

RESEARCH ARTICLE

Seed dispersal by frugivores from forest remnants promotes the regeneration of adjacent invaded forests in an oceanic island

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Forest remnants often act as refuges for native plant species within a degraded and highly fragmented forest matrix. Understanding whether these native patches can function as feeding grounds for frugivores and seed sources for native plant dispersal into the surrounding forest can provide critical information on ecosystem functions on a landscape scale and guidance on forest restoration. We used a large-scale natural system of eight granitic inselbergs in the Seychelles and recorded the identity and transport direction of seeds retrieved from the droppings of mist-netted birds across an invasion gradient. We found that inselberg forest remnants are important feeding areas for frugivores, acting as a source of native propagules to the surrounding invaded forests and potentially limiting the progression of non-native plant invasion. Two dominant non-native plant species (*Cinnamomum verum* and *Clidemia hirta*) were highly integrated into the frugivores' diets, competing with native plants for dispersal services. Despite the high non-native propagule pressure, the spill-over effect of native seeds into the invaded forest seemed to have a more durable positive effect on native plant recruitment fading out with distance to the inselberg edge. Our findings illustrate that remnant forest patches can generate positive spill-over of native seeds into degraded surrounding forests through directed seed transport by frugivores. This cross-boundary transport may slow down plant invasion and contribute to the recovery of adjacent degraded ecosystems. Forest remnants and avian frugivores therefore play a key role in the maintenance of native biodiversity and act as insurance for future restoration efforts.

Key words: forest restoration, frugivory, plant invasion, plant recruitment, remnant forest patch, seed transport

Implications for Practice

- Based on our findings that the non-native plant species *Cinnamomum verum* and *Clidemia hirta* compete with native plants for dispersal, we suggest that practitioners consider the removal of these species for the maintenance of native plant communities and the restoration of adjacent invaded areas.
- Management interventions against plant invasions in forest remnant patches are needed to ensure the viability of the native plant community and facilitate the regeneration of surrounding degraded areas.
- Given the potential of frugivorous birds in limiting the progression of plant invasion and providing assisted restoration across forest boundaries, identifying and protecting effective seed dispersers should be considered a priority in restoration planning.

Introduction

About two-thirds of the globally remaining forests persist as isolated patches embedded in a matrix of human-modified land cover (Driscoll et al. 2013; Haddad et al. 2015). Seed dispersers can act as connectors between forest fragments by actively moving across the landscape and transferring propagules between

patches and the surrounding disturbed matrix (Lundberg & Moberg 2003; González-Varo et al. 2017). The dispersal of seeds by frugivores allows plants to find favorable recruitment sites in or outside the forest fragments, expand their distribution, maintain their genetic diversity across forest interfaces, and avoid competition with siblings and natural enemies within small forest patches (Janzen 1971; Howe & Smallwood 1982; Traveset et al. 2014). Seed dispersal services, however, are

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heavily altered and disrupted by various human-caused processes, which is particularly problematic in fragmented forest ecosystems (Hagen et al. 2012).

One such disruptive process is the spread of non-native plant species in degraded ecosystems. The plasticity and generality of frugivory interactions often means that fruits of non-native plants are readily included in the diet of native frugivores, thereby facilitating the spread of non-native plants (Bartuszevige & Gorchoff 2006; Heleno et al. 2013; Heleno 2020). When non-native plants outperform natives, they can become invasive (Daehler 2003), negatively affecting the native vegetation through direct competition for resources (Hejda et al. 2009) and the dispersal of co-occurring native species due to changes in the activity of the dispersers (reviewed in Heleno 2020). The breakdown of plant-frugivore interactions can thus strongly affect the composition, functioning and persistence of invaded communities (Vilà et al. 2011). In a mixed forest landscape, however, forest patches with high availability of native propagules (i.e. native forest remnants) could also function as a source of native seeds to their surroundings and suppress the advance of the non-native species. Conversely, native forest patches could act as a recipient of non-native propagules transported by frugivores from the neighboring degraded forest, leading to the deterioration and potential loss of native forest remnants. Understanding these dynamics is important to both assess the impact of the spread of non-native plants on native biodiversity and ecosystem functioning, and to devise management interventions if required.

The movement and behavior of frugivores naturally determine the transfer of seeds across the landscapes (Carlo & Yang 2011; Morales et al. 2013; González-Varo et al. 2017). Recording the spatial behavior of the dispersers and the directionality of seed movement, however, has proven particularly challenging (Timóteo et al. 2018). Testing the direction of seed fluxes between plant communities in a natural setting requires the ability to record identity of the frugivores and the seeds involved in each dispersal event and to discern between the source and recipient plant communities. To circumvent this difficulty, most studies have considered seed dispersal as a function of distance traveled by seeds, independently of their specific dispersal direction from the source plant community to a specific deposition site (Spiegel & Nathan 2007; Rehm et al. 2019). Moreover, most research has focused either on frugivory and seed deposition or on seed germination and recruitment but studies combining both stages of the seed dispersal loop are still scarce (Wang & Smith 2002; Carlo & Yang 2011). In this study, we address the directionality of avian seed dispersal and seedling recruitment between remnant forest patches with different invasion levels and the surrounding highly invaded forest matrix. Moreover, we test for differences in plant recruitment inside and outside the forest patches and with distance from the edge of the native forest patch into the adjacent matrix.

We used a landscape model system (Kueffer & Kaiser-Bunbury 2014) on the island of Mahé, Seychelles, to study seed transport between mid-altitude granitic inselbergs (i.e. isolated steep-sided rock outcrops), which serve as refuges for native plant species, and the surrounding matrix of degraded vegetation dominated by non-native species. Inselbergs harbor the last

remnants of Seychelles' endemic flora (Fleischmann 1997), yet the quality of inselberg flora is variable, including plant communities that are almost pristine and undisturbed, actively restored and managed, moderately invaded, or heavily degraded. Much of the island's vegetation has been severely impacted by forest exploitation, fire and invasive species, and it now comprises mostly secondary forests dominated by non-native trees, mainly *Cinnamomum verum* J. Presl (Kueffer et al. 2007). We used inselbergs as replicated units to explore how frugivores, including several bird, one lizard and one bat species, and their ingested seeds move across the inselberg–forest interface and thereby contribute to the spread of propagules between these distinct ecosystems. Specifically, considering differences between native and non-native plant species, we ask whether (1) Forest remnants act as a source of propagules to the surrounding matrix; (2) Seedling and sapling density differs inside and outside the inselberg and with distance from the inselberg edge; and (3) The inselberg invasion level affects either seed transport or plant recruitment patterns.

Methods

Study Site

The study was conducted on Mahé, the largest granitic island of the Seychelles, Indian Ocean (-4.6953° , 55.4999° , 154 km^2 , 900 m a.s.l.). The Seychelles are characterized by a tropical climate with a wet and warm NW monsoon season (December to March) and the dry and cooler SE trade winds (May to October). Mean monthly temperature ($24^{\circ}\text{C} \pm 2$) and precipitation ($258 \text{ mm} \pm 29$) on the inselbergs can vary considerably with season and local weather (season 2018–2019; A. Costa et al., unpublished data). Inselberg plant communities are characterized by 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) and are composed of 22% of non-native plants (A. Costa et al., unpublished data). Several of the dominant native species produce fleshy fruits, including the deciduous *Memecylon elaeagni* Blume, *Paragenipa lancifolia* (Bojer ex Baker) Tirveng. & Robbr., *Pyrostria bibracteata* (Baker) Cavaco and four species of palms *Deckenia nobilis* H. Wendl. ex Seem., *Nephrosperma vanhoutteanum* (H. Wendl. ex Van Houtte) Balf.f., *Phoenicophorium borsigianum* (K. Koch.) Stuntz, and *Roscheria melanochaetes* (H. Wendl.) H. Wendl. ex Balf.f. (Robertson 1989; Friedmann 1994). The most common fleshy fruited exotic plant species on the inselbergs are *Psidium cattleianum* Afzel. ex Sabine, *Chrysobalanus icaco* L. (Chrysobalanaceae), *Clidemia hirta* (L.) D. Don, and *C. verum* (Kaiser-Bunbury et al. 2017). The degraded forest matrix is dominated by non-native species composed of old timber and cinnamon plantations and overgrown boulder fields comprising more than 80% of non-native species (Kueffer et al. 2007). The main fruiting period is December to March, but plants develop fruit throughout the year (A. Costa et al., unpublished data). Little is known about the seed dispersal community in the Seychelles. Potential dispersers on Mahé include the Seychelles fruit bat (*Pteropus seychellensis*) and six bird

species, of which the Seychelles Blue Pigeon (*Alectroenas pulcherrimus*), Seychelles Bulbul (*Hypsipetes crassirostris*), and the exotic Indian Mynah (*Acridotheres tristis*) are known frugivores (Kueffer 2006). The role of the Seychelles skink (*Trachylepis seychellensis*) as a disperser is still largely unknown. There are no ungulates, large carnivores or other large terrestrial dispersers on the island, and native giant tortoises that once roamed the island have disappeared long ago (Arnold et al. 1979).

Experimental Setup

Data were collected on eight inselberg plant communities of circa 1 ha in size with different levels of plant invasion. All study sites were surrounded by steep cliffs on at least three sides of the inselberg, separating inselberg vegetation from the surrounding forest (Fig. 1). Between 2011 and 2012, four of the inselbergs were cleared of all non-native plants with the aim to restore native plant communities, while the other four were left with both native and non-native species (Kaiser-Bunbury et al. 2015). Irregular maintenance of the “restored” sites resulted in encroachment of previously removed and recently arrived non-native plant species, mainly *C. hirta* and *C. verum* (A. Costa personal observation). Invasion level for each site was estimated as the ratio of the total crop of non-native to native ripe fruits using data on fruit abundances recorded monthly by counting all ripe fruits along linear transects. Transects were 2 m wide, divided into 25 m length sections distributed across the entire area of the sites and of variable length (75–150 m) in order to cover a similar proportion of area within each site (mean proportion of area sampled \pm SD: $6.39\% \pm 1.58$; correlation between site area and total transect length: $r = 0.71$; Table S1).

Seed Transport

To characterize the diversity, abundance, and origin of seeds exchanged between inselberg forests and the surrounding matrix, including the direction of seed transport, that is, the seeds arriving to and departing from inselbergs, we collected bird droppings from October 2018 to July 2019. Birds were caught by operating three mist-nets per site (6, 9, and 12 m) strategically placed parallel to the edge of inselberg cliffs (Gomes et al. 2017). Due to the steepness of the cliffs, the horizontal distance from the edge of the inselberg vegetation to the invaded forest is generally short (approximately 5 m). Further, the canopy height of the inselberg vegetation is low compared to that in the surrounding invaded forest (approximately 3 m vs. approximately 15 m). The placement of the mist-net under these conditions ensures that birds moving between these two vegetation types are effectively intercepted. The flight direction of each bird (i.e. *departing* from or *arriving* to the inselberg) was recorded based on the side of the net the bird entered into the trapping pocket (Fig. 1). While birds could potentially feed on natives on the inselbergs, fly into the invaded surrounding forest, and get caught upon their return to the inselberg, this scenario is unlikely. According to models on the optimal use of a patchy habitat (MacArthur & Pianka 1966; Charnov & Orians 2006), the optimal foraging choice for frugivores is to remain in a resource patch until fruit supply or productivity (i.e. ratio of resource calories ingested per unit foraging time) decreases. Hence, there is little reason to assume that frugivores will cross the habitat boundaries to forage in poorer patches within the short periods of gut retention times (e.g. *H. crassirostris* gut passage time in captivity circa 15 minutes; Kueffer 2006). We are therefore confident that the setup of the mist-nets is able to detect the main

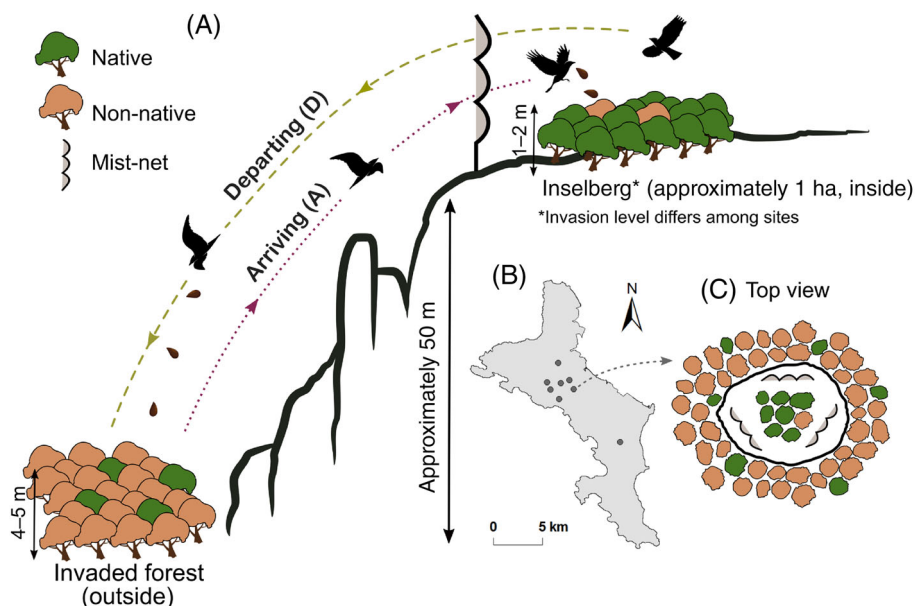


Figure 1. (A) Experimental design used to record the direction of seed dispersal from and toward the Seychelles' inselbergs. (B) Map of the study sites on the island of Mahé. (C) Birds' eye view of a study site: Thick solid black line represents the boundary between the inselberg (native forest remnant) and the surrounding invaded forest.

movement patterns of birds and the transport of seeds across the inselberg–invaded forest interface.

Mist-nets were operated for a total of 1,120 h (14 h per site and month) and inspected every 20 minutes. All birds were extracted and kept in cloth bags until seeds were ejected (defecated or regurgitated), or for a maximum of 30 minutes. Droppings were collected from the cloth bag and from the area beneath the mist-net where fresh droppings from the trapped bird could be found (González-Varo et al. 2014). Intact seeds in samples were counted and identified using a dissection microscope by comparing the seeds to a reference collection (García-Cervigón et al. 2018). Frequency of occurrence of seeds (hereafter FO) was calculated as the number of droppings containing at least one intact seed of each species (Correia et al. 2017). Number of fruits dispersed was calculated based on the number of seeds divided by the average number of seeds per fruit for each plant species (Table S2). FO and the number of fruits were strongly positively correlated ($r = 0.91$, $p < 0.001$, Fig. S1). Hereafter we only present data on FO to allow comparison of our findings with other seed dispersal studies.

Plant Recruitment

To evaluate plant recruitment success, we collected data on seedling and sapling densities along the inselberg–invaded forest interface. Plant recruitment surveys were conducted on inselbergs along parallel transects spanning the full length and width of the inselbergs. Because of the feeding behavior of the birds, we anticipated that detectable effects of native plant recruitment in the invaded forest were most marked relatively close to the inselberg boundaries. To survey a relatively homogeneous forest structure, we recorded plant recruitment along transects perpendicular to inselberg contour lines from the edge of the inselberg to 25 m into the surrounding invaded matrix (Table S1). In both sets of transects, all seedlings (< 50 cm height) and saplings (> 50 cm to circa 200 cm height) were identified and counted in 1 m² quadrats every three steps (approximately 2.5 m) on alternating sides of each transect between May and June 2019. A total of 555 quadrats were sampled inside the inselbergs and 400 quadrats in the surrounding invaded forest (Table S1). The density of seedlings and saplings was calculated for the quadrats inside and outside the inselberg, and also for the quadrats at each distance from the inselberg edge into the invaded matrix in 2.5 m intervals.

Statistical Analyses

All analyses were conducted in R 4.0.2. (R Core Team 2020). Poisson generalized mixed effects models (GLMMs) were fitted using the package “lme4” (Bates et al. 2015) and negative binomial models using “glmmTMB” (Brooks et al. 2017). Model design and selection followed the recommendations by Zuur et al. (2009) and Harrison et al. (2018). To quantify overdispersion in Poisson GLMMs, for each model the dispersion parameter was calculated as the ratio of the sum of the squared Pearson residuals to the residual degrees of freedom using the R function provided in Harrison (2014). When overdispersion was detected

(Hilbe 2011), we refitted the model with an observation-level random effect (OLRE), compared it to a model with a negative binomial distribution (Zuur et al. 2009; Harrison 2014), and selected the most parsimonious model based on the Akaike Information Criterion (AIC) (Burnham & Anderson 2002). 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).

To test for differences in seed transport depending on the directionality of dispersal (arriving vs. departing), plant origin (native vs. non-native), and invasion level (measured as the proportion of non-native fruits in each inselberg), we fitted GLMMs with a Poisson error distribution (log link) with direction, plant origin, and invasion level as fixed effects, using site ($n = 8$) as a random effect. We ran separate models to test the response on (1) the number of droppings with at least one seed (FO) and (2) the number of seeds. We performed post-hoc contrast tests for pairwise comparisons of significantly different groups, while correcting for multiple comparisons using the Tukey method with the “lsmeans” package (Lenth 2016).

To assess differences in plant recruitment by location (inside: inselberg vs. outside: invaded forest), plant origin, and inselberg invasion level, we fitted a GLMM with a negative binomial distribution (log link) with location, plant origin, location × plant origin, and invasion level as fixed effects. We included quadrat ($n = 955$) nested within site ($n = 8$) as a random effect in the model. The number of seedlings and saplings per quadrat with all plant species grouped based on origin was entered as response variables in separate models. Post-hoc contrast tests for pairwise comparisons were performed as indicated above.

We further tested the effect of the distance from the inselberg edge into the invaded forest on seedling and sapling density, and on native seedling and sapling species richness. First, we fitted two separate GLMM(s) with Poisson error distributions (log link) for the number of seedlings and saplings per quadrat as a response variable. Plant origin, invasion level, and distance were entered as fixed effects, as well as the interactions between distance × origin, and distance × invasion level. Secondly, native species richness per quadrat was fitted as the response variable, and invasion level, distance and their interaction, as fixed effects. In the density models, we included quadrat ($n = 400$) nested in site ($n = 8$) as a random effect, and in the native richness models, only site. Distance was re-scaled (subtracting the mean and dividing by the standard deviation) to improve model stability, likelihood and convergence and accuracy of parameter estimates (Harrison et al. 2018).

Results

Seed Transport

Overall, 381 birds were trapped (arriving = 172, departing = 209) and 32 recaptured (arriving = 13, departing = 19). From the individuals caught, 236 (61.9%) produced droppings (arriving = 109, departing = 127) and a total of 22,782 intact seeds were found in 98 droppings from 6 bird species.

Seychelles bulbul (*H. crassirostris*) was by far the main seed disperser, producing 87.8% of the droppings with seeds. Droppings contained seeds from 18 fleshy fruited plant species (Table S2), 16 natives, mainly *Dillenia ferruginea* (Baill.) Gilg, *M. elaeagni* and *Erythroxylum sechellarum* O. E. Schulz, and two non-natives, *C. verum* and *C. hirta*, both of which are invasive in the Seychelles. The vast majority of the retrieved seeds (97.9%, $n = 22,310$) were minute seeds (< 1 mm) of *C. hirta*, 1.9% of all seeds ($n = 437$) were from the 16 native species, and 0.15% were from the other invasive species *C. verum* ($n = 35$). Overall, native seeds were present in 66.3% of the droppings and non-native seeds were present in 55.1%.

Our data revealed strong evidence that considerably more droppings with seeds departed from the inselberg than arrived, independently of origin ($z = 3.01$, $p = 0.003$; Tables S3 & S4; Fig. 2A). By contrast, there was no evidence for differences in the number of droppings containing native and non-native seeds ($z = 1.02$, $p = 0.310$; Table S3), or differences in the number of seeds arriving to, and departing from the inselbergs ($z = 1.50$, $p = 0.134$; Table S3), neither for native nor non-native seeds (Table S4; Fig. 2B). However, there was strong evidence that the number of non-native seeds transferred in both directions was higher than that of natives ($z = -3.15$, $p = 0.002$; Tables S3 & S4; Fig. 2B). Neither the number of seeds ($z = 0.18$, $p = 0.859$) nor frequency of occurrence ($z = -0.60$, $p = 0.547$) was likely to change with the invasion level (Table S3).

Plant Recruitment

We recorded a total of 49,693 seedlings (inside = 23,402, 42.2 per m^2 ; outside = 26,291, 65.7 per m^2) from 17 of the 18 plant species transported by birds in our study. We also recorded abiotically dispersed seedling species, mainly non-native *Alstonia macrophylla* Wall. ex G. Don and endemic *Soulamea terminalioides* Baker, but they only comprised approx. 5.5% (inside = 3.7%, outside = 7.1%) of the total number of seedlings

registered. Results hereafter include only species dispersed by animals. The two non-native species accounted for 55.5% ($n = 27,563$) of all seedlings (48.3% *C. verum* and 7.2% *C. hirta*), and the remaining 44.5% ($n = 22,130$) belonged mainly to endemic broadleaves *M. elaeagni* (37.7%) and *E. sechellarum* (1.6%), and the palm *P. borsigianum* (1.6%). Interestingly, the native palms *M. elaeagni* (65.5%), *R. melanochaetes* (6.4%), and *D. nobilis* (5.4%) accounted for the majority of recorded saplings (92.6%, $n = 785$), whereas the two dominant non-native species *C. verum* and *C. hirta* accounted only for 7.4% of all recorded saplings ($n = 63$). Inselbergs harbored more saplings than the surrounding invaded forest (inside = 573, 1.03 per m^2 ; outside = 275, 0.69 per m^2).

Seedling density on inselbergs and in invaded forests was likely to reflect the dominant vegetation type, with more exotic seedlings outside and more native seedlings inside the inselbergs ($z = -22.21$, $p < 0.001$; Tables S5 & S6; Fig. 3A). Moreover, there was strong evidence that native sapling density was markedly higher than non-native sapling density in both forest types ($z = -3.68$, $p < 0.001$; Tables S5 & S6; Fig. 3B). Our data suggest that seedling or sapling density were independent from inselberg invasion level (Table S5).

Distance Effect

We did not detect any evidence that distance from the inselberg edge had an effect on seedling density, neither for native nor for non-native seedlings (Table S7; Fig. 4A). However, the density of native saplings was likely to decrease with distance from the inselberg edge, while the density of non-native saplings increased (Table S7; Fig. 4B).

There was no evidence for changes in native seedling ($z = 0.73$, $p = 0.467$) or sapling ($z = -0.54$, $p = 0.592$) species richness with distance from the inselberg to the invaded forest, or with the level of invasion (seedlings: $z = -1.13$, $p = 0.260$; saplings: $z = 0.12$, $p = 0.904$; Table S8).

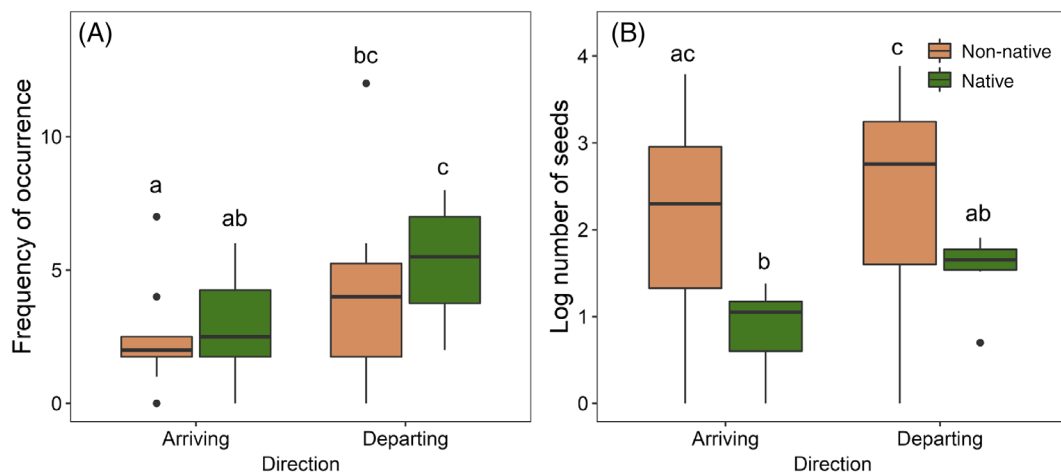


Figure 2. Boxplots depicting the total (A) number of droppings with seeds and (B) number of seeds (log-transformed) per site. Boxes illustrate the median (solid horizontal bar), 25th and 75th percentiles (upper and lower horizontal boxes) and $1.5 \times$ interquartile range of the data (whiskers). Different lowercase letters represent significant ($p < 0.05$) differences between predicted means using the most parsimonious GLMM and post-hoc pairwise comparisons with Tukey's test.

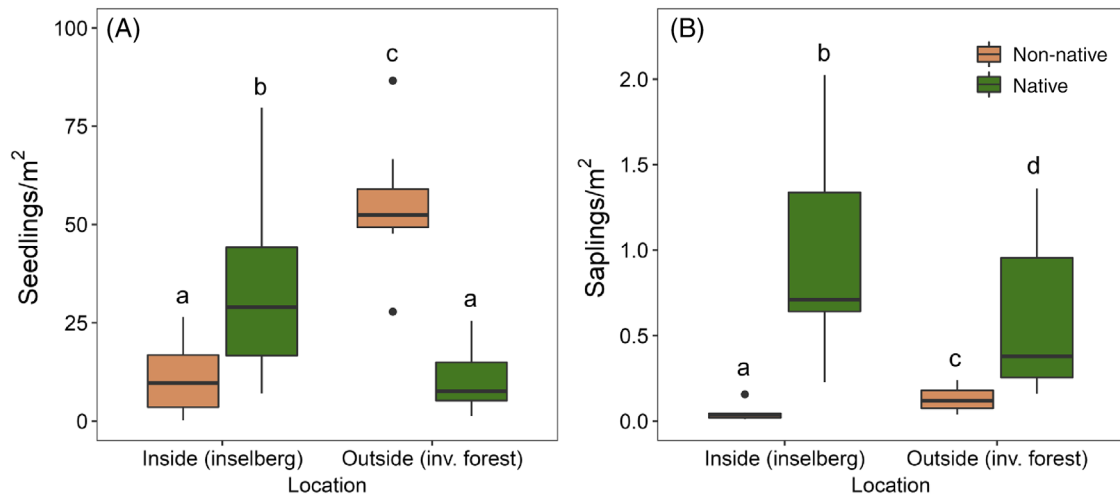


Figure 3. Boxplots depicting the mean number of (A) seedlings and (B) saplings per square meter and site. Boxes illustrate the median (solid horizontal bar), 25th and 75th percentiles (upper and lower horizontal boxes) and $1.5 \times$ interquartile range of the data (whiskers). Different lowercase letters represent significant ($p < 0.05$) differences between predicted means using the most parsimonious GLMM and post-hoc pairwise comparisons with Tukey’s test. Inside: Inselberg, outside: Invaded forest.

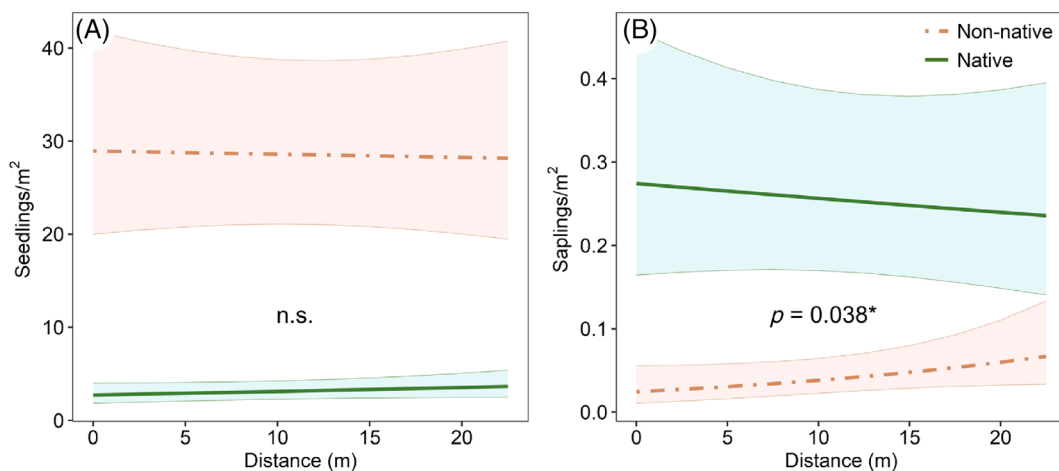


Figure 4. Effects of distance to the inselberg edge on (A) seedling and (B) sapling density. Lines represent model predictions and shaded areas 95% CI. (*) $p < 0.05$, “n.s.”: Non-significant.

Discussion

Our findings contribute new insights on the direction of seed dispersal between native forest remnants and the invaded matrix with implications for forest restoration and biological invasions. By providing a source of native seeds for dispersal and recruitment, inselberg vegetation promotes the resistance of native forest remnants to non-native propagule pressure. Yet previously disturbed sites may require assisted regeneration of native species or active restoration of degraded forests to re-create the resistance properties observed in the best preserved inselberg forests.

Specifically, we show that the quantity, identity, origin, and fate of seeds exchanged in both directions have strong implications for the dynamics of native plant communities at the landscape level. Although generally more seeds of non-native plants were

transported across the inselberg–invaded forest interface, the greater number of dispersal events from the inselberg to the invaded matrix indicates that plant communities on these mountain tops act as sources of native seeds for the surrounding degraded forest. These results imply that frugivorous birds use inselberg vegetation as a more important food source than the invaded forest. The impacts of plant establishment and recruitment were marked: despite the extensive propagule pressure of non-native plants, it appears that the spill-over effect of native seeds in the surrounding invaded forest had a positive effect on native plant recruitment, at least close to the inselberg edge. While the findings presented here apply specifically to our study system in the Seychelles, we believe that similar principles apply to other invaded islands and mainland plant communities, if they can draw on a predominately native frugivore community. The observed dynamics are less likely to apply

in severely depleted frugivore communities, such as on the islands of Guam (Rogers et al. 2021) or Rodrigues (Albert et al. 2021). Below we will discuss the ecological, conservation, and restoration implications of our findings.

Seed Transport

Despite the relatively small number of fleshy-fruited non-native plant species in our communities, a greater number of non-native seeds were transported in both directions. This indicates that the two non-native species, *C. verum* and particularly *C. hirta* (responsible for 98% of the total number of seeds dispersed), are highly integrated into the frugivores' diets. The great attractiveness of non-native fruits to frugivores could be explained by differences in fruit traits between invasive species and the most abundant native fruits in our community. The non-native species *C. verum* and *C. hirta* produce fruits with a higher nutritional quality and lower water content (i.e. greater ratio of dry pulp weight to total wet fruit weight) than native species on Mahé (Kueffer et al. 2009). Preference of frugivores for non-native fruits has been reported to promote, under some circumstances, competition between non-native and native plants for dispersers, which consequently can reduce seed dispersal success and recruitment of co-occurring native plants (Carlo et al. 2003; Traveset et al. 2012; Rumeu et al. 2019).

Interestingly, the dominance of non-natives fades in importance when the number of droppings that contain native or non-native seeds is considered. Non-native species in this study produce many small seeds, particularly in the case of *C. hirta*, and as these are often consumed and dispersed together, they likely suffer high post-dispersal density-dependent mortality (Harms et al. 2000; Correia et al. 2017). Small-seeded and fast-growing species like *C. hirta* may also show a lower tolerance of conspecific negative density dependence (CNDD) of seedlings compared to larger-seeded species, reducing seedling survival (Lebrija-Trejos et al. 2016). These notions support our data on plant recruitment, which showed that despite large propagule dispersal, non-native recruitment is considerably lower than native recruitment on and close to inselbergs. It is therefore important to emphasize the role of frugivorous birds using inselbergs as feeders and transporting seeds from the inselberg to the surrounding invaded forest, thereby providing propagules to the degraded forest and potentially promoting its restoration, or at least hindering the progression of the invasion.

Plant Recruitment

Our data suggest that despite the high non-native propagule pressure from the surrounding forest, inselbergs remain strongholds of native plant populations. Granitic inselbergs are sun- and wind-exposed rocky outcrops with scattered shrub vegetation and nutrient poor and acidic soils (pH ~ 4.5), while the adjacent secondary forests are shady, with denser vegetation and relatively nutrient-rich soils (Kueffer 2006). As native species evolved under these environmental conditions, inselbergs may offer some natural resistance to plant invasion (Porembski 2000), which is supported by the very low density of non-native plants on inselbergs that have

never been altered by humans (e.g. Bernica; Kaiser-Bunbury et al. 2011). The surrounding invaded forest represents a more suitable environment for germination and survival of non-natives, especially when kept partially disturbed and open by forest management. Our findings are consistent with the proposition that "stressful" habitats are more resistant to biological invasions (Rejmánek et al. 2013). Higher native seedling and sapling density on the inselbergs and in the surrounding forest, respectively, strongly indicates that native inselberg vegetation produced sufficient offspring for native plant recruitment both within and beyond the inselberg's native forest.

Overall survival rates of seedling to sapling stage seem to be low (natives = 3.55%, non-natives = 0.23%). These discrepancies in plant recruitment in the invaded forest are likely a result of higher establishment success of native species, despite the dominance of mature non-native plants in these forests (Schumacher et al. 2008). In a study conducted in forests predominately invaded by *C. verum*, Kueffer et al. (2007) found that the root mat created by adult cinnamon trees had a particularly strong negative effect on conspecific juveniles when compared to natives, showing remarkably low survival from the seedling to the sapling stage.

Nevertheless, our data on seed dispersal and plant recruitment suggest that inselbergs are threatened by the spread of non-native plants. Studies have shown that ecosystem responses to plant invasions are non-linear (Panetta & Gooden 2017), which suggests that losses in biodiversity and key ecosystem functions are likely to accelerate disproportionately with non-native plant invasion (Gooden et al. 2009; Thiele et al. 2010; Kaiser-Bunbury et al. 2011). That means inselbergs will require management interventions that aim to control non-native plant density and thereby ensure long-term benefits of native plant dispersal to inselberg plant refuges.

Distance Effect

The density of native saplings decreased while that of non-native saplings increased with distance from the native forest remnant, a pattern that did not exist for seedlings. Therefore, native seedling to sapling survival seems higher closer to the inselberg for natives and further away for non-natives. This suggests that inselbergs have a buffer effect that benefits native over non-native seedling survival, which fades with distance. The observed changes in sapling density with distance may be related to differences in habitat characteristics due to inherent attributes of inselbergs and their adjacent matrices (Hunter 2003). For instance, vegetation near the base of inselbergs receives increased moisture from run-off (Büdel et al. 2000), which, in some cases, can contribute to changes in soil chemistry and pH and a reduction of nutrients available to plants (Burke 2003). This decrease in soil fertility close to the inselberg is likely to benefit slow-growing natives, which are adapted to low-nutrient conditions compared to non-native saplings (Schumacher et al. 2009). Our results corroborate studies reporting transitional vegetation belts surrounding inselbergs (Porembski et al. 2000). Finally, as native and non-native seeds are expected to be similarly affected by dispersal through rainfall or gravity, higher non-native than native seedling density at the

base of the inselberg would be difficult to explain if abiotic primary or secondary seed dispersal played a significant role in driving these patterns. We conclude that the observed recruitment patterns are more likely related to differences in survival from seedling to sapling than to differences in seed deposition.

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Supporting Information

The following information may be found in the online version of this article:

- Figure S1.** Relationship between frequency of occurrence and number of fruits.
- Table S1.** Study sites characteristics.
- Table S2.** Number of seeds, FO, and number of fruits dispersed per plant species.
- Table S3.** Results of GLMMs on the effects of direction, plant origin and invasion level on seed transport.
- Table S4.** Post-hoc contrast tests results for seed transport.
- Table S5.** Results of GLMMs on the effects of direction, plant origin and invasion level on plant recruitment.
- Table S6.** Post-hoc contrast tests results for plant recruitment.
- Table S7.** Results of GLMMs on the effects of distance on plant recruitment.
- Table S8.** Results of GLMMs on the effects of distance on native species richness.