Oikos

## **OIK-07337**

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## Appendix 1: Additional details about the interaction network simulation approach

- In the network simulations, total interaction frequencies of plants took differences in plant
- 32 species abundance into account. We assumed a negative relationship between fruit size and
- interaction frequency (Donoso et al. 2017; González-Castro et al. 2015; Moles et al. 2005):

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35 (1)  $f_i = 1/x_i$ 

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- 37 where  $x_i$  represents the fruit volume value for plant i, and  $f_i$  represents the expected total
- interaction frequency (Donoso et al. 2017).

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- 40 Similarly, total interaction frequencies of bird species took differences in bird abundance into
- 41 account. We assumed a negative relationship between body mass and abundance (Cotgreave
- 42 1993; González-Castro et al. 2015); in this case, we assumed undercompensation (i.e. interaction
- frequency decreases less rapidly than bird size increases) as large birds tend to consume more
- 44 fruits per individual (García et al. 2014).

45

46 (2)  $g_j = (1/y_j) + \beta$ 

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- where  $y_i$  is the bird size value for bird j,  $g_i$  is the expected total bird interaction frequency, and  $\beta$
- being an undercompensation parameter, set to 10 % of the maximum value of 1/y. Donoso et al.
- 2017 found that results were robust to variation in the value of β. Because factors other than size
- 51 may influence species abundances, we investigated whether imperfect relationships between size
- and interaction frequencies had an effect on model results. To do this, we predefined an
- imperfect ( $r^2 = 0.6$ ) relationship between interaction frequency and fruit volume, and between
- 54 interaction frequency and bird size, using the R package faux version 0.0.1.0. We found that
- mean seed dispersal distances, derived from our simulations, were unchanged when
- 56 implementing these imperfect relationships between size and interaction frequencies.

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#### 61 language for statistical computing 62 63 Explanatory comments (#) 64 65 #-----# 66 67 68 #The dispsimulation function generates estimated seed dispersal distances for plant-69 bird interactions. This function takes as input an object with disperser body mass 70 (kg) for each interaction event in a network. 71 72 #Nbird = number of bird species in the community 73 #obsperbird = number of interaction events for each bird species 74 75 dispsimulation <- function (x) {</pre> 76 dispdist <- rep(NA, obsperbird \* Nbird)</pre> 77 for(i in 1:nrow(x)) { 78 #a mean GPT is selected from the allometric equation derived from empirical data 79 presented in this study. [i,3] indicates the column where bird body mass is located, 80 this may not fit with other data structures 81 meanGPThour $<-4.5*x[i,1]^0.5$ 82 83 #convert GPT to seconds (since speed is in m/s) 84 meanGPT <- meanGPThour\*3600</pre> 85 86 #calculate the shape and scale parameters for the gamma distribution using meanGPT 87 and variance (we chose variance = 100241, since this was the average GPT 88 variance calculated across 11 empirical studies in which variance was reported; 89 see Table S2) 90 scalevalue <- 75311 /meanGPT 91 shapevalue <- meanGPT^2/75311 92 93 #select a GPT value for this particular interaction from the GPT gamma distribution 94 GPT <- rgamma(1, shape = shapevalue, scale = scalevalue)</pre> 95 96 #then select a mean flight speed (calculated used the allometric equation presented 97 in Alerstam et al. 2007) 98 meanspeed $<-15.7*x[i,1]^0.17$ 99 100 #select a flight speed value for this particular interaction using meanspeed and 2.078 to parameterize rnorm. 2.078 is the flight speed sd average 101 102 reported in Alerstam et al. 2007 for those species with body mass lower than 1.77 kg 103 (which is the largest bird species across our 7 Andean communities) 104 speed <- rnorm(1, meanspeed, 2.078)</pre> 105 106 #calculate the max distance travelled (if flying straight without stopping) given the 107 selected GPT. 108 max\_distance <- speed\*GPT</pre> 109 110 #correction factor which accounts for birds resting/not always moving in a straight 111 line. 112 distance <- 0.002 \* max\_distance</pre>

Appendix 2: Source code for the mechanistic trait-based seed dispersal model in the R

```
113
       # NOTE! there may be a few cases where the speed value -selected from rnorm- could
114
115
       have a negative value.
       # For these few cases, the negative seed dispersal distance is replaced with NA.
116
          if (distance < 0){
117
            distance<-NA
118
          }
119
             dispdist[i] <- distance</pre>
120
121
122
       return(dispdist)
123
124
      }
```

## 125 Appendix 3

**Table A1.** Summary of feeding trial studies for the relationship between avian frugivore **body** mass and gut passage time.

Species	Body mass (g)	Mean retention time (min)	Std. deviation	
Acanthagenys refogularis	44	40.6	12.5	Murphy et al . 1993
Acridotheres cristatellus	123	18.4	NA	Shi <i>et al</i> . 2015
Alophoixus pallidus	42.8	44	11	Khamcha et al . 2014
Arizelocichla milanjensis	54	44	NA	Lehouck et al . 2009, personal communication
Bombycilla cedrorum	32	26.7	27.38	Ramirez & Ornelas 2009
Bycanistes bucinator	635	64	29	Lenz et al. 2011, personal communication
Ceratogymna atrata	1431	248.4	124.6	Holbrook & Smith 2000
Ceratogymna cylindricus	1038	218.4	95.2	Holbrook & Smith 2000
Dicaeum hirundinaceum	9	13.7	6.6	Murphy et al. 1993
Grantiella picta	20.7	24.4	9.77	Barea 2008
Hemiphaga novaeseelandiae	650	120	39.1	Wotton et al. 2008; Wotton et al. 2012
Hypsipetes amaurotis	78.7	20.8	NA	Fukui 2003
Megalaima asiatica	90.5	26.9	NA	Shi <i>et al</i> . 2015
Megalaima nuchalis	87.7	26.9	NA	Chang <i>et al</i> . 2012
Mionectes oleagineus	11.5	15.7	NA	Westcott & Graham 2000
Musophaga johnstoni	250	69.6	17.6	Sun <i>et al</i> . 1997
Myadestes melanops	32.1	24.5	NA	Murray 1988
Nestor notabilis	870	140.4	NA	Young et al . 2012
Notiomystis cincta	35	13.5	NA	Trass 2000
Onychognathus morio	135	35	NA	Mokotjomela <i>et al</i> . 2015
Onychognathus tristramii	120	135.1	NA	Spiegel & Nathan 2007
Penelope obscura	1770	346	NA	Guix & Ruiz 1997
Phainoptila melanoxantha	56	17.5	NA	Murray 1988
Phyllastrephus placidus	34.5	80.36	NA	V. Lehouck, personal communication
Prosthemadera novaeseelandiae	105	37	NA	O'Connor 2006
Pycnonotus aurigaster	44.4	22.6	NA	Shi <i>et al</i> . 2015
Pycnonotus jocosus	27.4	24	NA	Shi <i>et al</i> . 2015
Pycnonotus melanicterus	28.9	35	8	Khamcha et al . 2014
Pycnonotus xanthopygos	40	34.7	NA	Spiegel & Nathan 2007
Semnornis frantzii	57.3	26.6	NA	Murray 1988
Sturnus vulgaris	71	42.3	16.5	LaFleur et al. 2009; Karasov & Levey 1990
Tauraco corythaix	300	110.4	NA	Mokotjomela et al . 2015
Tauraco hartlaubi	235	42.9	NA	Lehouck et al . 2009, personal communication
Turdus helleri	66	45.73	NA	Lehouck et al. 2009, personal communication
Turdus merula	100	39.35	68.3	Morales et al . 2013
Turdus migratorius	79	48	NA	Karasov & Levey 1990
Zosterops lateralis	11	24.75	30.45	French 1996; Stanley & Lill 2002

We developed an allometric equation specific to frugivores. We only included studies that fed natural fruit to birds and excluded studies using artificial seeds or fruits, or marker dyes. We used the search strings "seed or fruit + gut + retention or passage". For some studies GPT medians were reported instead of means, if means could not be attained via author personal communication or digitisation from presented plots, the study was not included in our analysis. The allometric relationship between body mass and GPT presented by Robbins 1993 included data on 21 bird species across all diet types (including studies using liquid and marker dye to measure GPT). Only 4 of the 21 species were fed fruits. The 37 included species are widely distributed across the weight range of frugivore species found in the seven Andean communities. Generally, standard errors were reported instead of standard deviations; however, if standard errors and sample sizes were both reported we converted standard error to standard deviation.

# Table A2. Summary of field-based empirical studies for the relationship between avian frugivore

#### body mass and seed dispersal distances.

Species	Body mass (g)	Mean dispersal distance (m)	Max dispersal distance (m)	Source
Bycanistes bucinator	635	528	14790	Mueller et al . 2014
Ceratogymna atrata	1431	1521	6919	Holbrook & Smith 2000
Ceratogymna cylindricus	1038	1537	4628	Holbrook & Smith 2000
Corythaeola cristata	1000	240.5	NA	Sun <i>et al</i> . 1997
Dicaeum hirundinaceum	9.25	103.67	500	Ward & Paton 2007
Hemiphaga novaeseelandiae	650	84.7	1469	Wotton & Kelly 2012; Wotton et al. 200
Mionectes oleagineus	11.5	26.16	86	Westcott & Graham 2000
Musophaga johnstoni	250	137.5	NA	Sun <i>et al</i> . 1997
Myadestes melanops	31.5	84.7	364.7	Murray 1988
Onychognathus tristramii	119	1168	4800	Spiegel & Nathan 2007
Phainoptila melanoxantha	58	84.9	504.7	Murray 1988
Prosthemadera novaeseelandiae	105	222.5	NA	O'Connor 2006
Pycnonotus xanthopygos	40.5	303	900	Spiegel & Nathan 2007
Semnornis frantzii	63.25	62.6	215	Murray 1988
Turaco schuettii	250	149	NA	Sun <i>et al</i> . 1997
Turdus merula	100	89.48	2220	Breitbach et al . 2012

We included empirical seed dispersal studies which quantified seed dispersal distances by combining gut passage time and frugivore movement data. We did not include studies approximating SDD based on molecular data. We used ordinary least squares (OLS) to fit an allometric equation between bird body mass and mean seed dispersal distance for empirical field-based studies (Table S1). This resulted in the following equation: z = 504BM[kg]<sup>0.48</sup>, where z is seed dispersal distance and BM is disperser species body mass. The ratio between the allometric constant from the independent expectation (equation 7 in the main text; 504/254340) and the allometric constant from empirical studies presented here was used to calculate the correction factor (0.002; accounting for movements deviation from a straight line and time not moving).

Fig. A1. Relationship between **body mass** and mean **gut passage time** using data extracted from empirical feeding trials for frugivorous birds (see detailed information about the studies in Table S2). Body mass is positively related to mean gut passage time ( $r^2 = 0.69$ , p < 0.0001, n=39). The grey shaded region indicates the confidence interval for the regression.

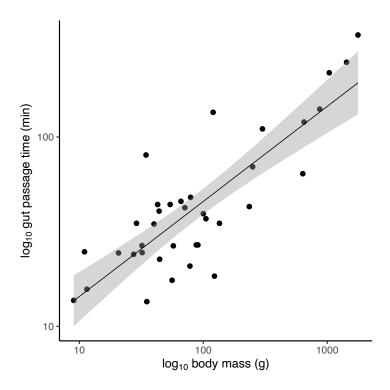
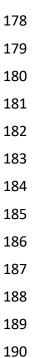


Fig. A2. Relationship between **body mass** and **mean dispersal distance** using data extracted from empirical studies of seed dispersal by frugivorous birds (see Table S2 for included studies). Body mass is positively related to mean dispersal distance ( $r^2 = 0.4$ , p = 0.007, n = 16). The grey shaded region indicates the confidence interval for the regression.



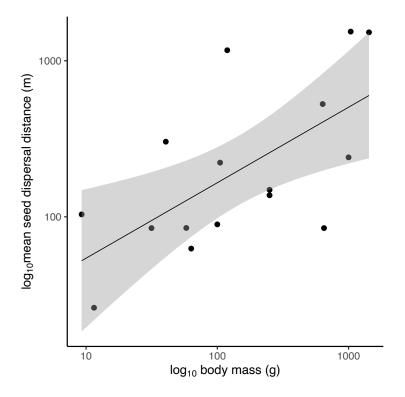
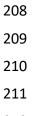
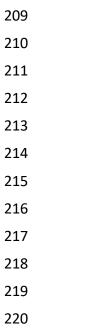
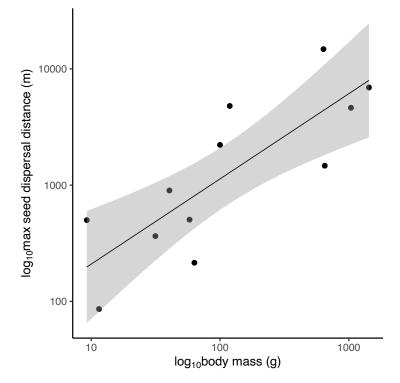


Fig. A3. Relationship between body mass and max seed dispersal distance using data extracted from empirical feeding trials for frugivorous birds (see Table A2). Body mass is positively related to max seed dispersal distance ( $r^2 = 0.62$ , p = 0.001, n=12). The grey shaded region indicates the confidence interval for the regression.

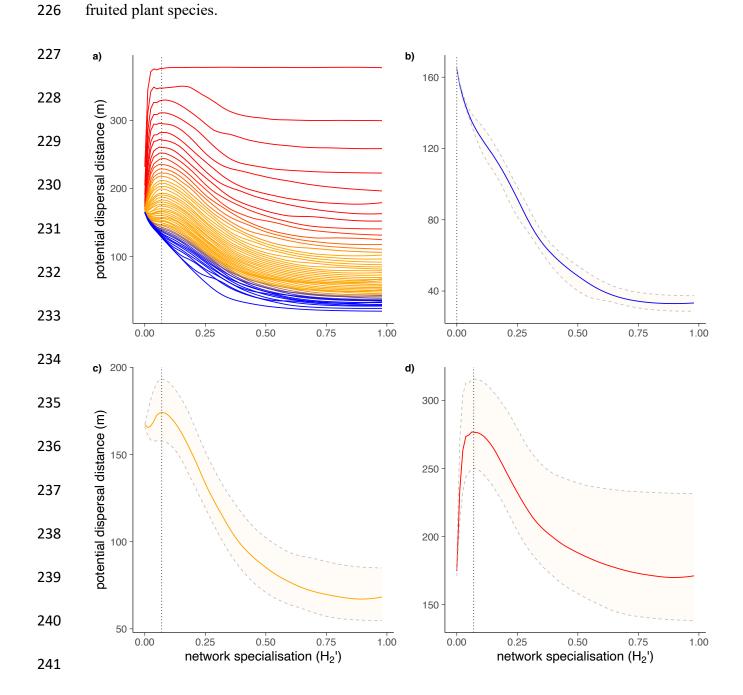






Appendix 4.

Fig. A4. Long-distance seed dispersal (LDD) results for (b) small, (c) medium, and (d) large



## **Appendix 5: Sensitivity analysis**

Morris's elementary effects method estimates the effect of each factor on the model output repeatedly, while the other factors take on different values from their entire ranges, and then averages these estimates into a measure of overall effect; these effects are called elementary effects. The elementary effects are statistically analysed to measure their relative importance (Thiele et al. 2004). We used the estimated mean of the distribution of the absolute values of the elementary effects,  $\mu^*$ , as a sensitivity measure to establish the overall impact of a parameter on the output. We performed the sensitivity analysis on five model parameters (k; Table 1), which were varied according to predefined ranges (see Table A3). The number of tested settings is given by  $r \times (k +$ 1), where r is the number of elementary effects computed per parameter. As we chose 160 elementary effects, this led to  $160 \times (5 + 1) = 960 \text{ model runs}$ . We ran the global sensitivity analysis for both, the mean and the 95% quantile of seed dispersal distances. We used the following methods to determine the range of the parameter values to be included in the global sensitivity analysis. For GPT<sup>exp</sup> we used the 95% confidence intervals of the exponent from the fitted allometric equation; for GPTvar we used the min and max values from feeding trial studies (Table A1); for  $FS^{\text{exp}}$  we took the range of 95% confidence intervals of the exponent from those calculated in a similar flight speed allometric equation presented in Alerstam et al. 2007; for FSsd we took the min and max standard deviation values from those reported from empirical flight speed data in Alerstam et al. 2007; for the CorrFactor we simply used a min value that was half of the estimated value and a maximum value that was twice the estimated value.

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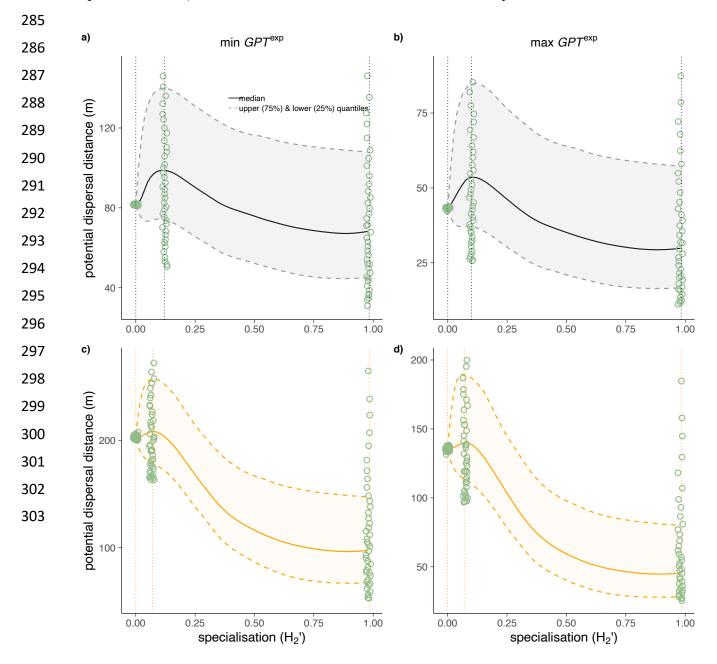
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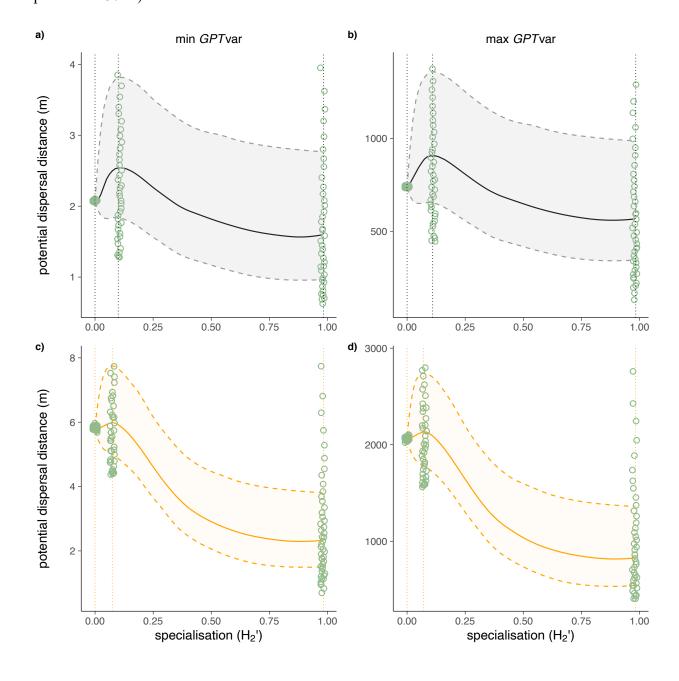
**Table A3.** Sensitivity analysis model parameters and results from the Morris screening method. The top three most influential parameters for median seed dispersal distances are bolded in black; the top three most influential parameters for the 95% quantile of seed dispersal are bolded in orange.  $\mu^*$  is an estimate of the overall influence of a factor on the model output (including interactions with other factors), and  $\sigma$  is an estimate of how much the influence of a factor depended on interactions and stochasticity.

			median		95% quantile	
parameter	description	range	$\mu^*$	σ	$\mu^*$	σ
gut passage time:						
$GPT^{\rm exp}$	exponent of the GPT Eq. 3	0.39-0.62	0.31	0.58	0.16	0.31
GPTvar	variance of the GPT gamma distribution, $s^2$ in Eq. 5 and 6	2613-931509	1	1	1	0.98
bird movement:						
$FS^{\mathrm{exp}}$	exponent of the FS Eq. 4	0.13-0.21	0.12	0.23	0.01	0.007
FS sd	standard deviation of the FS gaussian distribution	0-4.7	0	0	0	0
CorrFactor	fc in Eq. 7	0.001 - 0.004	0.58	0.96	0.55	1

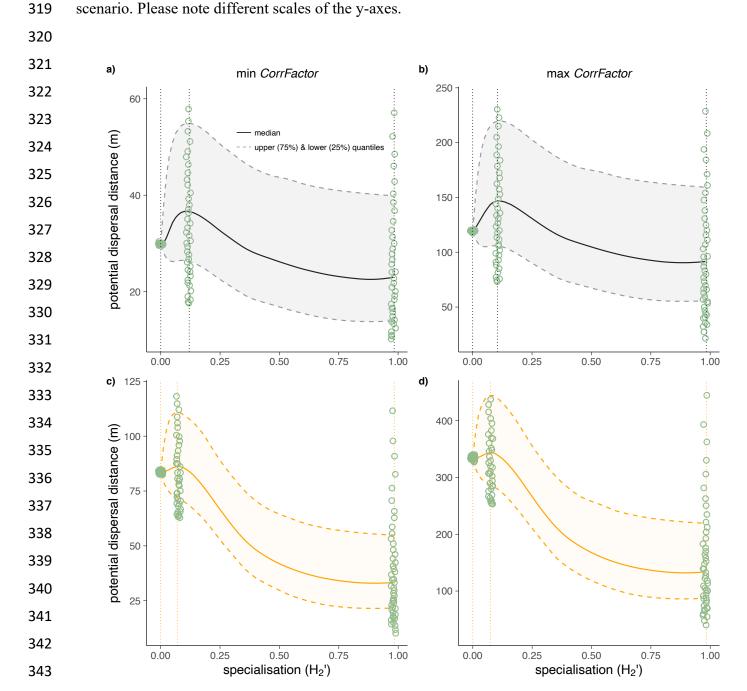
**Fig. A5.** The relationship between network specialisation ( $H_2$ ') and median community seed dispersal distances (TDK<sub>community</sub>) when using the a) min  $GPT^{\text{exp}}$  value, and b) max  $GPT^{\text{exp}}$ .  $GPT^{\text{exp}}$  is included in the top three most influential parameters for: mean and the 95% quantile of seed dispersal distances. Results show the same hump-shaped pattern between  $H_2$ ' and community-wide median seed dispersal distances. Absolute distance values for both the mean (min $GPT^{\text{exp}}$ : peak in seed dispersal = 98 m; max $GPT^{\text{exp}}$ : peak in seed dispersal = 53 m) and the 95% quantile values (min $GPT^{\text{exp}}$ : peak in seed dispersal = 209 m; max $GPT^{\text{exp}}$ : peak in seed dispersal = 140 m) are different. Please note different scales of the y-axes.



**Fig. A6.** The relationship between network specialisation ( $H_2$ ') and **mean** community seed dispersal distances (TDK<sub>community</sub>) when using the a) min GPTvar value, and b) max GPTvar. GPTvar is included in the top three most influential parameters for: mean, and 95% quantile seed dispersal distances. All figures show the same hump-shaped pattern between  $H_2$ ' and mean or LDD community-wide seed dispersal distances. c), and d) report results from the 95% quantile. Absolute seed dispersal distance values were very different for the mean (minGPTvar: peak in seed dispersal = 2.5 m; maxGPTvar: peak in seed dispersal = 909) and 95% quantile of seed dispersal distances (minGPTvar: peak in seed dispersal = 6 m; maxGPTvar: peak in seed dispersal = 2157 m).



**Fig. A7.** The relationship between network specialisation ( $H_2$ ') and community seed dispersal distances (TDK<sub>community</sub>) when using the a) min *CorrFactor* value, and b) max *CorrFactor*. *CorrFactor* is included in the top three most influential parameters for: mean, and 95% quantile seed dispersal distances. c), and d) report results from the 95% quantile. All figures show the same hump-shaped pattern between  $H_2$ ' and median or LDD community-wide seed dispersal distances. Absolute seed dispersal distance values were longer under the max *CorrFactor* scenario. Please note different scales of the y-axes.



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- Alerstam, T., Rosén, M., Bäckman, J., Ericson, P.G.P. & Hellgren, O. (2007). Flight speeds among bird species: allometric and phylogenetic effects. *PLoS Biol*, 5, e197.
- Barea, L.P., (2008). *Interactions between frugivores and their resources: case studies with the painted honeyeater Grantiella picta*. PhD Thesis, Charles Sturt University, Albury-Wodonga.
- Bender, I.M.A., Kissling, W.D., Blendinger, P.G., Gaese, K.B., Hensen, I., Kühn, I., et al. (2018). Morphological trait matching shapes plant–frugivore networks across the Andes. *Ecography*, 30, 1894.
  - Breitbach, N., Böhning-Gaese, K., Laube, I. & Schleuning, M. (2012). Short seed-dispersal distances and low seedling recruitment in farmland populations of bird-dispersed cherry trees. *Journal of Ecology*, 100, 1349–1358.
  - Calder, W.A. (1996) Size, Function and Life History, 2nd edn. Dover Publications, New York.
  - Chang, S-Y., Lee, Y.-F., Kuo, Y-M. & Chen, J-H. (2012). Frugivory by Taiwan Barbets (*Megalaima nuchalis*) and the effects of deinhibition and scarification on seed germination. *Canadian Journal of Zoology*, 90, 640–650.
  - Cotgreave, P. (1993) The relationship between body size and population abundance in animals. *Trends Ecol. Evol.* 8, 244 248.
  - Donoso, I., Schleuning, M., García, D. & Fründ, J. (2017). Defaunation effects on plant recruitment depend on size matching and size trade-offs in seed-dispersal networks. *Proc. R. Soc. B Biol. Sci.*, 284, 20162664.
  - French, K. (2011). French K. (1996). The gut passage rate of silvereyes and its effect on seed viability. *Corella* 20: 16-19, 1–4.
  - Fukui, A. (2003). Relationship between seed retention time in bird's gut and fruit characteristics. *Ornithological Science*, 2, 41–48.
  - García, D., Martínez, D., Stouffer, D.B. & Tylianakis, J.M. (2014). Exotic birds increase generalization and compensate for native bird decline in plant-frugivore assemblages. *J. Anim. Ecol.*, 83, 1441–1450.
- Guix, J.C. & Ruiz, X. (1997). Weevil larvae dispersal by guans in Southeastern Brazil.
   *Biotropica*, 29, 522–525.
  - González-Castro, A., Yang, S., Nogales, M. & Carlo, T.A. (2015). Relative importance of phenotypic trait matching and species' abundances in determining plant-avian seed dispersal interactions in a small insular community. *AoB Plants*, 7, plv017.
  - Holbrook, K.M. & Smith, T.B. (2000). Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, 125, 249–257.
- Khamcha, D., Savini, T., Westcott, D. A., McKeown, A., Brockelman, W. Y., Chimchome, V.,
   & Gale, G. A. (2014). Behavioral and social structure effects on seed dispersal curves
   of a forest-interior bulbul (*Pycnonotidae*) in a Tropical Evergreen Forest. *Biotropica*,
   46(3), 294–301.
- Karasov, W.H. & Levey, D.J. (1990). Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological Zoology*, 63, 1248–1270.

- LaFleur, N., Rubega, M. & Parent, J. (2009). Does frugivory by European starlings (*Sturnus vulgaris*) facilitate germination in invasive plants? *The Journal of the Torrey Botanical Society*, 136, 332–341.
- Lehouck, V., Spanhove, T., Demeter, S., Groot, N. E., & Lens, L. (2009). Complementary seed
   dispersal by three avian frugivores in a fragmented Afromontane forest. *Journal of Vegetation Science*, 20, 1110–1120.
- Leisler, B. & Winkler, H. (1991). Ergebnisse und Konzepte ökomorphologischer Untersuchungen an Vögeln. *J. Ornithol*, 132, 373–425.

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- Lenz, J., Fiedler, W., Caprano, T., Friedrichs, W., Gaese, B.H., Wikelski, M. & Böhning-Gaese,
   K. (2011). Seed-dispersal distributions by trumpeter hornbills in fragmented landscapes.
   *Proceedings of the Royal Society B: Biological Sciences*, 278, 2257–2264.
  - Mokotjomela, T.M., Hoffmann, J.H. & Downs, C.T. (2015). The potential for birds to disperse the seeds of *Acacia cyclops*, an invasive alien plant in South Africa. *Ibis*, 157, 449–458.
  - Moles, A., Ackerly, D., Webb, C., Tweddle, J., Dickie, J. & Westoby, M. (2005) A brief history of seed size. *Science* 307, 576 580. (doi:10.1126/science.1104863)
  - Morales, J.M., García, D., Martínez, D., Rodríguez-Pérez, J. & Herrera, J.M. (2013). Frugivore behavioural details matter for seed dispersal: a multi-species model for cantabrian thrushes and trees. PLoS ONE, 8, e65216.
  - Mueller, T., Lenz, J., Caprano, T., Fiedler, W. & Böhning-Gaese, K. (2014). Large frugivorous birds facilitate functional connectivity of fragmented landscapes. *Journal of Applied Ecology*, 51, 684–692.
  - Murphy, S.R., Reid, N., Yan, Z. & Venables, W.N. (1993). Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers: effects on seedling establishment. *Oecologia*, 93, 171–176.
- Murray, K.G. (1988). Avian seed dispersal of three neotropical gap-dependent plants.
   *Ecological Monographs*, 58, 271–298.
  - O'Connor, S-J. (2006) *Modelling seed dispersal by tui*. BSc (Hons) Project Report, University of Canterbury, Christchurch.
  - Ramírez, M. M. & Ornelas, J.F. (2009) Germination of *Psittacanthus schiedeanus* (mistletoe) seeds after passage through the gut of Cedar Waxwings and Grey Silky-Flycatchers. *Journal of the Torrey Botanical Society*, 136, 332–331.
- Rayner, J. M. V. (1988). Form and function in avian flight. Current Ornithology, 5, 1–66.
- Robbins. (1993). Wildlife feeding and Nutrition, 2<sup>nd</sup> edn. Academic Press, San Diego.
- Shi, T-T., Wang, B. & Quan, R-C. (2015). Effects of frugivorous birds on seed retention time and germination in Xishuangbanna, southwest China. *Zoological Research*, 36, 241–247.
- Spiegel, O. & 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.
- Stanley, M.C. & Lill, A. (2002). Avian fruit consumption and seed dispersal in a temperate Australian woodland. *Austral Ecology*, 27, 137–148.
- Sun, C., Ives, A.R., Kraeuter, H.J. & Moermond, T.C. (1997). Effectiveness of three turacos as seed dispersers in a tropical montane forest. *Oecologia*, 112, 94–103.
- Trass, A. P. (2000) *Invasion of woody species into weed infested areas*. MSc Thesis, Massey University, Palmerston North.

- Ward, M.J. & Paton, D.C. (2007). Predicting mistletoe seed shadow and patterns of seed rain from movements of the mistletoebird, *Dicaeum hirundinaceum*. *Austral Ecology*, 32, 113–121.
- Westcott, D.A. & Graham, D.L. (2000). Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia*, 122, 249–257.
- Wotton, D.M. & 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.
- Wotton, D.M., Clout, M.N. & Kelly, D. (2008). Seed retention times in the New Zealand pigeon (*Hemiphaga novaezeelandiae novaeseelandiae*). New Zealand Journal of Ecology, 32, 1–441 6.
- Young, L.M., Kelly, D. & Nelson, X.J. (2012). Alpine flora may depend on declining
   frugivorous parrot for seed dispersal. *Biological Conservation*, 147, 133–142.