

Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network

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Funding information

University of Washington Robert T. Paine Experimental Field Ecology Award; Walker Natural History Fund; National Science Foundation Graduate Research Fellowship

Abstract

Following defaunation, the loss of interactions with mutualists such as pollinators or seed dispersers may be compensated through increased interactions with remaining mutualists, ameliorating the negative cascading impacts on biodiversity. Alternatively, remaining mutualists may respond to altered competition by reducing the breadth or intensity of their interactions, exacerbating negative impacts on biodiversity. Despite the importance of these responses for our understanding of the dynamics of mutualistic networks and their response to global change, the mechanism and magnitude of interaction compensation within real mutualistic networks remains largely unknown. We examined differences in mutualistic interactions between frugivores and fruiting plants in two island ecosystems possessing an intact or disrupted seed dispersal network. We determined how changes in the abundance and behavior of remaining seed dispersers either increased mutualistic interactions (contributing to “interaction compensation”) or decreased interactions (causing an “interaction deficit”) in the disrupted network. We found a “rich-get-richer” response in the disrupted network, where remaining frugivores favored the plant species with highest interaction frequency, a dynamic that worsened the interaction deficit among plant species with low interaction frequency. Only one of five plant species experienced compensation and the other four had significant interaction deficits, with interaction frequencies 56–95% lower in the disrupted network. These results do not provide support for the strong compensating mechanisms assumed in theoretical network models, suggesting that existing network models underestimate the prevalence of cascading mutualism disruption after defaunation. This work supports a mutualist biodiversity-ecosystem functioning relationship, highlighting the importance of mutualist diversity for sustaining diverse and resilient ecosystems.

KEYWORDS

defaunation, ecological network, extinction, functional redundancy, mutualism, seed dispersal

1 | INTRODUCTION

Mutualistic interaction loss is a widespread impact of recent global change (Valiente-Banuet et al., 2015; Young, McCauley, Galetti, & Dirzo, 2016). Because mutualists often have multiple partners (Bascompte, Jordano, Melian, & Olesen, 2003), the disruption of a single interaction can affect a large portion of a community through

cascading interaction changes. Understanding how remaining interactions change following mutualism disruption in nature is critical for projecting the reverberating impacts of defaunation on species diversity (Brodie et al., 2014; Dunn, Harris, Colwell, Koh, & Sodhi, 2009) and ecosystem services ranging from crop pollination (Klein et al., 2007) to carbon storage in tropical forests (Bello et al., 2015).

In theory, reduced interactions with one partner can be compensated by increased interactions with another redundant partner (Bastolla et al., 2009; Kaiser-Bunbury, Muff, Memmott, Müller, & Cafisch, 2010; Memmott, Waser, & Price, 2004). Redundancy among mutualists is therefore commonly proposed as a process that buffers ecosystems from coextinction cascades (Howe, 2016; Tylianakis, Laliberté, Nielsen, & Bascompte, 2010). However, broad theoretical and empirical evidence suggests that species are typically complementary, rather than redundant, in their impact on ecosystem processes (Hooper et al., 2005; Tilman, Isbell, & Cowles, 2014), with the decline of species interactions (Valiente-Banuet et al., 2015) and their functional outcomes (McConkey & O'Farrill, 2016) typically thought to outpace the decline of species themselves. Mutualistic interaction networks containing complementary interactions are much less robust to species decline and extinction than networks containing redundant interactions that allow compensation (Schleuning, Fründ, & Garcia, 2015). Understanding whether and how interaction compensation occurs in mutualistic networks is critical for predicting the severity of global change drivers on mutualistic interactions, guiding the conservation of mutualists, and understanding the processes that underlie the stability of mutualistic networks.

Interaction compensation may occur via two mechanisms: through increases in the abundance of remaining partners ("density compensation"; Walker, 1992) or through changes in the effect of their individuals ("per capita compensation"; e.g., behavioral changes for animals). Network models used to study the impacts of mutualism disruption assume that compensation occurs, although the mechanism of compensation differs among models. Coextinction models are typically built so that a species will persist if at least one of its partners remains, regardless of that partner's abundance or how frequently the interaction was observed in nature (Fortuna & Bascompte, 2006; Memmott et al., 2004; Poccock, Evans, & Memmott, 2012). Although these topological models do not consider the mechanism of compensation explicitly, they assume that any partner species can fully compensate for the loss of all other partners. Dynamical network models, which have been used to understand the attributes of networks that confer stability and facilitate species coexistence (Bastolla et al., 2009; Rohr, Saavedra, & Bascompte, 2014; Thebault & Fontaine, 2010), also allow compensation. The extinction or population reduction of a focal species' partner decreases competition among other species of that trophic level, creating density compensation through an increase in the abundance of remaining partners. Models focused on network "rewiring"—the reassembly of interactions over space and time—show the potential for compensation when new interactions form after initial interactions are lost (Kaiser-Bunbury, Muff, et al., 2010; Ramos Jiliberto, Valdovinos, Moisset de Espanés, & Flores, 2012; Valdovinos, Moisset de Espanés, Flores, & Ramos Jiliberto, 2013). This is a form of per capita compensation because the per capita interaction rate increases from zero after rewiring. In all cases, these models find that compensating mechanisms ameliorate the negative cascading effects of mutualism disruption on mutualist diversity.

Whether compensation occurs in nature as it is assumed to in network models is largely unknown (Aslan, Zavaleta, Tershy, & Croll, 2013; Kurten, 2013; McConkey and O'Farrill 2016; Pattenmore & Wilcove, 2011). To study compensation at the scale at which it occurs, experimental studies would have to manipulate mutualist abundance across entire ecosystems. Such approaches are unethical or unfeasible, and so researchers have used observations within single networks to gain insight about the redundancy or complementarity of mutualistic interactions, which may provide information on the potential for compensatory responses following mutualism disruption. Many studies from individual intact networks have suggested that mutualistic interactions are complementary, rather than redundant (e.g., Blüthgen & Klein, 2011; Brodie, Helmy, & Brockelman, 2009; García & Martínez, 2012; González-Castro, Calviño-Cancela, & Nogales, 2015; McConkey & Brockelman, 2011; Poulsen, Clark, Connor, & Smith, 2002; Rother, Pizo, & Jordano, 2016; Wenny & Levey, 1998). Still, these data provide limited inferences for the prevalence or mechanism of interaction compensation because compensation involves the alteration of remaining interactions in response to the loss of other interactions, and such dynamics cannot be measured via observing a species' realized niche in a single intact community (Brodie, 2007; Kurten, 2013). Data from controlled mesocosms and small-scale experiments (e.g., Brosi & Briggs, 2013; Davies, Jenkins, Kingham, Hawkins, & Hiddink, 2012; Fründ, Dormann, Holzschuh, & Tschamtker, 2013; Stachowicz & Whitlatch, 2005) also suggest complementarity, but overlook potential abundance or per capita responses to mutualism disruption that may occur at larger spatial or temporal scales. An alternative and practical approach for assessing compensation at ecosystem scales are "accidental experiments" caused by unintentional mutualism disruption in space or time (HilleRisLambers et al., 2013).

Several studies that have used accidental experiments to test for interaction compensation suggest that compensation is weak or nonexistent (Biesmeijer et al., 2006; Cordeiro & Howe, 2003; Holbrook & Loiselle, 2009; Barrera Zambrano, Moncada, & Stevenson, 2008) or that interaction changes even underlie anticompensating responses, such as the loss of an interaction in a disrupted community despite the persistence of both partners (Aizen, Sabatino, & Tylianakis, 2012). Yet even in studies where mutualism disruptions in otherwise similar ecosystems allow appropriate comparisons, it has not been possible to assess the mechanism or prevalence of interaction compensation for two major reasons. First, existing studies have not presented information on the abundance of mutualists in the intact and disrupted communities (Aizen et al., 2012; Biesmeijer et al., 2006; Burkle, Marlin, & Knight, 2013; Holbrook & Loiselle, 2009). This precludes attribution of any observed interaction changes to changes in the abundance of mutualists or their per capita effect, thus obscuring the mechanism of compensation. The prevalence of compensatory responses is also obscured without abundance data. Without assessing abundance differences, a finding that a species has lower mutualistic interaction frequency in a disrupted community could indicate that the abundance and behavior of remaining mutualists are unchanged (no compensation response),

that the remaining mutualists have decreased in abundance or changed in behavior to exacerbate an “interaction deficit” (negative response; sensu Valiente-Banuet et al., 2015), or that the remaining mutualists have altered interactions to compensate partially (positive response), but insufficiently to achieve full compensation (Kurten, 2013). Second, mutualistic network studies have presented raw interaction counts without information characterizing the variability or uncertainty in interaction frequency (Aizen et al., 2012; Biesmeijer et al., 2006; Burkle et al., 2013). This prohibits statistical inference about difference in interaction frequency among communities and therefore complicates efforts to measure the magnitude of compensation. Taken together, existing research suggests that ecosystems may not possess the strong compensatory mechanisms assumed in theoretical network models, but these studies have not been designed to provide the empirical information necessary to assess the magnitude or mechanism of interaction compensation.

We tested for compensatory dynamics in seed dispersal interactions by comparing an intact seed dispersal network and a disrupted network, where two generalist frugivore species are functionally extirpated, in the Mariana Island chain in the western Pacific Ocean. We focused on compensation of seed dispersal interactions for plants, with two goals to (i) assess the alternatives that interaction frequency with remaining frugivores increases to compensate for mutualism disruption, is unaffected by mutualism disruption, or decreases to exacerbate interaction deficits, and (ii) determine the mechanism of these changes to interaction frequency, either caused by changes in remaining frugivore abundance or behavior. Oceanic islands are particularly suited for analyses of mutualistic networks and their disruption because global change drivers disproportionately threaten species on islands, their low species richness allows individual species to be well characterized in community-scale analyses, and inter-island studies can achieve strong comparisons (Kaiser-Bunbury, Traveset, & Hansen, 2010). By linking intensive observations of frugivory interactions with independent estimates of frugivore abundance, we explore changes to interaction frequency in the disrupted network that are attributable to differences in population density (density responses) and to behavioral differences in individual frugivores (per capita responses).

2 | MATERIALS AND METHODS

2.1 | Study system

This work was conducted on the islands of Saipan and Rota in the Mariana Islands. The main forest type on both islands is a limestone karst forest with low plant species richness relative to mainland tropical systems and a short canopy that ranges between 8 and 15 m. Both islands have a similar plant community composition. The period of peak fruiting is between May and August, coinciding with the beginning of the wet season that occurs between June and December. The islands receive approximately 2.0–2.5 m of rain annually (Lander, 2004). Birds are the primary dispersers in this system. The Mariana fruit bat (*Pteropus mariannus*) was likely an important

frugivore on both islands historically, but is currently considered endangered by the IUCN; estimates of population densities in suitable habitat on Saipan are <0.01 individuals per hectare and on Rota roughly 0.2 individuals per hectare (US Fish and Wildlife Service 2009). Carrying capacities for *Pteropus mariannus* is estimated at approximately 1.8 individuals per hectare (Mildenstein & Mills, 2013). The functional role of *Pteropus* bats as seed dispersers declines severely before they reach low population densities (McConkey & Drake, 2006), and because the densities in the Marianas fall well below the levels at which *Pteropus* bats are considered functionally extinct, we therefore focus only on diurnal interactions. Other frugivorous species include two introduced lizards, the emerald tree skink (*Lamprolepis smaragdina*) and the green anole (*Anolis carolinensis*), which may opportunistically consume fruit. On each island we conducted observations within three native limestone karst forest study sites, which possess similar plant communities with relatively high tree diversity (Rogers et al., 2017).

The avian species diversity differs between Saipan, which has a relatively intact seed disperser network, and Rota, which has a disrupted seed disperser network. Frugivorous birds on Saipan include the Mariana fruit dove (*Ptilinopus roseicapilla*), white-throated ground dove (*Gallicolumba xanthonura*), Micronesian starling (*Aplonis opaca*), bridled white-eye (*Zosterops conspicillatus*), and golden white-eye (*Cleptornis marchei*). On Rota, the endangered Rota bridled white-eye (*Zosterops rotensis*), which was previously considered a subspecies of *Zosterops conspicillatus*, persists in a restricted high elevation range, but has been absent from the majority of limestone forest on the island including our study sites for several decades (Amar, Amidon, Arroyo, Esselstyn, & Marshall, 2008). The golden white-eye is known on Rota only from bone evidence, as it was extirpated from Rota since human arrival (Steadman, 1999). The mechanism of decline for each of the white-eye species is poorly known, but coincided with anthropogenic factors including mammalian introductions and habitat modification. The Mariana fruit dove, white-throated ground dove, and Micronesian starling are the remaining frugivorous birds on Rota. Thus the major difference in the frugivore guild is the extirpation of small frugivorous passerines on Rota, although differences in abundance of other frugivores also exist between islands (Amar et al., 2008; Camp, Pratt, Marshall, Amidon, & Williams, 2009). We quantified these differences at our study sites as described below.

2.2 | Seed dispersal network

We detailed the seed dispersal network on each island by conducting observations during the peak fruiting season (May to August) across 2 years. Using binoculars, we performed extended direct observation of fruiting trees (Fricke, Tewksbury, Wandrag, & Rogers, 2017; Schleuning et al., 2011) from six tree species, *Aglaia mariannensis* (Meliaceae), *Carica papaya* (Caricaceae), *Melanolepis multiglandulosa* (Euphorbiaceae), *Pipturus argenteus* (Urticaceae), *Premna serratifolia* (Lamiaceae), and *Psychotria mariana* (Rubiaceae). These species were selected as focal species because they were observed fruiting during both years, were found on both islands, and were

observed to be dispersed by vertebrates. Hereafter we refer to these species by genus. Population densities measured within three forest plots on each island for *Aglaia* (121 ± 49 ; individuals per hectare; mean \pm SE), *Carica* (43 ± 27), *Melanolepis* (44 ± 10), *Pipturus* (13 ± 6), *Premna* (76 ± 20), and *Psychotria* (68 ± 20) were variable between sites within each island and the distributions of local population densities overlapped substantially between islands. As in other network studies, this analysis does not cover rare or rarely fruiting plant species present in these communities. Because the focus of our analysis is on comparisons of interactions between individual plant species and all of their frugivores across the two islands, our conclusions are not sensitive to the number of plant species included in the study. During observation sessions, observers identified frugivores to species, recorded how many diaspores were manipulated, and distinguished between interactions where the diaspore was dispersed (ingestion of the diaspore or movement of the diaspore away from the canopy), where pulp was removed without removing any diaspores, and where the diaspore was simply dropped from the tree. We only analyzed data on diaspores that were dispersed. Ongoing work is determining the potential role of the frugivores as seed predators as well as seed dispersers, although the conclusions of this study are qualitatively consistent if the white-throated ground dove, which potentially acts as a seed predator as well as a seed disperser, is excluded as a mutualist in the analysis. Observers conducted observations between 6:00 AM and 2:00 PM. Observation periods lasted between 2 and 8 hr, with 400 observation hours per species on average across the two islands (Table S1). Observers moved between islands and study sites over the course of the study period. Observations were conducted concurrently on both islands to minimize any temporal bias between islands. Observers also alternated between tree species. Observers recorded data on multiple tree individuals, with on average 52 individuals per species observed (range 23–88 individuals; Table S1). For *Carica*, we also used video recordings to record frugivory events. In addition to recording frugivory events, we estimated the total ripe fruit crop of each focal tree by counting every ripe fruit, or if many fruits were present, by counting the fruit present in a fraction of the canopy and then dividing by the fraction of canopy counted.

We obtained a frugivory rate (per diaspore probability of removal per hour) using parametric survival regression with the `survreg` function in the R package “survival” (Therneau, 2015). We used separate models for each tree species by frugivore species combination, obtaining in each case a frugivory rate for the focal frugivore-focal plant combination. Our approach included every diaspore as an individual and estimates the constant per diaspore probability of removal by the focal frugivore species. A challenge in accurately quantifying the per diaspore probability of removal by a focal frugivore is to achieve a temporally accurate denominator—seeds removed out of seeds available at any given time—while accounting for seeds removed over time by other frugivore species. Survival regression allowed us to account for this dynamic through right censoring. Diaspores that were remaining at the end of the observation period, diaspores that

were dropped, and diaspores removed by frugivores other than the focal frugivore in a given model, were right-censored in the survival analysis. The response variable was the survival term and the predictor variables were island (Saipan or Rota), the focal tree’s ripe fruit crop size, and an interaction term between island and crop size. When we did not observe any interactions between a tree species and frugivore species on one island, we only included crop size as the predictor variable. To account for nonindependence of diaspores on the same tree during a given observation, we included a tree-date ID as a cluster term. To obtain a frugivory rate for each island, we used this model to estimate the portion of diaspores removed per hour from a tree of the median crop size on each island. We produce 1,000 bootstrapped estimates of the frugivory rate by resampling with replacement from the tree-date IDs to achieve the same number of tree observation periods and refitting the models.

2.3 | Estimating avian abundance

During frugivory observations, we performed point counts for avian abundance. The distance to all individuals seen or heard was recorded during an 8 min period. We used the function `gdistsamp` in the R package “unmarked” to estimate avian abundance per hectare on each island (Fiske & Chandler, 2011). Although more than one point count was typically performed at locations where frugivory observations were performed, to achieve independence we randomly sampled one point count session from each location where observations were conducted. We produce 1,000 bootstrapped estimates of avian frugivore abundance by resampling with replacement from among the locations where point counts were conducted and refitting the models.

2.4 | Calculating density and per capita responses

We used estimates of abundance of each bird species on each island and frugivory rates for each bird-tree combination on each island to differentiate density and per capita responses to mutualism disruption. We did not have a priori information on which plant species have experienced mutualism disruption—possessing an interaction on Saipan with a frugivore extirpated from Rota—and therefore only calculated density and per capita responses to mutualism disruption for the species that we found to have experienced mutualism disruption. For each of these plant species, we started by calculating a per capita frugivory rate (frugivory rate/frugivore individuals per ha) for each observed bird-tree combination on each island. We then considered frugivory rates in three scenarios for each bird-tree combination.

- S1 Per capita frugivory rate on Rota * frugivore density on Rota = observed frugivory rate on Rota
- S2 Per capita frugivory rate on Saipan * frugivore density on Rota = predicted frugivory rate on Rota if frugivores behaved as they do on Saipan

S3 Per capita frugivory rate on Saipan * frugivore density on Saipan = observed frugivory rate on Saipan

Comparing these three scenarios allowed us to differentiate density and per capita compensation. Subtracting the frugivory rates in Scenario 2 from Scenario 1 indicates the per capita response in frugivory rate on Rota. Subtracting Scenario 3 from Scenario 2 indicates the density response. Note that these represent absolute, rather than relative, differences in frugivory rate. Take as an example that the observed frugivory rate of a frugivore species consuming fruits of a plant species is 0.2 on Rota and 0.1 on Saipan (per seed dispersal probability per hour) and the abundance is 4 on Rota and 2 on Saipan (individuals per hectare). In this case $S1 = 0.2$, $S2 = 0.2$, and $S3 = 0.1$, so the density response is $0.2 - 0.1 = 0.1$ and the per capita response is $0.2 - 0.2 = 0$. In other words, the frugivory rate on Rota has increased proportionately to frugivore density, and the difference in frugivory rate (difference of 0.1 per hour) can be attributed entirely as a density response. If instead the frugivory rate on Rota was 0.25, with other values otherwise equal, the density response would be 0.1 and the per capita response would be 0.05. Performing these calculations for each of the 1,000 bootstrapped replicates, we obtained median values and confidence intervals. To assess statistical significance, we interpreted overlap in 95% confidence intervals.

3 | RESULTS

We found differences in avian frugivore abundance between Rota, which possesses a disrupted frugivore guild, and Saipan, which possesses an intact frugivore guild. The golden white-eye (*Cleptornis marchei*) is absent from Rota and we did not observe the Rota bridled white-eye (*Zosterops rotensis*) at our study sites (Figure 1a). The golden white-eye and bridled white-eye (*Z. conspicillatus*) are the two most abundant frugivorous species on Saipan. The Mariana crow is present on Rota but absent on Saipan. The Micronesian starling was observed at roughly 40% greater densities on Rota relative to Saipan, the Mariana fruit dove was observed at similar densities at our study sites on Rota and Saipan, and the white-throated ground dove was observed at approximately 70% lower density on Rota relative to Saipan.

We recorded the removal of 11,380 diaspores across six plant species by eight frugivore species (Table S2). Most of the pairwise interactions observed in the intact network on Saipan were also observed in the disrupted network on Rota if the species were present there (Figure 1b). In one case an interaction was recorded on Rota that was not observed on Saipan (*Pipturus* – fruit dove), consistent with compensatory network rewiring. However, in three instances the opposite was true, with an interaction present on Saipan absent on Rota even though the species were present (Figure 1b). Other inter-island differences in the presence or absence of interactions were attributable to differences in species composition that are unrelated to network disruption. Specifically, the Mariana

crow has never occurred on Saipan and the non-native emerald tree skink is only present on Saipan and not Rota.

Of the six plant species in our network, five were partially dispersed on Saipan by species absent in our Rota sites. These are the species for which compensation may occur, and the seeds of each of these plant species can be handled by each of the frugivorous bird species remaining on Rota. The sixth, *Aglaia mariannensis*, was only consumed by the starling, which is abundant on both islands, therefore it was not included in our compensation analysis. As an overall measure of whether all frugivores together achieved compensation, we calculated the Rota:Saipan frugivory rate ratio (Figure 1c). Values less than 1 indicate interaction deficits, or frugivory rates on the defaunated island of Rota reduced relative to Saipan. Values overlapping 1 represent compensation after interaction loss on Rota. Values >1 indicate interaction surpluses, or relatively greater frugivory rates on Rota. We found a significant interaction deficit in four out of the five species, with median frugivory rates among these species reduced on Rota relative to Saipan between 56% and 95%. The interaction deficit was greatest in *Psychotria*, a species that had relatively few partners and experienced anticompensating network rewiring—the loss of an interaction on Rota that was present on Saipan even though the frugivore was present on both islands. We observed an interaction surplus in *Pipturus*, a species with many partners and which exhibited the only instance of compensatory rewiring—developing an interaction on Rota that was absent on Saipan (Figure 1c).

Having observed frugivory rates and frugivore abundances in the intact (Saipan) and disrupted (Rota) networks, we next decomposed the differences in interaction frequency for each plant-frugivore species combination into density and per capita responses (Figure 2a), assessed total density and per capita responses by summing across all frugivores species for each plant species (Figure 2b), and summed across both per capita and density responses to assess whether total responses were partially, fully, or anticompensating (Figure 2c). Figure 2a shows absolute differences in frugivory rates between the intact and disrupted network attributable to density responses and per capita responses for each bird-tree combination (Figure 2a). In 10 bird-tree interactions, the differences in frugivore abundance on Rota relative to Saipan caused significant density-related impacts on frugivory rate and, in seven bird-tree interactions, behavioral shifts led to significant positive or negative per capita responses (Figure 2a). The Micronesian starling, a generalist that occurs at higher densities in the disrupted community, caused the largest magnitude density-related increases in frugivory rates on Rota. However, when the density responses were summed for each plant species across the frugivore species present on Rota (Figure 2b, “All birds” column), there was lack of density-related changes in frugivory rates for every plant species except *Carica*. When the per capita responses were summed across all frugivore species (Figure 2b), there were two species, *Pipturus* and *Melanolepis*, that experienced a compensatory per capita response, with remaining frugivores increasing consumption on Rota relative to Saipan, and one species, *Carica*, with a negative

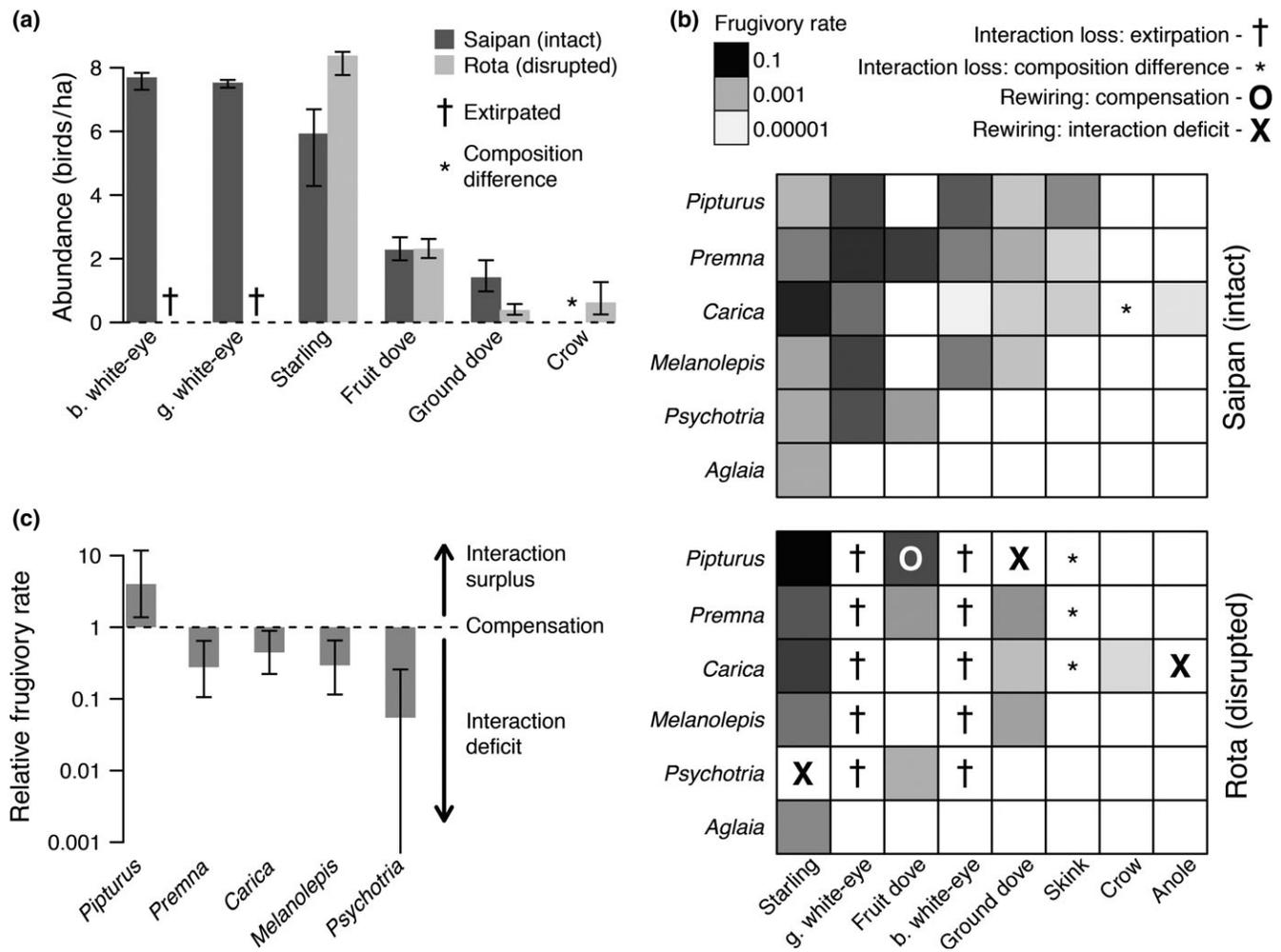


FIGURE 1 Abundances of birds (a), interaction networks on Saipan and Rota (b) and the Rota:Saipan frugivory rate ratio (c). Panels (a, c) show bootstrapped median values and 95% confidence intervals. Symbols in panels (b, c) indicate why species or interactions are absent or present on each island: daggers indicate the absence of species or interactions present on the other island due to frugivore functional extirpation; asterisks indicate the absence of species or interactions present on the other island due to differences in species composition unrelated to network disruption; capital “O” indicates compensatory rewiring; and capital “X” indicates rewiring contributing to an interaction deficit. Note in panel (c) that the 95% confidence interval for the frugivory rate of *Psychotria* on Rota extends to 0 but has been truncated to accommodate the log-scaled y-axis. Species are arranged in panel (a) by abundance in the intact community, and in panels (b, c) by decreasing total interaction frequency across both islands

per capita response, or a behavioral shift away from this species despite greater partner abundances.

Finally, we combined the density and per capita responses and compared this summed measure of interaction change against the level of interaction frequency “missing” in the disrupted network that would be necessary to achieve compensation (in other words, the interaction frequencies with the species present on Saipan that are absent from Rota; Figure 2c). In four of the five species, interaction changes did not achieve compensation, instead resulting in an interaction deficit. For *Premna*, *Carica*, and *Psychotria*, total responses did not differ from zero, meaning that the total interaction frequency with the remaining frugivore species in the disrupted network were statistically equal to the total interaction frequencies with those frugivore species in the intact community. For *Melanolepis*, a positive but weak total response yielded partial compensation, but only

roughly a fifth of what would be necessary to fully compensate for the interactions that were lost (Figure 2c). Only for *Pipturus* did interaction frequency increase sufficiently to compensate for the missing interactions, and this resulted in a significant interaction surplus for this species.

4 | DISCUSSION

In our comparison of seed dispersal interactions in a relatively intact and a disrupted mutualistic network on two islands in the Mariana Islands, we found little support for interaction compensation after the functional extirpation of two generalist frugivores. Using data on interaction frequency and independent assessment of abundance, we determined how changes in the abundance (density responses)

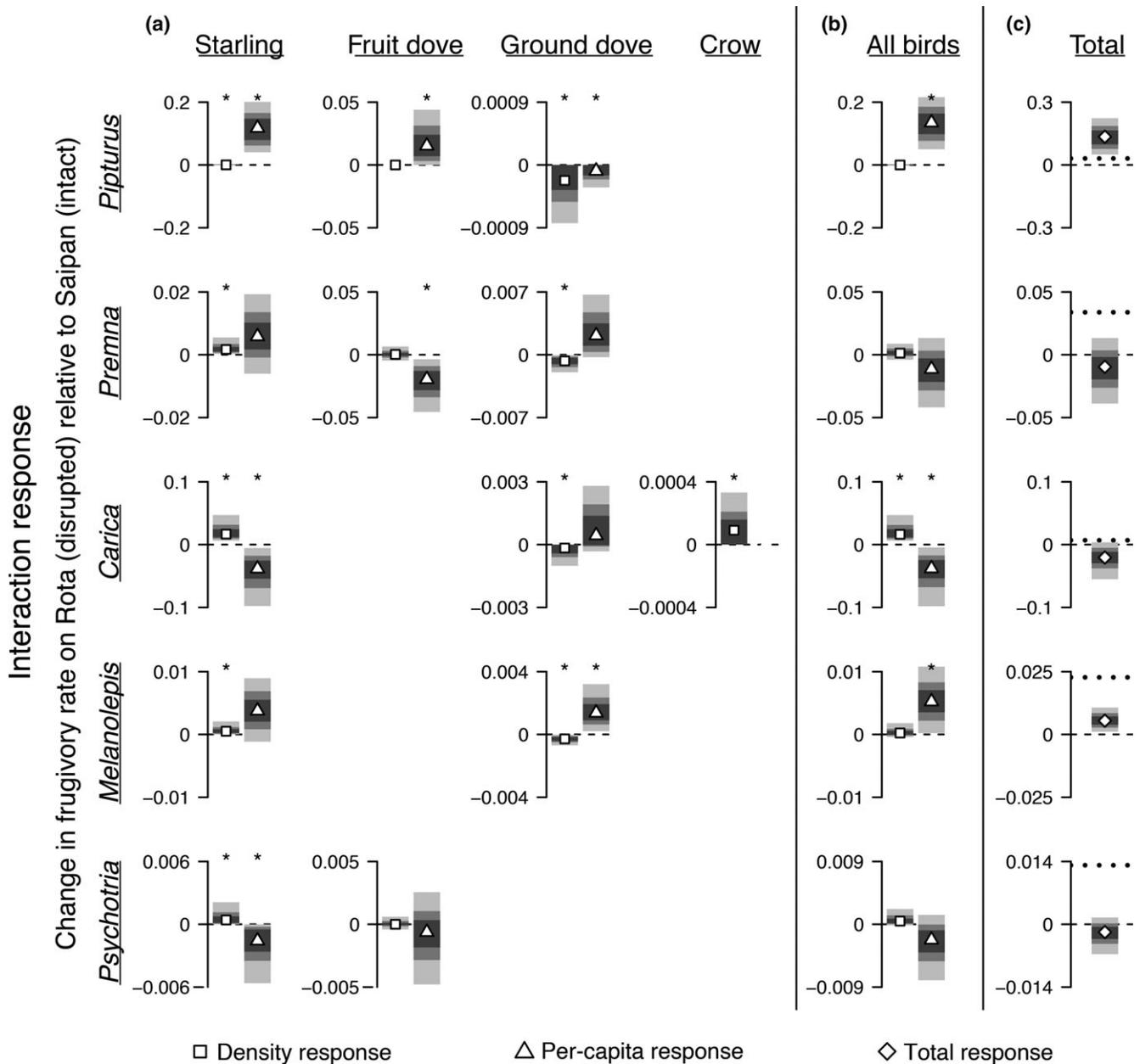


FIGURE 2 Assessing the mechanisms and magnitude of altered interaction frequency in the disrupted community. Panel (a) shows median changes in frugivory rates (probability of seed removal per hour) in the disrupted community via changes in frugivore abundance (“Density responses”) and through changes in the per capita effect of individuals (“Per capita responses”) and their associated 50%, 75%, and 95% confidence intervals. Columns represent frugivore species; rows represent plant species. In panel (a), all observed pairwise interactions including bird species present on Rota are shown. Asterisks indicate that estimates differ significantly from zero. In panel (b), the density response and per capita responses are summed across all bird species present on Rota. In panel (c), the density and per capita responses of all bird species are summed as a measure of the total interaction change on Rota relative to Saipan. The dotted line represents the interaction frequency necessary to achieve compensation by the remaining frugivores on Rota, calculated by summing the interaction frequencies of the species absent from Rota

and behavior (per capita responses) of frugivores contributed to interaction compensation or interaction deficit in the disrupted network. In many pairwise interactions, these changes yielded density or per capita compensation in frugivory rates. However, these compensatory responses were nearly always counteracted by anticomplementary changes caused by the density or per capita responses of

the same frugivore species or by other frugivore species. For example, although there are more starlings in the disrupted community, causing relatively higher consumption of *Premna* fruits (positive density response; Figure 2a), fruit doves in the disrupted community individually consume relatively fewer *Premna* fruits (negative per capita response). Only one of the five plant species experienced

significant community-level compensation in frugivory interactions (Figure 2c). We did observe network rewiring, but in sum it did not result in compensation because instances of the development of “new” interactions—interactions unobserved in the intact community but present in the disrupted one—were less common than the “loss” of interactions—interactions observed in the intact community that were unobserved in the disrupted one. Together, these mechanisms resulted in an interaction surplus in one plant species, which was among those with the greatest partner diversity and interaction frequency, and strong interaction deficits, with interaction frequencies 56–95% lower in the degraded network on Rota than in the intact network on Saipan, for the other four plant species (Figures 1c and 2c). These results do not support the hypothesized mechanisms or prevalence of compensation assumed in many mutualistic network models (Bastolla et al., 2009; Kaiser-Bunbury, Muff, et al., 2010; Memmott et al., 2004).

Behavioral changes caused larger differences in frugivory interactions than did changes in frugivore abundance. To date, density compensation is the form of compensation included in community models that are used to test the consequences of network perturbation (Bastolla et al., 2009), and it is much more frequently discussed as the mechanism of interaction compensation (e.g., Larsen, Williams, & Kremen, 2005; Schleuning et al., 2015; Winfree & Kremen, 2009). However, our results indicate that per capita responses can be large; we found that they were larger in magnitude than density responses in the great majority of cases (Figure 2a). Further, we show that the direction of the per capita responses can be either compensatory or anticomensatory. This contrasts with one way in which per capita compensation has been implicitly included in network models. Dynamical network models often use saturating functional responses where the mutualistic benefit provided by a given partner scales nonlinearly with that partner's abundance (Bastolla et al., 2009). In effect, this increases the per capita mutualistic benefit provided by a partner population after the partner has declined in abundance, introducing a per capita response that is exclusively compensating. In this study, per capita effects were inconsistent with this expectation, being large in magnitude but as frequently compensating as anticomensating.

Frugivore behavior can also depend on plant abundance and diversity, in addition to the frugivore abundance and diversity effects explored in this study. Field studies from single systems indicate heterogeneous intra- and interspecific responses, including frugivores responding to local conspecific fruit availability (Carlo & Morales, 2008) and frugivores favoring recruitment of rare species through rare-biased dispersal (Carlo & Morales, 2016). We believe that the large between-island differences observed in this study are not the result of intra- or interspecific plant abundance effects because we chose study sites with similar forest composition, conducted observations in areas of overlapping local conspecific densities across each island, and observed no apparent connection between the size of interaction change and the rarity or commonness of the plant species. Studies that link frugivore and fruit abundance to intra- or interspecific variation in interaction frequency have the potential to

enable mechanistic prediction of interaction changes and feedbacks between plant and animal populations following mutualistic network disruption. Increased efforts to measure the magnitude of compensatory dynamics in nature, to quantify the functional responses that relate mutualist abundance and diversity to interaction frequency (Schleuning et al., 2015), and to relate mutualistic interaction frequency to demography (Caughlin et al. 2015, Rogers et al., 2017) will be critical for advancing network models' capacity to predict impacts of defaunation on species diversity and ecosystem services.

When changes in the per capita effect of mutualists have been considered in network studies, it is typically though compensatory network rewiring, such as through the development of interactions in a disrupted community that were lacking in an intact one (Kaiser-Bunbury, Muff, et al., 2010; Ramos Jiliberto et al., 2012; Valdovinos et al., 2013). This has a strong potential for interaction compensation; models that allow a potential partner to rescue a species that has otherwise lost mutualists find increased robustness to coextinction (Kaiser-Bunbury, Muff, et al., 2010). Still, these models do not consider the opposite, anticomensating effect—that interactions with co-occurring partners can be lost in an altered network (Gilljam, Curtsdotter, & Ebenman, 2015). In the networks studied here, we found that anticomensating rewiring occurred more frequently than did compensating rewiring. The only instance where an interaction unobserved in the intact system was present in the disrupted one was the interaction between the Mariana fruit dove and *Pipturus*, the single plant species that experienced an interaction surplus in the disrupted network on Rota. This species would have experienced interaction compensation regardless of this individual case of compensatory rewiring. In contrast, there were three cases of anticomensating network rewiring. Although starlings, ground doves, and anole lizards are all present on Rota, they were not seen consuming *Psychotria*, *Pipturus*, and *Carica*, respectively—species they were seen consuming on Saipan. Of these four rewiring instances, the largest impact is the loss of the interaction between the Micronesian starling, a generalized frugivore, and *Psychotria*, the tree species that had the largest interaction deficit and which possessed the fewest partners among the species affected by mutualist extirpation. In general, we caution that cases of rewiring could be the result of well known spatiotemporal fluctuations or rare interaction sampling artifacts (Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008; Plein et al., 2013), rather than changes to interaction frequency that are large in magnitude and causally linked to network disruption. Therefore, care should be taken to assess the magnitude of rewiring-based interaction changes relative to other interaction changes that may be quantitatively more impactful. Across these islands, we found no evidence that rewiring is a widespread contributor to compensation.

Our findings suggest that the outcome of network disruption in this system was to strengthen interactions with species that have generalized interactions and to weaken interactions with species that have specialized interactions (Figure 1c). This is consistent with the network assembly process of preferential attachment, or the principle that “the rich-get-richer” (Olesen, Bascompte, Elberling, & Jordano, 2008). It is also consistent with the process of resource

breadth shifts in response to the competitive environment, causing complementarity to be high when interspecific competition is high (Ashton, Miller, Bowman, & Suding, 2010). Under both interpretations, the prediction is for a greater prevalence of interaction deficit in disrupted networks because the species most likely to lose their interactions (those with few partners or infrequent interaction) are least likely to strengthen interactions or develop new ones. Similar dynamics have been recently explored theoretically in the context of trophic networks. Gilljam et al. (2015) used dynamical models where trophic rewiring can be compensatory or anticomensatory to show that rewiring, when adaptive, increases coextinction risk. Thus network rewiring may not buffer ecosystems from coextinction in nature as it does in network models that assume consistently compensatory rewiring (Ramos Jiliberto et al., 2012; Staniczenko, Lewis, Jones, & Reed-Tsochas, 2010; Thierry et al., 2011; Valdivinos et al., 2013).

Our results show that interactions in the disrupted network did not change in a homogeneously compensating manner. This conclusion is critical for advancing our current knowledge of the links between the architecture of mutualistic networks, community stability, and species coexistence (Bascompte, Jordano, & Olesen, 2006; Bastolla et al., 2009; Rohr et al., 2014). Because the strong compensating dynamics assumed in network models provide a critical stabilizing mechanism that links network structure to stability (Bascompte et al. 2006; Blüthgen, 2010; Memmott et al., 2004)—and because we show that these dynamics may not be ubiquitous as assumed—the importance of network structure for stability and coexistence may be overestimated. Empirical data on changes to interactions following mutualism disruption should inform the functional responses included in network models that are used to predict the broader consequences of global change drivers on mutualist biodiversity (Bascompte & Stouffer, 2009; Kaiser-Bunbury & Bluthgen, 2015; Tylianakis et al., 2010). Given the patterns reported here, mutualistic interaction disruption following defaunation is likely to be more pervasive than would be concluded from existing models.

Whether and how compensation occurs in real networks is critical for establishing conservation priorities and making management decisions. If strong compensation occurs, then managers need only maintain a population of a single generalist animal to maintain ecological function among plants. Our results instead indicate the need for management efforts that maintain diverse mutualist assemblages in the Mariana Islands and elsewhere. On the neighboring island of Guam, where native seed dispersers have been functional extirpated following the introduction of the brown treesnake (Savidge, 1987), reestablishment of multiple seed dispersers will likely be necessary for sustaining plant populations threatened by bird loss (Rogers et al., 2017). This work broadens support that the biodiversity-ecosystem function relationships shown widely in other contexts apply to mutualist systems as well (Brosi & Briggs, 2013; Schleuning et al., 2015), emphasizing the need for conservation of mutualist biodiversity to maintain diverse, functioning, and resilient ecosystems.

ACKNOWLEDGEMENTS

For assistance in data collection we thank Sheela Turbek, Leonard-John Ventura, Nadya Muchoney, Kenji Tomari, and Caroline Cappello. We thank Matthias Schleuning and an anonymous reviewer for helpful comments on the manuscript. This work was supported by the University of Washington Robert T. Paine Experimental Field Ecology Award (to EF), the Walker Natural History Fund, and a National Science Foundation Graduate Research Fellowship (to EF).

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How to cite this article: Fricke EC, Tewksbury JJ, Rogers HS. Defauna leads to interaction deficits, not interaction compensation, in an island seed dispersal network. *Glob Change Biol*. 2017;00:1–11. <https://doi.org/10.1111/gcb.13832>