**Methods**

**Study system and species**

*H. novaeseelandiae* are large (c. 650 g adult) frugivorous pigeons. They live in lowland forests throughout NZ and are highly mobile, inferred from inter-annual changes in the numbers in northern forests and radio-telemetry data, but individuals can also be sedentary (Clout et al. 1991, Wotton 2007).

*V. lucens* are large angiosperm trees up to 20 m tall, with trunks up to 1.5 m wide, occurring mainly in temperate coastal areas of NZ (Salmon 1980). Hermaphroditic flowers are produced all year, with bright red fruits being present mainly between December and June. *P. ferruginea* are tall dioecious gymnosperm trees up to 25 m tall, with trunks up to 1 m wide, occurring in shady environments throughout NZ, from lowland forest to c. 1000 m elevation (Salmon 1980). Male trees have cones and female trees produce large red diaspores, mainly between December and June, consisting of a single seed surrounded by fleshy ovuliferous cone scales (McEwen 1988) – for convenience, these structures will henceforth also be referred to as ‘fruit’. The fruit of both tree species are long (*V. lucens*: 15.4 ± 0.2 mm, *n* = 286 fruit; *P. ferruginea*: 16.1 ± 0.1 mm, *n* = 702 fruit; Pegman 2012) and have single seeds that are hard and ‘woody’ surrounded by nutritious, edible, and ‘fleshy’ pulp, indicating that they are consumed by fruit-eating animals (Coates-Estrada and Estrada 1988, Tiffney 2004). Because fruits and birds vary in size within species, mid-sized birds such as tui (*Prosthemadera novaezelandiae*) or blackbird (*Turdus merula*) can consume smaller individual fruits of both tree species, but this occurs infrequently (Kelly et al. 2010). Mammals may also act as dispersers since seeds of our study species occasionally showed signs of predation such as open husks and teeth marks; however, this is again infrequent and Pegman (2012) showed that only 2.2 ± 1.3% of dispersed *P. ferruginea* seeds (*n* = 434 seeds across6 trees) had open husks, and mammal damage to dispersed *V. lucens* seeds was not observed.

We utilised these two tree species because (i) they are the two large-fruited NZ species for which there are data to parameterize our model, (ii) they differ in their environmental requirements, therefore not growing together, (iii) they have different reproductive strategies, and (iv) they have differing spatial distributions. Mean annual fruit production for *P. ferruginea* (c. 5000) is around twice that of *V. lucens*,and the proportion of annual fruit production that is actively dispersed by *H. novaeseelandiae* is c. 46% for both tree species (Pegman 2012). Field measurements showed that the distance between *P. ferruginea* trees (30.2 ± 6.1 m, *n* = 3 sites) is around twice the respective value for *V. lucens* (Pegman 2012). The two tree species also have different shaped seeds (*V. lucens* is irregular, whereas *P. ferruginea* is smooth), affecting frugivore gut passage time (Table 1, Supplementary material Appendix1, Traveset 1998). All of these factors may result in different outcomes for each tree species in our simulations.

**Model design**

Our model is concerned with how patterns in seed deposition emerge from interactions between frugivore behaviour and the environment, represented by different tree spatial patterns. The model is semi-mechanistic, spatially explicit, individual-based, stochastic, and event driven; it encompasses fruit production and avian frugivore foraging in simulated forests and was ‘built from the ground up’, having fundamental elements in common with other models of seed dispersal such as those described by Morales and Carlo (2006) and Will and Tackenberg (2008). We implemented our model in NetLogo 5.3 (Wilensky 1999). A complete description of our model following the ODD (Overview, Design concepts, Details) protocol of Grimm et al. (2010) and the code are provided in the Supplementary material Appendix 1 and 2 (see Fig. A1 in Appendix 1 for schematic overview).

In brief, our model represents the movement of variable numbers of individual birds (in our case, *H. novaeseelandiae*) through landscapes of fixed abundance of fruiting plants (in our case, *V. lucens* or *P. ferruginea*) whose spatial arrangement can be varied. Individual birds select the tree they move to based on the multiplicative interaction of its available fruit and the distance from the bird’s current location. The rationale for this interaction is that there is a positive correlation of frugivory with fruit abundance (Saracco et al. 2005) and that frugivores prefer local, rather than more distantly located, resources. For example, plants in denser neighborhoods have greater fruit removal rates than more isolated plants, even when the latter have desirable fruit (Levey et al. 1984, Morales et al. 2012). However, this rationale provides no indication about the mathematical function that most closely describes such relationships.

In our model, there is one feeding bout at a random point during the time spent at each tree during a mean of 120 minutes per day of perching time (Wotton 2007). A gut passage time for each feeding event is drawn from an appropriate probability distribution (see Supplementary material Appendix 1), seeds are deposited after that time elapses, and in due course the seed dispersal distribution emerges from this activity (Fig. 3b). There are no interactions among birds in the model with respect to their seed dispersal service (they do not flock due to current low densities, although they likely did so in the past) and so the final seed deposition pattern emerges from independent superposition of individual dispersal events across all birds. The parameters of the seed dispersal kernel are then fitted to the simulated seed deposition pattern (see below).

Other elements in our model reflect the biology of the systems we considered and include: (i) ‘roost’ trees i.e. trees that are attractive to birds but do not provide a food source (e.g. Beveridge 1964 and Johnson 2001 describe the use of *Weinmannia racemosa* in this way) and (ii) the occasional longer distance random movement by individual dispersers within the landscape, rather than on the basis of the attractiveness of trees. We also had a model setting that controlled background rate of fruit loss from trees due to wind, abscission, predation, mishandling by birds, etc.

**Model parameterisation, sensitivity and structural analyses, and *in silico* experiments**

The model parameterization was informed by data describing the foraging behavior of *H. novaeseelandiae* and the physiognomy of *V. lucens* and *P. ferruginea*, obtained through experiments, field observations, and from the relevant literature (see Table 1). We conducted a univariate sensitivity analysis, following the methods described by Hamby (1994), by imposing a ± 25% change on each specified baseline model input parameter and then calculating absolute ratios (*Sy, x*) of change in kernel parameters to assess how these seed dispersal characteristics changed with model parameterization (Table 2 and Supplementary material Appendix 4). The model parameters we tested were chosen because they were *a priori* deemed to be the most relevant to the questions we were focussing on or were the most uncertain. Because the sensitivity analysis suggested that it was a crucial driver of the model’s dynamics, we also conducted a structural analysis on the mathematical function governing frugivores’ choice of tree based on the distance from its current location (see Supplementary material Appendix 1, Eq. A2). Since we were assessing whether the degree of tree aggregation (sigma, σ) was a major driver of seed distributions, we used the entire biologically reasonable range (i.e. σ = 2 to 100 m) in the assessment of its sensitivity.

We then conducted a series of *in silico* plant-frugivore experiments to explore the extent to which seed dispersal kernels are influenced by interactions between tree spatial patterns and frugivore density. A factorial design was employed in which the density of *H. novaeseelandiae* (*nK*) varied between 0.1 and 10 ha-1, representing the range of plausible values (Pegman 2012). In support of this, Greene (2003) calculated *H. novaeseelandiae* densities of 0.1 to 2.6 ha-1 in Pureora Forest Park, NZ,reflecting seasonal movements linked to food availability. The degree of aggregation of trees (sigma, σ) was varied by tightening or relaxing clusters in the Thomas point process (Illian et al. 2008), used to simulate patterns of individual trees from aggregated (low σ) to diffuse (high σ), with c. 86% of all trees of a given cluster located within 2σ of the cluster centre (Illian et al. 2008, Supplementary material Appendix 1, Fig. A2). We varied σ from 10 to 200 m (representing nearest fruiting tree neighbors at c. 11 to 28 m) and held abundance constant at 1200 fruiting trees in 120 clusters per simulated landscape of 400 ha (i.e. 3 trees ha-1), based on field estimates of the density of both tree species (Pegman 2012). We also conducted experiments to assess the combined effects of low fruit availability and low fruit ripening on the seed dispersal kernels.

There were 30 simulations for each combination of factors, with each replicate comprising 120 minutes of daily frugivore perching time (time from arrival until departure from a tree, including foraging, Wotton 2007) across 14 days, adjusting frugivore gut passage time of seeds and fruit production according to the tree species examined (Table 1). Our analyses used seed dispersal events that occurred during the last three days of the model runs; this minimised the risk of ‘burn in’ effects, but still had ample sample size for robust parameter estimation. Each individual bird started the simulation at a randomly chosen tree, and the number of fruit removed from each tree and the dispersal distance of every seed were recorded.

Seed dispersal distributions were summed across individual birds to characterize the population level pattern for each tree species. A Weibull probability density function (Weibull 1951, Eq. 1) was fitted to the distributions by maximum likelihood estimation using the ‘fitdistr’ command in the MASS library in R–3.1.1 (R Development Core Team 2015). We used the Weibull distribution because it is flexible, approximating a number of other probability distribution functions that have been used to summarize seed dispersal kernels, and it quantifies the properties of dispersal kernels that we are interested in i.e. scale (mean seed dispersal distance) and shape (i.e. kurtosis-1; low shape values equate to high kurtosis and ‘fat’ long tails and *vice versa*).

 Eq. 1

where *x* = distance from tree, *α* = scale parameter, and *β* = shape parameter, all > 0.

For each analysis, we estimated the scale and shape parameters of the seed dispersal kernels; for these data, we were most interested in the scenario analyses that used empirically derived ‘field’, or ‘observed pattern’, estimates of tree aggregations while varying disperser densities, and *vice versa*. We also quantified the total number of dispersed seeds, seed rain map plots, frugivore foraging ranges (via convex hulls, computed in the R Spatstat library, Baddeley and Turner 2005) and the flight distances that resulted in them, and performed a spatial analysis of seed rain using a bivariate pair correlation function (Illian et al. 2008) based on spatial association between trees and deposition events.

**References**

Augspurger, C. K. and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. – Oecologia 61: 211–217.

Baddeley, A. and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. – Journal of Statistical Software 12: Online: http://www.jstatsoft.org/.

Bell, R. 1996. Seed dispersal by kereru (*Hemiphaga novaeseelandiae*) at Wenderholm Regional Park. – MSc thesis, Auckland University, New Zealand.

Beveridge, A. E. 1964. Dispersal and destruction of seed in central North Island podocarp forests. – Proceedings of the New Zealand Ecological Society 11: 48–56.

Bullock, J. M. et al. 2006. Measuring plant dispersal: an introduction to field methods and experimental design. – Plant Ecology 186: 217–234.

Campbell, K. L. 2006. A study of home ranges, movements, diet and habitat use of kereru (*Hemiphaga novaeseelandiae*) in the southeastern sector of Banks Peninsula, New Zealand. – MSc thesis, Lincoln University, Canterbury, New Zealand.

Clout, M. N. and Hay, J. R. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. – New Zealand Journal of Ecology 12 (supplement): 27–33.

Clout, M. N. et al. 1991. Seasonal movements of New Zealand Pigeons from a lowland forest reserve. – Notornis 38: 37–47.

Clout, M. N. and Tilley, J. A. V. 1992. Germination of miro (*Prumnopitys ferruginea*) seeds after consumption by New Zealand pigeons (*Hemiphaga novaeseelandiae*). – New Zealand Journal of Botany 30: 25–28.

Coates-Estrada, R. and Estrada, A. 1988. Frugivory and seed dispersal in *Cymbopetalum* *baillonii* (Annonaceae) at Los Tuxtlas, Mexico. – Journal of Tropical Ecology 4: 157–172.

Cordeiro, N. J. and Howe, H. F. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. – Proceedings of the National Academy of Sciences of the United States of America 100: 14052–14056.

Cortes, M. C. and Uriarte, M. 2013. Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. – Biological Reviews 88: 255–272.

Cousens, R. D. and Rawlinson, A. A. 2001. When will plant morphology affect the shape of a seed dispersal ‘kernel’? – Journal of Theoretical Biology 211: 229–238.

DeAngelis, D. L. and Mooij, W. M. 2005. Individual-based modeling of ecological and evolutionary processes. – Annual Review of Ecology and Systematics 36: 147–168.

Fedriani, J. M. et al. 2010. Spatial pattern of adult trees and the mammal-generated seed rain in the Iberian Pear. – Ecography 33: 545–555.

Forget, P. M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). – Biotropica 24: 408–414.

Greene, T. 2003. Distance sampling populations of New Zealand birds – estimating kaka and kereru abundance. – www.doc.govt.nz/Documents/science–and.../SciencePoster64.

Grimm, V. et al. 2010. The ODD protocol: a review and first update. – Ecological Modelling 221: 2760–2768.

Hamby, D. M. 1994. A review of techniques for parameter sensitivity analysis of environmental models. – Environmental Monitoring and Assessment32: 135–154.

Hanoteaux, S. et al. 2013. Effects of spatial patterns on the pollination success of a less attractive species. – Oikos 122: 867–880.

Hill, M. T. 2003. Diet, dispersal and distribution of kereru (*Hemiphaga novaeseelandiae*) in a lowland podocarp-hardwood forest. – MSc thesis, Massey University, Palmerston North, New Zealand.

Holmes, E. E. and Wilson, H. B. 1998. Running from trouble: long-distance dispersal and the competitive coexistence of inferior species. – The American Naturalist 151: 578–586.

Howe, H. F. and Miriti, M. N. 2004. When seed dispersal matters. – Bioscience 54: 651–660.

Illian, J. et al. 2008. Statistical Analysis and Modeling of Spatial Point Patterns*.* – John Wiley and Sons, Ltd, Chichester, U. K.

Johnson, S. 2001. *Prumnopitys ferruginea* (miro) seedling recruitment patterns in the Catlins, New Zealand, and dispersal by *Hemiphaga novaeseelandiae* (New Zealand Pigeon). – MSc Thesis in Environmental Science, University of Otago, New Zealand.

Kelly, D. et al. 2010. Mutualisms with the wreckage of an avifauna: the status of bird pollination and fruit-dispersal in New Zealand. – New Zealand Journal of Ecology 34: 66–85.

Levey, D. J. et al. 1984. Fruit choice in neotropical birds: the effect of distance between fruits on choice patterns. – Ecology 65: 844 – 850.

Levey, D. J. et al. 2008. Modeling long-distance seed dispersal in heterogeneous landscapes. – Journal of Ecology 96: 599–608.

Levin, S. A. et al. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. – Annual Review of Ecology, Evolution, and Systematics 34: 575–604.

McEwen, W. M. 1978. The food of the New Zealand pigeon (*Hemiphaga novaeseelandiae novaeseelandiae*). – New Zealand Journal of Ecology 1: 99–108.

McEwen, W. M. 1988. Cone and seed phenology in several New Zealand conifer tree species. – Tuatara 30 (1): 66–76.

Miskelly, C. M. et al. 2008. Conservation status of New Zealand birds. – Notornis 55: 117–135.

Morales, J. M. and Carlo, T. A. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. – Ecology 87: 1489–1496.

Morales, J. M. et al. 2012. Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in Patagonia. – Ecology 93 (4): 741– 748.

Morales, J. M. et al. 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for Cantabrian thrushes and trees. – PLoS ONE 8:e65216. doi: 10.1371/journal.pone.0065216.

Nathan, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. – Diversity and Distributions 11: 125–130.

Nathan, R. and Muller-Landau, C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – Trends in Ecology and Evolution 15: 278–285.

Nathan, R. et al. 2008. Mechanisms of long distance dispersal. – Trends in Ecology and Evolution 23: 638–647.

Pegman, A. P. McK. 2012. Reconstruction of seed dispersal via modeling, seedling recruitment, and dispersal efficiency of *Hemiphaga novaeseelandiae* in *Vitex* *lucens* and *Prumnopitys* *ferruginea* in New Zealand. – PhD thesis, Auckland University, New Zealand.

Pierce, R. J. and Graham, P. J. 1995. Ecology and breeding biology of kukupa (*Hemiphaga novaeseelandiae*) in Northland. – Science and Research Series 91. Wellington, Department of Conservation.

Powlesland, R. G. et al. 2011. Satellite tracking of kereru (*Hemiphaga* *novaeseelandiae*)in Southland, New Zealand: impacts, movements and home range. – New Zealand Journal of Ecology 35: 229–235.

R Development Core Team. 2015. R version 3.11.1: a language and environment for statistical computing. – R Foundation for statistical computing, Vienna, Austria. ISBN 3–900051–07–0, http://www.R–project.org.

Robledo-Arnuncio, J. J. et al. 2014. Space, time and complexity in plant dispersal ecology. – Movement Ecology 2: 16. doi: 10.1186/s40462–014–0016–3.

Rodriguez-Perez, J. et al. 2012. Adult proximity and frugivore’s activity structure the spatial pattern in an endangered plant. – Functional Ecology 26: 1221–1229.

Salmon, J. T. 1980. Native Trees of New Zealand. – Ed. Geoff Walker, Reed Methuen Publishers Ltd.

Santamaria, L. et al. 2007. Predicting spatial patterns of plant recruitment using animal-displacement kernels. – PLoS ONE 2 (10): e1008. doi:10.1371/journal.pone.0001008.

Saracco, J. F. et al. 2005. Crop size and fruit neighbourhood effects on visitation to fruiting trees. – Biotropica 37: 80–86.

Schotborgh, H. M. 2005. An analysis of home ranges, movements, foods and breeding of kereru (*Hemiphaga novaeseelandiae*) in a rural-urban landscape on Banks Peninsula, New Zealand. – MSc thesis, Lincoln University, Canterbury, New Zealand.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. – Vegetatio 107:15–29.

Schupp, E.W. et al. 2010. Seed dispersal effectiveness revisited: a conceptual review. – New Phytologist 188: 333–353.

Sekercioglu, C. H. et al. 2004. Ecosystem consequences of bird declines. – Proceedings of the National Academy of Sciences of the United States of America 101: 18042–18047.

Spiegel, O. and Nathan, R. 2007. Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. – Ecology Letters 10: 718–728.

Tiffney, B. H. 2004. Vertebrate dispersal of seed plants through time. – Annual Review of Ecology and Systematics 35: 1–29.

Traveset, A. 1998. Effect of seed passage through vertebrate frugivores’ guts on germination: a review. – Perspectives in Plant Ecology, Evolution and Systematics 1:151–190.

Uriarte, M. et al. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. – Ecology 92: 924–937.

Weibull, W. 1951. A statistical distribution function of wide applicability. – ASME Journal of Applied Mechanics, Transactions of the American Society of Mechanical Engineers: 293–297.

Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. – Ecological Monographs 70: 331–351.

Wilensky, U. 1999. NetLogo. http://ccl.northwestern.edu/netlogo/. – Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, Illinois, USA.

Will, H. and Tackenberg, O. 2008. A mechanistic simulation model of seed dispersal by animals. – Journal of Ecology 96: 1011–1022.

Wotton, D. M. 2007. Consequences of dispersal failure: kereru and large seeds in New Zealand. – PhD thesis, Canterbury University, New Zealand.

Wotton, D. M. et al. 2008. Seed retention times in the New Zealand Pigeon, *Hemiphaga novaeseelandiae*. – New Zealand Journal of Ecology 32: 1–6.

Wotton, D. M. and Kelly, D. 2011. Frugivore loss limits recruitment of large-seeded trees. – Proceedings of the Royal Society B: Biological Sciences 278: 3345–3354.

Wotton, D. M. and Kelly, D. 2012. Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. – Journal of Biogeography 39: 1973–1983.

Zurell, D. et al. 2010. The virtual ecologist approach: simulating data and observers. – Oikos 119: 622–635.