Jackfruit trees as seed attractors and nurses of early recruitment of native plant species in a secondary forest in Brazil

Milena Gomes · Eliana Cazetta · Ricardo Bovendorp · Deborah Faria

Received: 23 December 2020 / Accepted: 26 July 2021 / Published online: 7 August 2021
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

Abstract The Atlantic Forest is one of the most threatened tropical forests in the world, being drastically reduced, fragmented, and disturbed. The drastic process of anthropic occupation and exploitation of this biome has, in many cases, led to the introduction of exotic species, such as the jackfruits (Artocarpus heterophyllus). However, studies on the influence of jackfruits on the native biota are still scarce. Here we investigated the influence of fruit trees on the seed rain and early recruitment of seedlings in native remnants, comparing these patterns with those observed for a native species tapirira (Tapirira guianensis), which similarly to jackfruits, produces many fruits throughout the year, attracting a variety of frugivore species. Seed rain and seedlings observed under the jackfruits were both more abundant and equally rich to the assemblages reported under the native tapirira trees. In both species, co-specifics comprise a large part of the number of seeds (>70%) and seedlings (>45%) individuals and, although they attract similar seed assemblages, seedling composition diverge, particularly when co-specifics are excluded. We reported that jackfruits can attract a diverse seed and seedling assemblages, and we find no evidence that the presence of jackfruits negatively affects the arrival and initial recruitment of native plant species in the study area. These results should be analyzed with caution but considered when evaluating costs and benefits of management options to control exotic species.

Keywords Invasive alien species · Native species · Seed rain · Recruitment · Atlantic Forest

Introduction

Exotic species, i.e., those occurring outside their natural geographic boundaries, are increasingly becoming a common feature in human-dominated landscapes (D’Antonio et al. 2001). Some of these aliens become invasive, aggressively establishing populations into native ecosystems, eventually becoming a threat to native biotas (Stohlgren et al. 1999). Indeed, biological invasions are among the leading causes of biodiversity loss (Simberloff et al. 2013; Wonham and Carlton 2005), a process occurring globally at unprecedented levels (Simberloff et al. 2013). Even those protected, relatively more pristine areas are now facing the consequences of biological invasions (Pauchard and Alaback 2004; Sala et al.
of climate change (Finch et al. 2021). It has been rather amplificated considering the current predictions for such impacts are likely to be persistent and even anthropic influences on these dynamics (Dick et al. 2017; Ochocki and Miller 2017). Once arriving in new and suitable environments invasive species can affect native communities by altering competition and predation patterns, disrupting interaction networks, ultimately modifying the structure and functioning of the invaded system (Silva et al. 2021). Such impacts are likely to be persistent and even amplificated considering the current predictions of climate change (Finch et al. 2021). It has been assumed that invasive species can modify ecological interactions that have emerged throughout evolutionary times (Christian 2001; Traveset and Richardson 2014). Negative interactions between exotic and native plants are, therefore, expected as one of the most common and worrying consequences of biological invasions (Crooks 2002). However, a growing body of research also brings evidence that facilitating interactions between exotic and native species also occur, i.e., increases in densities and biomass of one or two interactive counterparts (Duffy and Baltz 1998; Schwindt et al. 2001). In some cases, the arrival of aliens can functionally replace native species lost or severely decreased by habitat disruptions (Rodriguez 2006), although critics claim for a more precautionary conclusion (Sotka and Byers 2019). Therefore, science needs to provide more evidence-based assessments that could increase our understanding of possible positive or negative impacts of alien and invasive species to support decision makers (Vimercati et al. 2020).

In Brazil, a country most recognized to host a rich and unique biota, the introduction of jackfruits (*Artocarpus heterophyllus*, Moraceae) is among the best reported cases with greatest invasive potential and, therefore, often considered among the major threats to local biota (Abreu and Rodrigues 2010). Native to Southeast Asia (Thomas 1980), the species was introduced in several countries for food, landscaping, and, in the case of Brazil, was also used to restore a degraded area in the colonial capital of Rio de Janeiro (Abreu 2008). Jackfruits produce large, nutritious, and abundant fleshy fruits highly appreciated by humans, but the species is also widely consumed by several animal frugivores, mainly mammals and birds (Lapenta and Procópio-de-Oliveira 2009; Mileri et al. 2012; Raíces et al. 2017; Taconi and Pires 2021). As a result of such massive consumption, large quantities of seeds may be dispersed (Faria et al. 2009; Oliveira et al. 2010), further expanding its distribution and increasing its potential to shape and structure plant and animal communities (Fabricante 2013). Although such situation often occurs in degraded areas, jackfruits are reported to be invading several protected areas in Brazil (Abreu 2008; Bergallo et al. 2016; Fabricante 2013; Raíces et al. 2017; Thomas 1980). Some studies alert that the presence of this species represents a significant threat to the phytodiversity of the Atlantic Forest (Abreu 2008; Barbosa 2016; Boni et al. 2009; Fabricante 2013; Mileri et al. 2012; Novelli et al. 2010), and managers are advised to take measures to control populations (Moura et al. 2020), including adult individuals’ girdling, seedling with- drawal, and chemical applications (Moura et al. 2020).

In the Atlantic Forest of southern Bahia, the largest remnants of coastal forests in the northeastern Brazil, jackfruits are widespread elements in the regional forest mosaic, particularly within the large area covered by cacao agroforestry, where this species is planted as fruiting and shading tree (Faria et al. 2009; Galindo-Leal and de Gusmao Camara 2003; Sambuichi et al. 2012). But it is also reported within native remnants, particularly those more degraded and secondary areas. For instance, a previous study has shown that a group of yellow-breasted-capuchins *Sapajus xanthosternos*, an endemic and threatened primate species inhabiting a protected area, consume and potentially disperse jackfruits (Canale et al. 2016). While foraging on such exotic species, which is more common on private properties surrounding the edge of Reserva Biológica de Una (Rebio-Una), these primates drop a rich and abundant seed rain comprising many native species consumed in mature and secondary forests (Bufalo et al. 2016; Cardoso et al. 2011; Oliveira et al. 2011). This primate species can potentially disperse jackfruit seeds within the forest reserve, with jackfruits also competing with native species for dispersal services (Canale et al. 2016). However, it is also important to understand whether seeds from native species drop under the jackfruits could potentially recruit or whether their development could be suppressed, for instance, by the high

© Springer
competition of jackfruit seedlings. Despite the potential of invading native areas, information regarding patterns of seed rain and seedling diversity and composition under the jackfruit crowns would feed the discussion on whether the ubiquitous presence of such exotics in disturbed areas could function as drain or sources for forest restoration (D’antonio and Meyerson 2002; Fridley et al. 2007).

In this context, we assessed patterns of seed rain and the early recruitment of seedlings under the canopy of jackfruits in a secondary forest within the limits of a protected area in the south of Bahia, Brazil. We also undertook the same assessment for a native tree species known as tapirira (Tapirira guianensis), which is a pioneer species locally abundant in both primary and secondary forests, also consumed by a variety of frugivores (de Oliveira et al. 2017; Guimarães 2003; Oliveira et al. 2010). We predict that, once both species can attract a rich assemblage of native frugivores, seed rain will be highly diverse (rich and abundant) under the canopy of both species, but the abundance and richness of seedlings from native species will be greater under the tapirira canopy because of the greater competitive pressure—possibly boosted by allelopathy—of jackfruit seedlings (Pere-domo and Magalhaes 2007; Costalonga and do Batitucci 2020).

Materials and methods

Study area

The study was carried out in the Una Biological Reserve, here in Rebio-Una (15° 17′ S, 39° 04′ W), located in the municipality of Una, Southern Bahia, Brazil (Fig. 1). It is a federally protected area representing one of the few and most important forest remnants of the Atlantic Forest of northeastern Bahia. The landscapes in the region are composed of forest fragments under different levels of regeneration, immersed in a complex matrix that includes pastures, secondary forest, and forest crops such as cocoa (Theobroma cacao), piaçava (Attalea funifera), and rubber trees (Hevea brasiliensis) (de Oliveira et al. 2017). The original vegetation is classified as wetland rainforest (Oliveira-Filho and Fontes 2000), a climatic type Af according to the classification of Köppen (Mori et al. 1983), characterized as wet and warm forests with annual precipitation of 1800 mm, with no defined dry season and with average temperature at about 24–25 °C (Mori et al. 1983).

Sampling design

We conducted the study from January to July 2017, when we selected 14 individual jackfruit trees and 14 tapiriras, with a minimum distance of 10 m from each individual. Both species presented fruiting periods within the monitored interval, and all selected individuals showed ripe fruits along the 7 months evaluated. All individuals were located within the limits of a foraging area of a group of capuchin monkeys, which were identified and monitored in a previous study carried out at Rebio-Una (Ferraco 2013). This foraging area is partially located within the Rebio-Una, comprising a mosaic of mature and secondary forests, but it also included small patches, shade cocoa, and rubber tree plantations located within private properties on the border of the reserve. Within this mosaic, we selected the sampling trees in two areas comprising a buffer of 200 m radius (0.13 km²); one with a predominance of tapiriras and without the presence of jackfruits and another with a dominance of jackfruits but without tapiriras (Fig. 1). The two sample areas are closely located (~ 1000 m apart), and are within the same mosaic of secondary forest, subject to similar composition of tree species and frugivore assemblages, and to soil, and climate conditions.

Seed rain and early recruitment

A total of 56 seedling plots were installed in the study area, 28 under the canopy of each focal species, 2 traps per plant. Each seed trap was fabricated with a 20 mm PVC tube, framing a 60 cm × 60 cm net (synthetic—comprising a sampling area of 360 cm²), and was installed suspended approximately 50 cm from the ground. In each monitored tree, we also installed one seedling recruitment plot, basically consisting of a 60 × 60 cm squared frame made by 20 mm PVC tube, located under each tree canopy within which all seedlings were reported. The area under the canopy of each tree was divided into four quadrants and the traps were randomly placed near the trunk of the monitored tree, although we pre-defined that each quadrant would contain only one type of trap. Once in a month we counted and identified all seed and seedling
individuals observed in each trap, accounting for all species, also excluding those co-specifics of each mother plant. After each counting, seeds were removed from traps, kept in paper bags, sent to the Laboratory of Applied Ecology at UESC where they were compared to a previous reference collection and identified at the lowest possible taxonomic level. By contrast, seedling recruitment was considered by the set of seedlings recruited in each trap after the start of the study, including seedlings and juveniles, and each individual was tagged (plastic label attached by a cotton thread) to avoid counting twice. Seedlings were considered as (1) individuals up to 3 mm thick at the base of the plant; (2) individuals with a single rod; (3) seedling recruitment was considered by the set of seedlings recruited in each trap after the start of the study, including seedlings and juveniles. Individuals with evidence of seed germination (follow the monthly follow-up for 6 months of the field). Seedlings were separated into morphospecies and identified at the family level whenever possible using the literature. We evaluated seed rain and recruitment plots each month for 6 months, except during July when sampling was not possible due to personal safety issues in the Rebio-Uma.

Statistical analyses

We used Generalized Linear Models (GLM) to examine the differences in seedling and seed richness and abundance among *A. heterophyllus* and *T. guianensis* species. For this analysis, we assume as a categorical explanatory variable the combination of two factors, being the type of factor (seeds and seedlings) and group factor (*A. heterophyllus* and *T. guianensis*). By combining these two factors, we obtained an explanatory variable with four levels, we thus acquire a complete factorial that demonstrates the effect of abundance and seedling and seed richness among the focal species. Referring to the dispersion effect of seed abundance and seedling abundance, we used Poisson error distribution (log-linear models) and when the data presented over-dispersion, we assumed the quasipoisson approximation to correct the data.
To evaluate the taxonomic composition of seeds and seedlings between both focal species, we performed a Permutational Multivariate Variance Analysis (PERMANOVA) (Anderson and Walsh 2013) based on Bray–Curtis dissimilarity matrices. To understand the possible differences in seed and seedling composition among predictors, we used the non-metric Multidimensional Scaling (NMDS) analysis.

Results

After monitoring the 28 focal trees, we reported a total of 199 seeds from 30 species (Table 1) and 134 seedlings of 22 species. Under the jackfruits, we observed a total of 129 seeds, 80% comprising jackfruit seeds and the remaining seeds from 14 different species. Of the 70 seeds found under the Tapirira, 70% of the seeds were of 22 different species of tapirira (Table 1). In the same period, a total of 134 seedlings of 22 species were observed recruiting under the canopy of the two focal species. Of these, 79 seedlings from 11 species were observed under the jackfruit trees, 76% comprising jackfruit seedlings, while under the tapirira we observed 55 seedlings from 6 species, with tapirira comprising 45% of these individuals (Table 2).

On average, seeds were more abundant than seedlings when all species are considered, but when co-specifics are discarded, i.e., after excluding seed and seedling from the mother plant, the average abundance of both seeds and seedling was significantly higher in jackfruits than those reported under the crown of the tapiriras (Fig. 2). However, we found no significant differences on average species richness of neither seeds nor seedlings between the two focal trees, even when co-specifics are excluded (Fig. 3).

We observed that each tree species comprised different assemblages of seeds under their crowns (Table 3), but only when co-specifics are included in the analysis, i.e., when seeds of jackfruits and tapirira are excluded from the assemblage reported bellow each mother plant, seeds composition did not differ between jackfruits and tapirira (Table 4). In this case, however, NMDS showed a larger variability on the composition among jackfruit individuals, whereas this was more similar among those tapirira trees (Fig. 4). By contrast, each tree species comprised different assemblages of seedlings even after controlling for co-specifics. Nevertheless, the NMDS revealed that, when co-specifics are excluded, the similarity of seedling composition between both tree species increases (Fig. 4).

Discussion

Our study shows that jackfruits are important perches attracting an abundant and rich seed rain, largely comprising a variety of native species. On average, seed rain and seedling assemblages under the jackfruits were both more abundant and equally rich to the assemblages reported under the native tapirira trees. In both species, co-specifics comprise a large part of the number of seeds (> 70%) and seedlings (> 45%) individuals. However, while both species attract similar assemblages of seeds, the composition of seedling assemblages diverge between focal species. Nevertheless, our analysis also showed that when co-specifics were excluded, the divergence between recruitment assemblage decreased.

The tropical climate along a large strip of the Atlantic Forest, with an intense frequency of rainfall and high average temperatures (Dean 1996), guarantees to the exotic species favorable conditions to abundant fruiting throughout the year. Each tree can produce more than 100 fruits, each averaging 500 seeds (Abreu and Rodrigues 2010). Furthermore, the dispersal of the jackfruit seeds occurs mainly through barocory, therefore, a major part of the fruits is deposited under the canopy of the mother plant (Abreu 2008; Bergallo et al. 2016; Abreu and Rodrigues 2010; Morton 1965), often with a high recruitment rate (Fabricante 2013; Silva 2014b). In many cases, the high availability of fruits and seeds produced by this exotic species is so high that it exceeds the consumption capacity of frugivores, such as reported for an insular area in Brazil (Oliveira et al. 2010). This deficit of consumers is likely to be greater in defaunated areas because the low abundance of consumers further increases the abundance of viable seeds and recruiting individuals under the canopy of the jackfruits.

In addition to seed predation, terrestrial mammals may also play an important role in the secondary dispersal of jackfruits, consuming and dispersing the fallen seeds under the mother plant. Raíces et al. (2017) evaluating the role of mammals in the Jackfruit
seed dispersal in Ilha Grande State Park, Brazil, found that the terrestrial mammalian species Didelphis aurita, Cuniculus paca, and Trinomys dimidiatus are among the main dispersers of jackfruit seeds. Plant species can compete for seed dispersers (Bergallo et al. 2016), particularly in highly defaunated areas. Therefore, the high local abundance of seeds of exotic species would increase its dispersal in detriment of this service to the remaining native species (Oliveira et al. 2010). In southern Bahia, primates represent one of the few frugivors capable of effectively disperse medium and large seeds, whose original dispersers are locally extinct due to hunting (Oliveira-Filho and Fontes 2000; Rocha et al. 2015). Oliveira et al. (2011), studying the use of agroforests in the same region where our study was concentrated reported that jackfruits are the only ubiquitous species registered in the diet of all groups of primates—the endemic golden-headed lion tamarins (Leontopithecus chrysomelas)—present in great abundance and being

### Table 1 Composition of seed species deposited under the canopy of the jackfruits (Artocarpus heterophyllus) and tapirira (Tapirira guianensis) in the Una Biological Reserve, Bahia, Brazil

| Family        | Species                     | Total collected | Jackfruit trees | Tapirira trees |
|---------------|-----------------------------|-----------------|-----------------|----------------|
| Anacardiaceae | *Tapirira guianensis*       | 22              | 0               | 22             |
| Arecaceae     | *Elaeis guianensis*         | 6               | 1               | 5              |
| Arecaceae     | *Euterpe edulis*            | 1               | 1               | 0              |
| Cannabaceae   | *Celtis ehrenbergiana*      | 4               | 1               | 3              |
| Erythroxylaceae| sp. I                      | 2               | 0               | 2              |
| Euphorbiaceae | *Brasilicroton mamoninha*   | 3               | 0               | 3              |
| Euphorbiaceae | sp. I                      | 1               | 0               | 1              |
| Euphorbiaceae | *Manihot glaziovii*         | 2               | 1               | 1              |
| Fabaceae      | *Andira surinamensis*       | 2               | 0               | 2              |
| Hernandiaceae | *Sparattanthelium botocudorum* | 2          | 0               | 2              |
| Malvaceae     | *Ceiba ventricosa*          | 3               | 2               | 1              |
| Malvaceae     | *Eriotheca globosa*         | 2               | 1               | 1              |
| Malvaceae     | *Theobroma cacao*           | 5               | 4               | 1              |
| Malvaceae     | *Trichilia casareti*        | 1               | 0               | 1              |
| Moraceae      | *Artocarpus heterophyllus*  | 104             | 104             | 0              |
| Moraceae      | *Brosimum glaziovii*        | 2               | 2               | 0              |
| Moraceae      | *Brosimum rubescens*        | 1               | 0               | 1              |
| Moraceae      | *Ficus clusiifolia*         | 2               | 0               | 2              |
| Moraceae      | *Ficus gomelleira*          | 2               | 0               | 2              |
| Peraceae      | *Chaetocarpus echinocarpus* | 3               | 1               | 2              |
| Polygonaceae  | *Coccoloba rosea*           | 3               | 0               | 3              |
| Rubiaceae     | sp. I                      | 2               | 2               | 0              |
| Sapindaceae   | *Capania scrobiculata*      | 1               | 1               | 0              |
| Sapindaceae   | *Matayba guianensis*        | 2               | 0               | 2              |
| Morfospecies  | I                           | 1               | 1               | 0              |
| Morfospecies  | II                          | 1               | 1               | 0              |
| Morfospecies  | III                         | 6               | 1               | 5              |
| Morfospecies  | IV                          | 2               | 0               | 2              |
| Morfospecies  | V                           | 5               | 1               | 4              |
| Morfospecies  | VI                          | 4               | 3               | 1              |
| Morfospecies  | VII                         | 1               | 0               | 1              |
| Morfospecies  | VIII                        | 1               | 1               | 0              |
consumed during periods of fruit shortage. In this case, primates consume fruits still hanging on the tree, that is, before falling ripe to the ground. However, at least in the case of the primate *S. xanthosthernos* monitored at Rebio-Unia, the dispersal effectiveness is quite small (de Oliveira et al. 2017). Although the *S. xanthosthernos* consumes jackfruits (Canale et al. 2016), fieldwork observations suggest that this primate can be a poor disperser of jackfruits and a better disperser of tapirira due to the difference in seeds size and consumption (unpublished data). Even though the entire region of southern Bahia is highly defaunated (Canale et al. 2012), it is possible that the low density of extant medium-sized species, particularly

### Table 2

| Family          | Species              | Total collected | Jackfruit trees | Tapirira trees |
|-----------------|----------------------|-----------------|-----------------|----------------|
| Anacardiaceae   | *Tapirira guianensis* | 25              | 0               | 25             |
| Apocynaceae     | sp. I                | 2               | 0               | 2              |
|                 | sp. II               | 1               | 0               | 1              |
| Burseraceae     | *Protium heptaphyllum* | 5               | 0               | 5              |
| Clusiaceae      | sp. I                | 2               | 0               | 2              |
| Euphorbiaceae   | *Mabea* sp.          | 1               | 0               | 1              |
|                 | *Sorocea* sp.        | 5               | 2               | 3              |
| Fabaceae        | *Inga* sp.           | 6               | 6               | 0              |
| Moraceae        | sp. I                | 1               | 1               | 0              |
|                 | *Artocarpus heterophyllus* | 60              | 60             | 0              |
| Myrtaceae       | sp. I                | 2               | 2               | 0              |
| Rubiaceae       | sp. I                | 4               | 0               | 4              |
|                 | sp. II               | 3               | 0               | 3              |
|                 | sp. III              | 1               | 0               | 1              |
| Sapindaceae     | sp. I                | 2               | 1               | 1              |
| Sapotaceae      | sp. I                | 1               | 1               | 0              |
| Vochysiaceae    | sp. I                | 2               | 0               | 2              |
|                 | Morfospespecies I    | 1               | 1               | 0              |
|                 | Morfospespecies II   | 2               | 1               | 1              |
|                 | Morfospespecies III  | 2               | 1               | 1              |
|                 | Morfospespecies IV   | 4               | 2               | 2              |
|                 | Morfospespecies V    | 2               | 1               | 1              |
inhabiting protected areas such as Rebio-Una, may help to disperse jackfruit seeds from the more urbanized areas surrounding this protected area to its interior (Cardoso et al. 2011; Mileri et al. 2012).

Although studies have shown that jackfruits can restrict the initial recruitment of native species, thus reducing the diversity of native plant assemblages (Abreu and Rodrigues 2010; Fabricante 2013; Morton 1965; Novelli et al. 2010), we did not find any evidence for such effect in our study. The seed rain and recruiting assemblage reported under the monitored jackfruit individuals are both as diverse and as abundant when compared to the native tapirira, one of the most common pioneer species in secondary and primary forests (Oliveira et al. 2011; Silva and Tabarelli 2000). Besides, seed rain composition is similar between both focal species, even considering that jackfruits and tapirira differ regarding the foraging frugivore assemblage. The native species tapirira exhibits a high production of small black fruits (width 0.68 cm; length 1.08 cm) attracting a dispersing fauna different from that reported for the exotic species, like several birds (Ortalis guttata, Eupsittula aurea, Pteroglossus aracari, Brotopheris tirica, and Cacicus cela) with varied strategies of capture and manipulation of the seeds (Guimaraes 2003; Ribeiro and Silva 2005; Silva 2014b). Such more diverse array of frugivores feeding on fruits of tapirira may partially explain a larger variability in the richness of seeds and seedlings under the crown of tapirira compared with jackfruits. That is, while the primary and secondary dispersal of the jackfruits (width 1.60 cm; length 2.10 cm) occurs, respectively, by barocory and terrestrial medium and large mammals such as Tapirus terrestris, Nasu nasua, Cuniculus paca, and Dasyprocta leporina (Alvino et al. 2005; Morton 1965; Oliveira et al. 2010; Thomas 1980; Taconi and Pires 2021), birds and small mammals are the main consumers and dispersers of tapirira fruits, even though primates also consume tapirira fruits. Despite these differences, when we excluded the presence of seeds produced by the mother plant, we found a high similarity in the composition of the seed rain between them. Both species present a rich, abundant, and diverse seed rain, together comprising at least 21

### Table 3

| Metric          | Assemblages          | Coefficients                      | Estimate | Std.Error | t.value | p    |
|-----------------|----------------------|-----------------------------------|----------|-----------|---------|------|
| **Abundance**   | All species²         | Tree species                      | 0.2834   | 0.2748    | -1.0310 | 0.30 |
|                 |                      | Seeds and seedlings               | 0.4845   | 0.2289    | 2.116   | 0.03*|
|                 |                      | Tree species and Seeds and seedlings | 0.2409 | 0.3595 | -0.670 | 0.50 |
| **Excluding co-specifics¹** | Tree species | 0.6061 | 0.2930 | 2.069 | 0.03* |
|                 |                      | Seeds and seedlings               | 0.1054   | 0.3249    | 0.324   | 0.74 |
|                 |                      | Tree species and Seeds and seedlings | 0.3684 | 0.3934 | 0.937 | 0.34 |
| **Richness**    | All species¹         | Tree species                      | 0.3409   | 0.2312    | 1.474   | 0.14 |
|                 |                      | Seeds and seedlings               | 0.0307   | 0.2481    | 0.124   | 0.90 |
| **Excluding co-specifics¹** | Tree species | -0.0532 | 0.3263 | -0.163 | 0.87 |
|                 |                      | Tree species and Seeds and seedlings | 0.5436 | 0.2963 | 1.834 | 0.06 |
|                 |                      | Seeds and seedlings               | 0.0540   | 0.3289    | 0.164   | 0.86 |
| **Tree species and Seeds and seedlings** | 0.1495 | 0.4083 | 0.366 | 0.71 |

Significant p values (p < 0.05) are assigned by *

Abundance or richness models followed the Poisson¹ or Quasi-Poisson² distributions

### Table 4

| Source of variation | F      | p      |
|---------------------|--------|--------|
| Total seeds         | 1249   | 0.0001*|
| Seeds without mother plant effect | 1651 | 0.0746 |
| Total seedlings     | 1544   | 0.0001*|
| Seedlings without mother plant effect | 2721 | 0.0025*|

Significant p values (p < 0.05) are assigned by *
species of native flora. Nevertheless, it is also possible that other factors not considered here influenced the observed pattern, in particular, the neighboring effect in dispersal of a given species could be enhanced by the co-occurrence of other fruiting species that are also consumed by the same dispersal vectors (Carlo 2005).

However, this similarity in the seed rain is not reflected in the composition of the recruiting assemblages. Indeed, among the major factors influencing plant recruitment are the availability—quantity and quality—of suitable sites for germination and antagonistic interactions, such as local competition—particularly regarding co-specifics—and predation pressure (Alvino et al. 2005; Crawley 1990). These factors may act as barriers limiting seedling recruitment at specific sites (Zimmerman et al. 2000). Differences in conditions under the canopy of the two species can determine different responses in the germination capacity, and survivor likelihood, of the seed assemblage. Among the emergent species highly abundant under the jackfruit canopies are some species characteristics of secondary succession. In particular, the genus Inga was very abundant and recruited exclusively under this exotic tree (Alvino et al. 2005). Inga and jackfruit seeds have similar characteristics, they are recalcitrant, have higher growth rates when exposed to light, and when water is reduced below 29%, the seeds are unable to germinate (Barrozo et al. 2014; da Silva 2014a). Although the jackfruit is classified as shade-tolerant species, its seeds germinate better in intermediate clearings than in shaded areas (Khan 2004). Nevertheless, it should be emphasized that the early recruitment of native plants under the jackfruits does not guarantee their establishment into the subsequent ontogenetic stages (Siqueira 2006). Most likely, as seedlings of this exotic species develop, these dynamics can change due to density-dependent mortality (da Fig. 4 Multidimensional Non-Metric Scaling (NMDS) of the composition of seeds (a, b) and seedling (c, d) assemblages, considering all seedlings assemblages (a, c) and when co-specifics (seeds from mother plant) are not considered (b, d) present under the canopy of the jackfruit (Artocarpus heterophyllus) and tapirira (Tapirira guianensis) trees, in southern Bahia, Brazil. Full circles (●) and add signs (+) depict the set of seedlings recruited under jackfruits and tapirira trees, respectively.
Silva 2014a). In fact, da Silva (2014a) evaluating the mortality of regenerant component of native species under jackfruit canopy revealed a lower abundance of native regenerants in the presence of the exotic species than in areas where the species was absent.

Implications for conservation

Habitat loss has led to a decrease in fruit availability in the southern region of Bahia, mainly from shade-tolerant species (Pessoa et al. 2017). The presence of jackfruits within, or on properties in the vicinity of Rebio-Una might play an important role in the maintenance of frugivore populations in the region, mainly during periods of fruit shortage (Pessoa et al. 2017). Due to this characteristic, any recommendation or management strategy should require a deep and careful evaluation. Strategies to eradicate exotic plant species might also imply more complex and, sometimes, unattended effects such as those impacting local frugivores (Oliveira et al. 2011). Our results reinforce that this exotic species does attract a rich and abundant seed rain, comparable to those reported in other native and abundant plant species. More important, despite the high abundance of both seeds and recruits of jackfruits, which could decrease the likelihood of native recruits by competition or even allelopathy, we find no evidence that this exotic species limits the early recruitment of the native seedlings. Nevertheless, we do not know whether this pattern remains unchanged over time, i.e., it is possible to picture the jackfruits acting as an exotic element with relevance to forest regeneration and recovery of degraded areas. In addition, other unmeasured factors could limit our conclusions, particularly regarding differences of possible underlying mechanisms determining the seed rain and recruitment patterns in each species assessed. However, we highlight that (1) small differences in the composition of native seedlings recruited may represent large differences in the long term, and (2) the jackfruits may present a greater competitive advantage in later recruitment stages, limiting the recruitment of native species in more advanced ontogenetic phases and acting as an ecological filter with adverse effects under forest regeneration. To propose either the use or the control of jackfruits as options for management actions, it is essential to investigate in more detail whether recruits will successfully be established. Short-term and very localized studies can limit our ability to adequately evaluate the ecological impacts of invasive species in natural systems (Crystal-Ornelas and Lockwood 2020). Thus, it is necessary to move forward to better understand the role of these exotic trees in the successional trajectory of the local community.

Acknowledgements The authors are grateful to Helena Bergallo and Margarita Florêncio by the insightful suggestions on an early draft, to Pavel Dodonov for his valuable help with the analysis and to Leticia Ferraço for sharing some important information regarding the jackfruits from Una region. This study was possible due to research grants from Sistema Nacional de Pesquisa em Biodiversidade—Sisbiota/Conselho Nacional de Desenvolvimento Cinético e Tecnológico—CNPq (Grant Number 563216/2010-70, Pró-Reitoria de Pesquisa e Pós-Graduação—PROPP/Universidade Estadual de Santa Cruz—UESC (Grant Number 00220.1100.1774). DF and EC were granted by a CNPq fellowships (Numbers 307990/2018-4 and 306373/2018-1, respectively) and MG was sponsored by a CNPq fellowship from Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade-PGECB. The present study is a publication number 42 of the REDE SISBIOTA.

Author contributions Conceptualization: DF and MG; Methodology: DF, MG, and EC; Formal analysis and investigation: MG; Writing—original draft preparation: MG, DF, and EC; Writing—MG, DF, EC, and RB; Funding acquisition: DF; Resources: DF; Supervision: DF.

Funding This study was possible due to research grants from Sisbiota/CNPq (Grant Number 563216/2010-70, PROPP/UESC (Grant Number 00220.1100.1774). DF and EC were granted by a CNPq fellowships (Numbers 307990/2018-4 and 306373/2018-1, respectively) and MG was sponsored by a CNPq fellowship from Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade-PGECB.

Data availability The data that support the findings of this study will be available in the dryad repository.

Declarations

Consent to participate All authors consented to participate in the manuscript.

Consent for publication All authors consent to publish the manuscript under acceptance.

References

Abreu RCR (2008) Dinâmica de populações da espécie exótica invasora Artocarpus heterophyllus L. (Moraceae) no Parque Nacional da Tijuca–Rio de Janeiro. Dissertation, Instituto de Pesquisa Jardim
Abreu RCR, Rodrigues PJF (2010) Exotic tree Artocarpus heterophyllus (Moraceae) invades the Brazilian Atlantic Rainforest/Árvore exótica Artocarpus heterophyllus (Moraceae) invade a Mata Atlântica brasileira. Rodriguésia 61:677–688

Alvino FO, Silva MFF, Rayol BP (2005) Potencial de uso das espécies arbóreas de uma floresta secundária, na Zona Bragantina, Pará, Brasil. Acta Amazon 35:413–420

Anderson MJ, Walsh DC (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol Monogr 83:557–574

Barbosa U (2016) Aspectos ecológicos e influência de Artocarpus heterophyllus Lam. na estrutura do componente arbóreo de fragmento florestal urbano. Dissertation, Universidade Federal Rural de Pernambuco

Barrozo LM, Ursulino EA, de Araujo LR, Sena DVA, de Medeiros DS, dos Santos JC (2014) Quality seeds Inga parviflora Lam., e Artocarpus heterophyllus Lam., na Reserva Biológica Paulo Fraga Rodrigues, antiga Reserva Biológica Duas Bocas, no Espírito Santo, Sudeste Brazil. Acta Amazon 35:413–420

Bergallo HG, Bergallo AC, Rocha HB, Rocha CFD (2016) Invasion by Artocarpus heterophyllus (Moraceae) in an island in the Atlantic Forest Biome, Brazil: distribution at the landscape level, density and need for control. J Coast Conserv 20:191–198

Boni R, Novelli FZ, Silva AG (2009) Um alerta para os riscos de bioinvasão de jaca, Artocarpus heterophyllus Lam., na Reserva Biológica Paulo Fraga Rodrigues, antiga Reserva Biológica Duas Bocas, no Espírito Santo, Sudeste do Brasil. CEP 29:140:500

Bufalo FS, Galetti M, Culot L (2016) Seed dispersal by primates and implications for the conservation of a biodiversity hotspot, the Atlantic forest of South America. Int J Primatol 37:333–349

Canale GR, Peres CA, Guidorizzi CE, Gatto CA, Kierulf MC (2012) Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PLoS ONE 7:e41671. https://doi.org/10.1371/journal.pone.0041671

Canale GR, Suscke P, Rocha-Santos L, Bernardo CS, Martins Kierulf MC, Chivers DJ (2016) Seed dispersal of threatened tree species by a critically endangered primate in a Brazilian Hotspot. Folia Primatol (Basel) 87:123–140. https://doi.org/10.1159/000447712

Cardoso NA, Le Pendu Y, Lapenta MJ, Raboy BE (2011) Fruigivory patterns and seed dispersal by golden-headed lion tamarins (Leontopithecus chrysomelas) in Una Biological Reserve, Bahia, Brazil. Mammalia 75:327–337. https://doi.org/10.1515/mamm.2011.042

Carlo TA (2005) Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. Ecology 86:2440–2449

Christian CE (2001) Consequences of abiological invasion reveal the importance of mutualism for plant communities. Nature 413:635–639

Costalonga SA, do Batitucci MCP (2020) Avaliação alelopática e fitoquímica de Artocarpus heterophyllus Lam. e Eriobotrya japonica (Thunb.) Lindl., duas espécies invasoras presentes em unidades de conservação do Espírito Santo, Brasil. Braz J Dev 6:56486–56505

Crawley MJ (1990) The population dynamics of plants. Philos Trans R Soc B 330:125–140

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166

Crystal-Ornellas R, Lockwood JL (2020) The “known unknowns” of invasive species impact measurement. Biol Invasions 22:1513–1525

D’antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restor Ecol 10:703–713

D’antonio C, Meyerson LA, Denslow JS (2001) Exotic species and conservation: research needs. In: Soulé ME, Orians GH (eds) Conservation biology. Research priorities for the next decade. Island Press, Washington, pp 59–80

da Silva CRB, Beaman JE, Dorey JB, Barker SJ, Congedi NC, Elmer MC, Galvin S, Tuiwawa M, Stevens MI, Alton LA, Schmarz MP, Kellermann V (2021) Climate change and invasive species: a physiological performance comparison of invasive and endemic bees in Fiji. J Exp Biol. https://doi.org/10.1093/comphys/coab038

Dean W (1996) A ferro e fogo: a história e a devastação da Mata Atlântica brasileira. Companhia das Letras, São Paulo

de Oliveira SN, de Carvalho Júnior OA, Gomes RAT, Guimarães RF, McMahon CM (2017) Landscape-fragmentation change due to recent agricultural expansion in the Brazilian Savanna, Western Bahia, Brazil. Reg Environ Change 17:411–423

Dick JT et al (2017) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. J Appl Ecol 54:1259–1267

Duffy JD et al (2007) The invasion paradox: reconciling patterns and process in species invasions. In: Poland TM, Patel-Weynand T, Fridley JD et al (eds) Conservation biology: existing, emerging and future invasive alien species. J Appl Ecol 54:1259–1267

Fabricante JR (2013) Sociabilidade de espécies da mata atlântica com a exótica invasora Artocarpus heterophyllus Lam. Revista de Biologia Neotropical 10:18–25

Faria D et al (2009) Forest structure in a mosaic of rainforest sites: the effect of fragmentation and recovery after clear cut. For Ecol Manag 257:2226–2234

Ferreira LL (2013) Efetividade da dispersão de sementes pelo macaco-prego-do-peito-amarelo (Sapajus xanthosternos, Primates: Cebidae) em um mosaico florestal da Mata Atlântica: implicações para a regeneração de florestas. Dissertation, Universidade Estadual de Santa Cruz

Finch DM, Butler JL, Runyon JB, Fettig CJ, Kilkenny FF, Jose S et al (2021) Effects of climate change on invasive species in invasive species. In: Poland TM, Patel-Weynand T, Finch DM, Ford MC, Hayes DC, Lopez VM, Vanessa M (eds) Forests and rangelands of the United States: a comprehensive science synthesis for the United States forest sector. Springer International Publishing, Heidelberg, pp 57–84

Fridley JD et al (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. https://doi.org/10.1890/0012-9658(2007)88[3:tipra]2.0.co;2

Galindo-Leal C, de Gusmao Camara I (2003) The Atlantic forest of South America: biodiversity status, threats, and outlook. Center for Applied Biodiversity Science and Island Press, Washington
Guimarães MA (2003) Frugivoria por aves em Tapiir a guianensis (Anacardiaceae) na zona urbana do município de Araruama, estado do Rio de Janeiro, sudeste brasileiro. Atualidades Ornitológicas 116:12
Khan ML (2004) Effects of seed mass on seedling success in *Artocarpus heterophyllus* Lam., a tropical tree species of north-east India. Acta Oecol 25:103–110
Lapenta MJ, Procopio-de-Oliveira P (2009) The fate of seeds dispersed by golden lion tamarins (*Leontopithecus rosalia*) in an Atlantic forest fragment, Brazil. Trop Conserv Sci 2:266–281
Mileri M, Passamani M, Eutrópio F, Oliveira A (2012) Removal of seeds of exotic jackfruit trees (*Artocarpus heterophyllus*, Moraceae) in native forest areas with predominance of jackfruit trees in the Duas Bocas Biological Reserve, Southeastern Brazil. Int J Ecosyst 2:93–98
Mori SA, Boom BM, Carvalho AM, Santos TS (2013) Southern Bahian moist forests. Bot Rev 49:155–232
Morton JF (1965) The jackfruit (*Artocarpus heterophyllus* Lam.):* its culture, varieties and utilization. Proc Fla State Hortic Soc 78:336–344
Moura CJR, Gaspar M, Bergallo HG, Lacerda AC, Ferreguetti A (2020) Closing the snack bar: developing methods for jackfruit tree (*Artocarpus heterophyllus* Lamk.) control in Brazil. FLORAM 27:1–10
Novelli FZ, Moreira RPG, Duca C, Silva AG (2010) O papel da barocoria na estruturação da população da jaqueira, *Artocarpus heterophyllus* Lam. na Reserva Biológica de Duas Bocas, Cariacica, Espírito Santo. Nat Line 8:91–94
Ochoki BM, Miller TE (2017) Rapid evolution of dispersal ability makes biological invasions faster and more variable. Nat Commun 8:14315. https://doi.org/10.1038/ncomms14315
Oliveira L, Hankerson S, Dietz J, Raboy B (2010) Key tree species for the golden-headed lion tamarin and implications for shade-cocoa management in southern Bahia, Brazil. Anim Conserv 13:60–70
Oliveira LC, Neves LG, Raboy BE, Dietz JM (2011) Abundance of jackfruit (*Artocarpus heterophyllus*) affects group characteristics and use of space by golden-headed lion tamarins (*Leontopithecus chrysomelas*) in Cabruca agroforest. Environ Manag 48:248–262. https://doi.org/10.1007/s00267-012-0958-3
Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. Biotropica 32:793–810
Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of South-Central Chile. Conserv Biol 18:238–248
Perdomo M, Magalhães LMS (2007) Ação alelopática da jaqueira (*Artocarpus heterophyllus*) em laboratório. Floresta Ambient 14:52–55
Pessoa MS, Rocha-Santos L, Talora DC, Faria D, Mariano-Neto E, Hamburger A, Cazetta E (2017) Fruit biomass availability along a forest cover gradient. Biotropica 49:45–55
Raíces DS, Ferreira PM, Mello JH, Bergallo HG (2017) Smile, you are on camera or in a live trap! The role of mammals in dispersion of jackfruit and native seeds in Ilha Grande State Park, Brazil. Nat Conserv Res 2:78–89
Ribeiro LB, Silva MG (2005) Comportamento alimentar das aves *Pitangus sulphuratus*, *Coereba flaveola* e *Thraupis sayaca* em palmeiras frutificadas em área urbana. Revista de Etologia 7:39–42
Rocha JS, Bommif FCG, Bernardo CSS (2015) Importância da reserva biológica de uma na conservação de mamíferos da Mata Atlântica do Sul da Bahia vol 1. XII Congresso de Ecologia do Brasil. https://www.seb-ecologia.org.br/revistas/indexar/anais/xiiceb/pdf/539.pdf. Acessed 6 Jan 2021
Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. Biol Invasions 8:927–939
Sala OE et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770
Sambuichi RHR et al (2012) Cabruca agroforests in southern Bahia, Brazil: tree component, management practices and tree species conservation. Biodivers Conserv 21:1055–1077. https://doi.org/10.1007/s10531-012-0240-3
Sampaio AB, Schmidt IB (2013) Espécies exoticas invasoras em unidades de conservação federais do Brasil. Biodiversidade Brasileira-BioBrasil 3:32–49
Schwindt E, Bortolus A, Iriarine OO (2001) Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biol Invasions 3:137–149
Silva AM (2014a) Avaliação da Regeneração de espécies nativas e da influência de *Artocarpus heterophyllus* L. na fitodiversidade de uma área de Floresta Atlântica. Dissertation, Universidade Federal Rural de Pernambuco
Silva C (2014b) Primeiro registro do sabiado-una (*Turdus flavipes* (Passeriformes: Turdidae)) para o estado de Sergipe, nordeste do Brasil. Atualidades Ornitológicas 177:18–19
Silva JMC, Tabarelli M (2000) Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. Nature 404:72–74
Simberloff D et al (2013) Impacts of biological invasions: what’s what and the way forward. Trends Ecol Evol 28:58–66. https://doi.org/10.1016/j.tree.2012.07.013
Siqueira JD (2006) Bioinvasão vegetal: dispersão e propagação de espécies nativas e invasoras exóticas no campus da Pontifícia Universidade Católica do Rio de Janeiro (PUC-Rio). Pesquisas Botânicas 57:319–330
Sotka E, Byers J (2019) Not so fast: promoting invasive species to enhance multifunctionality in a native ecosystem requires strong (er) scrutiny. Biol Invasions 21:19–25
Stohlgren TJ et al (1999) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. https://doi.org/10.1126/science.287.5459.1770
Taconi S, Pires AS (2021) Vertebrate frugivory on jackfruit trees in the Duas Bocas Biological Reserve, Cariacica, Espírito Santo. Nat Line 8:91–94
Thomas C (1980) Jackfruit, *Artocarpus heterophyllus* L., a tropical tree species conservation. Biodivers Conserv 1:45–113
Traveset A, Richardson DM (2014) Mutualistic interactions and biological invasions. Annu Rev Ecol Evol Syst 45:89–113
Usher M, Kruger F, Macdonald I, Loope L, Brockie R (1988) The ecology of biological invasions into nature reserves: an introduction. Biol Conserv 44:1–8
Vimercati G, Kumschick S, Probert AF, Volery L, Bacher S (2020) The importance of assessing positive and beneficial impacts of alien species. NeoBiota 62:525–545
Wonham MJ, Carlton JT (2005) Trends in marine biological invasions at local and regional scales: the Northeast Pacific Ocean as a model system. Biol Invasions 7:369–392

Zimmerman JK, Pascarella JB, Aide TM (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restor Ecol 8:350–360

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.