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Functional outcomes of mutualistic network interactions: A community-scale study of frugivore gut passage on germination

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Abstract

1. Current understanding of mutualistic networks is grounded largely in data on interaction frequency, yet mutualistic network dynamics are also shaped by interaction quality—the functional outcomes of individual interactions on reproduction and survival. The difficulty of obtaining data on functional outcomes has resulted in limited understanding of functional variation among a network's pairwise species interactions, of the study designs that are necessary to capture major sources of functional variation, and of predictors of functional variation that may allow generalization across networks.
2. In this community-scale study, we targeted a key functional outcome in plant–frugivore networks: the impact of frugivore gut passage on seed germination. We used captive frugivore feeding trials and germination experiments in an island ecosystem, attaining species-level coverage across all extant native frugivores and the plants they consume to (a) assess sources of functional variation, (b) separate effects of pulp removal from those of scarification via gut passage, and (c) test trait-based correlates of gut passage effect sizes.
3. We found antagonistic seed predation effects of a frugivore previously assumed to be a seed disperser, highlighting the need to consider functional outcomes rather than interaction frequency alone. The other frugivores each exhibited similar impacts for individual plant species, with benefits primarily caused by pulp removal rather than scarification, supporting the use of animal functional groups in this context. In contrast, plant species varied widely in impacts of gut passage on germination. Species with smaller seeds and more frugivore partners had larger benefits of gut passage, showing promise for network metrics and functional traits to predict functional variation among plants.
4. *Synthesis*. Combining network and demographic approaches, we assessed the degree and sources of variation in a key functional outcome of plant–frugivore interactions across an entire network. Using a detailed study design, our work shows how simpler study designs can capture primary sources of functional variation and that functional traits and network metrics may allow generalization across

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networks. Efficiently measuring and generalizing sources of functional variation within mutualistic networks will strengthen our ability to model network dynamics and predict mutualist responses to global change.

KEYWORDS

dispersal, ecological networks, endozoochory, functional traits, gut passage, mutualistic networks, plant–frugivore networks, seed disperser effectiveness

1 | INTRODUCTION

A central goal of mutualistic network research is to link patterns of interactions between mutualists to the dynamics of entire mutualistic communities (Bascompte & Jordano, 2014). Establishing these links offers opportunities to address fundamental and applied questions regarding co-evolutionary processes within complex communities (Guimarães, Jordano, & Thompson, 2011), mutualistic controls on demography (Bastolla et al., 2009), and consequences of mutualism disruption and reassembly under global change (Aslan, Zavaleta, Tershy, & Croll, 2013; Memmott, Craze, Waser, & Price, 2007; Tylianakis, Didham, & Bascompte, 2008). Research on mutualistic network interactions has progressed from early studies describing patterns in the presence or absence of interactions among partners (Bascompte, Jordano, Melián, & Olesen, 2003; Jordano, 1987) to later studies assessing quantitative patterns in, and correlates of, interaction frequency (Bartomeus et al., 2016; Eklöf et al., 2013; Encinas Viso, Revilla, & Etienne, 2012). However, the dynamics of mutualistic networks are defined not only by interaction quantity—the frequencies of interaction between partners—but also by the far less frequently studied component of interaction quality—the functional outcomes of the interactions on mutualist performance (e.g., growth, survival, reproduction; Schupp, Jordano, & Gómez, 2017).

Advancing the goals of mutualistic network research will require increased knowledge of the functional outcomes of network interactions. This is a major empirical hurdle especially for plants, in which the outcome of a pollination or seed dispersal interaction can play out over months or years (Howe, 2016; Schupp et al., 2017; Vazquez, Ramos Jiliberto, Urbani, & Valdovinos, 2015). Therefore, existing studies on functional outcomes of mutualisms have focused on one or several interacting pairs rather than entire networks (Genrich, Mello, Silveira, Bronstein, & Paglia, 2016; Nogales et al., 2017; Schupp et al., 2017). Lacking community-scale information on functional outcomes, mutualistic network models typically assume that all pairwise interactions have equal functional outcomes when predicting coextinction following mutualism disruption (Kaiser-Bunbury, Muff, Memmott, Müller, & Caflisch, 2010; Memmott, Waser, & Price, 2004; Pocock, Evans, & Memmott, 2012) and assessing the links between network structure and stability (Bastolla et al., 2009; Gao, Barzel, & Barabási, 2016; Rohr, Saavedra, & Bascompte, 2014). However, important functional differences exist among species in their dependence on mutualisms and the benefits they confer to their partners (Bronstein, 1994; Wheelwright & Orians, 1982), and conclusions regarding coextinction and stability in network models are sensitive to this variation (Fricke, Tewksbury, Wandrag, & Rogers, 2017; Traveset, Tur, & Eguíluz, 2017). Understanding the sources of variation in the functional outcomes of network interactions and developing approaches to generalize across networks can advance realistic models of mutualistic network dynamics and generate robust predictions of community responses to mutualism disruption.

In this study, we focus on plant–frugivore interactions, which have been a major focus of mutualistic network research (Bascompte & Jordano, 2007; Bastolla et al., 2009; Gao et al., 2016; Jordano, Bascompte, & Olesen, 2003). For plants, the demographic impacts of network interactions depend on the frequency of interaction, which remains the focus of network studies, as well as the quality of seed deposition, which is seldom analysed in depth (Schupp et al., 2017). Together, these quality and quantity components define seed dispersal effectiveness (sensu Schupp, Jordano, & Gómez, 2010; Schupp et al., 2017). We focus on the quality component of seed dispersal and target one key functional outcome for plants: the influence of gut passage by frugivores on seed germination.

Gut passage of seeds by frugivores typically increases germination, although existing studies that focus on a subset of plant–frugivore species pairs within a network have shown that the magnitude and sign of the effect can vary substantially among frugivore and plant species (Genrich et al., 2016; Traveset, Robertson, & Rodríguez-Pérez, 2007; Traveset & Verdú, 2002). Recent studies emphasize the need to adopt a community-level focus to understand the degree of this variation and the sources that cause it (González-Castro, Calviño-Cancela, & Nogales, 2015; Nogales et al., 2017). Oceanic islands, which typically have lower species diversity than mainland locations, offer tractable settings to study mutualistic interactions at a community scale (Kaiser-Bunbury et al., 2010). Recent studies in the Balearic and Galapagos islands have compared germination of seeds collected from scat to seeds removed from fruits to assess the effects of two or more frugivore functional groups on multiple plant species (González-Castro et al., 2015; Nogales et al., 2017), greatly advancing our understanding of community-level variation in gut passage effects among the functional groups of seed dispersers present at a study location.

More logistically intensive experiments on individual species pairs offer opportunities to understand the mechanism by which gut passage impacts germination and to assess the application of functional groupings in mutualistic network studies. Using feeding trials with captive frugivores can quantify seed predation by comparing

TABLE 1 Bird species included in the study. Parenthetical values indicate standard deviation

Bird species	Family	Mass (g)	Gape width (mm)	Number of individuals
Bridled white-eye (*Zosterops conspicillatus*)	Zosteropidae	8.2 (1.1)	5.7 (0.4)	4
Golden white-eye (*Cleptornis marchei*)	Zosteropidae	20 (3)	7.6 (0.3)	4
Micronesian starling (*Aplonis opaca*)	Sturnidae	80 (4)	15.2 (0.3)	5
Mariana fruit dove (*Alopecoenas xanthonurus*)	Columbidae	91 (14)	10.2 (0.2)	7
White-throated ground dove (*Ptilinopus roseicapilla*)	Columbidae	134 (14)	8.7 (0.9)	5

seeds consumed to seeds dispersed, can achieve sufficient sample sizes to assess individual plant–frugivore species pairs, and can hold the initial viability of seeds constant across treatments (Robertson, Trass, & Ladley, 2006; Traveset & Verdú, 2002). Trials comparing gut-passed seeds, manually depulped seeds, and whole fruits can separate effects of pulp and germination inhibitor removal ("deinhibition" effect) from effects of physical changes to the seed during gut passage ("scarification" effect), which are often smaller than deinhibition effects (Kelly et al., 2010; Robertson et al., 2006). Comparing germination of gut-passed seeds and seeds from whole fruit can also demonstrate how disperser extirpation would affect recruitment (Robertson et al., 2006; Samuels & Levey, 2005). In particular, measuring functional outcomes at a species pair level is critical for determining whether it is appropriate to generalize by grouping species into functional groups and for assessing the importance of individual frugivores within ecosystems facing defaunation.

An ongoing challenge is to develop a predictive understanding of functional outcomes within mutualistic networks that can be applied beyond the systems in which they are studied directly. For example, quantifying gut passage effects is key for determining which plant species are most vulnerable to mutualism disruption (Howe, 2016; Schleuning et al., 2016) and for constraining predictions for the role of coextinction in the current biodiversity crisis (Colwell, Dunn, & Harris, 2012; Koh et al., 2004). However, hundreds of thousands of plant–frugivore species interactions occur in nature and many are threatened by global change drivers such as defaunation (Aslan et al., 2013; Dirzo et al., 2014), making it impractical to measure these effect sizes directly. This further motivates community-scale studies because they offer the ability to evaluate which traits could predict the effect of gut passage on germination. Here, we focus on a plant functional trait and a network metric that reflect plant species' ecological strategies and may offer useful tools for predicting plant species' global change responses (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Lavorel & Garnier, 2002). A key functional trait commonly studied in the context of dispersal, fruit–frugivore interactions, and regeneration strategy is seed mass (Westoby, Falster, Moles, Vesk, & Wright, 2002). A key network metric that is often used to describe species' network roles and is related to their dependence on mutualistic interactions is the number of partners (species degree; Fricke et al., 2017; Mello, Rodrigues, Costa, & Kissling, 2015; Schleuning et al., 2014; Vázquez, Bluthgen, Cagnolo, & Chacoff, 2009). Plant functional traits and network metrics including seed size and the number of partners may be useful predictors of gut passage effect sizes.

We studied the influence of gut passage on germination in a network of fleshy-fruited plants and frugivores, bridging population ecology and network approaches by assessing this functional outcome across all pairwise species interactions. We address three objectives: First, to determine the major sources of functional variation among pairwise interactions. This allows us to assess whether it is appropriate to employ the common practice of lumping animals into functional groups under the assumption that they cause similar functional outcomes. Second, to separate the impacts of deinhibition and scarification. This elucidates the biological mechanisms underlying gut passage effects and can highlight the experimental designs necessary to capture variation in these effects. Third, to assess trait-based correlates of gut passage effect sizes, which may enable trait-based prediction of gut passage impacts across systems. On Saipan in the Mariana Island chain of the western Pacific, we attained broad coverage of the plant–frugivore network, measuring gut passage interactions between including all five of the island's remaining native frugivores, which are all birds, and 20 tree, vine, and shrub species, which make up the vast majority of bird-dispersed woody stems in the island's intact forests.

2 | MATERIALS AND METHODS

We used captive feeding trials and germination experiments with gut-passed seeds, manually depulped seeds, and whole fruits. We analysed gut passage effects using a hierarchical Bayesian approach, and in doing so separated the effects on germination of pulp removal (the "deinhibition" effect) and of physical changes to the seed during gut passage (the "scarification" effect). As predictors of gut passage effects, we consider seed mass and the number of frugivores.

TABLE 2 Plant species included in the study. Asterisks indicate introduced species

Plant species	Family	Mean seed mass (g)	Mean seeds per fruit (range)	Number of source plants
Aglaia mariannensis	Meliaceae	0.62	1.5 (1–2)	7
Aidia cochinchinensis	Rubiaceae	0.0014	18 (6–27)	27
*Capsicum frutescens**	Solanaceae	0.0040	11 (2–26)	57
*Carica papaya**	Caricaceae	0.012	721 (565–956)	8
*Coccinia grandis**	Cucurbitaceae	0.0010	126 (106–156)	15
Discocalyx megacarpa	Primulaceae	0.40	1 (1–1)	15
Elaeocarpus joga	Elaeocarpaceae	0.31	1 (1–1)	12
Eugenia palumbis	Myrtacea	0.40	1 (1–1)	8
Ficus prolixa	Moraceae	0.00036	189 (148–236)	12
Ficus tinctoria	Moraceae	0.00036	246 (158–310)	10
Meiogyne cylindrocarpa	Annonaceae	0.27	3.5 (1–7)	18
Melanolepis multiglandulosa	Euphorbiaceae	0.031	1.6 (1–3)	28
*Momordica charantia**	Cucurbitaceae	0.17	17 (12–23)	5
Morinda citrifolia	Rubiaceae	0.012	164 (143–203)	14
*Passiflora suberosa**	Passifloraceae	0.0047	26 (13–39)	9
Pipturus argenteus	Urticaceae	0.00013	45 (12–83)	22
Planchonella obovata	Sapotaceae	0.039	1.1 (1–3)	7
Premna serratifolia	Lamiaceae	0.0093	4 (4–4)	15
Psychotria mariana	Rubiaceae	0.025	2 (2–2)	31
*Triphasia trifolia**	Rutaceae	0.081	1.3 (1–3)	6

2.1 | Study system and species

Our experiments were conducted on Saipan (15.195°N, 145.755°E), the second largest island in the Mariana Island chain. The primary forest type has a limestone karst substrate and a canopy of 7–12 m. The island experiences a distinct wet and dry season, an average temperature of 27°C, and an average annual rainfall of roughly 2,000 mm (Lander, 2004). The frugivores on Saipan include five bird species, a bat species, and two introduced lizards. The frugivorous bird species are the Mariana fruit dove (*Ptilinopus roseicapilla*), the white-throated ground dove (*Alopecoenas xanthonura*), the Micronesian starling (*Aplonis opaca*), the golden white-eye (*Cleptornis marchei*), and the bridled white-eye (*Zosterops conspicillatus*; families, body size, and gape widths reported in Table 1). The only other native frugivore is the Mariana fruit bat (*Pteropus mariannae*), which maintains a remnant population on Saipan (<0.01 individuals per hectare; US Fish and Wildlife Service 2009), suggesting it is currently functionally extinct as a seed disperser (McConkey & Drake, 2006). In over a thousand hours of observation of fruiting trees on Saipan, we have observed very few instances of fruit consumption by the two introduced lizards (*Lamprolepis smaragdina* and *Anolis carolensis*; Fricke et al., 2017) and therefore focus on the five bird species for this study.

We assessed plant–frugivore interactions between the 5 avian frugivores and 20 bird-dispersed plant species (trees, shrubs, and vines) found in intact limestone forest (Table 2). We focused on the most commonly found fruiting species across forests in the Marianas, both native and nonnative; the 14 tree species make up 97% of bird-dispersed tree stems in limestone forest on Saipan (H. Rogers, unpubl. data; Table S1). We included three fleshy-fruited vine species we most frequently encountered fruiting in this forest type. To improve our understanding of plant–frugivore networks across forests in the Marianas more generally, the tree species included three species that are rare or may be absent on Saipan (*Triphasia trifolia*, *Elaeocarpus joga*, *Discocalyx megacarpa*), but are present in similar forests on the nearby island of Rota, where we collected fruits of those species. We refer to the plant species by genus, except when multiple species were included per genus. The pairwise interactions that occur in nature are a subset of all plant–frugivore combinations; we did not assess the outcome of individual plant–frugivore combinations if the frugivore could not consume seeds because of gape size constraints, the frugivore is not known to consume the plant species in the field, or the frugivore did not consume fruits after individuals were offered fruits on multiple occasions during captive feeding trials.

As correlates of gut passage effects for the plant species, we considered seed mass and the number of frugivore partners. We obtained average dry seed mass values from the literature or through direct measurement. We used data from fruiting plant observations to determine the number of frugivores (avian and non-avian) visiting each plant species. The methods are described in detail in Fricke et al. (2017). Briefly, observers at fruiting trees recorded interactions where seeds were consumed or taken away from the canopy,

excluding interactions where only pulp was removed or seeds were dropped. Observations were performed at multiple individual plants at multiple sites on Saipan and Rota, with a minimum of 50 hr of observation per plant species.

2.2 | Seed treatments

To assess the influence of frugivore gut passage on germination across fleshy-fruited plant species, we compared seeds in three treatments: seeds that were gut passed by captive birds, manually depulped seeds, and seeds within whole fruits. Ripe fruits for these experiments were collected in the field within 24 hr of the gut passage trials, except for fruits collected on Rota which were collected within 24–72 hr of the trials. We pooled the fruits collected from multiple trees and randomly allocated seeds from this "collection pool" across each of the treatments. We collected fruits from multiple adult individuals per species (Table 2) to avoid biases associated with plant individual effects.

Fruits allocated to the "whole fruit" treatment were typically planted without any manipulation. The exceptions were species with large, multiseeded fruits (*Carica*, *Coccinia*, *Momordica*, and *Morinda*) that typically break up if they fall to the ground. These species were divided into six smaller pieces to reflect this process. Fruits allocated to the "manually depulped" treatment were cleared of flesh using latex gloves and forceps but were not washed or treated with any solution. For the "gut passed" treatment, we offered fruits to birds and collected gut-passed seeds, testing multiple bird individuals for each fruit–frugivore species combination. We conducted feeding trials with wild-caught captive individuals of the five study species, which were housed individually in covered aviaries. Trials were typically conducted in the morning, with the maintenance diet removed at dusk the day prior. If the bird species was known to eat fruits of a given plant species in the wild but did not readily consume fruits in captivity, we hand-fed fruits to the birds. As birds defecated, gut-passed seeds were periodically collected from paper lining the aviary floor. We noted the number of fruits consumed and counted the number of seeds that passed intact. We recovered only small seed fragments from ground doves and assumed germination probabilities were near zero. Captive feeding trials were conducted from October 2015 to February 2016 and from June 2016 to August 2016.

2.3 | Monitoring germination

We sowed the seeds or fruits of each treatment on a 1:1 perlite and peat moss mixture in multicell trays in a shadehouse, with individual trays typically containing seeds of multiple treatments. We monitored germination three times per week between October 2015 and May 2017 during which time germination of each species peaked and then fell to no germination for at least several months. We periodically rotated trays to reduce the effect of any environmental heterogeneity within the shadehouse. Individual seeds were considered to have germinated at the earliest stage at which we could identify the plant to species; depending on species, this was possible at either the radicle emergence or cotyledon stage. We removed germinants to ensure they were not counted more than once. At the end of this period, we determined the viability of remaining seeds of species that were large enough to recover from the soil. Seeds were disintegrated or had empty seed coats in the vast majority of cases. Seeds that had not disintegrated were dissected and examined for potentially viable tissue and, if present, tested for viability using the tetrazolium test. We observed weak staining in several *Momordica* seeds, suggesting uncertain viability in ~2% of *Momordica* seeds, and otherwise found the remaining seeds were not viable. We concluded that the vast majority of seeds across all species that failed to germinate during our study were no longer viable. Seeds of *Elaeocarpus* and *Melanolepis* exhibited extremely low germination in all treatments, but were not viable at the end of the study period. This suggests that seeds were either initially unviable or were initially viable but have additional germination requirements that we did not provide. These two species were excluded from further analysis.

2.4 | Analysis

We used a hierarchical Bayesian generalized linear model to analyse the impact of gut passage on germination and disentangle the effects of deinhibition and scarification. Implementing the analysis in a Bayesian framework and including prior information on the distribution of the number of seeds per fruit offer an appropriate approach to model the unknown number of seeds within whole fruits. In the model (described in detail in the Supplementary Materials), the probability of germination reflects a baseline germination probability for seeds within whole fruits, with additional terms describing deinhibition and scarification effects for seeds of the relevant treatments. Seeds in the depulped treatment have deinhibition effects, whereas gut-passed seeds have deinhibition effects and additional effects of scarification.

We modelled the number of germinants out of the number of seeds of plant species p from seed collection pool k (representing the fruits of a species collected, mixed, and randomly assigned to treatments on a given day) within planting cell i passed by individual j of bird species b (n.germ_{bpijk}) as a binomial process. The probability of germination (p.germ_{bpjk}) was a linear function of a plant species-specific effect describing germination from whole fruits (β_{whole}), a deinhibition effect (β_{deinhib}), an overall scarification effect (β_{scar}), the bird species-specific effect of scarification ($\beta_{\text{bird.scar}}$), the plant species-specific effect of scarification ($\beta_{\text{plant.scar}}$), a bird–plant species interaction effect of scarification ($\beta_{\text{inter.scar}}$), and the effects of bird individual ($\beta_{\text{bird.id}}$) and plant collection pool ($\beta_{\text{plant.id}}$):

$$\text{n.germ}_{bpijk} \sim \text{Binomial}(\text{p.germ}_{bpjk}, \text{n.seed.true}_i)$$

$$\begin{aligned}\text{logit}(\text{p.germ}_{\text{bpjk}}) = {} & \beta_{\text{whole},p} + \beta_{\text{deinhib},p} + \beta_{\text{scar}} + \beta_{\text{bird,scar},b} \\ & + \beta_{\text{plant,scar},p} + \beta_{\text{inter,scar},bp} + \beta_{\text{bird,id},jb} + \beta_{\text{plant,id},kp}\end{aligned}$$

We implemented this model in three parts so that treatment effects were captured by the appropriate terms; all of the plant, bird, deinhibition, and scarification terms apply to seeds in the gut-passed treatments, the plant and depulping effects apply to seeds in the depulped treatment, and only the plant effects apply to seeds within whole fruits. For the number of seeds within whole fruits, we use informed Poisson prior distributions based on the distribution of seeds per fruit in the fruits we collected. As derived quantities, we output ratios of germination probabilities between gut-passed and whole fruit germination to assess the overall gut passage effect, between depulped and whole fruit germination to assess the deinhibition effect, and between gut-passed and depulped germination to assess the scarification effect. To assess statistical significance in these ratios, we assess whether the 95% credible intervals overlap one.

Finally, we analysed relationships between the gut passage effect (ratio of gut passed to whole fruit germination) and both seed size and the number of frugivores (species degree). In separate linear mixed effects models (Bates, Maechler, Bolker, & Walker, 2015), the response variable was the gut passage effect for each plant–frugivore combination in which seeds passed intact, the fixed effect was either log-transformed seed mass or the number of frugivores, and the random effect was frugivore species. We used likelihood ratio tests against a null model lacking the fixed effect to assess statistical significance.

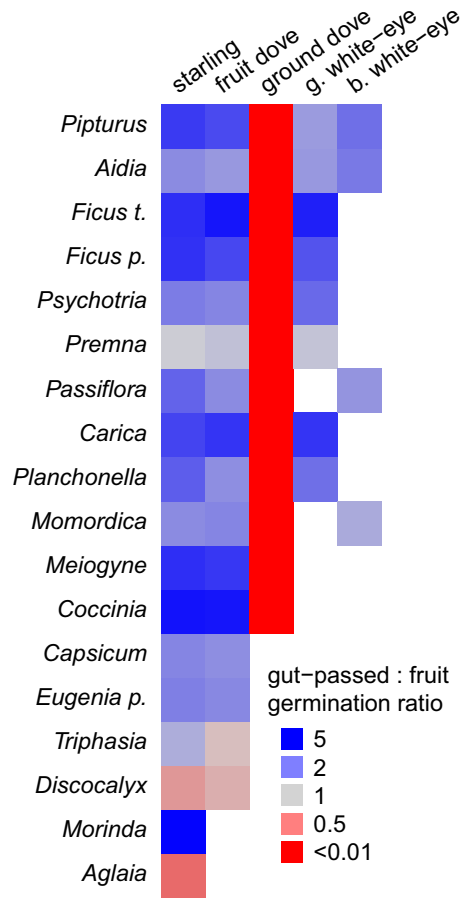

FIGURE 1 Effects of gut passage on germination within the plant–frugivore network. Colours represent the ratio of the probability of germination of gut-passed seeds to the probability of germination of seeds within whole fruits; bird–plant combinations that were not recorded in nature and were not tested are left blank [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Gut passage impacts on germination and sources of functional variation

Our analysis included over 44,000 seeds from 20 plant species in 19 genera and 16 families. We measured the effect of gut passage on germination as the ratio of germination for gut-passed seeds versus seeds within whole fruits for the 18 plant species whose seeds germinated (Figure 1, Figure S1, Table S2). The white-throated ground dove acted as a seed predator by destroying seeds during gut passage, whereas other frugivores passed seeds intact. Among the seed-dispersing bird species, gut passage typically increased germination and the effect of each seed disperser on germination of individual plant species was typically similar (Figure 1). Main effects of the seed-dispersing birds on germination and bird–tree interaction terms were more similar and smaller than the plant-specific effects (Figure S2). Thus, plant species exhibited larger differences in the benefits derived from seed disperser gut passage, and plant species identity was a larger source of variation than seed disperser species identity.

3.2 | Separating deinhibition and scarification effects

We measured the deinhibition effect as the ratio of germination of depulped seeds to germination of seeds in whole fruit and found that pulp removal improved germination for the majority of species (Figure 2). Of the 18 species that germinated, 12 species exhibited a positive deinhibition effect, and two species exhibited a negative deinhibition effect. Pulp removal did not significantly influence germination in the remaining four plant species. The deinhibition effect sizes varied widely among species, with the largest benefits of pulp removal quadrupling median germination probabilities. We measured the scarification effect as the ratio of gut-passed to depulped seed germination for the 46 plant–frugivore combinations in which seeds passed intact (Figure 3). In 13 of these plant–frugivore combinations, gut-passed seeds had greater germination than depulped seeds. In 30 combinations, gut-passed and depulped seeds had equal germination. In three combinations, gut-passed seeds had lower germination than did depulped seeds. Deinhibition effects were larger in magnitude than the effects of scarification, with median absolute deinhibition effects roughly 2.4 times larger than the total absolute scarification effects combining bird, plant, and interaction scarification terms (Figure S2).

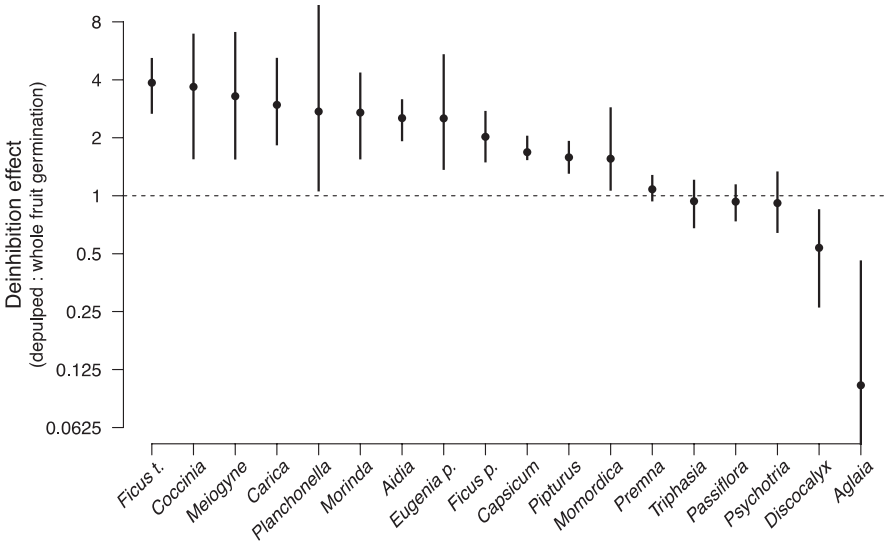

FIGURE 2 Isolating the effect of deinhibition via pulp removal on germination. Points represent the median ratio of the probability of germination between manually depulped seeds and seeds within whole fruits, bars indicate 95% credible intervals

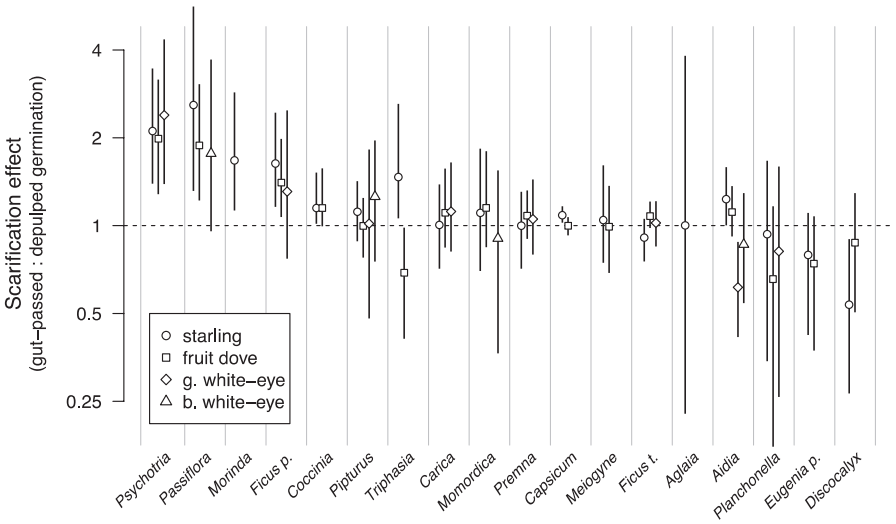

FIGURE 3 Isolating the effect of scarification via gut passage on germination. Points represent the median ratio of the probability of germination of gut-passed seeds to seeds that were manually depulped, bars indicate 95% credible intervals

3.3 | Assessing predictors of gut passage effects

Finally, we assessed predictors of overall gut passage effect sizes. Seed size was negatively related to the gut passage effect sizes; plant species with smaller seeds had larger benefits of gut passage by the seed-dispersing birds (Figure 4a; likelihood ratio test, $\chi^2 = 5.58$, $p = 0.018$). Plant species with more frugivore partners also experienced larger benefits of gut passage (Figure 4b; $\chi^2 = 5.55$, $p = 0.018$).

4 | DISCUSSION

We conducted experiments to quantify a key functional outcome of plant–frugivore network interactions—the impact of gut passage on germination—on the island of Saipan in the Mariana Island chain. The study assessed interactions between five bird species, which are all of the extant native frugivores on the island, and nearly all of the bird-dispersed plant species in the island's native forests. Our first objective was to assess the major sources of functional variation across the network. One major source of variation was the dichotomy between seed predators and seed dispersers, which distinguished the strongly negative functional effects of the white-throated ground dove (*Alopecoenas xanthonurus*) from the largely positive effects of the other seed-dispersing frugivores. The other major source of variation was plant species identity. Plant species had widely differing impacts of seed disperser gut passage on germination, but the impact of gut passage for individual plant species depended little on which of the seed-dispersing frugivores passed the seeds. Our second objective was to compare the effect of deinhibition via pulp removal versus the additional effect of scarification via gut passage, and we found that deinhibition effects were more variable and larger, consistent with previous studies (Kelly et al., 2010; Robertson et al., 2006). Our third objective was to assess predictors of functional variation, and we found significant relationships between gut passage effect sizes and a functional trait and a network metric (seed mass and the number of frugivores). This community

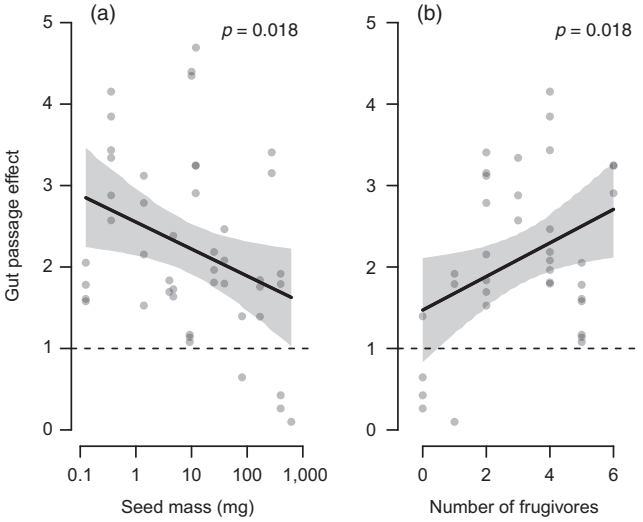

FIGURE 4 Correlates of gut passage effect sizes. The gut passage effect (ratio of gut-passed to whole-fruit germination) was negatively related to seed mass (a) and positively related to the number of frugivore species observed consuming fruits of the plant species (b)

perspective offers insight into opportunities for generalization and improved integration of functional outcomes for modelling community dynamics and network responses to disruption.

As ecologists work towards including functional outcomes into network models and characterizing networks much larger than the simple network studied here, key empirical challenges are to identify experimental approaches that efficiently capture the major sources of functional variation and to develop techniques for generalization that allow prediction of these effects across systems (Howe, 2016; Schupp et al., 2017; Vazquez et al., 2015). Based on our results, we make three primary conclusions.

First, by assessing the sources of variation in gut passage effects, we show that lumping frugivores into functional groups appears appropriate when considering effects of gut passage on germination, as there were not large or consistent differences across disperser species in their effects on germination. So long as the distinction between seed dispersers and seed predators was in place (which in this case involved complete seed predation, which may often not be the case; Shiels, 2011), we would have reached appropriate inferences by grouping the dispersers in this system a priori as "passerines/fruit dove," "small birds/large birds," or more simply "birds." The grouping of species into functional groups is already widely used in seed dispersal research, especially for considering differences in effectiveness of different groups of dispersers (González-Castro et al., 2015; Nogales et al., 2017). Our results emphasize that functional groupings for gut passage effects should be based on digestive morphology and diet rather than loosely on phylogeny and body size, which would have grouped the *Alopecoenas* ground dove and *Ptilinopus* fruit dove in this study. Although no species within *Alopecoenas* has, to our knowledge, been tested for gut passage effects, *Alopecoenas* doves have been treated as seed dispersers in previous research by ourselves and others (e.g., Fricke, Tewksbury, & Rogers, 2018; McConkey & Drake, 2015). The functionally antagonistic role of *A. xanthonurus* suggests the need for careful consideration of natural history and traits when grouping species. Our findings suggest that estimates developed at the functional group level can be appropriate in many settings where functional outcomes are relevant, including population projections, conservation planning, and network models.

Second, by separating effects of deinhibition and scarification, we found that comprehensive experimental designs may not be important for capturing most of the other variations in gut passage effects. In this system, plant species varied substantially in the effect of gut passage on germination, but a great majority of the effect size was explained by pulp removal, with smaller and inconsistent effects of gut passage by the different frugivores, consistent with previous studies (Kelly et al., 2010; Nogales et al., 2017; Robertson et al., 2006). Researchers focused on dynamics at the community scale may more quickly and cost-effectively describe plant species' dependence on gut passage by conducting experiments using only whole fruits and manually depulped seeds, or with gut passage trials using a subset of frugivores. Researchers focused on individual species, such as species of special conservation concern, may require gut passage trials to understand a plant species' dependence on frugivory or animal species' importance as a frugivore. Our results also indicate that experiments that only compare depulped and gut-passed seeds, which has been the experimental design for a majority of gut passage studies (Fuzessy, Cornelissen, Janson, & Silveira, 2016; Samuels & Levey, 2005; Traveset & Verdú, 2002), may dramatically underestimate the importance of other frugivores for plant populations. In more complex communities with other frugivores, such as ungulates, rodents, and primates, trials comparing the number of seeds ingested to the number of seeds passed may be important for assessing the impacts of frugivores that act as partial seed predators, destroying a subset of plant species or a subset of seeds within species. Even without trials, likely seed predation interactions may be determined by assessing digestive morphology (e.g., crops in birds) or relationships between seed size and the probability of predation versus dispersal in closely related animal taxa (Shiels, 2011). Approaches that efficiently target these sources of functional variation are critical if ecological understanding of the functional outcomes of mutualistic network interactions is to scale with the magnitude of mutualism disruption and at a pace relevant to conservation.

Third, by demonstrating trait- and network-based correlates of gut passage effects, this work highlights the potential for predictors of functional variation applicable to networks in other systems. Research that works towards a generalized understanding of the functional outcomes of mutualistic interactions provides an important complement to research focused on generalizing knowledge of the identity of partners and frequency of interaction (Bartomeus et al., 2016). Together, the functional outcomes of mutualisms and the frequency of interaction define the quality and quantity components of mutualistic interaction "effectiveness" (Schupp et al., 2017). However, ecologists currently have a much stronger

predictive understanding of which partners will interact and how frequently (quantity component) based on predictors including trait matching, partner abundances, and phenology (Bartomeus et al., 2016) than of the functional outcomes of those interactions on mutualist performance (quality component). Our work demonstrates two predictors of variation in the quality component for plants; we found that seed size and the number of partners both predicted the effect of disperser gut passage on germination. These patterns conform to the expectation for greater dependence on seed dispersal among small-seeded species under the competition-colonization trade-off (Tilman, 1994) and mirror recent studies showing that species with more mutualistic partners have greater dependence on mutualisms (Fricke et al., 2017; Mello et al., 2015; Schleuning et al., 2014). This study demonstrates that functional traits and network metrics can be useful tools for advancing a predictive understanding of the functional outcomes of mutualistic interactions on plant performance.

Assessing the effects of gut passage on germination is critical for understanding the population trajectories and potential management approaches for plant species facing the loss of seed dispersers. Populations of the plant species included in this study have lost their seed dispersers on the neighbouring island of Guam, where the introduced brown tree snake caused the extirpation of birds (Rogers et al., 2017; Savidge, 1987). In this system and elsewhere, plant species that benefit from gut passage are more prone to recruitment limitation as a result of disperser loss (Rogers et al., 2017; Traveset & Riera, 2005). Our data show that the loss of gut passage effects alone reduces germination of bird-dispersed plants on Guam by 50% on average. The loss of other benefits of dispersal (e.g., escape from distance-dependent mortality) exacerbates recruitment declines following disperser loss (Rogers et al., 2017; Wotton & Kelly, 2011). Determining the benefits that each disperser provides, and the redundancy or complementary of their effects, can be important for management decisions aimed at restoration of disperser function. Our results suggest that reintroduction of the white-throated ground dove would not restore seed disperser function, and that the other seed dispersers are broadly equivalent in the effect of gut passage. Due to the redundancy of the seed dispersers in terms of their gut passage effects, other components of dispersal quality or quantity may be more important for determining the species that could most effectively restore dispersal function to Guam's forests (Rehm, Chojnacki, Rogers, & Savidge, 2017). Although existing approaches that apply network concepts to conservation and management problems have focused on patterns in the identity and frequency of interaction (Tylianakis, Laliberté, Nielsen, & Bascompte, 2010), we emphasize that data on the functional outcomes of network interactions are critical for biologically meaningful network predictions and strong management recommendations.

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AUTHORS' CONTRIBUTIONS

H.R., E.F., and J.B. designed the study; J.B. collected the data; E.F. wrote the first draft of the manuscript, with substantial input from J.B., and performed the analysis; E.R. contributed to study design and implementation. All authors revised the manuscript.

DATA ACCESSIBILITY

Data and analysis code are archived in the Dryad Digital Repository: https://doi.org/10.5061/dryad.3555bh3 (Fricke, Bender, Rehm, & Rogers, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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