1974; Wood 1995; Pell & Tidemann 1997; Staddon et al. 2010
Mammals								
Possum (<i>Trichosurus vulpecula</i>)	11	10.0	23.3 (2.5–69, 9)	–	397 (1600, 24)	–	5428.8 (1440–17 280)	Owen & Norton 1995; Parkes & Thomson 1995; Nugent et al. 1997; Sweetapple & Nugent 1998; Cowan & Clout 2000; Nugent et al. 2000; Williams et al. 2000; Dungan et al. 2002; Glen et al. 2012
Pig (<i>Sus scrofa</i>)	2	9	35.6	–	1100 (3600)	–	2880 (11 520)	Thomson & Challies 1988; McIlroy 1989; Setter et al. 2002; O'Connor & Kelly 2012

⁺ Estimated based on body weight (see text for details); [#] breeding season; ^{*} non-breeding season; – no data available.

more pronounced fruit production peak than weeds, with most native fruits available from November to April (Fig. 2). Weed fruiting was spread more evenly throughout the year. Most fleshy-fruited weed species produce ripe fruits from January to May (Fig. 2). However, ripe fruits of many weed species are available from May to September, when native fruits are scarce (Fig. 2, Appendix S1). At least five weeds (*Berberis darwinii*, *Carpobrotus edulis*, *Cestrum parqui*, *Lantana camara* and *Phytolacca octandra*) can produce fruit year-round (Appendix S1). However, weed fruiting duration (5.6 ± 2.7 months, median = 5.0) did not differ from native species (5.4 ± 2.1 , 5.0). Bootstrap confidence intervals for fruiting duration overlapped almost completely (weeds: mean = 5.59, 95% bias-corrected and accelerated confidence interval

(bca CI) = 4.94 to 6.33; and natives: mean = 5.44, 95% bca CI = 4.90 to 6.00).

Major seed dispersers

Eight birds (non-native blackbird, song thrush, starling and myna, native silvereye, and endemic kererū, tūi, and bellbird) are major seed dispersers with the potential to spread fleshy-fruited weeds in New Zealand (Table 1). All eight species consume significant quantities of fruit (either seasonally or year-round), are widespread throughout the main islands of New Zealand, and generally do not damage or destroy ingested seeds. In addition, two invasive mammal species (possums and pigs) probably disperse several weed species.

Proportion of fruit in diet

All 10 major dispersers eat significant quantities of fruit, either seasonally or annually (>5% annual diet). Kererū are highly frugivorous, with fruit comprising up to 90% of their diet in northern New Zealand where native fruit is available all year (Dijkgraaf 2002). Blackbirds in Westland ate fruits year-round, but fruits were most important in late summer and autumn when they comprised >40% of blackbird diet (O'Donnell & Dilks 1994). Fruit comprises a small proportion of the annual diet of tūi, bellbirds, and silvereyes (Table 1), but is important seasonally (Gravatt 1971; O'Donnell & Dilks 1994; Murphy & Kelly 2001). Tūi and bellbirds in Westland ate fruit in all months, but fruit consumption peaked in April (48%) for tūi and June (16%) for bellbirds (O'Donnell & Dilks 1994). Silvereyes in Westland also ate fruit year-round, with peaks (12–18% of feeding observations) from April to August (O'Donnell & Dilks 1994). Fruits occurred in 14–100% of song thrush droppings at three sites near Nelson, although only 13 droppings were collected (Williams & Karl 1996).

New Zealand studies found fruits and seeds in the gut of 44% of starlings sampled throughout the year (Moeed 1980) and 59% of mynas (Wilson 1965, cited in Higgins et al. 2006). Starlings can form extremely large flocks and disperse huge quantities of seeds (c. 200–3700 seeds m⁻¹ month⁻¹ in peak fruiting season; Ferguson & Drake 1999; Anderson et al. 2006).

Possoms eat fruit in proportion to its availability, with fruit comprising up to 69% of their diet (Nugent et al. 2000; Williams et al. 2000). Feral pigs can include significant quantities of fruit in their diet (Table 1), but are limited to low-hanging fruits or those on the ground.

Native versus non-native fruits

Several studies report that endemic frugivores (kererū, tūi and bellbird) eat fewer non-native fruits than native silvereyes and non-native birds (blackbird, song thrush and starling, Fig. 3; Williams & Karl 1996; MacFarlane 2012; G. Henderson & D. Kelly unpubl. data). The percentage of non-native fruits eaten by non-native birds was highly variable but endemic birds consistently ate few non-native fruits (Fig. 3). Kererū in Auckland ate more non-native fruits in late winter and early spring when native fruits were scarce (Karan 2000). Non-native fruits were unimportant in the diet of bellbirds and tūi near Nelson, comprising less than 2% of fruit dry weight eaten (Williams & Karl 1996).

Number of weed species eaten

Blackbirds have been reported eating fruits and dispersing seeds of the greatest number of weeds (26 species) in New Zealand, closely followed by silvereyes and starlings (Table 1; Appendix S2). Of the endemic frugivores, kererū have been recorded eating fruits of the most weed species (17; Table 1, Appendix S2). Possoms have been recorded eating fruits of a similar number of weeds (10 species) to tūi, bellbirds and song thrushes. Pigs have been reported eating fruits and dispersing seeds of two weed species to date.

Frugivore feeding behaviour

New Zealand birds generally swallow fruits whole (Burrows 1994a; Mladovan 1998, cited in Bass et al. 2006), although blackbirds and song thrushes sometimes carry larger fruits than they can swallow away from the parent tree before consumption (Snow & Snow 1988; Hernández 2008). Blackbirds have been recorded moving fruits of the weeds *Syzygium smithii* and *S. australe* in this manner, sometimes more than 50 m (Karan

2000). Song thrushes, blackbirds and silvereyes can peck the pulp of fruits too large to swallow whole, either on the plant or on the ground (Snow & Snow 1988; Burrows 1994a; Stanley & Lill 2002).

Mammals have not been reported caching seeds in the wild in New Zealand. Possums eat large fruits such as *Passiflora tripartita* var. *mollissima* in pieces (Beavon & Kelly in press). In captive feeding trials, possums discarded c. 14% of seeds from fruits of several weed species eaten and swallowed remaining seeds (Williams et al. 2000). Possums ate the pulp and discarded seeds of all native miro (*Prumnopitys ferruginea*) fruits, the largest-seeded species in the study (mean seed width 9 mm; Williams et al. 2000). Captive pigs chewed and swallowed all native mataī (*P. taxifolia*) fruits offered to them (O'Connor & Kelly 2012). Thus, in New Zealand most small fruits are swallowed whole.

Effect of seed ingestion on germination

Frugivorous birds generally have little effect on seed germination (Robertson et al. 2006) and New Zealand avian dispersers are no exception (Beveridge 1964; LaRosa et al. 1985; Barnea et al. 1991; Clout & Tilley 1992; Burrows 1994a; French 1996; Trass 2000; Logan & Xu 2006; LaFleur et al. 2009). In contrast, because mammals chew they can crush seeds and act as seed predators in a way that most birds (excluding finches and some parrots) never do.

Possoms can damage significant proportions of ingested seeds (e.g. 78.7% for elder; Dungan et al. 2002), but some species (e.g. *Crataegus monogyna*) are largely unharmed (Bass 1990). Small seeds and those with hard seed coats tend

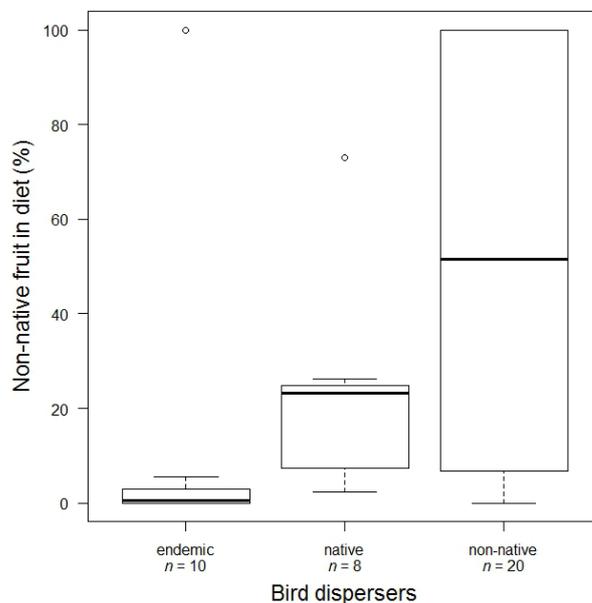


Figure 3. Percentage of non-native fruits eaten by endemic (kererū, tūi and bellbird), native (silvereye) and non-native (blackbird, song thrush and starling) bird dispersers in New Zealand. Data from Williams & Karl (1996; presence of seeds in faeces at three sites), MacFarlane (2012; presence of seeds in faeces at one site) and Henderson & Kelly (unpubl. data; fruit feeding observations at four sites). Data points are individual bird species at each site. Native and non-native fruits were present at all sites. Endemic, native and non-native birds were present at all sites except two where only native and non-native birds were present (Henderson & Kelly unpubl. data).

to be physically undamaged after ingestion by possums but larger seeds are crushed (Burrows 1994b; Williams et al. 2000; Young 2012). In a New Zealand native alpine plant community, 96.6% of seeds in possum droppings were intact, although seed viability was unknown (Young 2012). In captive feeding trials possums defecated 34% of ingested seeds intact across 12 plant species (mostly weeds, seed width 0.08–4.2 mm; Williams et al. 2000). Of these intact seeds, 24.7% germinated, compared with 42.2% of uneaten seeds (Williams et al. 2000). Possum ingestion significantly decreased germination of *Berberis glaucocarpa*, *Leycesteria formosa*, and *Pyracantha angustifolia* seeds, but increased germination of *Cotoneaster glaucophyllus* (Williams et al. 2000). About 15% of native seeds in 54 wild possum faecal pellets were destroyed, and possum ingestion reduced germination of *Coprosma robusta* seeds compared with birds (30% germination compared with 60–70%; Wyman 2013).

Pigs can destroy many seeds, particularly for larger seeded species. In controlled experiments, feral pigs damaged 23% of *Annona glabra* seeds ingested (Setter et al. 2002). *Prosopis pallida* and *Passiflora tripartita* var. *mollissima* seeds in feral pig droppings had 19.3% (Lynes & Campbell 2000) and 1.6% (Beavon & Kelly in press) of seeds damaged, respectively. Under field conditions, *P. tripartita* var. *mollissima* seed germination was greater for pig-ingested seeds than hand-cleaned seeds and seeds with pulp, but less than in whole fruits (Beavon & Kelly in press). In captive feeding trials, pigs destroyed 86% of medium-sized (≥ 7 mm seed width) native *Prumnopitys taxifolia* (mataī) seeds (O'Connor & Kelly 2012). Mataī seeds that were defecated intact by pigs germinated as well as hand-cleaned seeds (O'Connor & Kelly 2012).

Distribution and habitat use

Blackbirds, song thrushes and silvereyes are the most widely distributed avian seed dispersers, and are found virtually

throughout mainland New Zealand (Robertson et al. 2007). Starlings are also widely distributed (Robertson et al. 2007), although they are absent from mountainous areas (Heather & Robertson 2005). Endemic seed dispersers (tūi, bellbird and kererū) are widespread throughout New Zealand but have a more patchy distribution and are often uncommon or absent in Northland, Waikato, southern Hawke’s Bay, Wairarapa, and eastern parts of the South Island (Robertson et al. 2007). Mynas are largely restricted to the North Island from New Plymouth and Hawke’s Bay northwards (Robertson et al. 2007). Possums and pigs are generally found throughout New Zealand, although they remain scarce or absent in some areas (Cowan 2005; McIlroy 2005). In 2000, pigs occupied 93 000 km² or 34% of New Zealand (Fraser et al. 2000).

Endemic birds are observed in native forest more frequently than native silvereyes and non-native birds (Fig. 4). Non-native birds are most commonly recorded in farmland (Fig. 4). Starlings and mynas are common at forest edges, but rarely venture far into intact forests (Heather & Robertson 2005).

Possums occur mainly in native and exotic forests, but can also be found in native and exotic grasslands, montane scrublands, shelter belts, orchards and cropping areas, thermal areas, swamps, sand dunes, and urban areas (Cowan 2005). Preferred habitats of feral pigs are native and exotic forests, dense gorse or bracken stands near farmland, marginal or reverting farmland, and river flats and tussock grassland with patches of shelter (Wodzicki 1950; Roberts 1968).

Many of the seed-dispersers in New Zealand travel readily between habitat types. Blackbirds, silvereyes (Williams 2006), kererū (Wotton & Kelly 2012), bellbirds (MacLeod et al. 2012) and tūi (van Heezik et al. 2008) use both urban areas and native forest, facilitating the spread of weeds from cities and towns to native ecosystems. In Canterbury, possums regularly moved between subalpine shrubland and adjacent forest (Young 2012).

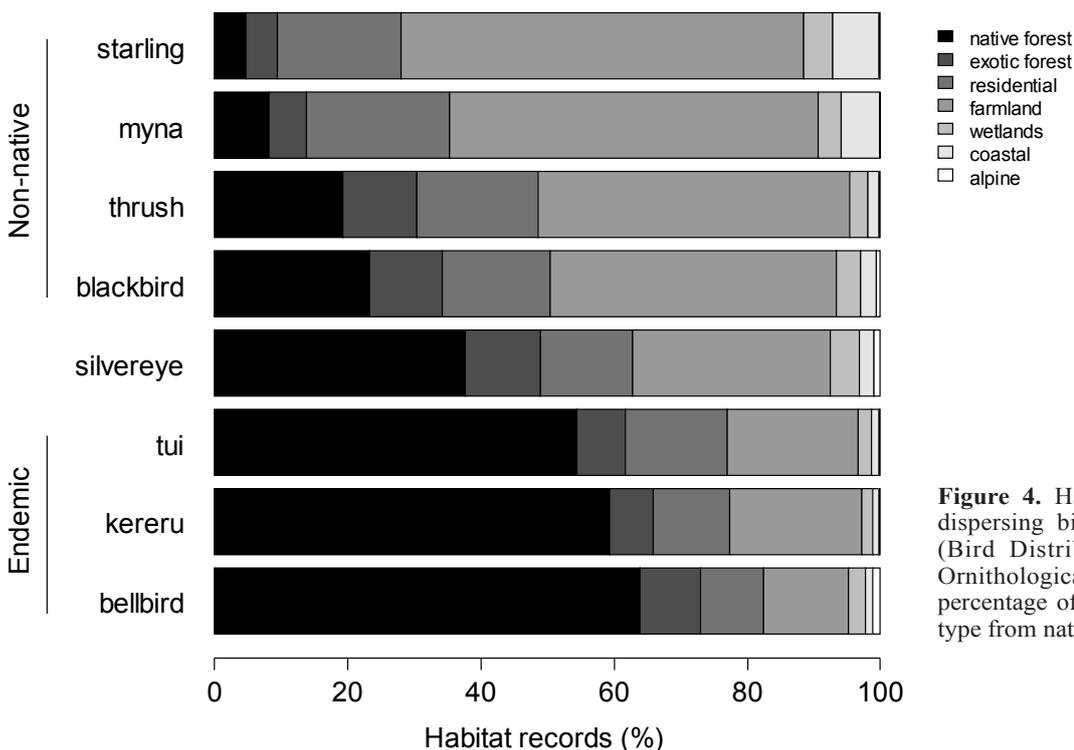


Figure 4. Habitats used by major seed-dispersing bird species in New Zealand (Bird Distribution Data 1999–2004 © Ornithological Society NZ). Data show percentage of observations in each habitat type from nationwide bird surveys.

Seed dispersal distance

Most bird-dispersed seeds are deposited less than 100 m from the source plant, regardless of the bird species (Burrows 1994b; O'Connor 2006; Williams 2006; Wotton & Kelly 2012). Some notable exceptions include transport of seeds to islands by starlings (Brookie 1983; Ferguson & Drake 1999; Anderson et al. 2006) and long-distance dispersal by tūī (O'Connor 2006), kererū (Wotton & Kelly 2012) and possibly myna (Wilson 1971; Heather & Robertson 2005). Seed dispersal distances have been directly estimated for only two dispersers in New Zealand: kererū (Wotton & Kelly 2012) and tūī (O'Connor 2006). Kererū mean seed dispersal distance was 85 m, with 80–88% of seeds dispersed within 100 m, and less than 1% of seeds moved 1000–1500 m (Wotton & Kelly 2012). However, with long (mean 2 h) seed retention times (Wotton et al. 2008) and some flights exceeding 30 km (Harper 2003; Powlesland et al. 2011), kererū may occasionally disperse seeds tens of kilometres (Wotton & Kelly 2012).

Tūī are strong fliers and can travel up to 10 km between foraging areas and overnight roosts (Stewart & Craig 1985). During the breeding season, tūī in Auckland foraged within c. 500 m of their nest (Bergquist 1985b). Tūī around New Plymouth tended to roam in a localised area within a day, often returning to the same food sources (O'Connor 2006). Tūī seed dispersal distances averaged 223 m, with 85% of seeds dispersed less than 200 m and c. 2% of seeds dispersed 2000–2200 m (O'Connor 2006). Bellbirds have small home ranges (Table 1), although may travel long distances occasionally (Moncrieff 1928).

In Australia, silvereyes stayed at fruiting plants for very short periods (French et al. 1992; Stanley & Lill 2002), with 91.7% moving more than 10 m to trees immediately surrounding feeding sites (Stanley & Lill 2002). Silvereyes have short seed retention times (mean 20 min; Table 1). Blackbird territories in New Zealand range from 0.45 to 0.81 ha (Gurr 1954; Bull 1958). However, blackbirds may feed outside their territories (Snow & Snow 1988), and in New Zealand can roost up to 1.6 km away (Gurr 1954). Although blackbirds in England tend to leave fruiting trees soon after feeding, they often return to the same site and regurgitate seeds before feeding again, thus failing to disperse seeds (Snow & Snow 1988). In England, blackbirds have been recorded carrying fruits 160–300 m to feed their young (Snow & Snow 1988).

Song thrushes also carry fruit to their chicks (Snow & Snow 1988). Like many frugivorous birds, song thrushes had smaller home ranges during the breeding (mean 1.1 ha in England) than non-breeding (3.3 ha) season (Peach et al. 2004). Male song thrushes had larger breeding home ranges than females (1.5 and 0.5 ha respectively) and home ranges were larger on farmland within 100 m of a garden year-round (Peach et al. 2004). Song thrushes preferred gardens for nesting and foraging and individuals nesting on farmland travelled longer distances to visit gardens (Peach et al. 2004).

Starlings can travel up to 30 km to reach overnight roosts (Heather & Robertson 2005). Starlings use offshore islands as overnight roosts or staging posts to reach such roosts (Brookie 1983), and there are major roosts on at least 24 New Zealand offshore islands (Atkinson 1997). Starlings dispersed seeds of several weed species 4 km from the mainland to Tiritiri Mātangi Island (Anderson et al. 2006).

Mynas can be sedentary during the breeding season (Pell & Tidemann 1997), which extends from October to mid-April in Auckland (Counsilman 1974) and from late August to early March in Hawke's Bay (Wilson 1971). Most food is collected

within the breeding territory, which ranges from 0.09–2.27 ha (Counsilman 1974; Wilson 1971). However, mynas may flock at major food sources (including ripening fruits) within c. 800 m of their territory (Wilson 1971). Except for breeding females, mynas roost communally each night (Wilson 1971). However, during the non-breeding season (when many weeds have ripe fruits) mynas can travel between 1.6 and 12 km from overnight roosts to winter foraging areas each day (Wilson 1971; Wood 1995; Heather & Robertson 2005).

Possums occupy home ranges of 1.3–3.4 ha, and male possums have larger home ranges (mean 1.9 ha) than females (1.3 ha; Cowan & Clout 2000). Young possums dispersing from their place of birth can move up to 3 km a night and 10 km a week (Cowan & Clout 2000). Possums are likely to move hundreds rather than tens of metres during the time it takes for seeds to be defecated (1–12 days, median 3.8; Williams et al. 2000).

Feral pigs near Murchison occupied home ranges of 28–209 ha (McIlroy 1989). Home range size and movements are determined primarily by food availability, and are usually correlated with body mass and population density (McIlroy 2005). Home ranges of feral pigs can be smaller during summer and autumn than winter (McIlroy 1989). Most feral pigs tend to be sedentary, and have been recorded travelling on average between 0.8 and 1.7 km (maximum 3.6 km) per day (McIlroy 1989). Feral pigs have long seed retention times (mean 48 h; Setter et al. 2002) compared with birds and can potentially disperse seeds long distances.

Seed deposition patterns

Although bird droppings sometimes occur in the open without any overhead perching sites, birds generally defecate seeds while perched or immediately after they take off, rather than during flight (McDonnell & Stiles 1983; Burrows 1994b). Bird-dispersed seeds therefore tend to be concentrated beneath favoured perch or roosts sites, which serve as plant recruitment foci (McDonnell & Stiles 1983; Ferguson & Drake 1999; Anderson et al. 2006; Chimera & Drake 2010). In one study from the eastern South Island, nearly all hawthorn (*Crataegus monogyna*) seedlings were found within 2 m of potential bird perches (woody vegetation ≥ 0.5 m tall; Williams et al. 2010).

Blackbirds, silvereyes and kererū often fly to a nearby non-fruiting tree after feeding on fleshy fruits (Snow & Snow 1988; Stanley & Lill 2002; DMW pers. obs.). Silvereyes in Australia generally flew to tall canopy trees after feeding on fruiting shrubs (Stanley & Lill 2002), and both starlings and mynas favour roost sites in isolated stands of tall trees (especially macrocarpa, *Cupressus macrocarpa*, for starlings). Starlings also prefer to roost on cliffs or islands as noted above (Heather & Robertson 2005).

Relative frugivore importance

Few New Zealand studies have quantified the relative importance of different frugivores to weed dispersal. At Kowhai Bush, Canterbury, song thrushes removed the most *Berberis glaucocarpa* fruits (42.9%), followed by silvereyes (32.6%), blackbirds (24.3%) and starlings (0.1%) (MacFarlane 2012). Bellbirds never fed on *B. glaucocarpa* fruits, while kererū were absent from the site and tūī were rare (MacFarlane 2012).

Across four Canterbury sites (two urban and two rural), more than half (55.5%) of visits to non-native fruiting plants over a 12-month period were by silvereyes (G. Henderson &

D. Kelly unpubl. data). Blackbirds were the next most common frugivores (30.1% of visits), followed by bellbirds (4.8%), starlings (3.8%), and song thrushes (2.4%). House sparrows (*Passer domesticus*), greenfinches (*Carduelis chloris*), and chaffinches (*Fringilla coelebs*) made less than 2% of all visits to non-native plants, while kererū were never recorded feeding on non-native fruits (G. Henderson & D. Kelly unpubl. data).

In subalpine areas possums dispersed far more seeds (78% of all seeds dispersed, 162.5 seeds m⁻² yr⁻¹) than other non-native mammals; the sampling method did not allow a comparison with seed dispersal by birds (Young 2012). However, possums deposited most seeds in sites unsuitable for seedling establishment (Young 2012). At a forested site with low possum density (1 possum ha⁻¹), possums dispersed less than 3% of all seeds, while birds dispersed the rest (Wyman 2013).

Minor seed dispersers

Birds

Range-restricted bird species, minor frugivores, and seed predators are unlikely to play a significant role in the dispersal of weeds. Range-restricted frugivores include stitchbird (*Notiomystis cincta*), saddleback (*Philesturnus carunculatus*), kōkako (*Callaeas wilsoni*), weka (*Gallirallus australis*), kiwi (*Apteryx* spp.), parakeets (*Cyanoramphus* spp.), kākāpō (*Strigops habroptilus*), kea (*Nestor notabilis*), and kākā (*Nestor meridionalis*) (Clout & Hay 1989; O'Donnell & Dilks 1994; Robertson et al. 2007; Thorsen et al. 2011; Young et al. 2012). Minor frugivores include rifleman (*Acanthisitta chloris*), brown creeper (*Mohoua novaeseelandiae*), yellowhead (*M. ochrocephala*), grey warbler (*Gerygone igata*), tomtit (*Petroica macrocephala*), fantail (*Rhipidura fuliginosa*), greenfinch, chaffinch, house sparrow, dunnoek (*Prunella modularis*), blue duck (*Hymenolaimus malacorhynchus*), dotterels (*Charadrius* spp.), pūkeko (*Porphyrio porphyrio*), and gulls (*Larus* spp.) (MacMillan 1981; Clout & Hay 1989; O'Donnell & Dilks 1994; Williams & Buxton 1995; Thorsen 2003; Thorsen et al. 2011; MacFarlane 2012). For most of these species we could not find any reports of weed frugivory. However, on Little Barrier Island *Phytolacca octandra* fruits were the most important component of red-crowned parakeet (*Cyanoramphus novaeseelandiae*) diet during winter (26.2 ± 10%; Greene 1998). Pūkeko eat *Passiflora tripartita* var. *mollissima* fruits (Williams & Buxton 1995) and the Australian gull *Larus pacificus* dispersed seeds of two non-native plants in Tasmania, including *Lycium ferocissimum* (Calvino-Cancela 2011a).

Finches and parrots tend to destroy most or all seeds ingested, and are generally considered seed predators. Studies have demonstrated this for greenfinches, chaffinches, house sparrows, yellowhammers (*Emberiza citrinella*), sulphur-crested cockatoos (*Cacatua galerita*), and crimson rosellas (*Platycercus elegans*) (Moncrieff 1928; Bull 1958; Esler 1988; Snow & Snow 1988; Burrows 1994b). However, intact weed seeds have been found in some goldfinch (*Carduelis carduelis*) and chaffinch droppings (Williams & Karl 1996; Heleno et al. 2011), and seeds ingested by the larger native New Zealand parrots are not always damaged (Clarke 1970; Young et al. 2012). In Canterbury, kea ate fruits of 19 native plant species and defecated almost all seeds intact (Young et al. 2012). Seeds of five native species ingested by kea germinated readily (Clarke 1970).

Rodents

There are four introduced rodents in New Zealand: ship rats (*Rattus rattus*), Norway rats (*R. norvegicus*), kiore (*R. exulans*), and mice (*Mus musculus*). Ship rats, Norway rats, and kiore tend to consume small fruits (<10 mm) and seeds (Grant-Hoffman & Barboza 2010). Seeds and fruits comprised 74% of ship rats' diets in podocarp–broadleaved forest in the central North Island (Sweetapple & Nugent 2007). Kiore eat significant quantities of fleshy fruits (40% of diet; Shiels et al. 2013), often carrying them to husking stations where they feed (Campbell et al. 1984). Kiore eat weed fruits including *Lycium ferocissimum* (Campbell et al. 1984) and *Passiflora* spp. (West 1996), although the fate of seeds was not reported. Ship rats eat *Passiflora tripartita* var. *mollissima* fruits (Beavon & Kelly in press).

In captive feeding trials in New Zealand, few seeds survived ingestion by ship rats (5%), kiore (0.2%), mice (0%) (Williams et al. 2000) or Norway rats (0%; Beavon & Kelly in press). Overall for rodents there was little relationship between seed size and survival (Williams et al. 2000). However, the smallest-seeded species in one study (*Leycesteria formosa*, seed width 0.08 mm, mass 0.4 mg) was the only species to survive ingestion by kiore (1.8% survival; Williams et al. 2000). Some (25–34%) *Leycesteria formosa* seeds also survived ship rat ingestion, as did 6.3% of *Cotoneaster simonsii* (4.1 mm, 9.88 mg), 12.5% of *Pyracantha angustifolia* (2.1 mm, 3.15 mg), and 32.2% of native *Solanum aviculare* (2.24 mm, 0.6 mg) seeds (Williams et al. 2000). However, several species with seeds smaller than *C. simonsii* had all ingested seeds destroyed by ship rats (Williams et al. 2000). In similar captive trials in Hawai'i, ship rats destroyed ingested seeds of all but two species, which had the smallest seeds by far (<1.5 mm long and 0.7 mg mass; Shiels 2011). Only tiny seeds (<1 mm length) have been found intact in mouse stomachs (Shiels et al. 2013).

Ship rats and/or kiore used husking stations in Tonga but the vast majority (98.7%) of 13 720 plant items recorded at stations were empty seed husks (McConkey et al. 2003). Although the fruit pulp may be consumed quickly and seeds left intact, both kiore and ship rats can return weeks or months later to eat the seed kernel (Campbell et al. 1984; Wotton 2007). In addition, ship rats generally moved seeds less than 1 m (Wotton 2007). In some cases ship rats eat only part of the seed, which may still germinate (Shiels & Drake 2011; Wotton & Kelly 2011). In Hawai'i, fruits of *Psidium cattleianum* were highly attractive to ship rats, which removed 100% of fruits in field trials within 6 days but destroyed 82% of seeds in captive trials (Shiels & Drake 2011). In a New Zealand study, mice, kiore and ship rats all cached some fruits or seeds (51.3%, 28.9% and 41.6% of individuals respectively) in captivity (Williams et al. 2000). However, to date the only evidence of seed caching under field conditions that we know of is by ship rats in the subantarctic (Shaw et al. 2005).

Other mammals

Other mammals may also play a role in dispersing weed seeds in New Zealand but our knowledge is limited. Hedgehogs (*Erinaceus europaeus*) eat native fleshy fruits (Hendra 1999; Young 2012), and intact *Rosa rubiginosa* seeds have been recorded in their droppings in New Zealand (Jones et al. 2005; Jones & Norbury 2011). In Spain, hedgehogs ate fallen *Prunus avium* fruits and defecated more than 99% of seeds intact, but the effect on seed viability was unknown (Hernández 2008). In New Zealand subalpine habitats, 98.5% of native seeds

(all ≤ 6 mm seed length) found in hedgehog droppings were intact (Young 2012) but again their viability was unknown.

Red deer (*Cervus elaphus*), hares (*Lepus europaeus*), sheep (*Ovis aries*) and chamois (*Rupicapra rupicapra*) ate native fleshy fruits in New Zealand subalpine habitats and >90% of seeds in droppings were intact (Young 2012). Hares may be important seed dispersers in Canterbury high country due to their high abundance even though the number of seeds per faecal pellet is low (Young 2012). *Rosa rubiginosa* seeds were ubiquitous from February to May in hare gut samples collected over several years in Canterbury high country (Blay 1989). Rabbits dispersed viable seeds of several fleshy-fruited plant species in Western Australia (Calvino-Cancela 2011b), and may play a similar role in New Zealand. Deer ate *Lonicera japonica* fruits in North America, although the effect of gut passage on germination was unknown (Williams et al. 2001). Cattle and sheep have both been reported eating *Phytolacca octandra* fruits in New Zealand, and intact seeds of this species have been found in cattle droppings (Hilgendorf & Calder 1967).

Lizards

New Zealand lizards can eat significant quantities of fruit seasonally (Whitaker 1987; Wotton 2002) and are effective short-distance (<20 m) dispersers of some native plant species (Wotton 2002; DMW unpubl. data). There is one record of intact *Phytolacca octandra* seeds in common gecko (*Woodworthia maculatus*) droppings (Wotton 2002).

Discussion

Does fruit size limit dispersal of any weeds?

Although New Zealand weeds have wider fruits (mean 14.3 mm; this study) than native plants (6.4 mm; Lord et al. 2002), fruit size limits the number of potential dispersers for few weed species. Observations of birds other than kererū feeding on two weed species with large (>15 mm width) single-seeded fruits are probably pulp theft and not legitimate seed dispersal. However, blackbirds and song thrushes may occasionally carry large fruits several metres before eating the pulp (Snow & Snow 1988; Karan 2000; DMW pers. obs.).

Mammals have teeth and can chew fruits before swallowing them, and are thus less limited than birds in the size of fruits they can eat. However, mammals often destroy seeds while chewing (Shiels & Drake 2011; O'Connor & Kelly 2012). For some mammals the proportion of ingested seeds damaged may be related to seed size, with the smallest seeds passed intact and many or all medium to large seeds destroyed (Williams et al. 2000; Shiels & Drake 2011). For other mammals there is no relationship between seed size and the proportion of seeds destroyed (Herrera 1989). Currently, we do not know the exact nature of any relationship between seed size and seed damage (including whether seed-size thresholds exist), and how general any relationships are across mammal species.

Does fruiting phenology differ between weeds and natives?

Our results show that weed fruiting in New Zealand is spread more evenly throughout the year than native fruiting, and fruits of many weed species are available when native fruits are scarce. Weeds that fruit when native fruits are scarce may be more readily consumed by, or attract a greater diversity

of, frugivores (Corlett 2005) and thus spread more rapidly (Gosper et al. 2005). Weeds that fruit year-round (e.g. *Berberis darwinii*, *Lantana camara*) have access to the greatest range of potential dispersers and may enable native animals to adapt rapidly to a novel food source (Gosper 2004). In Australia, non-native plant species that fruited over a short period had lower rates of fruit removal (Gosper 2004) and were less invasive (Gosper & Vivian-Smith 2009b). Weeds often fruit when few natives are in fruit (Cordeiro et al. 2004; Gosper 2004; Corlett 2005; Chimera & Drake 2010; Gosper & Vivian-Smith 2010; White & Vivian-Smith 2011), have a longer fruiting season than natives (Gosper & Vivian-Smith 2010), and/or produce a super-abundance of fruits (Meyer 1998; Cordeiro et al. 2004; Chimera & Drake 2010; Gleditsch & Carlo 2011).

Which animals are the main dispersers of fleshy-fruited weeds?

We have confirmed William's (2006) finding that blackbirds, silvereyes and starlings are probably the main weed seed dispersers in New Zealand. All three birds are widely distributed and disperse more than 20 weeds – approximately twice as many species as song thrushes, tūī, bellbirds and possums. Silvereyes and blackbirds are more likely to disperse seeds within forest, while starlings appear particularly effective at dispersing seeds long distances (Anderson et al. 2006). The endemic kererū is highly frugivorous, and is the key disperser for three weed species with large single-seeded fruits. Song thrushes, tūī, bellbirds, mynas, possums and pigs are also likely to be important weed dispersers, but they have a narrower distribution and/or disperse fewer weed species than blackbirds, silvereyes and starlings. Possums and pigs are also seed predators, depending on the weed species. Possums probably disperse several small-seeded weeds (Williams et al. 2000) and species with hard seed coats (Young 2012).

Minor dispersers that are range-restricted or generally seed predators may effectively disperse weed seeds in some instances. For example, in areas such as Wellington where kākā are common they may play a role in spreading weeds. Likewise, ship rats and kiore probably disperse very-small-seeded weed species.

How might disperser attributes influence weed dispersal?

Differences in fruit handling behaviour can influence seed dispersal effectiveness (Levey 1987). Pecking at fruits provides less efficient dispersal than swallowing fruits whole as relatively few seeds may be ingested (Burrows 1994a). Dispersal distances are likely to be shorter when large fruits are carried before consumption. Additionally, birds feeding on large fruits may simply be robbing the pulp without being a legitimate disperser (Burrows 1994a; Stanley & Lill 2002). Silvereyes feed on several large-fruited (>10 mm wide) weeds (Appendix S2) for which they may be pulp thieves rather than dispersers (Burrows 1994a; Stanley & Lill 2002). For example, silvereyes only peck at *Crataegus monogyna* fruits rather than swallowing them whole (Williams 2006), so are unlikely to disperse the single, medium-sized seed. Likewise, silvereyes ate *Ficus carica* fruits in both Australia (Stanley & Lill 2002) and New Zealand (Gibb 2000), but their droppings contained no seeds (Stanley & Lill 2002). Although silvereyes can avoid ingesting seeds as small as 1.43 mm³ (Stanley & Lill 2002), small-seeded species (e.g. *Actinidia chinensis*, 2.2 mm long; Hopping 1976) have been found in their droppings (Logan & Xu 2006).

Animal movement patterns and seed dispersal distances may be influenced by time of year, gender, and body size. Animal home ranges can be larger in non-breeding than breeding seasons (Peach et al. 2004; Heather & Robertson 2005) and in males than females (McIlroy 1989; Peach et al. 2004). Likewise, larger frugivores tend to disperse seeds longer distances than smaller frugivores, in addition to dispersing more seeds and a wider range of species (Wotton & Kelly 2012).

How might landscape attributes influence weed dispersal?

Landscape attributes can also alter frugivore behaviour and movement patterns (McConkey et al. 2012), and thus influence weed invasions and spread (Neilan et al. 2006). Overseas studies have shown that seeds are dispersed further in fragmented landscapes than in continuous habitat (Lenz et al. 2011), and in structurally simple farmland than in structurally complex farmland or forest (Breitbach et al. 2010). Many of the main seed dispersers in New Zealand will travel readily between habitat fragments separated by agricultural or urban matrices (e.g. O'Connor 2006; Powlesland et al. 2011). Consequently, weed spread may be more rapid in highly fragmented landscapes.

The availability of perches and vegetation structural complexity can influence fruit removal and seed deposition patterns by birds (Debussche & Isenmann 1994; Wunderle 1997; Gosper et al. 2005). Increased woody vegetation cover after cessation of grazing may have facilitated the spread of bird-dispersed hawthorn (*Crataegus monogyna*) in the eastern South Island by providing safe nesting and perching sites for blackbirds and safe sites for hawthorn establishment (Williams et al. 2010).

Management implications

Management options for reducing weed spread via seed dispersal fall into three main categories: (1) direct control of weeds; (2) direct control of dispersers; and (3) manipulation or targeting of habitat and landscape features that influence disperser behaviour.

Weed control

Reducing or preventing fruit production may help limit weed spread (Coutts et al. 2011). Several studies have shown that weed populations with more fruits (Sargent 1990; Gosper et al. 2005; Spotswood et al. 2012) or reproductive adults (Aslan 2011) have greater rates of fruit removal. Fruit production could be limited by undertaking weed control before the onset of fruiting, either annually for well-established populations, or before maturity for newly established populations. Host-specific biocontrol agents that destroy seeds before they are dispersed can reduce population growth rates, maximum seed dispersal distances, and the establishment of new invasion foci (Le Maitre et al. 2008).

Invasive plants can provide food for native frugivores, especially in modified landscapes, resulting in a potential management dilemma (Neilan et al. 2006; Gosper & Vivian-Smith 2009a; Gleditsch & Carlo 2011). However, maintaining weed populations as food sources for native birds may have several negative consequences in addition to spread from the unmanaged site. These include reduced dispersal of co-occurring native plants via competition for dispersers (Gleditsch & Carlo 2011; Heleno et al. 2013a), and displacement of native plants and their associated fauna. Invasion by fleshy-fruited plants may also create positive feedback cycles when increased fruit availability supports more frugivores, which

then contribute to increased seed dispersal effectiveness and weed spread (Gosper & Vivian-Smith 2009a; Gleditsch & Carlo 2011). In addition, endemic New Zealand birds are generally limited by predation from non-native mammals, not food supply (Innes et al. 2010). Removal of *Berberis glaucocarpa* had no effect on bellbird behaviour or territory size, which makes sense since bellbirds did not feed on *B. glaucocarpa* fruits (MacFarlane 2012).

One way around any potential conflict between weed control and sustaining native fauna is to provide an alternative native food source at the time when the invasive species fruits, to mitigate any impacts of control (Williams & West 2000; McConkey et al. 2012). Native plants with fruits consistently more attractive to local dispersers (Gosper & Vivian-Smith 2009a) or that fruit during winter may be especially useful.

Models indicate seed dispersal distance is a key driver of weed spread (Higgins & Richardson 1999; Coutts et al. 2011). Where feasible, management should focus on reducing dispersal distances by targeting weed control in areas likely to be sources for long-distance dispersal. For example, controlling fleshy-fruited-weed populations where starlings feed may reduce the likelihood of long-distance dispersal and weed invasion of sensitive sites.

Control of dispersers

Weed dispersal could be reduced by controlling non-native seed dispersers directly. While management options for non-native bird control may be limited (and potentially controversial), non-native mammals are already controlled in many areas of New Zealand to reduce their impacts on native ecosystems and prevent the spread of bovine tuberculosis. The contribution of non-native mammals to dispersal of environmental weeds (Williams et al. 2000; Beavon & Kelly in press) provides an additional reason for their control.

Habitat and landscape attributes

Because perch sites frequently act as foci for weed invasion (Ferguson & Drake 1999; Stansbury 2001; Anderson et al. 2006; Bass et al. 2006), they could be sentinel sites when monitoring for new weed incursions. To limit weed spread to islands, mainland sources of weed infestations should be removed wherever possible (Atkinson 1997; Anderson et al. 2006).

Future research

Despite the importance of seed dispersal in the spread and management of fleshy-fruited invasive weeds, surprisingly little research has been carried out either globally (Westcott & Fletcher 2011) or in New Zealand. This review has highlighted several areas where further research is needed in New Zealand. First, although we have confirmed phenological differences in fruiting between natives and weeds, it is not known whether timing of fruit production influences seed dispersal success. Second, research on the dispersal effectiveness (Schupp 1993) of fruit-eating animals would help determine the relative importance of each disperser to weed spread (especially larger mammals: Kelly et al. 2010). Third, there are significant gaps in our understanding of how local vegetation context and landscape-scale processes influence dispersal of fleshy-fruited environmental weeds (Lenz et al. 2011). Finally, although fleshy-fruited weeds are common in New Zealand, two-thirds of the environmental weeds are adapted for dispersal by other mechanisms; a review of dry-fruited weed dispersal in New Zealand would be useful.

Acknowledgements

We are grateful to Dave Kelly, Kim McConkey, Peter Bellingham and two anonymous reviewers for helpful comments on earlier drafts. We thank Ian Westbrooke for statistical advice, Clayson Howell for taxonomic advice, and Geoff Henderson, Dave Kelly, Ralph Powlesland and Carl Gosper for unpublished data.

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Editorial Board member: Peter Bellingham
Received 30 July 2014; accepted 9 October 2014

Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Fruit size (range and/or mean), number of seeds per dispersal unit, seed size, seed dry mass and the availability of ripe fruits for 97 fleshy-fruited environmental weeds adapted for vertebrate dispersal in New Zealand

Appendix S2. Potential seed dispersers recorded feeding on fleshy-fruited weeds in New Zealand

Appendix S3. References for appendices

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