

Research



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Author for correspondence:

E. Rehm

e-mail: emrehm@gmail.com

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Animal movement drives variation in seed dispersal distance in a plant–animal network

E. Rehm¹, E. Fricke², J. Bender³, J. Savidge⁴ and H. Rogers²

¹Department of Ecology, Evolution, and Marine Biology, University of California at Santa Barbara, Santa Barbara, CA, USA

²Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA, USA

³Lincoln Park Zoo, Chicago, IL, USA

⁴Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins, CO, USA

ER, 0000-0002-5804-0027; EF, 0000-0002-0520-4200

Frugivores play differing roles in shaping dispersal patterns yet seed dispersal distance is rarely quantified across entire communities. We model seed dispersal distance using gut passage times and bird movement for the majority (39 interactions) of known bird–tree interactions on the island of Saipan to highlight differences in seed dispersal distances provided by the five avian frugivores. One bird species was found to be a seed predator rather than a disperser. The remaining four avian species dispersed seeds but differences in seed dispersal distance were largely driven by interspecific variation in bird movement rather than intraspecific variation in gut passage times. The median dispersal distance was at least 56 m for all species-specific combinations, indicating all species play a role in reducing high seed mortality under the parent tree. However, one species—the Micronesian Starling—performed 94% of dispersal events greater than 500 m, suggesting this species could be a key driver of long-distance dispersal services (e.g. linking populations, colonizing new areas). Assessing variation in dispersal patterns across this network highlights key sources of variation in seed dispersal distances and suggests which empirical approaches are sufficient for modelling how seed dispersal mutualisms affect populations and communities.

1. Background

Seed dispersal plays an important role in shaping plant population and community patterns [1,2]. Greater dispersal away from the parent plant can reduce negative conspecific distance and density-dependent mortality [3,4], maintain connectivity between disjunct populations [5], promote colonization of new habitats [5], and increase species migration rates [6]. Given that the vast majority of tropical trees and many temperate tree species rely on animals for seed dispersal services [7], understanding seed dispersal patterns within plant communities offers opportunities to assess whether individual seed dispersers provide similar or differing roles across plant species, determine the key sources of variation in seed dispersal patterns, and improve predictions about the outcome of disperser loss and reintroduction.

Yet our understanding of the community-level variation of seed dispersal remains limited as efforts often focus on a single or few species-specific interactions [8]. Plant species often interact with several dispersers and those dispersers are likewise interacting with many species of plants. Therefore, disperser roles may differ among plant species such as when a plant relies on a group of dispersers for long-distance seed dispersal [9,10] while other plants receive little or no benefit from those same dispersers. Taking a community approach to seed dispersal studies will clarify the changing dispersal patterns for a broad array of plant–animal interactions and allow development of

empirical approaches that efficiently characterize key sources of variation in dispersal.

To overcome the difficulties of studying all species-specific interactions within a community, efforts have focused on patterns of dispersal for different plant and animal functional types [9–13]. These efforts have started to reveal some community-level patterns such as how disperser body size and plant seed mass influence the dispersal process [10,12,14]. However, clumping species into functional groups may mask important differences in seed dispersal performed by dispersers of the same functional type or dispersal may vary independently of a given plant functional trait [15].

Another approach to making studies of community seed dispersal patterns more manageable is to break the seed dispersal process into component parts. For example, seed dispersal is a complicated series of events with the movement of seeds away from a parent tree being one of the early steps in this process [8,16]. This movement is often quantified as seed dispersal distance and is commonly modelled by combining seed gut passage times (GPTs) with disperser displacement to form a dispersal curve for that specific interaction. Although such distances have been regularly modelled for a variety of systems, to date, most efforts have modelled seed dispersal distance for one or a limited number of plant–animal interactions due to the difficulty of quantifying large numbers of interactions within diverse communities [17]. Therefore, inferences about community patterns in seed dispersal distance are limited or unclear [16].

Dispersal distance among dispersers can be complementary [15,18] or show large overlap in dispersal distance for the same plant species [19,20]. Similarly, patterns of seed dispersal distance by a single disperser species dispersing multiple plant species are equally inconsistent as dispersers may disperse seeds of multiple plants at similar [19,21–23] or different spatial scales [19–21,24]. While it is clear there is substantial variation in seed dispersal distance among plant–animal combinations, there is still little understanding if variation in seed dispersal distance is driven by variation in GPT among seed dispersers and plant species, disperser displacement alone, or a combination of both.

Tropical islands often have a high preponderance of fleshy fruits adapted for vertebrate dispersal combined with overall lower levels of diversity making seed dispersal studies in these systems tractable for understanding community-level dispersal dynamics [11,12,25]. We demonstrate the relative influences of bird and plant species identities on dispersal distance in a plant–animal interaction network on the island of Saipan. We combine avian movement and gut passage times for nearly all interacting limestone karst-forest tree and bird species to produce seed dispersal kernels for all avian dispersers and a substantial portion of the forest tree community. By modelling seed dispersal kernels across the forest tree community, we can identify and understand the drivers of variation in seed dispersal distance and consider how disruptions in the dispersal network may influence community seed dispersal patterns.

2. Material and methods

(a) Study site and species

This study took place from April 2015 to October 2016 on the island of Saipan (115 km²) in the Mariana Archipelago (15°11'

N, 145°44' E). The native limestone karst-forests of Saipan contain roughly 40 species of tree and shrub, with 10 species making up approximately 90% of tree stems. This study focused on the dispersal of 15 woody shrub and tree species (figure 1; electronic supplementary material, table S1) by five native forest bird species. These plant species produce fleshy fruits that are known components of frugivore diets, make up 94% of bird-dispersed tree stems in this forest type, and range in seed mass from 0.0001 g (*Pipturus argenteus*) to 0.62 g (*Aglaia marianensis*; electronic supplementary material, table S1). Additional tree species were excluded as they were rare within the study area, did not produce sufficient fruit during the study, or were not bird-dispersed. Tree species included 15 native and two naturalized species (*Carica papaya* and *Triphasia trifolia*; electronic supplementary material, table S1).

The five extant avian frugivores on Saipan are: Bridled White-eye (*Zosterops conspicillatus*), Golden White-eye (*Cleptornis marchei*), Mariana Fruit Dove (*Ptilinopus roseicapilla*), Micronesian Starling (*Aplonis opaca*), and White-throated Ground Dove (*Alopecoenas xanthonura*). All bird species were known to consume fruits and therefore considered potential seed dispersers. Species varied in the amount of fruit included in the diet from purely frugivorous (e.g. Mariana Fruit Dove) to omnivorous (e.g. Bridled White-eye) and in body size (5–150 g). For additional life-history traits such as home range size and habitat selection see Rehm *et al.* [26]. The Mariana fruit bat (*Pteropus mariannus*) is an additional frugivore on Saipan and likely influences dispersal patterns, especially for large-seeded plant species. However, the bat is functionally extinct on Saipan and was therefore not included in the current study. In addition, other dispersers have been extirpated within the Mariana Islands prior to or shortly following human settlement but their roles as seed dispersers are unknown [27].

(b) Gut passage times

To determine GPT, we conducted feeding trials with fruits from tree species fed to wild-caught birds. Fruits were collected from multiple trees and mixed before feeding to birds. Only healthy and non-breeding individuals were taken into a captive facility and were given at least 24 h to adjust to the enclosures before feeding trials began (electronic supplementary material, table S2). Birds were maintained on a standard maintenance diet of fruit, dried mealworm, and vitamin supplement. The maintenance diet was removed the evening prior to a feeding trial, allowing birds to pass all seeds overnight.

Trials began at 0600 h and birds were offered whole or partial (if the whole fruit was large and multi-seeded, as is the case for *C. papaya*) fruits. Birds were given sufficient time to passively feed and were hand-fed only if they would not feed voluntarily. Bridled White-eyes were not hand-fed due to their small body size. Golden White-eyes were not hand-fed as they readily consumed all fruits presented to them. Once a bird consumed the first fruit, it was allowed 10 min to consume additional fruits before the remaining fruit was removed. We used video monitoring to determine when and where seeds were defaecated or regurgitated, then counted the number of seeds per defaecation at the end of the trial. There were just two combinations where a bird species regurgitated seeds, Micronesian Starling consuming *A. mariannensis* and Mariana Fruit Dove consuming *Melanolepis multiglandulosa*. In these cases, regurgitation was treated like a gut passage for simplicity but the interpretation of dispersal distance should be treated with caution as bird movement likely varies depending on seed handling technique. GPT was calculated as the time from ingestion to the time of deposition. When birds fed voluntarily, time of ingestion was calculated beginning at the midpoint between the time when the first fruit and last fruit were consumed, a maximum 10 min

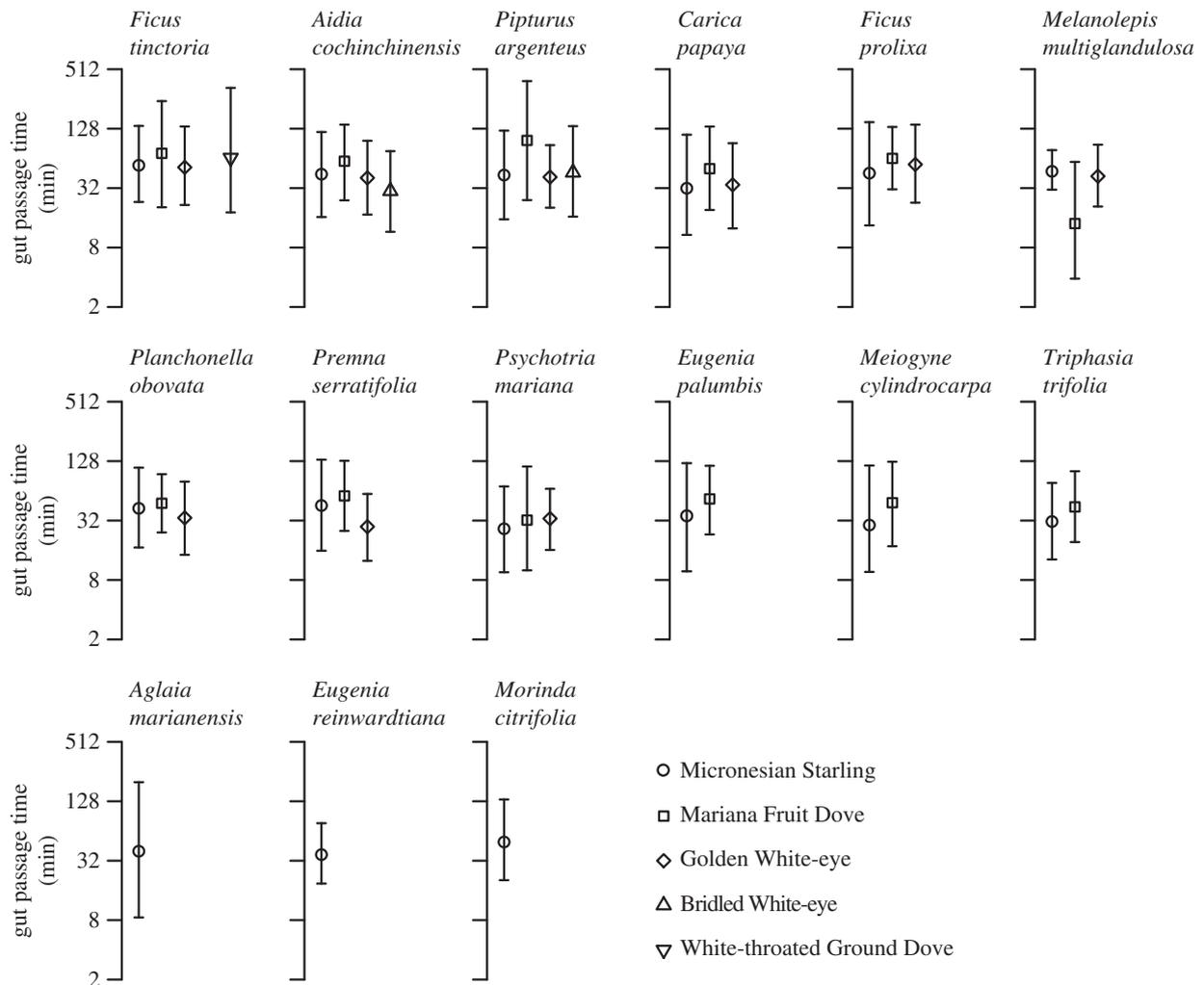


Figure 1. Posterior predictive distribution of gut passage times for 39 plant–bird interactions on the island of Saipan. Points represent median values and bars represent 95% credible intervals. Note the fourfold increasing scale on the y-axis.

interval. Since multiple fruits were often consumed within this period, we assume that seeds were passed in the same order they were consumed and calculated GPT accordingly. For birds that were hand-fed, exact ingestion time was known.

We used faecal samples collected from birds caught in the wild (E Rehm 2015–2016, unpublished data) and foraging observations (E Fricke 2013–2016, unpublished data) to determine which plant–animal combinations to include in this study. We excluded only one combination, Bridled White-eye and *Premna serratifolia*, even though it was observed in the wild [28] as we were unable to obtain GPT data. Bridled White-eyes did not eat *P. serratifolia* fruits in captivity and we did not hand feed Bridled White-eyes due to their small body size.

We used two White-throated Ground Dove, three Bridled White-eye, four Golden White-eye, five Micronesia Starling, and six Mariana Fruit Dove for feeding trials. We did not use more than two White-throated Ground Doves because most seeds (greater than 99%) fed to these two individuals were destroyed and all faecal samples collected in a related study lacked seeds. Individual birds were often used to determine the gut passage of multiple tree species but, when possible, multiple individuals of bird species were used to test a single tree species (electronic supplementary material, table S3).

(c) Bird movement

Bird movement was determined using standard very high frequency (VHF) radio tracking techniques. Non-breeding adults were captured using mist nets, fitted with radio transmitters

(BD-2, BD-2X Holohil Systems Limited, Ontario, Canada, for non-White-eye or custom built 0.34–0.68 g from JDJC Corporation, Iowa, USA for White-eye) using a leg-loop harness, and given a unique combination of metal and coloured leg bands. Potential bias can arise from different size transmitters and therefore their differing strength of signals. We compensated for this potential bias by having more persons conducting the tracking on smaller transmitters (four to five individuals instead of three to four individuals for larger transmitters) and by tracking the smaller-bodied birds with small transmitters at closer ranges as smaller birds tended to have smaller movement distances and were not disturbed by the presence of humans. We waited 24 h after transmitter attachment before beginning telemetry activities.

To determine movement patterns of birds on timescales relevant to the gut passage, we tracked birds during 2 h sessions. Locations were estimated every 10 min resulting in 13 locations per complete 2 h tracking session. The number of individuals tracked per species ranged from 10 to 15, the number of tracking sessions completed per individual ranged from 1–12, the number of days individuals were tracked ranged from 1 to 118, and tracking for all species spanned across portions of a wet and dry season, covering the peak fruiting season for nearly all focal plant species (electronic supplementary material, table S4). For more details on the tracking methods, see Rehm *et al.* [26].

(d) Data analysis

We used a hierarchical Bayesian framework to model GPTs from the captive feeding trials and movement patterns from bird

telemetry, and then used predicted movement distances and GPTs to develop dispersal kernels. Detailed descriptions of the gut passage and movement models are provided in the electronic supplementary material.

For the GPT model, we assumed that GPTs were lognormally distributed [29], with time_{ijbp} representing the GPT of pile i by bird individual j of bird species b passing seeds of plant species p . Mean log-transformed GPT ($\mu_{\text{time},ijbp}$) depends linearly on an intercept (β_0), effects of bird ($\beta_{\text{bird},b}$) and plant ($\beta_{\text{plant},p}$) species, their interaction ($\beta_{\text{inter},bp}$) and a bird individual effect ($\beta_{\text{indiv},jb}$):

$$\log(\text{time}_{ijbp}) \sim N(\mu_{\text{time},ijbp}, \sigma_{\text{time},bp}^2)$$

$$\mu_{\text{time},ijbp} = \beta_0 + \beta_{\text{bird},b} + \beta_{\text{plant},p} + \beta_{\text{inter},bp} + \beta_{\text{indiv},jb}$$

Bird species individual effects shared a species-specific variance term and are centred at zero.

For the bird movement model, we modelled displacement of birds from their location at the beginning of each tracking session, representing a hypothetical location of seed ingestion. We characterized telemetry measurement error by conducting beacon tests, calculating the distance between observed and true locations, and fitting the scale parameter of a Rayleigh distribution using maximum-likelihood methods. Observed displacement values i of bird individual j (disp.obs_{ij}), with Rayleigh-distributed measurement error, follow a saturating function of expected displacement values over time (t):

$$\text{disp.exp}_j = \frac{\alpha_j \times t}{1 + \alpha_j * \beta_j}$$

The individual-level α_j and β_j terms were drawn from gamma distributed terms α_b and β_b for each bird species b .

We developed posterior predictive distributions for gut passage times and parameters of the movement model to characterize displacement over time, sampling every 100th iteration to obtain 1000 samples. Replacing t in the movement model with predicted GPTs for each plant–animal combination for which we obtained GPT data, we calculated a two-dimensional dispersal kernel for each plant–animal combination.

3. Results

We modelled seed dispersal distance for 39 interactions between five avian seed dispersers and 15 tree species based on gut passage trials involving roughly 5000 seeds and more than 600 h of radio tracking. White-throated Ground Doves ingested seeds of many species but destroyed nearly all seeds consumed. The only exception was from a single, small-seeded tree species, *Ficus tinctoria*, but in this case, Ground Doves passed less than 1% of the total seeds consumed. Bridled White-eyes passed only two small-seeded plant species despite being offered a wide variety of fruits, as gape limitations prevent them from consuming most species. Conversely, Micronesian Starlings passed (14 species) or regurgitated (1 species) all 15 tree species and Mariana Fruit Doves passed (11 species) or regurgitated (1 species) 12, whereas Golden White-eyes passed nine.

When considering tree species consumed by at least three dispersers, posterior estimates of median GPT among disperser species varied greatly for some plant species (excluding regurgitated species) and little for others (figure 1). For example, the shortest median posterior estimate GPT for *Pipturus argenteus* was 41.7 min by Golden White-eyes compared to the longest median GPT of 97.0 min by Mariana Fruit Doves. Conversely, some plant species showed little variation in GPT by multiple dispersers such as *Psychotria mariana*,

which Micronesian Starling passed in 25.8 min (median posterior estimate of GPT) while Golden White-eyes and Mariana Fruit Doves passed seeds in 32.8 and 32.6 min, respectively.

Similarly, for a given disperser species that consumed at least three tree species, median GPT varied greatly across tree species (excluding regurgitated species) for Mariana Fruit Doves (lowest median posterior estimate GPT of 32.3 min for *P. mariana* and maximum of 97.0 min for *P. argenteus*) whereas Micronesian Starlings and Golden White-eyes exhibited median GPTs that were more similar across most tree species (figure 1). We did not obtain GPT estimates for enough tree species for Bridled White-eyes and White-throated Ground Doves to identify patterns.

For all species, movement away from a given starting location saturated quickly, with birds tending to have movements centred around a starting location (figure 2). Micronesian Starlings had the longest estimated median movements at all time intervals but there was substantial variation around this median (figure 2). White-throated Ground Doves, Bridled White-eyes, and Golden White-eyes all exhibited similar movement patterns and moved much shorter distances than Micronesian Starlings. Mariana Fruit Doves had movement patterns intermediate of Micronesian Starlings and the other species.

Owing to the saturating movement patterns, modelled seed dispersal distances were largely driven by animal movement with GPT variation across dispersers and tree species playing minor roles in determining how far seeds were dispersed. All bird species were predicted to disperse some seeds at local scales (less than 50 m; figure 3). For Golden White-eyes, Bridled White-eyes, and White-throated Ground Doves, the 99th percentile of predicted seed dispersal distances for all modelled plant species was less than 120 m. Conversely, when pooled across all plant species for which seeds were dispersed, Micronesian Starlings and Mariana Fruit Doves dispersed seeds greater than 120 m 43.7% and 21.0% of the time, respectively.

We define long-distance dispersal as dispersal greater than 500 m as this distance represents a realistic distance threshold between plant populations on Saipan [5]. While long-distance dispersal events of greater than 500 m were rare, Micronesian Starlings were the main driver of these events. For all 15 plant species, Micronesian Starlings dispersed seeds greater than 500 m between 0.6 and 2.1% of the time. When pooled across all plant–bird interactions, 94.4% of all dispersal events greater than 500 m were performed by Micronesian Starlings with Mariana Fruit Doves performing the remaining 5.6%.

4. Discussion

Vertebrate seed dispersal is an important and widespread process, particularly in tropical forest communities. Yet this process is also complex and difficult to quantify because it involves many plants and animals, each of which may have different effects on seed fate. The factors driving variation in seed dispersal distance and thus the roles of dispersers across an entire plant community remain unclear, hindering community-level predictions on the seed dispersal process. On the island of Saipan, we modelled seed dispersal distance by all five extant avian frugivores of 15 forest tree species,

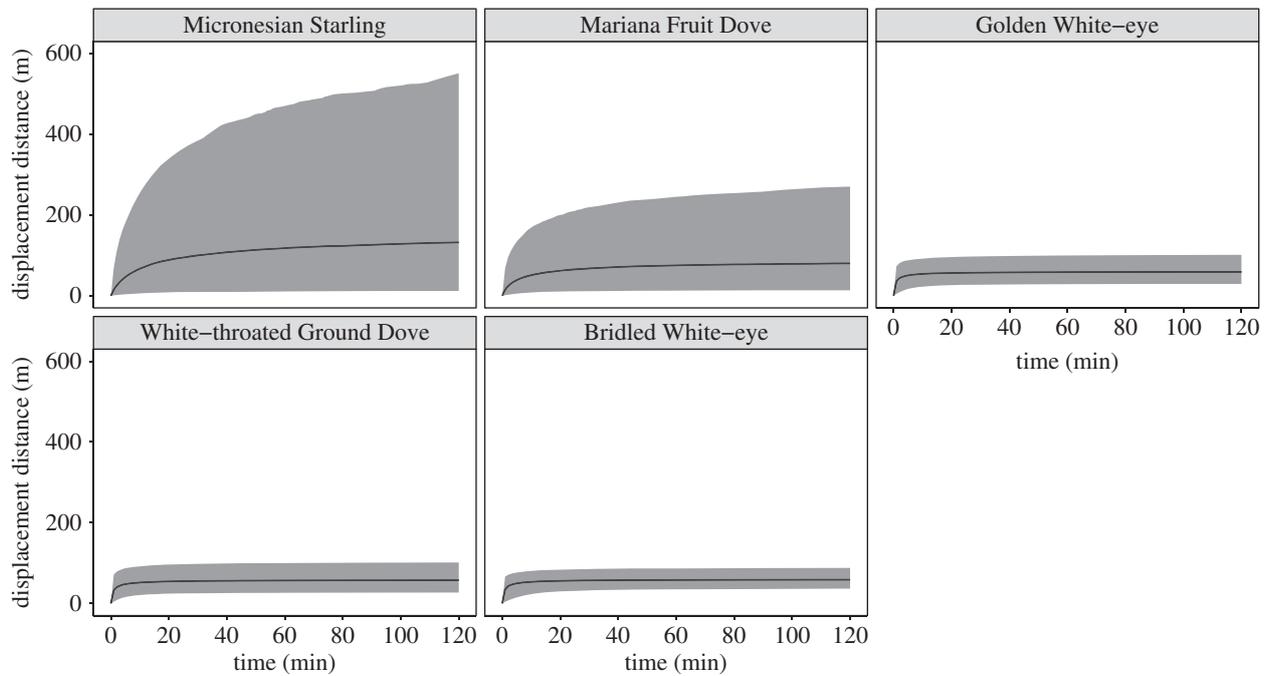


Figure 2. Posterior median and 95% credible intervals (shaded area) of modelled displacement by time for five avian seed dispersers on the island of Saipan.

including 39 bird–tree interactions. One bird species, the White-throated Ground Dove was an ineffective seed disperser because it acted as a seed predator. The remaining avian species showed overlap and disparities in dispersal distance for a given tree species suggesting that species contribute differently to the total dispersal kernel.

By studying a large portion of the plant–animal interaction network, we determined that the cause of variation in seed dispersal distance across the community was driven largely by movement of the seed dispersers rather than differences in GPT across disperser or plant species. For example, *P. mariana* seeds had relatively fast GPTs while *P. argenteus* seeds took three times longer to pass through the gut of Mariana Fruit Doves. Yet Mariana Fruit Doves dispersed seeds of *P. mariana* only slightly shorter distances than *P. argenteus* (67 versus 76 m median dispersal distance; figure 3). This relatively small influence of GPT on seed dispersal distance was surprisingly consistent across different seed disperser and tree species combinations.

The saturating nature of animal movement over time for all bird species restricted seed dispersal to a few hundred metres around their starting point, considered to be the location of a frugivory event for our study. However, even short-distance dispersal (approx. 10 m) may alleviate density- and distance-dependent mortality effects for some plant species [30]. The two smaller-bodied white-eye species had high redundancy in seed dispersal distances, with most seeds dispersed less than 100 m. By contrast, longer distance dispersal appears to be driven by the larger-bodied Micronesian Starling and Mariana Fruit Dove. While Micronesian Starlings and Mariana Fruit Doves have some overlap in their dispersal distances, Micronesian Starlings were more than 10 times more likely to disperse seeds greater than 500 m and dispersed seeds at short distances as well. Therefore, most species are providing important seed dispersal services, with considerable overlap in dispersal at short distances but long-distance dispersal being performed by just two species.

The importance of Micronesian Starlings and Mariana Fruit Doves to this plant–animal interaction network is further highlighted by the number of tree species that these birds disperse. Micronesian Starlings and Mariana Fruit Doves each consumed a broad diversity of plant species, although Micronesian Starlings have a larger gape width, consumed a larger diversity of plant species in this study, and have been observed consuming the broadest diversity of plant species during frugivory observations in this system [28]. White-eyes have limited gape widths restricting their interactions with most tree species. However, white-eyes may still provide seed dispersal services for plant species by removing fruits and consuming pulp a short distance away from the parent tree before dropping seeds. These types of interactions certainly occur in the wild and could be an important contribution to total dispersal kernels but were omitted in this study. Additionally, the native Mariana fruit bat likely plays some role in shaping the total seed dispersal kernel but was not included in this study.

Our findings show that larger-bodied organisms tend to disperse seeds over longer distances, which is in agreement with previous studies that lumped dispersers into functional groups based on body size [10,15]. However, we caution against *a priori* functional groupings because doing so could mask important species-specific differences [17]. For example, grouping the larger-bodied Micronesian Starling, Mariana Fruit Dove, and White-throated Ground Dove together would hide the contribution to long-distance seed dispersal by Micronesian Starlings, as well as the status of the Ground Dove as a seed predator rather than a disperser.

Our data show that seed dispersers that are similar in one functional trait (e.g. similar GPTs across frugivores, body size) can differ widely in another functional trait (e.g. substantial differences in the scale of movement). Approaches that apply functional groupings to all functional traits of dispersal may be less accurate than applying functional groupings to single functional traits. In our case, all bird species are in the same functional group based on GPTs

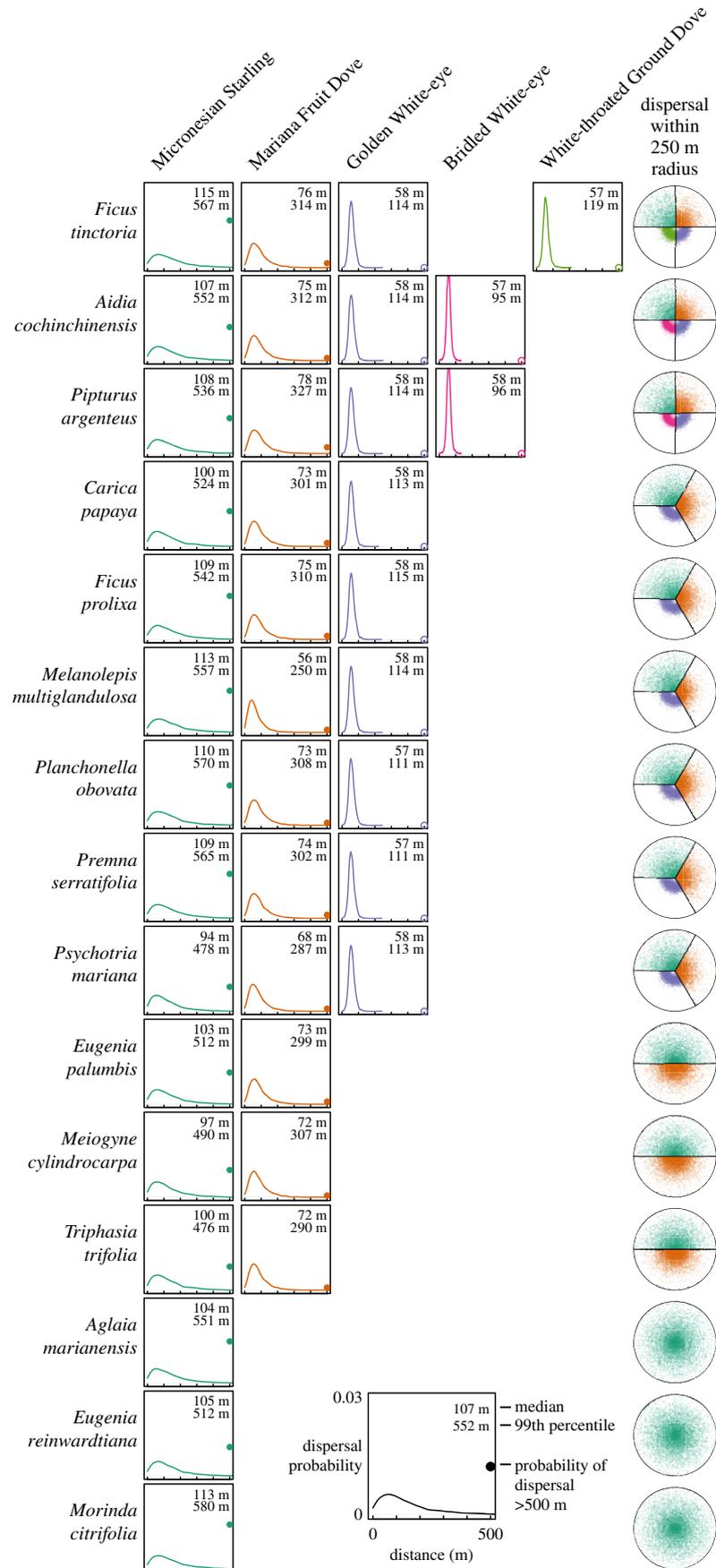


Figure 3. Posterior predictive seed dispersal distances by five avian seed dispersers of 15 tree species on Saipan. Each panel represents a modelled species-specific interaction. For each interaction, we show standard dispersal curves, median and 99th percentile dispersal distances (numbers in top right of panel), and probability of seed dispersal greater than 500 m (filled dots represent probabilities greater than 0 and hollow dots represent probability = 0). The final column represents potential seed dispersal in two dimensions for bird species dispersing that given plant species.

but differ greatly in movement patterns. Characterizing movement patterns for each bird species and GPTs for only a subset of bird species or bird–plant combinations would have been sufficient to characterize the community-level variation in dispersal distances. However, if bird species were grouped based on functional types and movement patterns were characterized for just a subset of species representing each functional type, then community-level dispersal distance patterns may have been incorrectly described and characterized.

The importance of animal movements in explaining variation in dispersal distances found here could be amplified by our study taking place within a fragmented landscape where the contiguous, native-dominated forest is present in remnant patches. The fragmented nature of the remaining forest likely imposes restrictions on animal movement, highlighted by the majority of all bird locations occurring within largely forest-dominated home ranges [26]. These individuals infrequently cross forest/non-forest habitat boundaries [31], indicating that there is little incentive to leave forested habitat patches. Therefore, seed dispersal may be restricted to within habitat fragment movements and explain the saturating nature of animal movements that drove dispersal distance in our study. Similarly, in a fragmented landscape in South Africa, Trumpeter Hornbills dispersed the majority of seeds within a forest fragment while fewer seeds were dispersed between forest fragments [32,33]. Given that large areas of previously intact forest are now fragmented [34,35], studying seed dispersal in impacted landscapes could elucidate important differences in community patterns in differing landscapes.

The overlap and disparities in seed dispersal distance and diet breadth displayed here provide important insight into the potential impacts of network disruptions and species loss to seed dispersal services. Such perturbations are most common on tropical islands where a large portion of the plant community depends on animals for seed dispersal and species extinctions are relatively high [25,36–38]. The introduction of the nocturnal and predatory snake, *Boiga irregularis*, to Guam, the southernmost island in the Mariana Archipelago resulted in the loss of all avian seed dispersers except for a small remnant population of Micronesian Starlings [39,40]. As Micronesian Starlings dispersed the largest number of tree species and dispersed seeds farther than other avian species, this remnant population is likely still providing critical dispersal services on Guam, albeit over a limited spatial scale as the remnant population is restricted to a small, mostly developed area in the northern part of the island. If *B. irregularis* were to invade Saipan, then the loss of all or some avian species would disrupt seed dispersal but the severity of that disruption would depend on which

avian seed dispersers are lost. If both white-eye species were lost but Micronesian Starlings and Mariana Fruit Doves persist, the bulk of short-distance seed dispersal would be lost but some short- and most long-distance seed dispersal would still occur. Conversely, if only the two white-eye species remained, long-distance seed dispersal would be severely reduced and certain plant species would completely lose their avian seed dispersers.

Dispersal away from a parent plant is just one step in the dispersal process [8]. We show that seed dispersal distance can vary within a seed dispersal network and that the majority of this variation is based on the movement patterns of each disperser rather than their GPTs or the identity of the plant. However, movement of seeds alone does not demonstrate that a frugivore species is an effective disperser [8]. The next step is to evaluate seed disperser effectiveness by considering the quantity of seeds consumed, effects of gut passage on germination, and the quality of seed deposition sites by each bird species [8]. For example, in addition to dispersing seeds the farthest and dispersing seeds of the largest number of studied tree species, Micronesian Starlings also regularly cross habitat boundaries and potentially dispersed seeds into degraded habitats whereas other species do so less frequently [31]. By understanding community patterns, and the variation therein, for the entire seed dispersal process, we will be able to make more informed predictions about forest dynamics and trajectories in human-modified landscapes.

Data accessibility. All data and R code for analysis is available on github at <https://github.com/EBL-Marianas/SaipanDispersalKernels>. Summary data of posterior model outputs and a more detailed description of models are in the electronic supplementary material.

Competing interests. We declare we have no competing interests.

Authors' contributions. E.R., E.F., J.B., J.S., and H.R. designed the study. E.R. coordinated data collection on animal movements and assisted with gut passage time trials. J.B. coordinated data collection on gut passage time trials. E.F. conducted statistical analysis on gut passage time, animal displacement, and seed dispersal model development. E.R., E.F., and J.B. wrote the manuscript. All authors critically revised and approved the final manuscript.

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