

An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia

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ABSTRACT

Aim We studied how the abundance of the highly invasive fruit-bearing tree *Miconia calvenscens* DC. influences seed dispersal networks and the foraging patterns of three avian frugivores.

Location Tahiti and Moorea, French Polynesia.

Methods Our study was conducted at six sites which vary in the abundance of *M. calvenscens*. We used dietary data from three frugivores (two introduced, one endemic) to determine whether patterns of fruit consumption are related to invasive tree abundance. We constructed seed dispersal networks for each island to evaluate how patterns of interaction between frugivores and plants shift at highly invaded sites.

Results Two frugivores increased consumption of *M. calvenscens* fruit at highly invaded sites and decreased consumption of other dietary items. The endemic fruit dove, *Ptilinopus purpuratus*, consumed more native fruit than either of the two introduced frugivores (the red-vented bulbul, *Pycnonotus cafer*, and the silvereye, *Zosterops lateralis*), and introduced frugivores showed a low potential to act as dispersers of native plants. Network patterns on the highly invaded island of Tahiti were dominated by introduced plants and birds, which were responsible for the majority of plant–frugivore interactions.

Main conclusions Shifts in the diet of introduced birds, coupled with reduced populations of endemic frugivores, caused differences in properties of the seed dispersal network on the island of Tahiti compared to the less invaded island of Moorea. These results demonstrate that the presence of invasive fruit-bearing plants and introduced frugivores can alter seed dispersal networks, and that the patterns of alteration depend both on the frugivore community and on the relative abundance of available fruit.

Keywords

French Polynesia, frugivory, fruit abundance, introduced birds, invasive plant, *Miconia calvenscens*, mutualism, species interactions.

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INTRODUCTION

Species invasions pose a threat to biodiversity, particularly on remote tropical islands (Reaser *et al.*, 2007) where rates of endemism are high (Kier *et al.*, 2009). The introduction of alien species presents an opportunity for novel mutualistic associations to develop between vertebrate frugivores and the seeds they disperse, which may disrupt relationships between native species (Traveset & Richardson, 2006; Aizen *et al.*, 2008). Native fleshy-fruited plants and frugivores are linked to

each other in seed dispersal networks (Jordano, 1987) in which patterns of interaction depend in part on the relative abundance of interacting species in a community (Vázquez *et al.*, 2007). Thus, the changes in the relative abundance of available fruit that can occur when invasive fleshy-fruited plants become dominant may alter interactions between native species. The presence of highly invasive fleshy-fruited plants on oceanic islands offers a unique opportunity to explore how the local abundance of a single species influences seed dispersal, in part because of the relative simplicity of island ecosystems

(Vitousek, 2002) which makes community-wide studies more tractable than in other locations. Evaluating seed dispersal patterns at the community scale has the potential to provide insight that would not otherwise be available (Tylianakis *et al.*, 2009). For example, invaded communities may retain similar numbers of native species even when patterns of interaction have shifted disproportionately in favour of invasive species (Tylianakis *et al.*, 2009). Considering a few species in isolation might therefore mask changes at the community level that could have implications for ecosystem resilience and stability (Bascompte *et al.*, 2006; Tylianakis *et al.*, 2009). Furthermore, network analysis allows information relevant to conservation to emerge, such as the loss of interactions between species, the identification of vulnerable species, and quantification of the relative contributions of frugivorous species to dispersal of native plants.

The abundance of fruit-bearing plants in a community is known to influence avian foraging patterns, which are cumulatively reflected in the properties of seed dispersal networks (Levey, 1988; Loiselle & Blake, 1991; Herrera, 1998; Ortiz Pulido & Rico Gray, 2000; Blendinger *et al.*, 2008). An increase in the relative abundance of one species may influence others by attracting frugivores to an area, creating a neighbourhood effect in which multiple species benefit from increased seed dispersal (Sargent, 1990; Carlo, 2005; Gleditsch & Carlo, 2010). On the other hand, competition can also occur, whereby the choice to eat a more abundant species leads to decreased consumption of other neighbouring species (Saracco *et al.*, 2005; Carlo & Morales, 2008). Diet switching triggered by highly abundant invasive species may lead to a corresponding decline in seed dispersal services to native plants, with consequences for plant regeneration and community stability (Traveset & Richardson, 2006).

Investigating how species invasions alter seed dispersal is particularly urgent on remote oceanic islands where introduced species are associated with population reductions and extinction of native species (Vitousek *et al.*, 1997; Reaser *et al.*, 2007). The extreme low diversity of native frugivores on many islands in the Pacific can place disproportionate importance on a small number of species that act as the sole dispersers of native plants (Cox *et al.*, 1991). Declining populations or changes in the diets of extant native frugivores could lead to corresponding declines in dispersal services to native plants. At the same time, the introduction of multiple alien frugivores to many islands in the remote Pacific creates opportunities for ecological substitution if introduced species become dispersers of native plants (Kaiser-Bunbury *et al.*, 2010).

We investigated patterns of seed dispersal on the islands of Tahiti and Moorea in French Polynesia, where multiple species of fruit-bearing plants and frugivorous birds have been introduced (Monnet *et al.*, 1993; Fourdrigniez & Meyer, 2008). Avian extinction (especially of native pigeons) following the arrival of Polynesians in the past 1000 years has left the islands with only a subset of the original avifauna (Steadman, 2006). The existing community of frugivores on Tahiti and Moorea is extremely small, consisting of one surviving

endemic pigeon and three recent passerine introductions. In 1937, the introduction of the fruit-bearing tree *Miconia calvescens* DC. (Melastomataceae) resulted in the catastrophic invasion of 60–70% of the island of Tahiti (Meyer & Florence, 1996). The shade-tolerant invasive tree does not require disturbance or deforestation to facilitate invasion, and is notable for its ability to invade into high elevation forests where human impacts are minimal (Meyer & Florence, 1996). In this study we examined how *M. calvescens* abundance affects seed dispersal network properties and avian foraging patterns by comparing Tahiti to the nearby and less invaded island of Moorea (c. 25% invaded) (Meyer, 2010). Specifically, our objectives were: (1) to examine the diet of frugivores to determine whether invasive tree abundance at a site is related to changes in diet; (2) to quantify differences in the diets of native and introduced frugivores to determine which species are most responsible for the dispersal of native fruit; and finally (3) to build seed dispersal networks for the islands of Tahiti and Moorea to compare community-wide interaction patterns in a highly invaded ecosystem to one that is less invaded.

MATERIALS AND METHODS

Study area

This study was conducted at three sites on Tahiti (high *M. calvescens* abundance) and three sites on Moorea (low *M. calvescens* abundance) in the Society Archipelago of French Polynesia (17°38' S 149°30' W and 17°32' S 149°50' W). Both are relatively small and young tropical oceanic islands. Tahiti (0.6–1.1 Ma) is the largest and highest island in French Polynesia, covering 1045 km² and reaching 2241 m in elevation at its highest peak. Moorea, located 20 km from Tahiti, is smaller and older (1.1–2.5 Ma), covering only 142 km² with its highest peak reaching 1207 m. The flora of French Polynesia is rich in endemic plant species (520 endemic out of 885 native vascular plant species) including one of the highest proportions of endangered plants in the Pacific, with a total of 47 threatened plants according to IUCN Red Lists, and six plant species already extinct (Meyer & Salvat, 2009).

We chose sites in secondary forests composed of mixed native and alien tree species at elevations between 100 and 800 m (Table 1). Both islands were cleared at low elevations by Polynesians for agriculture followed by abandonment after European arrival (Lepofsky, 1999). While the history of Polynesian land use is not as well known for Tahiti, on Moorea, archaeological excavation in the Opunohu valley (including the locations of all three of our sites) has revealed evidence of extensive forest clearing (Lepofsky *et al.*, 1996). We avoided stands of forest dominated by the introduced trees *Falcataria moluccana* (Mimosaceae) and *Inocarpus fagifer* (Fabaceae) and placed sites in forests with a diversity of native and introduced species. Plant communities on the two islands are not identical, and it was not possible to control for all factors other than the abundance of *M. calvescens*. In spite of this limitation, we made an effort to locate sites in similar

Table 1 Number of faecal samples collected for three bird species at six sites on Tahiti and Moorea. Faecal samples were collected using mist nets and indirectly from under perch trees. Total numbers of samples for each island are shown in bold.

	<i>Miconia calvescens</i> basal area (m ² ha ⁻¹)	<i>Pycnonotus cafer</i>	<i>Ptilinopus purpuratus</i>	<i>Zosterops lateralis</i>	Elevation (m)	Forest type (surrounding forest)
Tahiti		324	3	175		
Aorai	15.38	219	0	88	600	Mixed native
Marau	6.14	30	0	43	800	Heavily invaded
Taravao	21.92	75	3	44	600	Heavily invaded
Moorea		131	201	344		
Belvedere	0.4	20	100	114	250	Mixed native
Cocotiers	0.7	68	101	114	350	Mixed native
Vaiana	2.2	43	0	116	150	Moderately invaded

habitats and with similar plant communities in order to vary invasive tree abundance between sites while keeping other factors as consistent as possible.

Study species

Miconia calvescens grows in dense stands on both Tahiti and Moorea, but the invasion is less extensive on Moorea where it has been present only since the 1960s (Meyer, 1998). The tree produces a fleshy fruit *c.* 7 mm in diameter that is purple-black when ripe. Fruits contain between 50 and 250 seeds, each approximately 0.6 mm in diameter. Single trees can produce up to eight million seeds each per year and are rarely devoid of fruit (Meyer, 1998).

Frugivores included in this study are the grey-green fruit dove, *Ptilinopus purpuratus* (Gmelin, 1789) (Columbiformes, Columbidae), the red-vented bulbul, *Pycnonotus cafer* (Linnaeus, 1766) (Passeriformes, Pycnonotidae), and the silvereye, *Zosterops lateralis* (Latham, 1801) (Passeriformes, Zosteropidae). Native mammals are entirely absent, and other potential frugivores include only the introduced Polynesian rat (*Rattus exulans*), the black rat (*Rattus rattus*), and the common myna (*Acridotheres tristis*) (J.Y. Meyer, pers. obs.). We chose to exclude the myna from this study because it consumes relatively little fruit and is not abundant at sites above 200 m (E.N. Spotswood, unpublished data). The Polynesian rat is present at our sites, but was also excluded because its home range is relatively small and it acts only as a local disperser of small seeds (Meyer & Butaud, 2009). Lizards are present and are potential seed dispersers, but all are small in size (< 60 mm snout–vent length) (Whitaker, 1970; Crombie & Steadman, 1986; Ineich & Blanc, 1988), and were also excluded due to their small home ranges and body size.

The native *Ptilinopus purpuratus* is endemic to the Society Archipelago where it is widespread from sea level up to 600 m on Moorea and 1000 m on Tahiti (Holyoak & Thibault, 1984). *Pycnonotus cafer*, first seen naturalized on Tahiti in the late 1970s (Bruner, 1979), spread rapidly across the island and is now found up to 2100 m in elevation (J.Y. Meyer, pers. obs.). *Zosterops lateralis* was introduced to Tahiti in 1937 (Guild, 1938), and is now the most abundant land bird on Tahiti and

Moorea (Thibault & Monnet, 1990) where it is found up to 2240 m (J.Y. Meyer, pers. obs.).

Species abundance

All sites were located adjacent to pre-existing vegetation plots established between 2005 and 2007. In each plot the diameter at breast height (1.3 m) of every stem was measured in two 10 m × 10 m quadrats on Tahiti and a single 20 m × 20 m quadrat on Moorea. We calculated the basal area of *M. calvescens* in order to provide an index of the level of invasion at each site (Table 1).

We estimated the relative abundance of each frugivore species at each of our sites using 7-min intensive point counts (Ralph *et al.*, 1993). Three point counts were carried out at each plot between 06:45 and 09:00 h on two separate visits between March and October of 2008. Fixed census points were located within 200 m of mist net stations, and were used consistently throughout the census period. The relative abundance of birds was calculated by comparing the number of birds seen or heard within 100 m for each point count. Differences in abundance between species were assessed using ANOVA followed by Tukey's honestly significant difference (HSD) test. Differences in abundance between islands were assessed separately for each species using a Student's *t*-test.

Characterizing diet

We captured birds using mist nets and collected faecal samples to determine diet directly. Mist nets were 2.5 m wide and 12 m long (mesh size 30 and 36 mm), raised to 50 cm off the ground on poles reaching 3 m in height. Birds were captured on 2–9 days per month from September 2007 to November 2008 (four nets per day) and again in 2010 from June to August (12 nets per day). Total net hours, calculated as the number of m² of mist net area covered multiplied by the number of hours of operation, amounted to 52,770 m² hours on 64 days of mist netting. Nets were opened between 05:30 and 06:00 h and closed either after a half day at 11:00 h or after a full day at 17:30 h. Nets were closed during periods of rain or high wind. All birds were fitted with a numbered aluminum

band and standard measurements taken (wing length, weight, fat deposits and reproductive status) (Pyle, 1997).

Each bird was placed in a thin breathable paper envelope inside a cloth bag until a faecal sample was produced or until 45 min had elapsed. All seeds were counted and identified using a dissecting microscope and a reference collection. We weighed each faecal sample, recorded the size and colour of each fruit, and quantified the proportion of faecal contents by category using a point sampling method. Samples were spread evenly across a Petri dish marked with a grid of 50 evenly distributed points. To obtain point estimates, we counted the number of points falling on each type of dietary item present in the sample (e.g. insects versus fruit). Arthropod remains were identified to the highest taxonomic category possible. All samples were stored in 90% ethanol.

Because *Pycnonotus cafer* was extremely difficult to capture using a mist net, samples were also collected indirectly from this species by identifying perch trees at each of our study sites and collecting droppings on dense vegetation under the trees. It is possible that there could be a systematic bias in dietary data obtained from perch sites compared to those collected directly. To account for this, we included sample type as a factor in our analysis linking bird diet to the density of *M. calvescens* at a site (described in detail below). This type of sample did not allow us to estimate recapture rates or to control for the independence of samples. *Pycnonotus cafer* lives in family groups and is territorial, especially during the breeding season (Kumar, 2004), and it is likely that faecal samples collected under the same perch tree are not independent because they represent replicates from a small group of individuals over time. Thus, dietary estimates for *P. cafer* may be less generalizable than for the other two species in this study.

Relating dietary contents to *Miconia calvescens* abundance

To determine whether bird dietary contents are related to *M. calvescens* density (measured using basal area), we analysed *Pycnonotus cafer* and *Zosterops lateralis* faecal samples separately. We excluded *Ptilinopus purpuratus* from this analysis because we lacked sufficient data from Tahiti to make adequate comparisons across all sites. Models for *Pycnonotus cafer* dietary contents included the presence and abundance of *M. calvescens* seeds, other alien seeds, and native seeds. Models for *Zosterops lateralis* dietary contents included the presence and abundance of *M. calvescens* seeds, other seeds (all species combined, excluding *M. calvescens*) and insects (calculated as the percentage of total points from point sampling). Covariates included in models of *Pycnonotus cafer* and *Zosterops lateralis* diets were *M. calvescens* basal area, island and period of capture, and the proportion of other dietary contents (calculated as the percentage of total hits using point sampling). We included both the island of capture and *M. calvescens* basal area in all saturated models because there are other factors that vary between islands beyond invasive tree abundance. Models that

contain both factors therefore indicate that both *M. calvescens* abundance and other factors not measured that vary between islands are important in explaining the variability in dietary contents.

We assessed whether the presence and proportion of dietary contents in faecal samples was related to *M. calvescens* basal area by constructing a zero-altered negative binomial (ZANB) generalized linear model (GLM hurdle model). Zero-altered hurdle models account for zero inflation caused by large numbers of plant species that are rare in bird diets and are therefore often absent. This modelling approach consists of two steps in which (1) a GLM with a binomial error structure examines the probability of a species occurring in a faecal sample (1 – presence) versus the probability of absence of the same species (0 – absence); and (2) a GLM with a negative binomial error structure examines the variation in numbers of seeds of a given plant species found in faecal samples where the plant was present (1 – present samples only). This method allows for the possibility that the mechanisms that determine presence and abundance can be different (Potts & Elith, 2006; Zuur *et al.*, 2009). In our case the quantity of each food item consumed by birds is a product of two separate decisions in which a bird decides whether to consume a plant (binomial probability of presence) followed by a decision about how many fruit of a given plant to consume (negative binomial count process).

Model selection was carried out using a backwards stepwise procedure starting with a saturated model. Least important factors were eliminated from the saturated model one at a time on the basis of Akaike's information criterion (AIC) until no more factors could be eliminated without deterioration in model fit (indicated by AIC values at least one point higher than the current model). All models were fit using R version 2.12 (R Development Core Team, 2010) with the 'pscl' package (Zeileis *et al.*, 2008; Jackman, 2011).

Native fruit consumption

To determine whether the consumption of native fruit varied by frugivore, we related the proportion of hits (using point sampling) of native fruit in each faecal sample to the island and period of capture (divided into three seasons, February–May, June–August, and September–November), the frugivore species, the proportion of alien fruit and insects (calculated as the percentage of total hits using point sampling), and the *M. calvescens* basal area at a site. Each analysis was performed using zero-altered hurdle models as described above.

Seed dispersal networks

Seed dispersal network properties are known to be sensitive to the exclusion of rare species (Blüthgen, 2010), and it is therefore important to verify whether dietary data accurately represent the links between species before the construction of networks. We used sample-based rarefaction to examine whether our sampling was sufficient to adequately characterize

the diets of birds on Tahiti and Moorea. We excluded the diet of *Ptilinopus purpuratus* on Tahiti from this analysis because we had limited samples from Tahiti. We used the incidence based nonparametric Chao coverage estimator which generates rarefaction curves based on the distribution of rare species (Colwell & Coddington, 1994). All rarefaction computations were performed using ESTIMATES version 8.2 (Colwell, 2005).

To assess whether network properties are altered on the highly invaded island of Tahiti compared to Moorea, we constructed seed dispersal networks for both islands using an interaction matrix with birds representing columns and plants representing rows. We constrained our networks to reflect differences in the relative abundance of our study species using estimates from point counts. Networks were built by using randomization to sample dietary data in numbers proportional to relative abundance for each species on each island. We defined the frequency of interaction as the number of faecal samples containing a given plant species in each network (Vázquez, 2005) instead of numbers of seeds because plants are highly variable in how many seeds are produced per fruit. Network properties were calculated for each of 1000 networks built using bootstrap sampling. For each iteration, we calculated seven unweighted network properties and one weighted network property, as well as two estimates of centrality for each plant species in the network (Table 2). Network properties were selected on the basis of relevance to prior research and their potential to guide the conservation of disturbed habitats using recommendations provided in Tylianakis *et al.* (2009). Unweighted properties consider only numbers of links between species whereas weighted properties incorporate both the presence and the frequency of interactions (Blüthgen *et al.*, 2008), and included R , N , $NODF$, R_p , R_n , I_n , I_a and L (see

Table 2 for definitions of each property). Nestedness (N) was calculated using the Nestedness Temperature Calculator in BINMATNEST (Rodríguez Gironés & Santamaría, 2006). This method re-arranges the matrix of rows (consumers) and columns (resources) to maximize nestedness, and then calculates deviations from the resulting matrix. The N metric produces values between 0 (high nestedness) and 100 (low nestedness). We also calculated one alternative measure of nestedness, the nestedness metric based on overlap and decreasing fill (NODF), which provides more reliable results compared to the N metric (Almeida-Neto *et al.*, 2008). NODF uses row and column marginal totals and paired overlaps in the presence and absence of links between species to calculate nestedness values which range between zero (low nestedness) and 100 (high nestedness) (Almeida-Neto *et al.*, 2008). The weighted property Evenness (E_2), based on the Shannon diversity index, follows the form (Blüthgen *et al.*, 2008):

$$E_2 = H_2 / \ln L$$

where L is the number of all links in the network and H_2 is the Shannon diversity index. In addition, we calculated two species-level properties to estimate the centrality of plant species. Measures of centrality quantify the importance of different nodes in the network on the basis of its position (Martín González *et al.*, 2010). We used closeness centrality (CC), which measures the proximity of a node to all other nodes (Martín González *et al.*, 2010), and betweenness centrality (BC), which evaluates the importance of each species as a connector to other parts of the network. Nodes with ($BC > 0$) connect areas of the network that would otherwise be isolated (Martín González *et al.*, 2010). In CC , the distance of a focal species i to all other species in the network is evaluated using

Table 2 Network properties included in analysis of seed dispersal networks on Tahiti and Moorea (see text for further details of each network metric).

Network metric	Property	Definition
R	Richness	Number of links in network
N	Nestedness	Describes the extent to which species that interact with specialists form a subset of the species that interact with generalists
$NODF$	Weighted nestedness	An alternative weighted quantitative metric for nestedness
R_p	Richness plants	Number of plant species in network
R_n	Richness natives	Number of native plant species in network
I_n	Interactions (native)	Percent of total interactions including native species
I_a	Interactions (alien)	Percent of total interactions including alien species
L	Linkage density	Number of links per species (R /number of species in network)
E_2	Interaction evenness	Based on the Shannon diversity index, describes the heterogeneity of associations between species based on interaction frequencies (see text)
CC_a	Closeness centrality (alien)	Describes how close a focal species is to all other species in the network (all alien species)
CC_n	Closeness centrality (native)	Describes how close a focal species is to all other species in the network (all native species)
BC_a	Betweenness centrality (alien)	Describes the importance of a species as a connector to different parts of the network. $BC > 0$ indicates species that act as connectors (alien species only)
BC_n	Betweenness centrality (native)	Describes the importance of a species as a connector to different parts of the network. $BC > 0$ indicates species that act as connectors (native species only)

Nestedness (N) was calculated using the Nestedness Temperature Calculator in BINMATNEST (Rodríguez Gironés & Santamaría, 2006).

NODF is a nestedness metric based on overlap and decreasing fill (Almeida-Neto *et al.*, 2008).

$$CC_i = \sum_{j=1, i \neq j}^n \frac{d_{ij}}{n-1}$$

where n is the number of species and d_{ij} is the shortest distance between species i and j measured in number of links (Martín González *et al.*, 2010). BC of a species i is the fraction of shortest paths which pass through that species in the network and is evaluated using

$$BC_i = 2 \sum_{j < i, i \neq j} \frac{g_{jk}(i)/g_{jk}}{(n-1)(n-2)}$$

where n is the number of species in the network, g_{ik} is the number of shortest paths linking any two species, and $g_{ik}(i)$ is the number of those shortest paths that pass through i (Martín González *et al.*, 2010). Because the number of frugivores was very low, CC and BC values are not meaningful for birds, and only plant centrality values were considered. In our analysis, we grouped plant species by status (alien versus native) in order to determine how alien and native plant centrality values varied between islands. All network calculations were performed using the R bipartite package (Dormann *et al.*, 2009) and all island comparisons were made using a Wilcoxon rank sum test.

RESULTS

Species abundance

Miconia calvescens basal area varied from 0.4 m² ha⁻¹ on Moorea to 21.92 m² ha⁻¹ at the site with highest abundance on Tahiti (Table 1). Bird abundance varied significantly by species (birds seen or heard per point count, $F = 25.419$, $P < 0.0001$; Fig. 1) and *Zosterops lateralis* was significantly more abundant (Tukey's HSD $P < 0.0001$) at our sites than *Pycnonotus cafer* or *Ptilinopus purpuratus*. *Ptilinopus purpuratus* was more abundant on Moorea (Student's t -test $P = 0.027$)

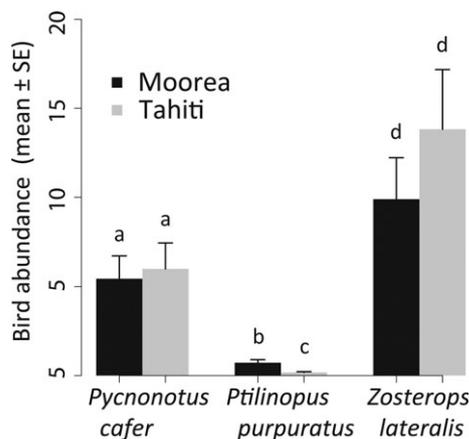


Figure 1 Relative abundance of the three frugivores (*Ptilinopus purpuratus*, *Pycnonotus cafer* and *Zosterops lateralis*) on Moorea and Tahiti. Abundance is calculated as all birds seen or heard during 7-min point counts. Different letters indicate significant differences (see text for details).

compared to Tahiti, while the abundances of *Zosterops lateralis* ($P = 0.21$) and *Pycnonotus cafer* ($P = 0.83$) were similar on both islands.

Characterizing diet

We collected a total of 1178 faecal samples from individuals of the three species of frugivore during the study period (Table 1). Recapture rates varied by species, with 0% recapture for *Pycnonotus cafer*, 5.8% for *Zosterops lateralis* and 20.1% for *Ptilinopus purpuratus*. Most samples from *Pycnonotus cafer* were collected from under perches ($n = 427$), whereas samples from *Zosterops lateralis* and *Ptilinopus purpuratus* were collected from captured birds.

Ptilinopus purpuratus was the most frugivorous of the three species, with fruit parts and seeds found in 99% of faecal samples. Fruit was found in 94.7% of *Pycnonotus cafer* faecal samples and 43.3% of *Zosterops lateralis* samples. Other dietary items included arthropod remains, flower parts and vegetative material. All three species consumed both native and alien fruits, though in varying quantities (Table 3). The colour and size of introduced fruits in bird diets were similar to those of native fruits (see Appendix S1 in Supporting Information), and black fruit comprised roughly 30% of fruit (both native and introduced) while red/orange fruit comprised roughly 20% and green fruit roughly 20%.

Miconia calvescens was the most common item in the diet of all three frugivores, and was present in 68.1% of all *Pycnonotus cafer* faecal samples, 38.3% of *Zosterops lateralis* samples and 44.6% of *Ptilinopus purpuratus* samples (Table 3). *Miconia calvescens* also vastly outnumbered any other species in terms of the numbers of seeds consumed, accounting for 76.8% of all seeds in faecal samples ($n = 215,904$).

Relating dietary contents to *Miconia calvescens* abundance

Miconia calvescens basal area was related to the abundance (hurdle models, $P = 0.0002$) but not the presence ($P = 0.836$, Appendix S2b) of native seeds in *Pycnonotus cafer* faecal samples (Fig. 2a). *Miconia calvescens* seeds were more abundant ($P = 0.016$) but present in equal numbers ($P = 0.781$) at sites with higher basal area, and alien seed presence and abundance were unaffected by basal area. In *Zosterops lateralis* diets, *M. calvescens* basal area was related to both fruit and insects (Fig. 2b, Appendix S2c). Insects were present more often ($P = 0.015$) but were less abundant when present ($P = 0.0004$) at sites with higher basal area. *Miconia calvescens* seeds were equally abundant ($P = 0.344$) but were present more often ($P = 0.02$) at sites with higher basal area.

The consumption of all fruit by *Pycnonotus cafer* was influenced by the island of capture. The consumption of other fruit by *Zosterops lateralis* was influenced by the island of capture, but not the consumption of *M. calvescens* or insects. Island was not related to *M. calvescens* or insect consumption in *Zosterops lateralis*.

Table 3 Composition of diets of three frugivores on Moorea and Tahiti. % represents the percentage of total faecal samples containing seeds. Mean seeds is the average number of seeds per faecal sample. Native species consumed only by *Ptilinopus purpuratus* are highlighted in bold. Rows highlighted in grey represent the total number of plant species in each category.

Plant species	<i>Pycnonotus cafer</i>				<i>Ptilinopus purpuratus</i>		<i>Zosterops lateralis</i>			
	Moorea		Tahiti		Moorea		Moorea		Tahiti	
	%	Mean seeds	%	Mean seeds	%	Mean seeds	%	Mean seeds	%	Mean seeds
Introduced	5	7	5	3	5	13	3	5	3	5
<i>Miconia calvenscens</i>	14.29	31.19	90.91	148.92	43.65	485.54	24.59	10.54	66.1	48.24
<i>Rubus rosifolius</i>	5.44	0.41	6.67	2.2	0	0	0.54	0.06	11.86	2.67
<i>Cecropia peltata</i>	2.72	0.09	24.55	3.85	0	0	0	0	0.56	0.01
<i>Schinus terebenthifolius</i>	0	0	1.52	0.02	0	0	0	0	1.69	0.04
<i>Cananga odorata</i>	0	0	0	0	3.05	0	0	0	0	0
<i>Psidium guajava</i>	0	0	0.3	0.02	0.51	0.18	0	0	0	0
<i>Passiflora suberosa</i>	0.68	0.01	0.3	0	0.51	0.06	0	0	0	0
<i>Lantana camara</i>	16.33	0.33	7.27	0.12	2.03	0.26	2.43	0.05	1.69	0.02
<i>Pseudelephantopus spicatus</i>	0	0	0	0	0.51	0.01	0	0	0	0
<i>Oxalis corniculata</i>	0	0	0.3	0.02	0	0	0	0	0	0
Native	5	3	13	1	3	1	3	1	1	1
<i>Tarenna sambucina</i>	38.78	3.53	0	0	56.35	81.08	0	0	0	0
<i>Cyclophyllum barbatum</i>	0.68	0.01	0	0	15.23	0.36	0	0	0	0
<i>Wikstroemia foetida</i>	0	0	0	0	8.12	0.42	0	0	0	0
<i>Rhus taitensis</i>	5.44	0.08	4.55	0.07	0.51	0.04	1.35	0.01	2.82	0.13
<i>Freycinetia impavida</i>	2.04	3.72	0	0	18.27	103.75	0.27	0.05	0	0
<i>Meryta lanceolata</i>	0	0	0	0	3.05	0.42	0	0	0	0
<i>Ficus prolixa</i>	0	0	1.82	1.6	2.54	19.36	0	0	0	0
<i>Ixora mooreensis</i>	0	0	0	0	3.05	0.09	0	0	0	0
<i>Xylosma suaveolens</i>	0	0	0	0	1.52	2.07	0	0	0	0
<i>Fagraea berteriana</i>	1.36	0.03	0	0	0.51	0.79	1.08	0.09	0	0
<i>Coprosma taitensis</i>	0	0	0.61	0.02	0	0	0	0	0	0
<i>Premna serratifolia</i>	0	0	0	0	1.02	0.04	0	0	0	0
<i>Melastoma malabathricum</i>	0	0	0	0	0.51	0.01	0	0	0	0
<i>Pittosporum taitense</i>	0	0	0	0	0	0	0.27	0	0	0
<i>Macaranga attenuata</i>	0	0	0	0	0.51	0.01	0	0	0	0
Unknown	2.04	0.04	1.82	0.85	9.64	20.57	1.08	0.01	1.69	0.07

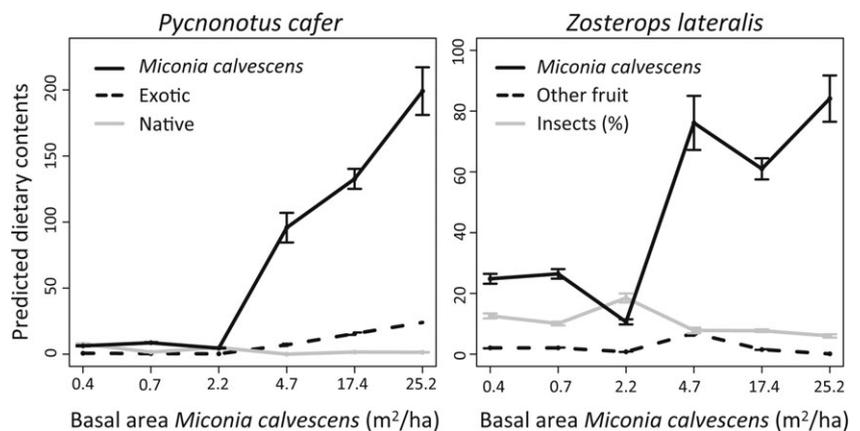


Figure 2 Predicted dietary contents (number of seeds or % insects \pm SE) of (a) *Pycnonotus cafer*, and (b) *Zosterops lateralis*, as a function of *Miconia calvenscens* basal area. Predictions are from best-fitting hurdle models for the relationship between diet and *M. calvenscens* basal area.

The season of capture predicted dietary contents for *Zosterops lateralis* but not *Pycnonotus cafer* (Appendix S2). Season influenced the abundance but not the presence of other fruit in *Zosterops lateralis* diets, and other fruit were signifi-

cantly more abundant ($P = 0.024$) during the months of June through August (Fig. 2b). *Miconia calvenscens* was present less often ($P = 0.0003$) but was more abundant ($P = 0.005$) during the months of September through November, while insects

were both more abundant ($P < 0.0001$) and more frequent ($P < 0.0001$) from March through May.

Pycnonotus cafer samples collected under perches contained alien seeds more often (present in 151 samples or 35.36%, $P = 0.023$) but in similar abundance ($P = 0.068$) compared to samples collected from captured birds. Native seeds were only present in a single sample collected via direct capture (3.57%), compared to 87 samples collected under perches (20.03%, $P = 0.036$). Sample type had no impact on the presence or abundance of *M. calvescens* seeds.

Native and alien plant consumption

Ptilinopus purpuratus consumed more native than alien plants on Moorea, and natives were present in 76.6% of samples compared to 49.3% for introduced species. Native fruit were more likely to be present in *Ptilinopus purpuratus* samples (present in 75.5% of samples, hurdle models, $P < 0.0001$, $n = 204$) than *Pycnonotus cafer* (present in 19.3% of samples, $P = 0.47$, $n = 455$) or *Zosterops lateralis* samples (present in 2.9% of samples, $P = 0.008$, $n = 519$). *Ptilinopus purpuratus* consumed higher numbers of native seeds per faecal sample on Moorea (mean seed abundance \pm SD = 204.85 \pm 432.31, $n = 202$) compared to *Pycnonotus cafer* (7.56 \pm 37.73, $n = 131$) and *Zosterops lateralis* (0.12 \pm 1.28, $n = 344$). *Ptilinopus purpuratus* also consumed the largest total number of

plant species ($n = 29$) and the highest number of native species ($n = 12$), including seven species which were not consumed by other frugivores. *Pycnonotus cafer* consumed a total of 10 species while *Zosterops lateralis* consumed only six (Table 3). Both the presence and proportion of samples of native fruit varied by season, with the highest consumption recorded during the period from June to August (Appendix S2a).

Seed dispersal networks

Introduced species were well infiltrated into seed dispersal networks on both islands (Fig. 3), but were more dominant on Tahiti where they accounted for a total of $94.81 \pm 2.99\%$ (mean \pm SE) of all interactions (all network properties can be found in Table 4). Rarefaction indicated that diets were well characterized for *Ptilinopus purpuratus* on Moorea and for *Pycnonotus cafer* and *Zosterops lateralis* on both islands (Appendix S3). *Ptilinopus purpuratus* played a minor role in the seed dispersal network on Tahiti due to reduced population size. Networks contained more total links, greater numbers of plant species, and more native species on Moorea compared to Tahiti. On average, birds were linked to a greater number of plant species, as well as to more native plants on Moorea, and evenness was higher. Nestedness values were not consistent between metrics. The N metric produced higher nestedness for Tahiti than for Moorea, whereas the NODF

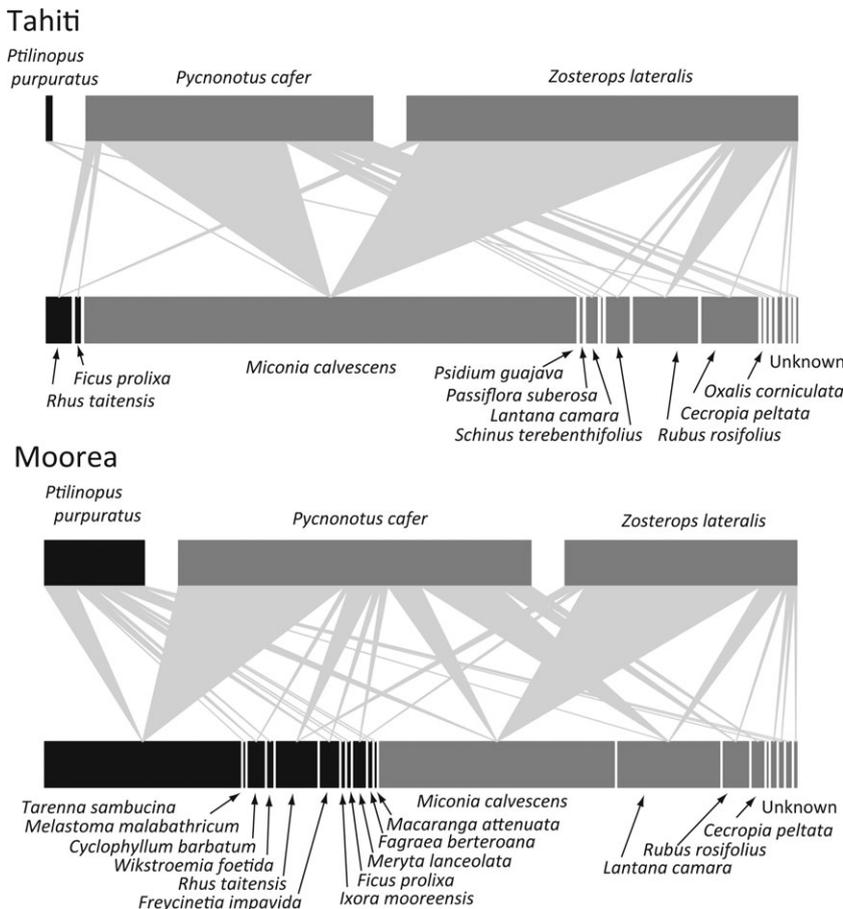


Figure 3 Seed dispersal networks for Tahiti and Moorea taken from simulated networks integrating the relative population of frugivores with dietary information. Native species are represented in black and alien species in grey. Birds are shown on the upper bar, plants on the lower bar, and grey lines between them represent the presence of a link between two species. The width of each bar represents the proportion of all interactions in the network represented by that species. The frequency of interactions is calculated based on the presence of a plant in a faecal sample.

Table 4 Network properties for Moorea and Tahiti represented as means with 95% confidence intervals (CI) and *P*-values from Wilcoxon signed rank test for differences in each property between island. Betweenness centrality (BC) values represent the number and percentage of all plant species that had a BC > 0.

	Moorea	CI	Tahiti	CI	<i>P</i> -value
<i>R</i>	35.21	(33.03–37.39)	24.72	(23.09–26.26)	< 0.0001
<i>N</i>	36.37	(34.11–38.62)	14.59	(13.67–15.48)	< 0.0001
NODF	12.91	(12.11–13.71)	8.65	(8.11–9.19)	< 0.0001
<i>R_p</i>	23.95	(22.46–25.43)	16.68	(15.63–17.70)	< 0.0001
<i>R_n</i>	11.34	(10.64–12.05)	2.98	(2.79–3.17)	< 0.0001
<i>I_n</i>	45.59	(39.95–45.23)	4.98	(3.73–4.22)	< 0.0001
<i>I_a</i>	55.34	(51.91–58.77)	94.82	(88.94–100)	< 0.0001
<i>L</i>	3.11	(2.91–3.29)	2.33	(2.19–2.48)	< 0.0001
<i>E₂</i>	0.67	(0.63–0.72)	0.54	(0.50–0.57)	< 0.0001
CC _n	0.032	(0.0316–0.0327)	0.012	(0.012–0.0124)	< 0.0001
CC _a	0.0274	(0.02769–0.0279)	0.0473	(0.0463–0.0482)	< 0.0001
BC _n	4–5	9.5–11.9%	1	2.30%	
BC _a	3–4	7.1–9.5%	4–5	9.5–11.9%	

metric showed the opposite pattern. Average CC centrality measures were similar for alien and native plant species on Moorea, and the BC metric showed similar numbers of native and alien species with BC values greater than zero. However, on Tahiti, average values of CC were more than three times higher for alien species compared to native species. Likewise, only a single native species had a BC > 0, while 4–5 alien species had BC > 0.

DISCUSSION

Relating dietary contents to *Miconia calvescens* abundance

In this study, birds responded to the abundance of *M. calvescens* at a site by increasing their consumption of its fruit. *Pycnonotus cafer* consumed fewer native fruits at more invaded sites, and *Zosterops lateralis* consumed fewer insects and other fruits. Alien fruit consumption by *Pycnonotus cafer* was unrelated to *M. calvescens* basal area, probably because the most abundant introduced species in *Pycnonotus cafer* diets were *Lantana camara* and *Cecropia peltata*, two species that are unlikely to be related to the presence of *M. calvescens* because both are shade-intolerant pioneer plants. These results are consistent with many other studies that have documented that the abundance of fruit influences consumption by frugivores at multiple spatial scales (Levey, 1988; Carlo *et al.*, 2004; Ortiz-Pulido *et al.*, 2007; Blendinger *et al.*, 2008; Gleditsch & Carlo, 2010). The negative relationship between *M. calvescens* abundance and other dietary contents suggests dietary switching (Carnicer *et al.*, 2009), in which the choice to consume one resource leads to decreased consumption of other fruit or other kinds of resources (Saracco *et al.*, 2005; Blendinger & Villegas, 2011).

Zosterops lateralis consumed almost no native fruit, but switched their diets from larger quantities of insects to more *M. calvescens* at sites with highest basal area. *Zosterops lateralis* ate more *M. calvescens* on Tahiti, but this pattern was not constant through time. Increases in fruit consumption and

corresponding decreases in insect consumption on both islands during the rainy season are probably linked to seasonal patterns in breeding, moulting and raising young, and spatial and temporal patterns of resource use may reflect patterns of availability of both insects and fruit (Carnicer *et al.*, 2009).

Pycnonotus cafer dietary contents were not affected by the period of capture, which could be because the majority of faecal samples were collected under perch sites where we could not determine the exact date of consumption. Faecal samples collected under perches contained greater numbers of native fruit on Moorea and smaller numbers of alien fruit on Tahiti than those collected directly. While dietary results for this species should be interpreted with caution, we believe that differences in the contents of samples collected under perches are caused primarily by our inability to verify the precise date of deposition.

Native fruit consumption

Ptilinopus purpuratus consumed more native fruit than either alien frugivore. Shared evolutionary history resulting in the buildup of complementary traits that enable plants and animals to interact has been proposed to explain why species that have evolved in the same environment might interact with each other more frequently than expected by chance (Thompson, 2006). For example, traits such as fruit colour and shape can converge among species that are dispersed by similar frugivores (Bascompte & Jordano, 2007). In our study, similar colour, size and shape among native fruit may provide cues to endemic frugivores that help maintain links between native species. While we did not study the effects of colour on choice in our birds, the colour and size of fruits found in frugivore diets were similar between introduced and alien fruits, suggesting that the cues birds are using to choose fruits are consistent regardless of plant origin (Appendix S1).

On Moorea, nearly half of all *Ptilinopus purpuratus* faecal samples contained seeds of alien species, the majority of which were *M. calvescens*. Integration of alien fruit into the diets of native frugivores has occurred in a variety of other habitats

(Richardson *et al.*, 2000). In our study, the low diversity of native frugivores, coupled with the low potential of alien frugivores to disperse native fruit, indicates that shifts in the diet of the *Ptilinopus purpuratus* could have larger consequences than in other locations. These results are consistent with findings from pollinator communities on islands elsewhere that have found endemic 'super-generalists' pollinators (Olesen *et al.*, 2002) and flying foxes (*Pteropus* spp.) that act as 'strong interactors' (Cox *et al.*, 1991). In both cases, low biodiversity in animal communities leads to a greater dependence of plants on a smaller number of animal species for pollination and dispersal. The super-generalist nature of *Ptilinopus purpuratus* interactions with plants has important conservation implications because in this study, at least seven species of native plants do not have alternative dispersers if the bird becomes rare, changes its diet, or goes extinct.

We did not assess whether birds are effective dispersers of the seeds they consume (Schupp, 1993). However, in a related study we compared germination rates for digested seeds to hand-cleaned seeds in three species of native plants. Germination of digested and undigested seeds was similar for two species and 10% better for the native tree *Tarennia sambucina* after digestion by *Ptilinopus purpuratus* (Spotswood, 2011), suggesting that endemic frugivores are capable of dispersing native seeds that remain viable. In addition, we compared germination rates for *M. calvescens* seeds, and found slight improvements in germination after digestion by the *Pycnonotus cafer* and in hand-cleaned seeds compared to seeds digested by *Zosterops lateralis* and *Ptilinopus purpuratus*. However, germination rates were > 80% for all groups, demonstrating that all frugivores are capable of dispersing viable seeds (Spotswood, 2011).

Alien frugivores showed low potential to act as surrogate dispersers of native fruits, and the dispersal of native plants is therefore likely to depend disproportionately on *Ptilinopus purpuratus* into the future. Other studies have also found that introduced frugivores often show poor potential to replace natives. In Mauritius, red-whiskered bulbuls (*Pycnonotus jocosus*) consumed the fruit of only two native species compared to eight introduced (Linnebjerg *et al.*, 2010). Introduced white-eyes (genus *Zosterops*) consumed mostly introduced fruit in Hawaii (Foster & Robinson, 2007), while in the Bonin Islands, native and introduced white-eyes had similar diets (Kawakami *et al.*, 2009). The dominance of links between introduced species on Tahiti suggests that facilitation between introduced frugivores and alien plants could be occurring. These results are suggestive of an invasional meltdown in which reciprocally beneficial interactions between co-occurring introduced species trigger cascades of changes to native ecosystems (Simberloff & Von Holle, 1999).

Seed dispersal networks

This study demonstrates that it is possible to evaluate how invasive species influence community-wide patterns of interaction between plants and frugivores using seed dispersal

network analysis. Variation in the abundance of *M. calvescens* is only one of the potential causes of differences in network patterns on Moorea and Tahiti. Several of the models that explained the greatest variation in the diets of *Pycnonotus cafer* and *Zosterops lateralis* also included the island of capture as a covariate, indicating that factors beyond the abundance of *M. calvescens* also contributed to dietary differences. The larger area of the island of Tahiti could explain some of this variation (Whittaker & Fernández-Palacios, 2007), while other biotic and abiotic factors that were not measured could also be important. Nevertheless, the relationships between *M. calvescens* abundance and dietary contents strongly suggest that local abundance is a dominant factor influencing network properties.

Measures of network richness, including the total number of links and linkage density, were higher on Moorea due to the larger number of plants present in the diets of birds. Additionally, the network on Tahiti was dominated by invasive species, while the network on Moorea contained more links and a greater frequency of interactions between birds and native plants. These differences were caused by the very low abundance of *Ptilinopus purpuratus* on Tahiti, and by differences in diets of the two introduced frugivores due to the greater abundance of *M. calvescens* on Tahiti. The ecological impact of alterations in network structure in disturbed habitats has not been well studied empirically (Tylianakis *et al.*, 2009), but theoretical literature suggests the potential for changes in ecosystem stability and resilience (Bascompte & Jordano, 2007; Tylianakis *et al.*, 2009). In our study, the smaller number of links to fewer plants and lower linkage density on Tahiti reflected a loss of links between birds and plants, which could translate to a reduced dispersal potential for native plants on Tahiti.

Lower network evenness on Tahiti was caused by differences in the relative frequency of interactions. On Tahiti, networks were dominated by a few strongly linked species while on Moorea, interactions were more evenly distributed across species. On Tahiti, links were concentrated among introduced species, and 75% of all interactions were between birds and *M. calvescens* compared to 35% of interactions on Moorea. Similar changes in interaction evenness were also documented in a disturbed host-parasitoid food web where interaction evenness was lower due to the dominance of a single interaction (Tylianakis *et al.*, 2007). While it is unclear whether increased evenness promotes stability (Tylianakis *et al.*, 2009), our results show that dispersal services on Tahiti are concentrated on a smaller proportion of the total community of available fruit.

Network nestedness comparisons between islands were inconclusive because the two metrics yielded opposing results. The N metric is known to produce unreliably high estimates of nestedness in simulated matrices where values should be very low, which could have occurred in this study given the small size of networks (Almeida-Neto *et al.*, 2008). While matrix shape, size and fill should ideally not influence nestedness values, Almeida-Neto *et al.* (2008) found correlations between

matrix fill for both the N metric and NODF, and correlations between matrix size and nestedness for the N metric. The relationship between N and matrix size was particularly pronounced for matrices with fewer than 500 cells, which tended to produce high values of nestedness. Our networks contained 126 cells and were on average 20–40% filled, with higher fill on Moorea, and these structural properties of the matrices could be partially responsible for differences in estimated nestedness values. These results highlight the need for careful interpretation of nestedness metrics, given the potential for different metrics to produce different results.

Measures of centrality indicated that on Moorea, both native and alien plant species are important to the cohesiveness of the network and have the potential to affect many other species. However, on Tahiti, alien species act as central connectors, while native species had very low CC values and only a single species with $BC > 0$. The centrality measure CC was low on both islands compared to other studies of pollinator networks (Martín González *et al.*, 2010), probably reflecting the extreme simplicity of these networks. Only the most generalized species in a network will typically have BC values greater than zero, usually indicating that a species is connected with almost half of the other species in the network. High BC and CC values could indicate the presence of keystone species, which have the potential to impact a network more than most species, and whose extinction could cause cascades of linked extinctions (Estrada, 2007; Martín González *et al.*, 2010). In our study, connector species on Moorea included both native and alien species, indicating that native species remain important in the functioning of the network as a whole. Despite the presence of native plants in networks on Tahiti, only alien species were highly central and were primarily responsible for linking other alien species to the network.

CONCLUSIONS

This study demonstrates that the use of networks can be helpful in uncovering how patterns of seed dispersal are affected by invasive plants. Our results revealed that on the island of Tahiti, which is highly invaded by *M. calvescens*, networks were dominated by interactions between alien plants and birds. In addition, *Ptilinopus purpuratus*, the sole endemic frugivore in our systems was responsible for a disproportionate fraction of interactions with native plants, several of which relied on it entirely for seed dispersal. A focus on a subset of the community of interactions might have missed the importance of *Ptilinopus purpuratus*, which is much less abundant than *Zosterops lateralis* and *Pycnonotus cafer*, but is important because of the strength of its interactions with native plants. The presence of a single dominant fleshy-fruited invasive plant and the low diversity of flora and fauna on remote oceanic islands made this system ideally suited for the use of networks to understand how invasions influence community-wide dispersal patterns. Future studies in more complicated habitats could provide additional insight into the generalizability of our findings.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Fruit colour and size traits for species found in diets of the three frugivores on Moorea and Tahiti.

Appendix S2 Best-fitting zero-altered hurdle models for (a) the proportion of native fruit in the diets of the three frugivores, (b) consumption of exotic fruit, *Miconia calvescens*, and native fruit by *Pycnonotus cafer*, and (c) consumption of *M. calvescens*, other fruit, and insects by *Zosterops lateralis*.

Appendix S3 Rarefaction curves for the total and native richness of diets of *Pycnonotus cafer* and *Zosterops lateralis* on Tahiti and Moorea and *Ptilinopus purpuratus* on Moorea.

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