

RESEARCH ARTICLE

Seasonal variation in impact of non-native species on tropical seed dispersal networks

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Abstract

1. Invasive non-native species can alter animal-mediated seed dispersal interactions and ultimately affect the stability of recipient communities. The degree of such disturbances, however, is highly variable and depends on several factors, two of which have received little attention: the relative timing of native and non-native fruiting phenologies, and the associated variation in relative resource availability across the fruiting period. Both are likely to alter plant–seed disperser interactions threatened by biological invasions.
2. Here we investigated the impact of plant invasions on the seasonal dynamics of frugivory and seed dispersal networks across a large-scale experimental setup and a plant invasion gradient on a tropical island. We recorded fruit and frugivore abundances, and plant–frugivore interactions across eight inselbergs (i.e. rocky outcrops) with different levels of plant invasion during 10 months on the island of Mahé, Seychelles. By combining four sampling methods of plant–frugivore interactions we constructed quantitative seed dispersal networks at all sites across two 5-month seasons: the on-peak and off-peak fruiting season.
3. Our findings showed that, by fruiting mostly synchronously with natives, non-native plants compete with natives for dispersal services, predominantly carried out by native frugivores. Variation in native seed dispersal was driven by plant invasion and seasonality. Specifically, native seed dispersal declined with the degree of invasion; dispersal frequency increased with fruit abundance more strongly during the off-peak fruiting season; and networks became increasingly specialised during off-peak. These results indicated that during the main fruiting peak seed dispersal services were saturated, which likely intensified the competition between native and non-native fruits. When resources were scarce during off-peak fruiting season, native and non-native frugivores were more selective in their fruit choice at sites dominated by non-native plants.

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4. We showed that native plant and frugivore populations and native seed dispersal interactions were more vulnerable in invaded plant communities, where non-native plants compete with natives for dispersal services potentially reducing native recruitment. As invasive non-native plants dominate many ecosystems world-wide, particularly on islands, our findings showed that controlling plant invasions in vulnerable native communities can be critical to maintain native ecosystem functions and biodiversity.

KEYWORDS

frugivory, fruiting phenology, invasion ecology, invasive alien species, mutualisms, oceanic islands, seed dispersal networks

1 | INTRODUCTION

Mutualistic interactions, such as those between plants and their seed dispersers, are vital for maintaining the structure, stability and functioning of ecological communities (Bascompte & Jordano, 2014). Invasive non-native species can alter the composition of recipient communities (Hejda et al., 2009; Levine et al., 2003) with effects on diversity and on the intricate network of biotic interactions that sustain ecological communities (Heleno, 2020; Vilà et al., 2011). For instance, the introduction of non-native frugivores can change the recruitment patterns of native plant species both directly, e.g. by dispersing the seeds of non-native plants (Mandon-Dalger et al., 2004), or indirectly, e.g. by reducing the services provided by native seed dispersers (Traveset & Richardson, 2014).

The magnitude of such disturbances is highly variable and is contingent on multiple factors. There is increasing evidence that the relative timing of non-native and native fruiting phenologies plays a critical role in the rate at which non-native species invade native communities as it may determine the potential for diverting seed dispersal services (Heleno, 2020). For example, when non-native species fruit synchronously with natives they can directly compete for seed dispersal services. This competition can divert frugivore visits away from native plants (Heleno, 2020; Kueffer et al., 2009), thereby reducing native seed rain and recruitment (Rowles & O'Dowd, 2009; Traveset et al., 2012). Conversely, non-native plant species with phenologies that exploit unoccupied temporal niches in native communities (i.e. those that fruit outside of the main native fruiting season), will likely attract a high number of seed dispersers which might facilitate the invasion (Heleno, Olesen, et al., 2013; Williams & Karl, 1996). The time of fruiting can also affect the assembly of available seed dispersers and even the main direction of dispersal (González-Varo et al., 2021). However, to date, few studies evaluated the importance of (a-) synchronous fruiting phenology on seed dispersal services and recruitment patterns. Furthermore, most of our knowledge on the effects of non-native species on seed dispersal interactions is derived from static (i.e. temporally aggregated) seed dispersal interaction networks (e.g. Heleno, Olesen, et al., 2013; Heleno, Ramos, et al., 2013; Vizentin-Bugoni et al., 2019), and it remains uncertain

how plant–seed disperser interactions are affected by the variable pressure of biological invasions under natural conditions.

Species interactions vary considerably across multiple time-scales (CaraDonna et al., 2021; Costa et al., 2020; Trøjelsgaard & Olesen, 2016). Within a season, the addition or loss of interactions will be determined by which species temporarily co-occur, along with species relative abundance and the availability of suitable resources (phenological matching; CaraDonna et al., 2021; Olesen et al., 2010; Vázquez et al., 2009). For instance, given that frugivores show high plasticity in their foraging behaviour and fruit preferences (Carnicer et al., 2009), seed removal rates and the number and identity of plant–frugivore interactions, strongly depend on the fruiting neighbourhood (Albrecht et al., 2015; Carlo & Morales, 2008; Rumeu et al., 2019). This temporal variation in the identity and strength of interactions arises even in tropical ecosystems (e.g. Kaiser-Bunbury et al., 2014; Ramos-Robles et al., 2016), where seasonality is less marked than in temperate regions. In this context, the analysis of aggregated networks that span several seasons cannot fully capture the dynamics of interactions and is likely to provide an incomplete overview of the seasonal effects of biological invasions on species interactions and community dynamics (Arroyo-Correa et al., 2020). Therefore, explicitly incorporating the temporal dimension, is likely very important to understanding how non-native species integrate and affect native seed dispersal networks.

Here we investigated the impact of plant invasions on the seasonal dynamics of seed dispersal function and networks across a large-scale experimental setup and a plant invasion gradient on a tropical island. We primarily focus on the direct effects of plant invasion on native plant and frugivore communities and their interactions, but also explore indirect effects mediated through native and non-native frugivores. We collected data on fruit and frugivore abundances and feeding interactions over time to address the following questions:

1. How does the proportion of non-native fleshy fruits alter seed dispersal frequency of native plants, and do these effects differ between seasons?

2. How do seasonality and the level of plant invasion affect the structure of seed dispersal networks and determine the roles of native and non-native frugivores?

Given the tropical climate and relatively small size of the island and the lack of migratory bird species in the frugivore community, we anticipated little changes in the frugivore assemblages between seasons. We, therefore, predicted that both fruit traits of non-native plants and relative densities of fruits of native and non-native plants are primary drivers of changes in frugivore movement and foraging behaviour and that these drivers differ between seasons. Specifically, we expected that non-native plants fruiting outside the main fruiting period have a higher probability of attracting seed dispersers (Muñoz & Ackerman, 2013) and that those non-natives fruiting alongside with native plants, both inside and outside the main season, will compete with, and divert seed dispersal services away from native plants (Heleno, Ramos, et al., 2013; Kueffer et al., 2009). These indirect effects between native and non-native plants could equally be mediated through native and non-native frugivores. Finally, we predicted strong temporal variation in plant–frugivore interactions as a result of changes in the fruit availability and plant community composition (Arroyo-Correa et al., 2020; CaraDonna et al., 2021), with more links, and greater diversity and overlap of plant–frugivore interactions during the fruiting peak (Albrecht et al., 2015).

2 | MATERIALS AND METHODS

2.1 | Study system

The study was carried out on eight inselbergs (steep-sided granitic rock outcrops) of ca. 1 ha on Mahé, the largest granitic island of the Seychelles archipelago, Indian Ocean (4°40'S, 55°26'E, 154 km², 900 m a.s.l.; Figure S1). Mahé has a tropical climate (Walsh, 1984) characterised by a wet and warm NW monsoon season from December to March, corresponding to the peak of the fruiting period on the inselbergs, and a drier and cooler SE trade winds season from May to October, leading to a marked two-seasonal dynamic. All study sites are surrounded by a similar forest matrix of degraded vegetation dominated by non-native species composed of old timber and cinnamon plantations (Kueffer et al., 2007; Kueffer & Kaiser-Bunbury, 2014). Inselberg plant communities are composed of woody shrubs and small trees, with an average canopy height of 1–2 m and a few trees that grow to 4–5 m (Kaiser-Bunbury et al., 2011). Inselberg vegetation is the last stronghold of many endemic plant species across the island with only a few dominant non-native plants, particularly *Cinnamomum verum* (Fleischmann, 1996; Kueffer et al., 2007). Likewise, introduced birds such as the Indian Mynah *Acridotheres tristis*, the Malagasy Turtle-Dove *Streptopelia picturata*, the Zebra

dove *Geopelia striata* and the Madagascar Fody *Foudia madagascariensis* are well established across the island.

We surveyed plant and frugivore species phenology, abundance and their interactions on inselbergs with different levels of plant invasion. Between 2011 and 2012, all non-native plants were removed from four inselbergs to restore plant communities, while the other four inselbergs were left with both native and non-native species (Kaiser-Bunbury et al., 2017). Intermittent maintenance of the 'restored' sites resulted in re-invasion and the arrival of new non-native plant species, mainly *Clidemia hirta* and *C. verum* (pers. obs.), leading to different levels of invasion. We measured the invasion level of the sites by calculating two indices: the ratio of non-native to total plant individuals across the whole study period (proportion of non-native plants, Appendix S1), and the ratio of non-native to total ripe fruits per month (proportion of non-native fruits). Please see Appendix S1 for further details on how plant abundance (individuals) was recorded.

2.2 | Fruit and frugivore abundances and phenology

We collected data on fruit (monthly) and frugivore (2 days/month) abundances between September 2018 and August 2019 across all eight study sites. Fruit abundances were recorded along fixed transects (Table S2), and we used standardised point-counts to estimate frugivorous bird and bat *Pteropus seychellensis* abundances by recording all individuals detected within a 50 m radius, in which detectability is high due to open inselberg vegetation. Point counts were always carried out by the same observer, the vegetation did not show any seasonal changes that may affect detection probability and the number of potential disperser species on the island is relatively low, which facilitated species identification. We recorded the abundance of the Seychelles skink *Trachylepis seychellensis*, the only non-flying species recorded feeding on fruit, through direct observations along transects (see Appendix S1 for detailed methods).

2.3 | Plant–frugivore interactions

From October 2018 to 10 July 2019 consecutive months that include the period before, during and after the main fruiting season (Figure 1), we sampled monthly plant–frugivore interactions at each site by combining the following four complementary sampling methods: (1) identification of intact seeds in faeces from trapped birds and reptiles in mist-nets and baited traps, respectively, (2) identification of intact seeds in faeces collected on faecal traps where the dispersers were identified based on DNA barcoding, (3) recording photos and videos of plant–frugivore interactions captured by motion-triggered camera traps and (4) direct frugivory observations. We registered one plant–frugivore interaction whenever an animal consumed at least one fruit per visit

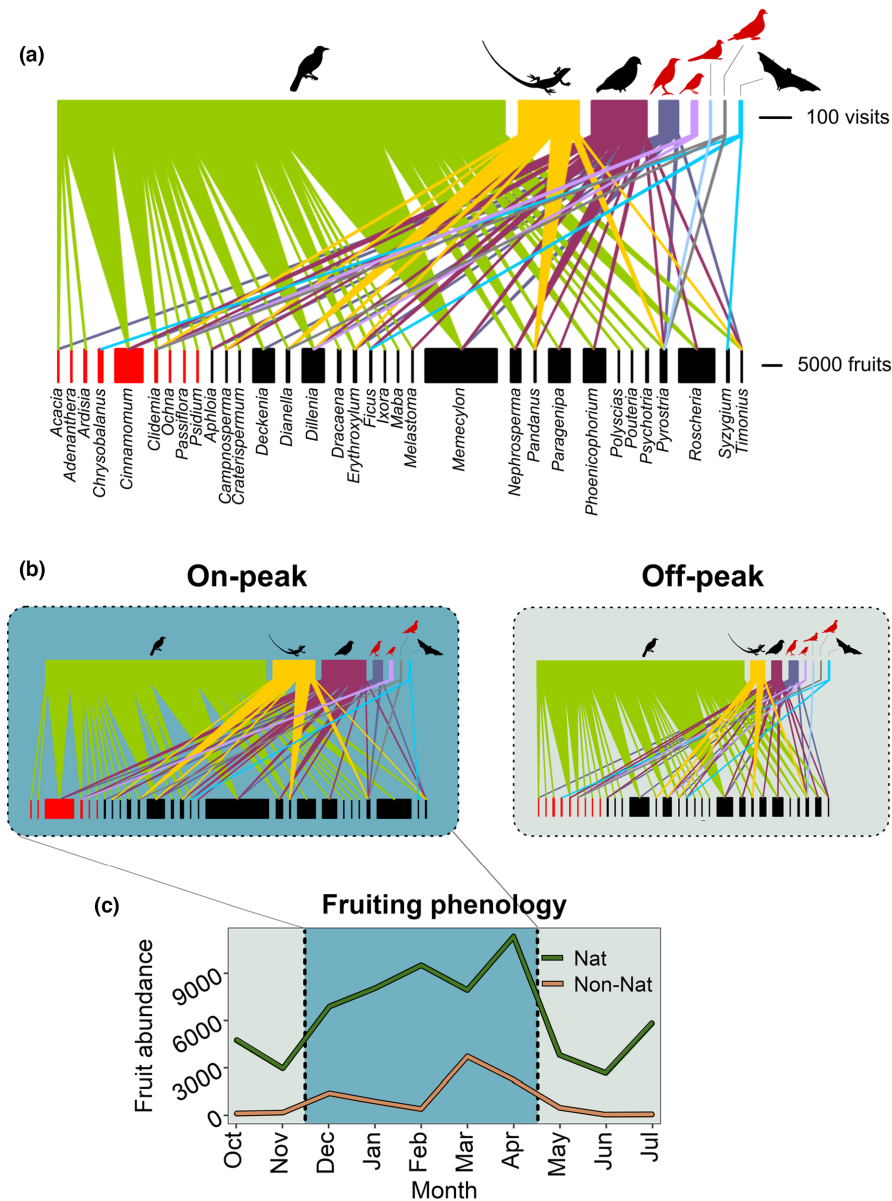


FIGURE 1 Plant-frugivore interaction networks on the island of Mahé, Seychelles. (a) Pooled network for the entire extended fruiting season (10 months) and (b) sub-networks represent the interactions within the main fruiting season (on-peak) and outside the peak of the fruiting season (off-peak). Lines between frugivores (top bar) and plant species (bottom bar) represent pairwise interactions and its horizontal width is proportional to the pooled interaction frequency across four sampling methods (analysis of droppings from mist-netted birds and from faecal traps, camera trapping, and direct frugivory observations). The width of the bars reflects species abundances, non-native species are coloured in red and natives in black. Frugivore species names from left to right in (a): Seychelles bulbul *Hypsipetes crassirostris*, Seychelles skink *T. seychellensis*, Seychelles blue pigeon *Alectroenas pulcherrimus*, Indian mynah *Acridotheres tristis*, Madagascar Fody *Foudia madagascariensis*, zebra dove *Geopelia striata*, Malagasy turtle-dove *Streptopelia picturata* and Seychelles fruit bat *Pteropus seychellensis*. The fruit bat was incorporated to the network through camera-trap recordings and direct observations and we did not include introduced rodents in the networks. All networks are drawn to the same scale. (c) Fruiting phenology (total fruit crop recorded along transects across the 8 sites) of native and non-native species. Plant origin: Nat = native; non-Nat = non-native.

to a plant individual and recorded a new observation if the visitor moved to and fed on a different plant. Please refer to Appendix S1 for detailed descriptions of the four methods to collect data on plant-frugivore interactions. The Seychelles Parks and Gardens Authority and the Seychelles Bureau of Standards granted us permission to conduct the work (permit reference A0157 with date 3 May 2018).

2.4 | Seed dispersal networks

We reconstructed seed dispersal networks for each site by generating quantitative interaction matrices based on the pooled frequency of occurrence of interactions between plant species i and disperser species j across all sampling methods following Heleno et al., 2022. We considered each sample as an individual record of interaction

ij using the following criteria for the different recording methods: (a) faecal samples: 1 record = 1 dropping of seed disperser j with the presence of intact seeds of plant i ; (b) direct observations and trapped seeds: 1 plant individual at which seed disperser j was observed ingesting fruits of plant species i and (c) remote observations: 1 camera-trap photo or video where seed disperser j was recorded ingesting fruits of plant i (Heleno et al., 2022; Timóteo et al., 2018). While all strategies to combine quantitative interaction matrices have their own caveats, by pooling the frequency of occurrence of interactions across all sampling methods, we always sum their contribution on the same currency (i.e. frequency of samples with evidence of an interaction). This combination of complementary sampling methods allowed us to maximise the completeness and taxonomic resolution of the network, thus bringing us closer to a realistic representation of the entire food web (Heleno et al., 2022; Jordano, 2016; Quintero et al., 2021).

To explore the effect of seasonal variation in fruit availability and frugivore activity on seed dispersal networks, we distinguished between two 5-month periods: the wet season or 'on-peak' fruiting season (December to April) and the dry season or 'off-peak' fruiting season (October to November and May to July). We assembled two seed dispersal sub-networks for visualisation purposes (on-peak and off-peak; Figure 1a,b) and considered interaction data from each of the 16 sub-networks (8 sites \times 2 periods) for the statistical analyses (Figure S3).

The structure of the 16 interaction sub-networks from each season (on and off-peak) and across the 8 sites with variable levels of plant invasion was described with key species- and network-level indices. We focused on standard metrics of quantitative bipartite network structure as commonly applied in across-network comparisons (Bascompte & Jordano, 2007; Tylianakis et al., 2007). The metrics chosen were (1) normalised degree, (2) species-level specialisation d' (Blüthgen et al., 2006), (3) species strength (Bascompte et al., 2006), (4) network size, (5) number of links and (6) network-level specialisation H_2' . Network metrics were calculated using the R package 'BIPARTITE' (Dormann et al., 2008) and are described in the Supporting information (Appendix S2).

2.5 | Statistical analyses

To evaluate the response of frugivores to fruit availability, we ran three generalised linear mixed models (GLMMs) with a negative binomial error distribution (log link) with the abundance of native ripe fruits, birds and skinks as response variables (Table 1a–c, respectively). The model exploring native fruit abundance included the proportion of non-native plants and season (on-peak vs. off-peak) as fixed effects. Only species fruiting in at least two study sites (24 out of 31 species) were considered in this model. To incorporate the effect of plant individuals on overall native fruit abundance, we fitted the log-transformed number of plant individuals as an offset term (fruits per capita). Random effects included plant species identity and sections nested within transects within sites. Both, the bird

and skink models, included the proportion of non-native fruits, fruit abundance and season as fixed effects. In the bird model we also fitted bird origin (native vs. non-native) and the interaction term bird origin \times season as a fixed effect and site and animal species as random effects. For skinks, we added site as a random effect and the log-transformed transect area (m^2) as an offset term to predict the abundance of skinks, while adjusting for the area sampled. Fruit abundance was rescaled by subtracting the mean and dividing by the standard deviation prior to analysis to improve model stability, convergence and accuracy of parameter estimates (Harrison et al., 2018). To account for the nonlinear relationship of fruit availability through the year, all three models included a z-scored Julian day quadratic fixed effect. We performed post-hoc contrast tests for pairwise comparisons of significant interactions, while correcting for multiple comparisons using the Tukey method with the 'LSMEANS' package (Lenth, 2016).

To quantify the synchrony of fruiting phenology between native and non-native plants we calculated the coefficient of overlap (Weitzman, 1970) using the R package OVERLAP (Ridout & Linkie, 2009). The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap). We then explored whether frugivore and plant species phenology (i.e. number of months where frugivores and fruits were present in the seed dispersal networks) was affected by species origin (native vs. non-native), season (on-peak vs. off-peak) and the proportion of non-native fruits by including them as fixed effects in a GLMM with Poisson errors and a log link. Separated models were fitted for the number of months that (i) dispersed plants were fruiting (Table 1d) and (ii) frugivores were dispersing (Table 1e). We included species and site as random effects in both models.

To investigate whether seed dispersal of native plants in each season decreased in the presence of non-native fruits, we added the dispersal frequency of native plants as a response variable in a GLMM with a negative binomial error distribution (log link). Animal origin, proportion of non-native fruits, season, fruit abundance and season \times fruit abundance were fitted as fixed effects, and site and plant species as random effects (Table 1f).

Additionally, to evaluate frugivore feeding preferences for native vs. non-native fruits, we calculated the Manly–Chesson (MC) selectivity index (Chesson, 1978) between fruit availability (natives and non-natives) and 'use' of each fruit type. The values of MC range from 0 (complete avoidance) to 1 (complete preference). The index is equal to 1/number of food types in the environment, if fruits are consumed in proportion to their abundance in the environment (i.e. no preference), and higher or lower if a food type is positively or negatively selected, respectively (Mittelbach, 2002). Therefore, with only two fruit types, an index of 0.5 would indicate 'no preference'.

Finally, we tested whether species phenologies affect the structure of seed dispersal networks, by assessing how key species- and network-level descriptors change across the season and invasion levels using linear mixed models (LMMs). Species-level metrics were explored by including frugivore origin, season and origin \times season as fixed effects (Table 1g–i). To test network level metrics, we fitted full factorial models with season and proportion of non-native fruits

TABLE 1 Results of the statistical models. GLMM reference level for plant and animal origin is 'non-native' and for season 'off-peak'. Day represents a continuous count of days (Julian day)

Response variable	Random effects	Predictors	Estimate (SE)	p value
Abundance: GLMM (negative binomial)				
(a) Native ripe fruit abundance	Site/transsect/section, plant species, offset: log (no. plant individuals) $N_{obs} = 1542$; $N_{site:transsect:section} = 112$; $N_{plant\ spp} = 24$	Intercept Prop. of non-native plants Season Day Day ²	2.02 (0.41) 3.51 (1.00) 0.30 (0.12) 0.14 (1.37) -8.21 (2.31)	<0.001 <0.001 0.012 0.004 <0.001
(b) Bird abundance	Site, animal species $N_{obs} = 458$; $N_{site} = 8$; $N_{ani-spp} = 5$	Intercept Prop. of non-native fruits Fruit abundance (scaled) Animal origin Season Day Day ² Animal origin × Season	1.33 (0.46) -0.06 (0.29) 0.04 (0.04) -0.18 (0.70) -0.37 (0.12) -0.48 (0.64) -3.55 (1.10) 0.32 (0.12)	0.004 0.822 0.324 0.793 0.002 0.453 0.001 0.008
(c) Reptile abundance (<i>T. seychellensis</i>)	Site, offset: log (m ² per transect) $N_{obs} = 337$; $N_{site} = 8$	Intercept Prop. of non-native fruits Fruit abundance (scaled) Season Day Day ²	-4.28 (0.13) -0.25 (0.33) 0.00 (0.04) -0.04 (0.13) -0.56 (0.79) -2.04 (1.02)	<0.001 0.448 0.980 0.737 0.479 0.046
Phenology: GLMM (Poisson)				
(d) No. months plants fruiting	Site, plant species $N_{obs} = 202$; $N_{site} = 8$	Intercept Prop. of non-native fruits Plant origin Season	0.73 (0.21) 0.16 (0.25) -0.01 (0.22) 0.18 (0.09)	<0.001 0.527 0.974 0.045
(e) No. months frugivores dispersing	Site, animal species $N_{obs} = 116$; $N_{site} = 8$	Intercept Prop. of non-native fruits Animal origin Season Prop. of non-native fruits × Animal origin	-0.68 (0.45) -2.33 (1.16) 1.50 (0.60) 0.28 (0.14) 1.96 (1.25)	0.135 0.046 0.012 0.039 0.117

TABLE 1 (Continued)

Response variable	Random effects	Predictors	Estimate (SE)	p value
Dispersal frequency: GLMM (negative binomial)				
(f) Dispersal of native plants	Site, plant species $N_{obs} = 360$; $N_{site} = 8$; $N_{plant\ sp} = 24$	Intercept	0.13 (0.29)	0.648
		Fruit abundance (scaled)	0.38 (0.15)	0.010
		Prop. of non-native fruits	-1.19 (0.42)	0.005
		Animal origin	1.21 (0.24)	<0.001
		Season	0.02 (0.11)	0.846
		Fruit abundance × Season	-0.35 (0.15)	0.024
Species-level metrics (frugivores): LMM				
(g) Normalised degree (log-transformed)	Site $N_{obs} = 71$; $N_{site} = 8$	Intercept	0.06 (0.03)	0.037
		Animal origin	0.08 (0.03)	0.021
		Season	-0.01 (0.04)	0.719
		Animal origin × Season	0.03 (0.04)	0.496
(h) Species strength (log-transformed)		Intercept	-0.48 (0.17)	0.005
		Animal origin	0.80 (0.20)	<0.001
		Season	-0.12 (0.23)	0.600
		Animal origin × Season	0.18 (0.27)	0.505
(i) Specialisation (d')		Intercept	0.37 (0.08)	<0.001
		Animal origin	0.21 (0.09)	0.018
		Season	0.10 (0.10)	0.290
		Animal origin × Season	-0.14 (0.12)	0.239
Network-level metrics: LMM				
(j) Network size ($P \times D$) (log-transformed)	Site $N_{obs} = 16$; $N_{site} = 8$	Intercept	1.78 (0.08)	<0.001
		Season	0.02 (0.10)	0.838
		Prop. of non-native fruits	-0.56 (0.66)	0.406
		Season × Prop. of non-native fruits	0.69 (0.72)	0.360
(k) No. links (log-transformed)		Intercept	1.35 (0.05)	<0.001
		Season	0.02 (0.05)	0.745
		Prop. of non-native fruits	-0.71 (0.36)	0.080
		Season × Prop. of non-native fruits	0.77 (0.38)	0.078
(l) Specialisation (H_2')		Intercept	0.42 (0.05)	<0.001
		Season	0.058 (0.04)	0.171
		Prop. of non-native fruits	1.34 (0.27)	0.002
		Season × Prop. of non-native fruits	-0.98 (0.28)	0.014

as explanatory variables (Table 1j–l). All models included site as a random factor, and normalised degree, species strength, network size and the number of links were log-transformed to meet model assumptions.

All analyses were conducted in R 4.1.1 (R Core Team, 2021). GLMMs were fitted using packages 'lme4' (Bates et al., 2015) and 'GLMMTMB' (Brooks et al., 2017), and LMMs using the 'lmerTest' package (Kuznetsova et al., 2017). Model design and selection followed the recommendations by Zuur et al. (2009) and Harrison et al. (2018). When overdispersion was detected for any of the Poisson GLMMs, we refitted the model with a negative binomial distribution (Hilbe, 2011). GLMM model diagnostics were performed using a simulation-based approach to calculate scaled (quantile) residuals and test typical model misspecification problems such as overdispersion and zero-inflation using the 'DHARMA' package (Hartig, 2020).

3 | RESULTS

3.1 | Fruit and frugivore abundance and phenology

We recorded a total of 76,361 ripe fruits from 40 plant species (31 native and 9 non-native), of which 87.4% were native and 12.6% non-native (Table S3; Figure S4). Ripe fruits of both native and non-native species were more abundant during the fruiting peak (on-peak) than off-peak (54,917 vs. 21,444 fruits, Wilcoxon signed rank test, $p = 0.014$; Figure 1c). The most abundant fruits were those of *Memecylon elaeagni*, *Roscheria melanochaetes* and the non-native *C. verum*, representing the 27.4%, 13.4% and 10.0% of the total ripe fruit crop observed in our communities, respectively. The number of native ripe fruits per plant increased with the proportion of non-native plants ($p < 0.001$; Table 1a), while the number of unripe fruits was not affected ($p = 0.053$, Table S4).

A total of eight seed disperser species were recorded: the Seychelles skink *T. seychellensis*, the Seychelles fruit bat *Pteropus seychellensis*, and six bird species. Four of these dispersers were non-native (all birds), and the other four were native (Figure 1a). The Seychelles Bulbul *Hypsipetes crassirostris* was the most abundant disperser species, followed by the non-native Madagascar fody *Foudia madagascariensis* (Table S5). We did not consider *G. striata* in our abundance analyses since it was present only in one of the eight study sites. Native and non-native frugivore abundances were independent of total fruit availability and the proportion of non-native fruits (Table 1b). Although skink and native bird abundances kept constant across seasons, post-hoc results showed a significantly higher number of non-native frugivores at the study sites during off-peak (Table 1b,c; Table S6).

Fruiting of non-native species largely coincided with the main peak of native fruit production, that is, between December and April (Figure 1c; coefficient of overlap = 0.89) and lasted for a similar extent than natives (natives = 4.93 ± 0.35 , non-natives = 4.19 ± 0.91 months; Table 1d; Figure S4). Native frugivores

were active dispersers for longer throughout the study period than non-native frugivores (6.26 ± 0.57 vs. 1.87 ± 0.43 months; Table 1e; Figure S5) and native and non-native plants were dispersed for a similar duration (Table 1e; Figure S6).

3.2 | Dispersal of native plants

Overall, we recorded 1879 interactions (i.e. dispersal events; on-peak = 1064; off-peak = 815) and 74 unique plant–frugivore links (on-peak = 60; off-peak = 62) between 8 animal species and 33 plant species (22 native and 9 non-native; Figure 1a, Table S7). The dispersal frequency of native plants declined with the proportion of non-native fruits (Table 1f; Figure 2). Across the entire study, native frugivores dispersed seeds of native plants more frequently than non-native frugivores (Table 1f). There was a positive relationship between fruit availability and dispersal frequency of natives, mainly outside the main fruiting season (Figure 3).

According to the Manly–Chesson selectivity index, frugivores showed a strong preference for non-native fruits during the months of lower fruit availability (natives = 0.17; non-natives = 0.83; 'no preference scenario' = 0.5), which was absent during the main fruiting season (natives = 0.56; non-natives = 0.44).

3.3 | Network structure and species roles

The Seychelles bulbul *H. crassirostris* was not only the most abundant frugivore but also the main seed disperser in the networks, accounting for 94% of all plant species dispersed (on-peak = 93%;

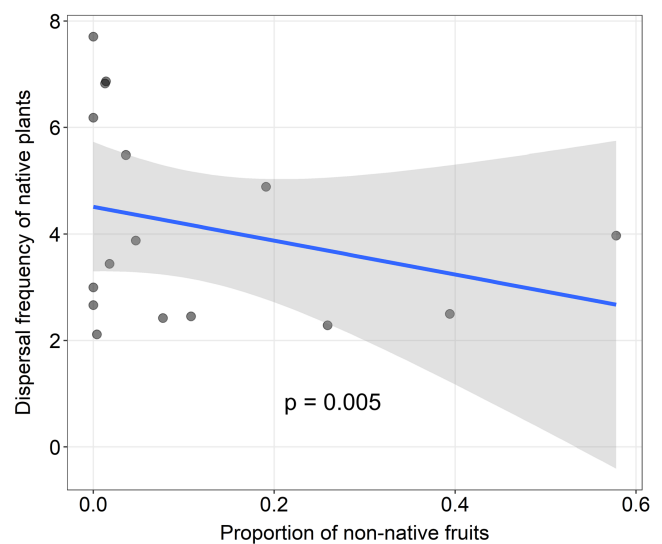


FIGURE 2 Scatterplot showing a decline in dispersal frequency of native plants (each point represents the mean number of interactions per site and season) with an increase in the proportion of non-native fruits per site (ratio of non-native to total ripe fruits). Lines represent the best fitting linear prediction and shaded areas 95% confidence intervals.

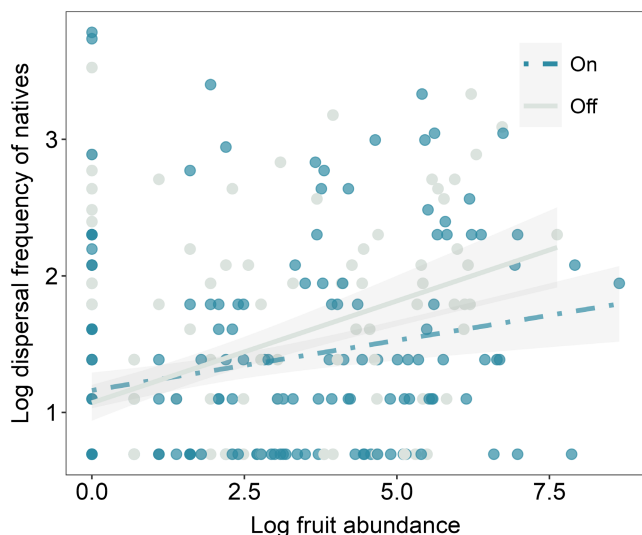


FIGURE 3 Native seed dispersal frequency increased with fruit abundance (both on log scale), but this relationship was stronger during the off-peak (grey, solid line) than on-peak (blue, dashed line) fruiting season ($p = 0.024$, Table 1f). During off-peak, when resources are scarce, native seed dispersal was relatively more dependent on total fruit abundance at each site. Lines represent the best fitting linear prediction and shaded areas 95% confidence intervals.

off-peak = 97%) and 76% of all interactions (on-peak = 69%; off-peak = 84%). As such, the species had a significant impact on network structure, such as species degree, species strength and specialisation (d'), all of which were similar between seasons but higher for native frugivores compared to non-natives (Table 1g–i; Figure 4). Network size and the number of links did not change significantly between the two seasons (Tables 1j–k). Network specialisation (H_2'), however, increased with the proportion of non-native fruits, and this effect was stronger outside the main fruiting season (Table 1; Figure 5).

4 | DISCUSSION

Many islands around the world have suffered the disruption of ecosystem functions due to the impact of invasive species (Kaiser-Bunbury et al., 2010; Traveset & Richardson, 2014). Here, we showed that by displaying a similar fruiting phenology, non-native fleshy-fruited plants compete with native plants for dispersal services. Further, we identified two processes in which seasonal variation in fruit availability and the level of plant invasion played a critical role for native plant–frugivore dynamics. Firstly, the frequency of dispersed seeds increased linearly with the availability of fruits, but this effect was much clearer outside the main fruiting season, suggesting that during the fruiting peak there are too many fruits for too few frugivores. This saturation of frugivores, and consequently of seed-dispersal services, intensified the competition between native and non-native fruits during the main fruiting season with negative consequences for native seed dispersal. Secondly, at times of low

fruit availability as fruits became harder to find, frugivores selected more non-native fruits at sites dominated by non-native plants. These findings indicate that both critical ecosystem functions and native plant and frugivore populations are under increased pressure in invaded plant communities, which constitute most of the remaining forested areas on Mahé. Below we will explore the underlying mechanism that are likely to be responsible for the observed patterns and discuss ecological and conservation consequences of our findings.

4.1 | Fruit and frugivore abundance and phenology

In our study system, non-native and native plants fruited mostly synchronously and for a similar duration. This synchrony has two main implications for native seed dispersal dynamics: during the main fruiting season an excess of highly attractive non-native fruits compete for frugivores with native fruits, reducing native seed dispersal. Outside the fruiting peak, when resources are scarce, plant invasion impedes native plant–frugivore interactions, with likely negative consequences for both mutualistic partners. Elsewhere it was shown that native seed rain (Gleditsch & Carlo, 2011; Heleno, 2020) and recruitment (Heleno, Ramos, et al., 2013; Traveset et al., 2012) were reduced when non-native and native plants compete for dispersal services.

During the peak of the fruiting season, non-native frugivores were rarer on the inselbergs than off-peak, while native frugivores remained constant. The most likely driver of the observed changes in non-native frugivore abundance during the fruiting season is increased rainfall (December–March; Walsh, 1984), particularly at higher elevations (Boyle et al., 2010). Avian frugivores have been observed to move along an elevation gradient depending on the season (Santillán et al., 2018), and a similar pattern is possible here, driven by excess fruit and more favourable weather conditions in the lowland. It is unsurprising that the most prominent native frugivore, the Seychelles bulbul, as a forest dweller adapted to the mid and high altitudes and reliant on native fruits (predominant on inselberg communities) does not show these elevational movements.

4.2 | Dispersal of native plants

The dispersal of native plants increased with fruit availability, mainly during those months when resources were scarce (i.e. off-peak season). The weaker relationship between fruit availability and dispersal during the fruiting peak and a similar dispersal frequency in both seasons, could be explained by a frugivore satiation during the period when most plants are fruiting and the frugivorous fauna cannot keep up the consumption of fruits. Similar effects of abundant fruit supplies on vertebrate frugivore communities have been described by Hampe (2008) and Rumeu et al. (2019) in temperate regions. Therefore, during the main fruiting peak only a fraction of the available fruit crop on the inselbergs is dispersed, especially at sites with

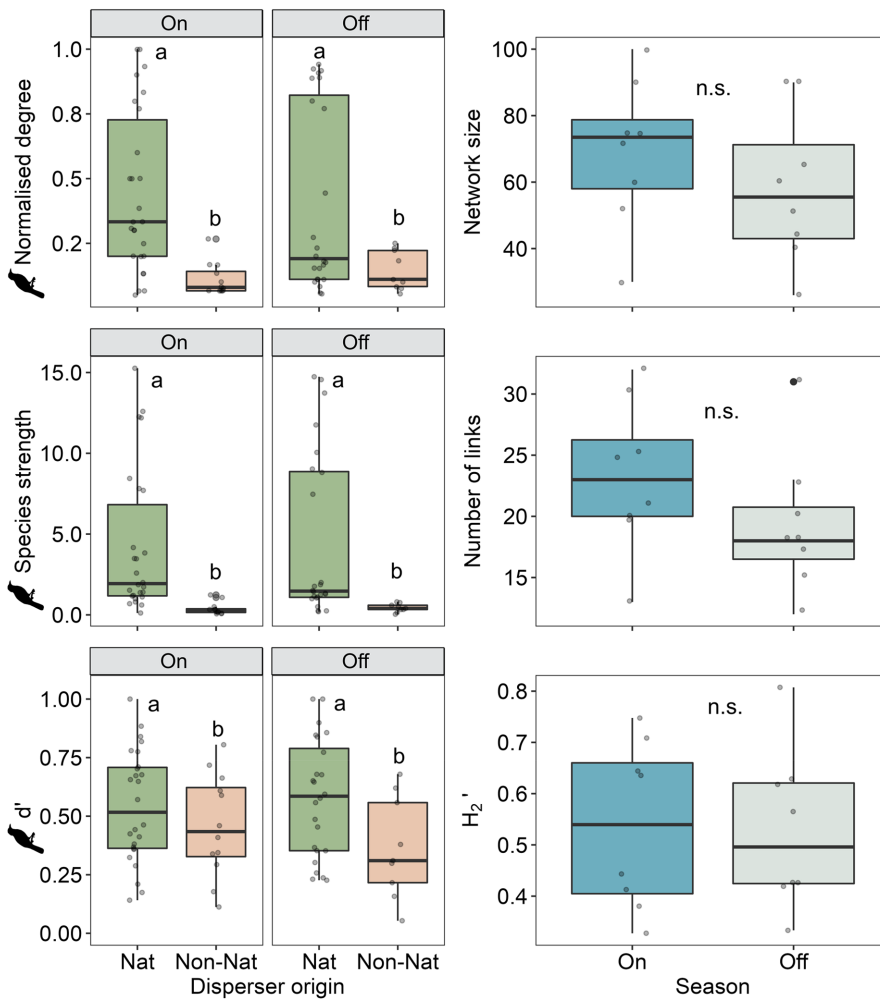


FIGURE 4 Boxplots depicting species-level metrics by frugivore species and site (left) and network-level metrics by site (right). Metrics include normalised degree, species strength, species specialisation (d'), network size, number of links and network specialisation (H_2'). Boxes indicate the 25th to 75th percentiles, the middle line is the median, and the maximum length of the whiskers is 1.5 times the interquartile range. Nat = native; non-Nat = non-native; On = on-peak; Off = off-peak. Different lowercase letters represent significant differences between groups ($p < 0.05$), (*) $p < 0.05$, (**) $p < 0.01$.

higher presence of non-native plants. In this context, the saturation of the frugivorous fauna intensifies the competition between native and non-native fruits for seed dispersal services, particularly at invaded sites. These results highlight a yet underappreciated mechanism by which native plant recruitment can be truncated due to the presence of synchronously fruiting introduced plants.

4.3 | Network structure and species roles

Overall, network size and structure were largely consistent across the study period. Interestingly, however, network specialisation H_2' increased with the presence of non-native fruits, particularly during off-peak. During on-peak the ability of frugivores to find and feed on native fruits is likely to depend on the relative density of native fruits across the inselbergs. With increasing plant invasion, native fruits become harder to detect due to their lower relative density, an effect that is possibly amplified by the physical obstruction created by non-natives, particularly *Chrysobalanus icaco* and *C. verum*. In predominately native plant communities, networks were equally generalised on- and off-peak, which suggests that foraging behaviour changed little with season. In invaded communities, however, we observed higher specialisation

during off-peak, which was somewhat surprising given our expectation that frugivores become less specialised when resources are scarce. Two complementary effects may be responsible for the observed change in foraging behaviour of the frugivores: native fruit crops were scarcer and smaller, which made them harder to find in the first place, and when fruits were found they provided a lower energetic reward. Kueffer et al. (2009) showed that on Mahé the fruits of the most abundant non-native tree *C. verum* have a much higher energetic content per dry pulp and lower water content (resulting in a greater relative yield) than those of native plants. It is plausible that frugivores in invaded communities changed their foraging behaviour due to differences in nutritional and energetic values between native and non-native fruit at times of resource scarcity (Brown, 1988; Charnov, 1976), becoming more selective on high-energy non-native fruit crops that deliver more energy per foraging effort (Albrecht et al., 2018). This interpretation is supported by the selectivity analysis, which showed higher selectivity of non-native fruit by frugivores during off-peak. Given the low fruit availability of native and non-native plants on the inselbergs during off-peak, avian frugivores may also use invaded adjacent forests to feed on high-energy non-native fruit. Because native and non-native plants in our study system are similar in fruit colour and size and in plant habit and height,

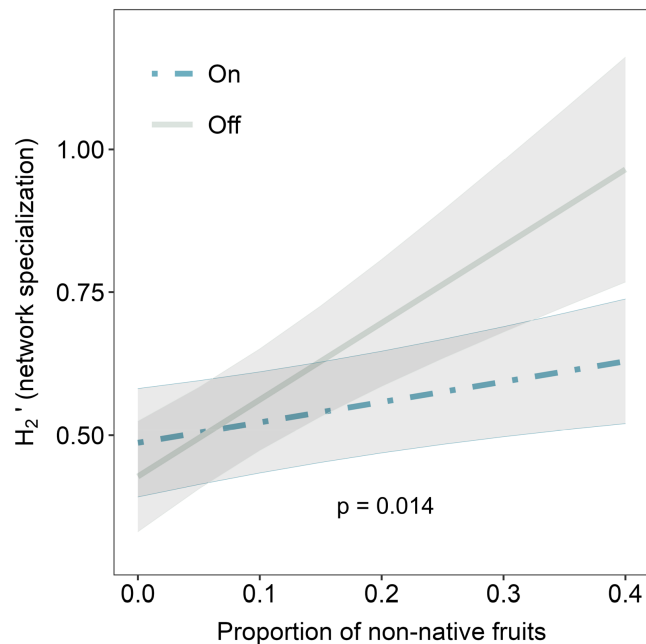


FIGURE 5 Network specialisation (H_2') increased with degree of invasion (proportion of non-native fruits), and this relationship was stronger during the off-peak (grey, solid line) than on-peak (blue, dashed line) fruiting season ($p = 0.014$, Table 1). Lines represent model predictions and shaded areas 95% confidence intervals. On = on-peak; off = off-peak.

these characteristics are unlikely to drive fruit selection by frugivores, but other cues (e.g. chemical composition) would require a more rigorous comparison. The ecological and conservation implications of these changes in foraging behaviour with invasion are stark. Native species fruiting during off-peak have a lower chance of dispersion, and equally native frugivores have to switch diet and experience changes in foraging effectiveness, with potentially negative consequences for fitness (Martin, 1985). Furthermore, increased specialisation in invaded plant communities during off-peak may increase the vulnerability of seed dispersal function and frugivores (Kaiser-Bunbury & Blüthgen, 2015), which is a direct consequence of plant invasion.

In some ecosystems, non-native frugivores can augment seed dispersal of native frugivores, or even act as functional surrogates of extinct or functionally extinct dispersers (Didham et al., 2005). Across the whole study period, native frugivore species dispersed a greater number of seeds and were actively dispersing for longer periods than non-natives, which includes the native skink species *T. seychellensis*. In addition, native frugivores dispersed more plant species, were more selective and they were more important for the dispersal of the entire plant community than non-native frugivores. In this study, we considered all frugivores to legitimately disperse viable seeds. Some frugivores, however, may act as seed predators by destroying a variable proportion of the ingested seeds. Instead of grouping frugivores into seed dispersers (mutualists) or seed predators (antagonists), we recognise that all frugivores vary along a continuum of seed dispersal effectiveness (SDE). With this in mind, it

is likely that the two main native avian frugivores, the Seychelles bulbul *H. crassirostris* and the Seychelles blue pigeon *A. pulcherrimus*, contribute more to effective seed dispersal than suggested solely by the number of feeding events compared with the non-native omnivores Malagasy Turtle-Dove *S. picturata*, Zebra dove *G. striata*, Indian Mynah *A. tristis* and Madagascar Fody *F. madagascariensis* (Billerman et al., 2022; Rocamora & Henriette, 2017). These species may contribute overall little to seed dispersal because of their tendency to destroy seeds during feeding and digestions (pers. obs.). These findings highlight the importance of native frugivores for native plant dispersal in these patches of native forest. Further, non-native frugivores are unlikely to replace a loss of seed dispersal function as a result of native frugivore decline or extinction.

Although we cannot draw any conclusions on the SDE (Schupp et al., 2010) of the frugivores in the Seychelles as such experimental SDE studies on the community level are very rare (Carlo & Yang, 2011; Traveset et al., 2014, but see González-Castro et al., 2015), our interaction data, which have been primarily derived from animal droppings (75% of the interactions), suggest the dispersal of intact seeds, rendering the frugivores legitimate seed dispersers. Further indirect evidence for the effectiveness of the frugivores reported here is provided by a study by Costa, Heleno, Dufrene, Huckle, Gabriel, et al. (2022), which found extensive native recruitment in invaded forest which lacks adult native species. Taken together, these findings suggest that the frugivore community in our study provide effective seed dispersal services.

5 | CONCLUSIONS

Our study showed that the effects of non-native plants on seed dispersal interactions vary markedly across fruiting seasons. By fruiting synchronously with native plants, non-native fleshy-fruited plants negatively affected the dispersal of native plants. Our highly resolved temporal data revealed changes in foraging behaviour due to plant invasion, which are likely to generate additional constraints on frugivore populations and may limit native recruitment. It is therefore critical to consider different temporal scales when assessing the impact of human-mediated stressors, here invasive plant species, on native ecosystem functions (see CaraDonna et al., 2021). Finally, remnant or restored native plant communities are important for protecting native plant–frugivore interactions and the regeneration potential of these forests.

AUTHORS' CONTRIBUTIONS

Alba Costa, Christopher N. Kaiser-Bunbury and Ruben Heleno conceived the ideas and designed the methodology. Alba Costa, Eleanor Huckle and Yanick Dufrene collected the data. Ronny Gabriel assisted with the implementation of the experiment. Alba Costa analysed the data; Xavier Harrison advised on statistical analyses; Dana G. Schabo and Nina Farwig supervised and advised on laboratory analyses. Alba Costa, Christopher N. Kaiser-Bunbury and Ruben Heleno led the writing of the manuscript. All

authors contributed to revisions of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. Ruben Heleno is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available at the Dryad Digital Repository <https://doi.org/10.5061/dryad.wm37pvmqw> (Costa, Heleno, Dufrene, Huckle, Gabriel, Harrison, et al., 2022).

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