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RESEARCH

Seed dispersal mechanisms and dispersal potential of environmental weeds in New Zealand

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Abstract: Seed dispersal distances drive the rate of spread for invasive plants and are strongly influenced by dispersal mechanisms. We investigated weed seed dispersal mechanisms and dispersal potential in New Zealand. We collated data on dispersal mechanisms for 318 species that produce seed in New Zealand. We modelled maximum seed dispersal distances of 286 species for which data were available using dispersal mechanism, growth form, seed release height, and seed mass. Internal dispersal by vertebrates was the most frequent mechanism, both among weed species (56%, 60% of which had fleshy fruits) and all weed species × dispersal mechanism interactions (34%). Wind was the next most frequent mechanism (39% of species, 24% of mechanisms), followed by water (29%, 18%), attachment (16%, 10%), ant (8%, 5%), and ballistic dispersal (5%, 3%). Most weed species (56%) have only one known dispersal mechanism, 37% are dispersed by multiple mechanisms, and 7% have no known mechanism. Non-standard mechanisms (those not predicted by plant morphology) were used by 44% of weed species and comprised 51% of all mechanisms. Modelled maximum seed dispersal distances show that most weed species have the potential for long-distance dispersal: 70% of species were predicted to be dispersed > 100 m, 17% > 1 km, and 0.3% > 10 km. Dispersal distances were greatest for vertebrate-dispersed seeds (mean = 973 m), then seeds dispersed by wind (146 m), ants (75 m), and ballistic mechanisms (14 m). Many weed species are dispersed by non-standard mechanisms (especially vertebrates) that have the potential to move seeds much further than standard mechanisms and thus accelerate range expansion. We predict that non-standard mechanisms are even more frequent than reported to date, as they have been rarely studied in New Zealand. Examining the combined effect of multiple mechanisms is critical to understanding the historic and future spread of weeds.

Keywords: anemochory; biological invasions, dispersal distance, endozoochory, epizoochory, granivory, hydrochory, invasive plants, myrmecochory, polychory

Introduction

Seed dispersal is the main process by which plants colonise new sites. How a plant disperses determines where and when it can spread in a landscape (Westcott & Fletcher 2011). Dispersal ability has the strongest effect on the rate of plant spread, including for invasive species (Higgins & Richardson 1999; Theoharides & Dukes 2007). Thus, predicting how rapidly invasive plant species will spread, including in response to climate change, depends on the accurate estimation of seed dispersal distances (Higgins & Richardson 1999). There is some evidence that species that reproduce by seed have faster rates of spread than clonal species (Pyšek & Hulme 2005), while the invasion capacity of some species is minimal without seed dispersal (e.g. Aurambout & Endress 2018). Identifying seed dispersal mechanisms and estimating dispersal distances are fundamental to describing potential weed spread and developing effective management strategies (Westcott & Fletcher 2011).

Seed dispersal research has largely been dominated by the classical dispersal syndrome paradigm (Green et al. 2022), where the means of dispersal is predicted based on diaspore (the dispersal unit) morphology (van der Pijl 1982). Seed dispersal syndromes include movement by wind (anemochory), water (hydrochory), gravity (barochory), animal ingestion (endozoochory), external attachment to animal feathers, fur, or feet (epizoochory), explosive propulsion (ballistic), and ants (myrmecochory). However, seed dispersal syndromes are subjective and are poor predictors of actual dispersal mechanisms (particularly for seed dispersal by vertebrates; Green et al. 2022), long-distance dispersal (Higgins et al. 2003), range size (Alzate & Onstein 2022), and spread of invasive plants (Pyšek & Hulme 2005; Moyano et al. 2022).

Both biotic and abiotic dispersal mechanisms may apply

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to a wider range of species than expected on the basis of their seed morphology alone (Chambers & MacMahon 1994; Nathan 2007; Reynolds et al. 2015; Green et al. 2022). These so-called non-standard dispersal mechanisms may occur when the alternative mechanism is a well-described classic dispersal mechanism (e.g. wind) or by unusual mechanisms that are poorly studied (Higgins et al. 2003). Non-standard mechanisms often result in rare long-distance dispersal events (Higgins et al. 2003), which are particularly important in driving plant range expansion and the spread of invasive plants (Higgins & Richardson 1999). Consequently, dispersal potential may increase with the number of dispersal mechanisms used by a given species, due to a greater likelihood of using mechanisms capable of moving seeds further.

While seed dispersal mechanisms have a strong influence on how far seeds are dispersed, plant traits such as height and seed size also play a role. Taller plants and those with smaller seeds spread faster (Zhang et al. 2023) and have larger ranges (Alzate & Onstein 2022). Plant height is also positively correlated with mean seed dispersal distance across species, and with maximum distances for species with wind, ballistic, and unassisted dispersal syndromes (Thomson et al. 2011). For wind-dispersed species, tree height is more important for local or shorter-distance dispersal, while seed terminal velocity influences long-distance dispersal (Tackenberg et al. 2003; Wyse & Hulme 2021). Although seed mass is far less important than plant height for predicting seed dispersal distances, it is positively correlated with maximum dispersal distances for ballistic dispersal and negatively correlated with maximum distances for wind-dispersed species (Thomson et al. 2011). Some studies show that large seeds promote naturalisation, while small-seeded species are more likely to be invasive (Gioria et al. 2023). Species with extremely light so-called "dust seeds" that disperse individually should, in theory, be able to disperse widely irrespective of seed shape (Eriksson & Kainulainen 2011). Nevertheless, the few studies that have estimated dispersal range in dust seeds suggest that most are deposited close to the parent plant, although rare long-distance dispersal events are possible (Eriksson & Kainulainen 2011).

We previously reviewed seed dispersal by frugivores of fleshy-fruited environmental weeds in New Zealand (Wotton & McAlpine 2015). Environmental weeds (sensu Falk-Petersen et al. 2006) are non-native plants that invade natural ecosystems and have the potential to affect native biodiversity or ecosystem function (hereafter referred to as weeds). In this follow-up study, we review seed dispersal of an updated list of environmental weeds in New Zealand (McAlpine & Howell 2024), including fleshy- and dry-fruited species. We specifically address the following questions: (1) What is the frequency of each seed dispersal mechanism in the New Zealand weed flora? (2) How frequent are non-standard dispersal mechanisms? (3) Are predicted dispersal distances greater when both non-standard mechanisms and dispersal syndromes are modelled than when only syndromes are included? (4) Is there a positive relationship between the number of dispersal mechanisms used and dispersal distance? and (5) Which species have the potential to disperse seeds long distances, and do any of these currently have a restricted distribution?

There is no single definition of long-distance dispersal, so for the purposes of our study we define it as > 100 m, following the approach of Cain et al. (2000). We focus on patterns in the weed flora, rather than making predictions for individual weed species. We also discuss the importance of context in predicting seed dispersal, focusing on abiotic mechanisms (see Wotton & McAlpine 2015 for a similar discussion of vertebrate dispersal).

Methods

We reviewed information from the literature to assign seed dispersal mechanisms for each of 318 environmental weed species included in our review. We used an updated list of 386 environmental weeds in New Zealand (McAlpine & Howell 2024) from which we excluded 14 species that lack seeds (12 ferns or fern allies and two seaweeds), 34 species that are not known to produce seed in New Zealand, and 20 species where seed set is rare and thus likely to contribute little to weed spread (Appendix S1 in Supplementary Material). For all 318 species, we searched for reports of seed dispersal mechanisms in Google Scholar using the terms "seed" and "dispersal", including studies from New Zealand and overseas. We also searched the Seed Information Database (https://ser-sid.org), New Zealand floras (Webb et al. 1988; Healy & Edgar 1980; Edgar & Connor 2000; New Zealand Flora Online, https://www.nzflora.info), publications on seed dispersal mechanisms or vertebrate diets (see references in Appendix S2), and the New Zealand Plant Conservation Network website (www.nzpcn.org.nz).

We assigned seed dispersal mechanisms in the following categories: internal (internal dispersal of seeds by fruit- or seed-eating vertebrates), attachment (external attachment to vertebrate feathers, fur, or feet), wind, water (including dispersal by rivers, streams, flowing surface water, and sea currents), ballistic (seeds self-propelled by the plant), ant (seeds carried by ants), bird nesting material (dispersed by birds in material used to build nests), and scatter-hoarding (dispersed by vertebrates that fail to retrieve cached seeds). Multiple seed dispersal mechanisms were assigned for a species when there was evidence for this. We excluded human-mediated seed dispersal from our study.

For endozoochory by non-frugivores, we included only those reports where at least some seeds were intact. We included overseas reports of animal dispersal even if the animal species responsible is not present in New Zealand, as animal seed dispersal tends to be generalised (Wheelwright & Orians 1982) or occurs by chance (Sorensen 1986). We took a non-conservative approach by including all reported mechanisms, regardless of whether they were based on traits (i.e. syndromes) and/or empirical evidence, or no evidence was cited. Non-standard mechanisms are almost certainly underreported (Green et al. 2022) and the trait-based models we used (Tamme et al. 2014; see below) tend to underestimate seed dispersal distances (e.g. Herrmann et al. 2016), so our approach seeks to counterbalance these conservative effects.

To determine the frequency of non-standard mechanisms, we also assigned seed dispersal syndromes for each species based on putative adaptations for dispersal. First, we categorised species as dry- or fleshy-fruited (berries, drupes, compound drupelets, arillate fruits, or elaiosomes) using descriptions from New Zealand floras (Webb et al. 1988; Healy & Edgar 1980; Edgar & Connor 2000; New Zealand Flora Online). We then assigned the internal syndrome to all fleshy-fruited species, except those with elaiosomes or other fleshy appendages reported as adapted for ant dispersal, which were assigned the ant syndrome. For dry-fruited species, seed dispersal syndromes were obtained from the literature, or assigned by us based on seed or diaspore morphology (49 species) in the following categories: attachment, wind (seeds with wings or plumes), water (buoyant seeds), ballistic, scatter-hoarding, and unspecialised (no apparent adaptations for dispersal). We did not include gravity as a syndrome, as it acts by default on all seeds (Thorsen et al. 2009), and instead assigned species reported as dispersed by gravity to the unspecialised syndrome. We tested whether the number of dispersal mechanisms per species differed between fleshy-fruited and dry-fruited species using a Poisson generalised linear model in *R* v. 4.4.3 (R Core Team 2024).

We estimated maximum seed dispersal distances for the New Zealand weed flora using an *R* script for mixed-effects models (Tamme et al. 2014), which required some recoding to work. Tamme et al.'s (2014) models use both the dispersal mechanism (animal, ant, ballistic, wind, or "wind none") and plant traits that influence dispersal distance (growth form, seed terminal velocity, seed release height, and seed mass) to predict maximum seed dispersal distances. The wind none category applies to species that are dispersed by wind but have no special adaptations for dispersal (Tamme et al. 2014), which have shorter dispersal distances than wind-dispersed species with special adaptations such as wings or plumes (Nathan 2007). The models represent a single combined animal (vertebrate) dispersal category including internal, attachment, and scatter-hoarding (Tamme et al. 2014). We also included bird nesting material in the animal category (nine instances), as empirical dispersal distances are similar to those of other vertebrate dispersal modes (Warren et al. 2017). The models do not include water as a dispersal mechanism, so we could not estimate distances for seeds dispersed by water. The models were based on dispersal distances obtained from field observations and models parameterised with field data and explain on average 52.5% of the variation in dispersal distances (Tamme et al. 2014).

When parameterising their models, Tamme et al. (2014) included several species identified in the literature as unspecialised but dispersed by wind (e.g. *Calluna vulgaris* and *Erica cinerea*; Bullock & Clarke 2000) in the wind syndrome, rather than wind none. We therefore modelled species with an unspecialised (non-standard) wind dispersal mechanism (wind none) using both the wind and wind none categories, but we included only the wind distances in our analyses (wind none distances are included in Appendix S2).

We collated plant trait data for growth form, seed release height, and seed mass to use in the models. We used maximum plant height (excluding unusually large values, as reported in brackets in flora species descriptions) as a proxy for seed release height. Plant growth form is a proxy for seed release height, which enables dispersal distances to be modelled even when height data are unavailable (Tamme et al. 2014). The models only accommodated the growth forms herb, shrub or tree, but the approximate height of all species was known, so we assigned vines to the shrub category unless they were known to grow in tree canopies (none grow only at ground level). Grasses, sedges, rushes, and reeds were all assigned to herb, except for two large species of *Cortaderia* (pampas grass) that we assigned to shrub. Species described as either a shrub or tree were assigned to shrub if they grow up to 10 m (most are usually much shorter than 10 m), and to tree if they grow taller than 10 m (except for *Acacia mearnsii*, where height data were from Australia, but plants can reach more than 10 m in New Zealand). While terminal velocity can influence dispersal distances (Tamme et al. 2014), these data were unavailable for most species and so we did not include it in the models.

Plant trait data were obtained from New Zealand and Australian floras (Webb et al. 1988; Healy & Edgar 1980; Edgar & Connor 2000; New Zealand Flora Online; https://www.nzflora.info; Flora of Australia https://profiles.ala.org.au/opus/foa) and published literature when possible (van Kraayenoord et al. 1995; Webb et al. 1995; Smith 1996; Heenan et al. 1999; Sykes 2002; Lusk & Kelly 2003; Camarero et al. 2005; Heenan et al. 2008; Shiels 2011; Miller 2016; Figueiredo et al. 2019; Xu et al. 2020; Perrie & Sheppard 2021; Quijano-Abril et al. 2021; Wyse & Hulme 2021). In some cases, trait data were unavailable from the published literature, so we used information from websites, particularly the New Zealand Plant Conservation Network (www.nzpcn.org.nz), and also occasionally Weedbusters (www.weedbusters.org.nz), Bioeconomy Science Institute (https://agpest.co.nz) and the US Department of Agriculture Plants Database (https://plants.sc.egov.usda.gov/). Seed mass data were obtained primarily from the Seed Information Database (https://ser-sid.org).

We modelled seed dispersal distances for 286 weed species (excluding 23 species with no known dispersal mechanism and nine species dispersed only by water). We modelled the mean maximum dispersal distance for each mechanism used by each weed species (i.e. both standard and non-standard dispersal mechanisms, 359 dispersal mechanisms in total) using a statistical model that included dispersal mechanism, growth form, seed release height, and seed mass (Tamme et al. 2014). When seed mass and/or seed release height data were unavailable, we ran simpler models that excluded these traits. Seed mass data were unavailable for 26 species (using 28 mechanisms), seed release height data for 45 species (48 mechanisms), and both seed mass and height data for a further 14 species and mechanisms. Models included a random effect (family nested within order) to account for taxonomic structure (Tamme et al. 2014). Taxonomic structure was determined by checking the Global Biodiversity Information Facility (GBIF) database using the R package "taxize" v. 0.9.98 and the GBIF backbone (Chamberlain & Szocs 2013; Chamberlain et al. 2020). For species where the family or order was absent from Tamme et al.'s (2014) model training data, the predicted distance was at the order or species level.

We tested whether maximum modelled dispersal distances achieved for each species differed when only syndromes were included (i.e. non-standard mechanisms excluded) and when syndromes plus non-standard mechanisms were included, using a paired t-test in *R* (R Core Team 2024). We also tested whether there was a relationship between the number of dispersal mechanisms used by a species and the maximum dispersal distance achieved, using the "glmmTMB" package v. 1.1.8 (Brooks et al. 2017) to fit a lognormal generalised linear model in *R* (R Core Team 2024). We assessed model assumptions by inspecting residual plots, and there were no concerning patterns. We also identified the maximum dispersal distance of environmental weed species that currently have a restricted distribution in New Zealand (latitudinal range < 5 degrees and < 100 records) using occurrence records from GBIF (https://www.gbif.org/, downloaded 24 August 2025).

Results

Dispersal mechanisms

Of the 318 weed species we considered, 111 species (35%) had fleshy fruits adapted to dispersal by frugivores (including ants) and 207 species (65%) had dry fruits (Appendix S2). The number of dispersal mechanisms per species ranged from zero to five (Fig. 1; 495 dispersal mechanisms were recorded across all species). Although most weed species (177, 56%) had only a single reported dispersal mechanism, many species (118, 37%) used multiple mechanisms (Fig. 1). Twenty-four weed species (8%) had four or five reported dispersal mechanisms, while 23 species (7%) had no known dispersal mechanisms (Fig. 1). Fleshy-fruited species had fewer dispersal mechanisms (1.2 ± 0.6, mean ± s.d.; estimate = −0.35, s.e. = 0.10, $z = -3.45$, $P = 0.0006$) than dry-fruited species (1.7 ± 1.2.; estimate = 0.55, s.e. = 0.05, $z = 10.4$).

The most frequent dispersal mechanism both among weed species and weed species × dispersal mechanism interactions was endozoochory, which was reported for 56% of all weed species and 34% of mechanisms (Fig. 2). Sixty percent of endozoochorous species had fleshy fruits (Fig. 2). Wind was the next most frequent dispersal mechanism, followed by water, then attachment (Fig. 2). Vertebrates dispersed 61% of weed species and accounted for 38% of all weed species × dispersal mechanism interactions (internal, attachment, scatter-hoarding, and bird nesting material combined). Ant, ballistic, and bird nest building material dispersal were infrequent, while scatter-hoarding was rare (Fig. 2). Forty-four percent of weed species (139 species) used non-standard seed dispersal mechanisms not predicted by their morphology, and 51% of all weed species × dispersal mechanism interactions were non-standard.

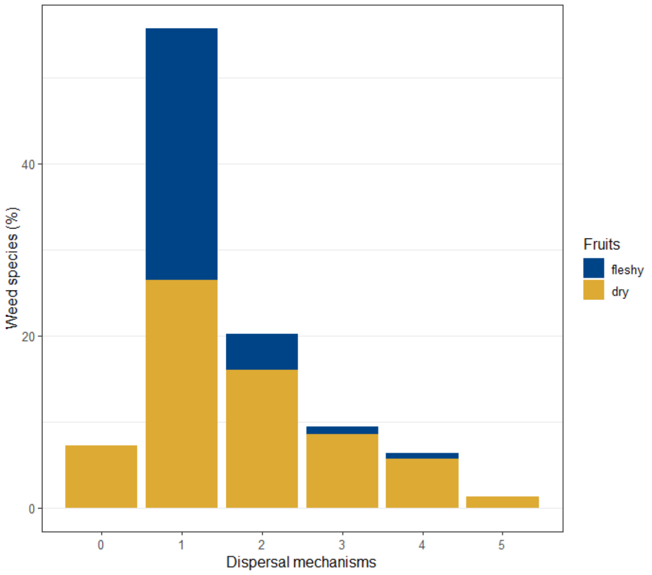

Figure 1. The number of reported seed dispersal mechanisms used by fleshy- and dry-fruited environmental weed species in New Zealand.

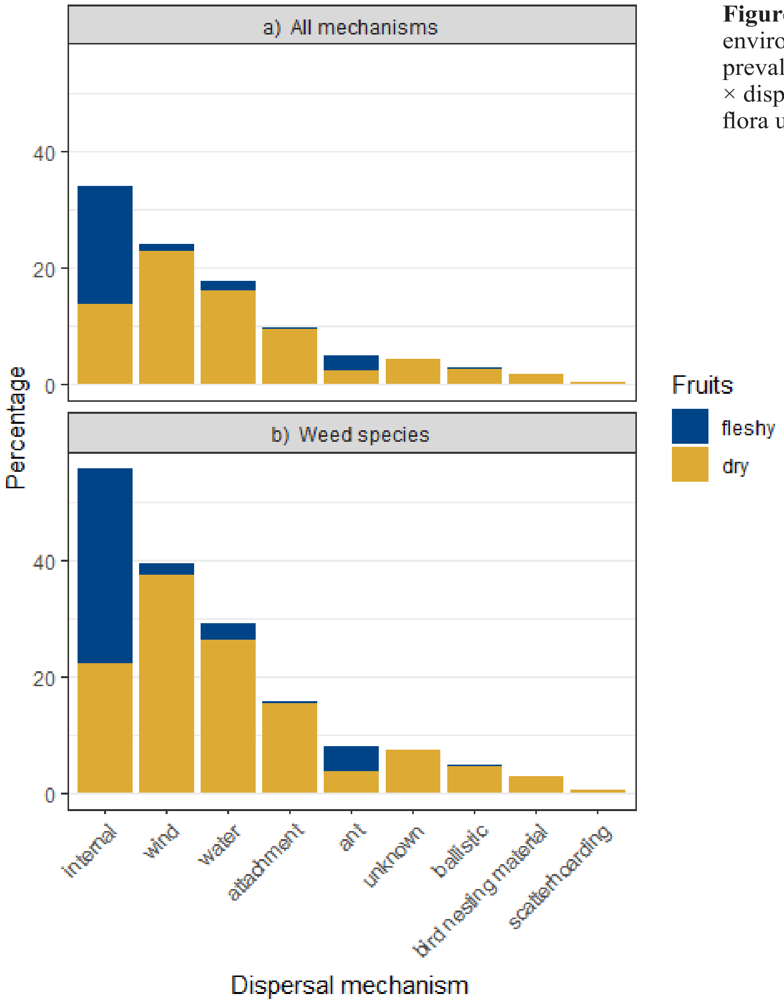

Figure 2. Seed dispersal mechanisms of fleshy- and dry-fruited environmental weed species in New Zealand. (a) Percentage prevalence of each mechanism across all known weed species × dispersal mechanism interactions, and (b) percentage of weed flora using each dispersal mechanism.

Dispersal distances

Most weed species were predicted to have the potential to disperse seeds over long distances. Across all dispersal mechanisms, 6% of modelled maximum dispersal distances were < 10 m, 61% were > 100 m, 14% > 1 km, and 0.3% > 10 km. For species with multiple dispersal mechanisms, considering the maximum distance across those, 4% of species were dispersed < 10 m, 70% > 100 m, 17% > 1 km, and 0.3% > 10 km.

Modelled maximum dispersal distances were greatest for animal-dispersed seeds (973 ± 1650 m, mean ± s.d.), followed by seeds dispersed by wind (146 ± 176 m), ants (75 ± 53 m), and ballistic mechanisms (14 ± 10 m; Fig. 3). Even the shortest modelled maximum animal dispersal distances were 40 m, and longer than the shortest distances for all other mechanisms (< 5m; ant, ballistic, and wind).

When non-standard mechanisms were excluded and only dispersal syndromes were analysed, the maximum modelled dispersal distance achieved for each species was shorter (mean ± s.d. = 531 ± 1163m; median = 183 m; t = −5.57, d.f. = 219, $P < 0.0001$) than when including both syndromes and non-standard mechanisms (mean ± s.d. = 801 ± 1583 m; median = 332 m). There was a positive relationship between the number of dispersal mechanisms used and the maximum modelled dispersal distance achieved for each weed species (estimate = 0.20, s.e. = 0.04, z = 4.54, $P = 0.00006$). All fifty weed species with maximum modelled dispersal distances > 1 km achieved this via animal dispersal, although some were also predicted to be dispersed shorter distances by other mechanisms (Appendix S2).

Eight weed species that currently have a restricted distribution in New Zealand (< 5° latitudinal range and fewer than 100 records) have the potential to disperse > 100 m (Fig. 4). An additional two species have a latitudinal range of < 5° but slightly more than 100 records, and also have the potential to disperse > 100 m (*Epilobium hirsutum* (144 records) and *Phragmites karka* (134)).

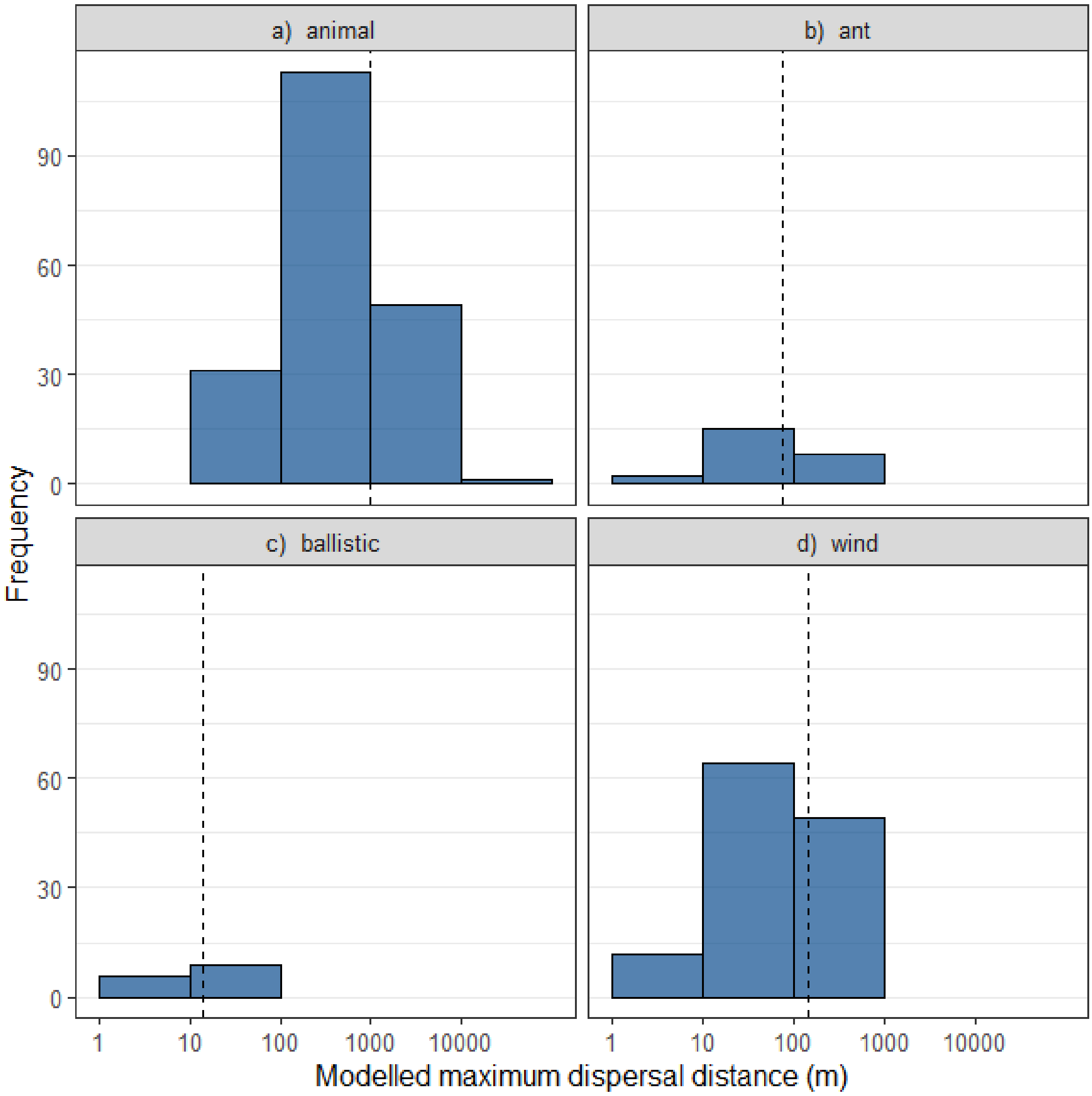

Figure 3. Modelled maximum seed dispersal distances for all known dispersal mechanisms used by the environmental weed flora in New Zealand. The dashed line indicates the mean modelled maximum distance for each mechanism (animal = dispersed by vertebrates via internal ingestion, external attachment, scatter-hoarding, or nesting material). Note the x-axis is on a log scale.

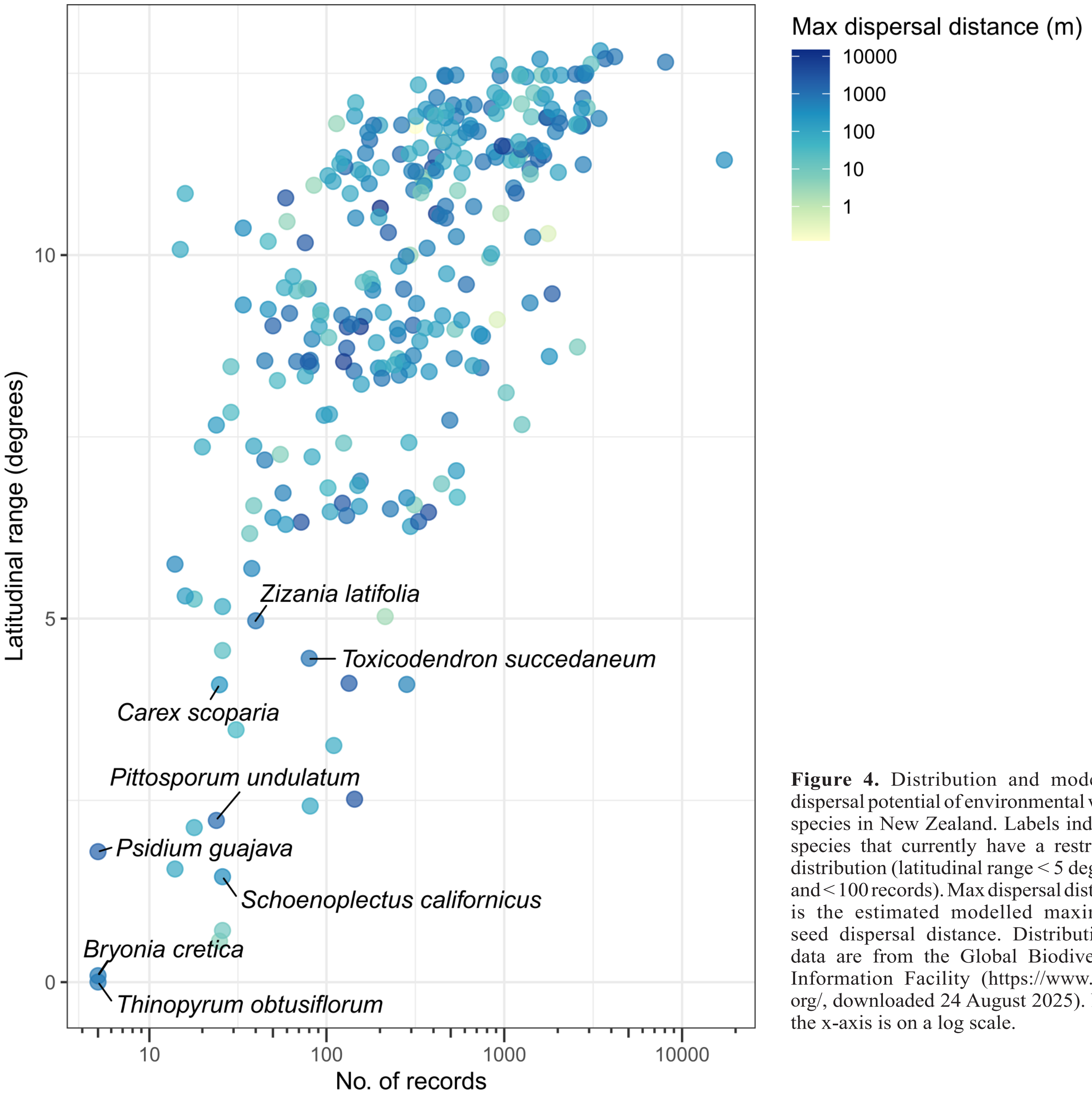

Figure 4. Distribution and modelled dispersal potential of environmental weed species in New Zealand. Labels indicate species that currently have a restricted distribution (latitudinal range < 5 degrees and < 100 records). Max dispersal distance is the estimated modelled maximum seed dispersal distance. Distributional data are from the Global Biodiversity Information Facility (https://www.gbif.org/, downloaded 24 August 2025). Note the x-axis is on a log scale.

Discussion

Dispersal mechanisms

Non-standard seed dispersal probably plays a significant role in weed spread (Green 2016), with many species dispersed by mechanisms that are not predicted by their seed morphology or dispersal syndrome (Pakeman et al. 2002; Green et al. 2022; González-Varo et al. 2024). For example, in New Zealand non-fleshy fruits are dispersed by vertebrate ingestion of seeds (e.g. *Cytisus scoparius* dispersal by possums (Dungan et al. 2002) and *Melianthus major* dispersal by birds (Simpson 1971)), or in nesting material (Bull 1958; Wiser & Allen 2006). Seeds of fleshy-fruited *Crataegus monogyna* and *Rubus* species are also dispersed by attachment (Albert et al. 2015; Reynolds & Cumming 2016). Likewise, some wind-dispersed *Pinus* species that are invasive in New Zealand are dispersed by attachment, via ingestion by water birds, or in bird nesting material (Appendix S2; Müller-Schneider 1986, cited in Camarero et al. 2005; Albert et al. 2015; Reynolds & Cumming 2016; Warren et al. 2017; Almeida et al. 2025). Some weed species may also disperse as vegetative fragments using the same or alternative mechanisms as seeds.

We found that 44% of New Zealand's environmental weed flora use non-standard dispersal mechanisms and that 40% of endozoochorous weed species have dry fruits, but these are almost certainly underestimates (Green et al. 2022), as non-standard seed dispersal mechanisms have rarely been studied, particularly in New Zealand. The use of methods to detect non-standard dispersal can increase the number of species using classical dispersal syndromes compared to that predicted by morphology (e.g. Kaproth & McGraw 2008; Morris et al. 2011; Green et al. 2022) and identify unusual (or understudied) mechanisms such as dispersal in nesting material (e.g. Dean et al. 1990). However, our findings may be biased by differences in research effort among mechanisms. Examining the combined effect of multiple mechanisms is essential for determining the ecological consequences of dispersal (Nathan 2007; Rogers et al. 2019) and probably the historic and future spread of many weed species (Robledo-Arnuncio et al. 2014; Green 2016).

As the number of mechanisms used by weed species increases, so does dispersal potential, presumably because adding more dispersal mechanisms increases the likelihood of using one that can move seeds further. Ant-, wind-, and ballistic-dispersed species can increase their dispersal distance if they are also dispersed by vertebrates, while ballistic-dispersed species can also be dispersed further by ants. The number of mechanisms a plant uses could, therefore, influence rates of weed spread, but this hypothesis requires further testing. Different mechanisms may not only disperse seeds of a given species over contrasting distances (Vittoz & Engler 2007; Tamme et al. 2014), but their activity may also vary over different spatial and temporal scales, and they may respond differently to environmental change (Nathan 2007; Robledo-Arnuncio et al. 2014). Diplochory (two-stage dispersal, e.g. ballistic + ant, water + animal, or wind + water) was not specifically accounted for in our modelling but would also increase dispersal distances (Kaproth & McGraw 2008; Navarro-Ramos et al. 2024). Dispersal distance predictions for diplochorous species could be estimated by combining distances for each mechanism, where available.

Vertebrates are important in the spread of environmental weeds in New Zealand, dispersing 61% of weed species. Our study, using an updated environmental weed list (McAlpine & Howell 2024), confirms that approximately one-third of weed species in New Zealand have fleshy fruits dispersed primarily by frugivores (Wotton & McAlpine 2015). Frugivorous (Williams 2006; Wotton & McAlpine 2015) and granivorous birds (Simpson 1971; Burrows 1994), possums (*Trichosurus vulpecula*; Dungan et al. 2002; Beavon & Kelly 2015), pigs (*Sus scrofa*; Beavon & Kelly 2015), ship rats (*Rattus rattus*; Williams et al. 2000), goats (*Capra hircus*; Harrington et al. 2011), hedgehogs (*Erinaceus europaeus*; Jones & Norbury 2011), and livestock (Molloy et al. 1967) all act as weed vectors in New Zealand. To our knowledge, there have been no studies on seed dispersal by deer in New Zealand; however, deer frequently disperse seeds overseas, both internally and attached to their fur or hooves (e.g. Welch 1985; Albert et al. 2015; Quin et al. 2023).

Several of New Zealand's environmental weeds have no known dispersal mechanism but have traits, such as small seeds, and occur in environments where dispersal by waterbirds may be important (Green et al. 2023). Elsewhere, water birds disperse the seeds of many plant species considered to have an unspecialised dispersal syndrome, including environmental weeds (Costea et al. 2016; Green 2016; Almeida et al. 2022, 2025). In New Zealand, mallards (*Anas platyrhynchos*) disperse seeds of several non-native species by endozoochory (Bartel et al. 2018), but have been reported as dispersing only one weed species (*Glyceria declinata*; Simpson 1971). Seeds of five weed species have been recorded in pūkeko (*Porphyrio porphyrio*) gizzards in New Zealand: *Glyceria fluitans*, *Glyceria maxima*, *Holcus lanatus*, *Lolium perenne* and *Poa annua* (Carroll 1966; Marchant & Higgins 1993). Water dispersal of weed seeds is probably underreported since even non-buoyant seeds can travel long distances in rivers during high flows or floods (Hyslop & Trowsdale 2012).

Dispersal distances

Range expansion rates in plant species are driven by long-distance dispersal events (Clark et al. 1998), which are predicted by seed dispersal mechanisms (Vittoz & Engler 2007). Wyse and Hulme (2021) reported that long-distance dispersal potential was the best predictor of spread rate in invasive *Pinus* species in New Zealand. Most environmental weed species in New Zealand have the potential for long-distance dispersal, and more than half are dispersed by vertebrates, which have the greatest capacity for moving seeds over long distances (Tamme et al. 2014; Costea et al. 2016; Nazareno et al. 2021). We identified at least eight species with a restricted distribution in New Zealand but a high dispersal potential (> 100 m), although some species may be under-recorded rather than genuinely range-restricted. Nevertheless, dispersal potential and species distribution could inform prioritisation of weed species management. Two of the eight species are subject to national eradication programmes (*Bryonia cretica* and *Zizania latifolia*; Ministry for Primary Industries-managed National Interest Pest Response species).

For wind- and ballistic-dispersed species, our modelled maximum distances are comparable to maximum dispersal distances reported from empirical studies (Appendix S3). The maximum ant dispersal distances modelled in our study (mean 77 m maximum distance for all ant dispersed weed species) are comparable to reported ant dispersal distances of 70–180 m (Gómez & Espadaler 2013).

Using trait-based empirical models allowed us to estimate and compare the dispersal potential of both dispersal syndromes and non-standard mechanisms for nearly the entire New Zealand environmental weed flora, using readily available data. Where more accurate dispersal distances are required for individual weed species, species-specific mechanistic modelling should be undertaken (Morgan & Venn 2017; Killick 2017). Trait-based predictions of invasion risk have provided inconsistent results, with some studies showing that taller plants and those with small seeds are more likely to be invasive (Moodley et al. 2013), while others report that a persistent soil seed bank is the only trait that increases invasiveness (Gioria et al. 2021). Persistent soil seed banks enable species to disperse their seeds in time and thus increase opportunities for range expansion (Gioria et al. 2023). While dispersal syndromes perform poorly in trait-based predictions of invasiveness at a global scale (Moyano et al. 2022), using empirical seed dispersal mechanisms may be a useful approach. Including non-standard dispersal mechanisms is important for accurate prediction of dispersal distances alongside dispersal syndromes. Weed risk assessments in New Zealand and Australia currently include information on seed dispersal syndromes (Owen 1997; https://www.agriculture.gov.au/biosecurity-trade/policy/risk-analysis/weeds/system/). These assessments could be improved by including empirical dispersal mechanisms as well, and for fleshy-fruited species, incorporating traits that are strongly correlated with invasion risk, such as fruit size (Gosper & Vivian-Smith 2009).

The processes that move seeds are often complex and poorly defined (Higgins et al. 2003; Robledo-Arnuncio et al. 2014). It is perhaps unsurprising, therefore, that there is little evidence of a link between dispersal syndromes and long-distance plant dispersal (Higgins et al. 2003), vascular plant range size (Alzate & Onstein 2022), or spread of invasive plants (Pyšek & Hulme 2005; Moyano et al. 2022). Furthermore, plant spread is influenced by actual dispersal mechanisms rather than the dispersal syndromes assigned to them, which may also explain the lack of correspondence. Many invasive species lack apparent adaptations for seed dispersal yet successfully naturalise and spread (Mologni et al. 2024). These species may be more efficient at exploiting human-mediated vectors (Mologni et al. 2024) or non-standard dispersal mechanisms. While morphological dispersal adaptations can determine local dispersal, they are less important in long-distance dispersal, where non-standard vectors dominate (Nathan et al. 2008).

The importance of context in predicting dispersal

Local environmental conditions can also strongly influence patterns of seed dispersal (Robledo-Arnuncio et al. 2014). Theoharides and Dukes (2007) suggested this context-dependence and variations in the local success of weed species may explain the lack of predictive power in models of dispersal distance. For animal-dispersed species, habitat-specific (directed) deposition results from the combination of disperser preferences (e.g., movement patterns and seed deposition activity) and local environmental conditions (e.g., habitat fragmentation and vegetation structural complexity; Robledo-Arnuncio et al. 2014; Wotton & McAlpine 2015; Herrmann et al. 2016). For wind-dispersed species, seed deposition can be influenced by topography, canopy structure, and habitat connectivity (Bohrer et al. 2008; Trakhtenbrot et al. 2014; Damschen et al. 2014). For instance, mechanistic models predicted that the long-distance wind dispersal potential of *Pinus* species was greater for seeds in forests than for seeds dispersed from a lone tree (Wyse & Hulme 2021). Wind-dispersed plants growing on cliffs release their seeds from a greater height and hence have the potential to disperse their seeds much further (Killick 2017).

A combination of strong winds and high turbulence maximises seed dispersal distance in wind-dispersed species (Soons & Bullock 2008 and references therein). Many wind-dispersed species are more likely to release their seeds in gusty, windy conditions that favour long-distance dispersal, and may also influence the direction of seed dispersal and spread (Greene et al. 2008; Soons & Bullock 2008).

Seed dispersal of wind-dispersed species may be biased in the direction of prevailing winds, or stronger winds that have a dominant direction (Greene et al. 2008; Soons & Bullock 2008). Strong directional bias may occur when the wind direction is correlated with shifts in relative humidity (Greene et al. 2008; Soons & Bullock 2008). For most wind-dispersed plants, seed abscission occurs primarily when relative humidity is low such as during foehn-type winds (Greene et al. 2008); similar effects could occur in the eastern South Island of New Zealand in the lee of the Southern Alps. In coastal areas, relative humidity may interact with daily patterns of air circulation (Greene et al. 2008). Relative humidity typically reaches a minimum in early afternoon, coinciding with a peak in afternoon sea breezes that move air from the sea toward land. Thus, for coastal plants, most wind-dispersed seeds will be transported inland (Greene et al. 2008).

For species dispersed by rivers and streams, once seeds enter the water, dispersal distances and deposition sites are primarily influenced by local hydrodynamics (Nilsson et al. 2010; Hyslop & Trowsdale 2012). Oceanic currents and surface wind influence dispersal distances in the sea (Van der Stocken & Menemenlis 2017). In rivers and streams, seed deposition is concentrated in areas with low flow but dispersal distances exponentially increase with surface flow (Andersson et al. 2000, cited in Hyslop & Trowsdale 2012; Hyslop & Trowsdale 2012). Species whose seed release coincides with seasonal floods, or with a seed bank that can be re-suspended by flood waters, may be more likely to be dispersed by floods (Kehr et al. 2014). Seed deposition patterns during floods may be correlated with sediment deposition (Hayashi et al. 2012), but remain poorly understood (Hyslop & Trowsdale 2012).

Stream vegetation can also strongly influence dispersal distances, with more vegetation resulting in shorter dispersal distances due to seed entrapment (de Jager et al. 2019). Plant traits are mediated by local habitat conditions: large seeds are less likely to become entrapped in stream vegetation and are therefore dispersed further than small seeds (de Jager et al. 2019). Woody debris and flotsam can also trap seeds, but with the effect of increasing dispersal distances regardless of floating ability as material rafts downstream (Nilsson et al. 2010; Hyslop & Trowsdale 2012). Seeds dispersed by rivers can only move downstream, which means that weeds in upper catchments have greater potential to spread long distances via hydrochory (Hyslop & Trowsdale 2012). Most riparian species can be dispersed upstream by other mechanisms, primarily water birds (e.g. Pollux et al. 2005), as well as other animals or wind, although upstream dispersal is less frequent (Wubs et al. 2016).

Conclusion

More research is needed to observe the dispersal of seeds in the field and to document the range of mechanisms used by the environmental weed flora in New Zealand. This need is particularly pressing for vertebrate dispersal, which has the greatest capacity to disperse seeds long distances but, except for frugivory, is understudied. While there have been attempts to predict dispersal mechanisms from other plant traits, these have had limited success (Thomson et al. 2010).

It would also be useful to update the trait-based dispersal models to enable predictions of dispersal distances by hydrochory, based on recent findings such as the relationship between seed size and dispersal distance by water (de Jager et al. 2019). More dynamic models could also be developed to predict range expansion rates of environmental weeds and to disentangle establishment and dispersal limitation. The influence of seed dispersal distance (including non-standard mechanisms) on weed range size would be worth further exploration, alongside the many other potential predictors of range size (Sheth et al. 2020). Meanwhile, our results can be used to provide reasonable predictions of how rapidly most weed species in New Zealand could spread, including into newly suitable habitats, with a changing environment (Bradley et al. 2010). By identifying the relative dispersal potential of weed species, this research can also guide the identification and management of actual or potential weed threats to our native ecosystems.

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Additional information and declarations

Author contributions: DMW conceived the research questions, collated and analysed the data, prepared graphs and wrote and edited the manuscript. GLWP contributed to developing the research questions, modelled seed dispersal distances, graphed weed distributions, and edited the manuscript. KGM conceived the project, assisted with collating plant height data, and edited the manuscript.

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Supplementary Material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Environmental weed species excluded from this study, with reasons for their exclusion.

Appendix S2. Seed dispersal mechanisms, plants traits, modelled maximum dispersal distances and dispersal mechanism references for the New Zealand environmental weed flora.

Appendix S3. Comparison of modelled and empirical dispersal distances for environmental weed species.