Seed Removal Rates in Forest Remnants Respond to Forest Loss at the Landscape Scale

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Abstract: Seed removal is a key component of seed dispersal and may be influenced by both landscape-scale and local attributes, and it has been used as an indicator of the intensity of interactions between ecosystem components. We examined how the seed removal rates, which integrate the activity of seed dispersers and seed predators, vary with landscape-scale forest cover. We collected data under 34 trees belonging to two zoochoric species (*Helicostylis tomentosa* (Poepp. and Endl.) J. F. Macbr. and *Inga vera* Willd.) in 17 remnants in the Brazilian Atlantic forest, with different percentages of forest cover. The seed removal rate was estimated using a fast method based on the abundance of intact fruits and fruit scraps on the ground. The amount of forest cover affected the rate of seed removal in a humpbacked shape, with a maximum seed removal rate at intermediate forest cover. Seed removal rates must be related to the amount of food resources offered and diversity of dispersers and predators in the region. In landscapes with intermediate forest amount, there is a better balance between supply and demand for fruits, leading to a higher seed removal rate than more deforested or forested landscape. Our results also show that local factors, such as crop size and canopy surface, together with forest cover amount, are also important to the removal rate, depending on the species. In addition, our results showed that plant–animal interactions are occurring in all fragments, but the health status of these forests is similar to disturbed forests, even in sites immersed in forested landscapes.

Keywords: animal extirpation; forest health indicator; frugivory; satiation; tropical forest

1. Introduction

The Anthropocene is characterized by the pervasive influence of human activity in every biome on Earth. Human impact has drastically increased and it is now comparable in magnitude to natural processes affecting many aspects of the global biosphere [1]. Anthropogenic activities are responsible for drastic land use changes, in which forests are replaced by agricultural and pasture areas [2]. This longstanding process of habitat conversion and consequently habitat loss is the main threat to biodiversity worldwide [3,4]. Therefore, there is an increasing demand for scientific information to mitigate habitat loss effects, but first it is necessary to quantify the status of these new ecosystems [5].

Assessing community diversity through conventional methods is extremely difficult and time consuming [6–8], especially in mega diverse environments such as tropical forests. Therefore, methods that quickly access species diversity have been increasingly used since large programs such as the

Conservation International's Rapid Assessment Program have been proposed [9]. Since then, rapid methods have been developed to access the diversity of different taxonomic groups, such as tape recordings for birds [10], acoustic inventories for bats [11], monitoring species by camera traps [12], and assessing forest structure by drone and lidar [13,14]. Recently, Boissier et al. [5] proposed a method to estimate ecological processes through the rate of interaction between plants and animals. This is of paramount importance because species interaction is an often-missed component of biodiversity loss that can even precede species loss [15]. This rapid seed removal method allows the easier implementation of large-scale studies and provides a snapshot of the proportion of removed seeds by frugivores and seed predators [5,16–18]. While not integrative of animal activity over the year, since seed removal of a given species can be estimated only during the fruiting period, it provides a realistic picture of it. Indeed, animals adapt the use of their home-range according to the seasonal availability of food resources, even in degraded or provisioned habitats, as demonstrated for primates [19–21]. The rapid seed removal method is able to estimate a functional aspect of ecosystem health, as it is an indicator of ecological sustainability [22].

The seed removal rate integrates the activity of seed predators and also of primary and secondary seed dispersers. Zoochoric seed dispersal is a primordial regeneration process for most tropical tree species because it prevents local extinction and allows seedlings and saplings to escape density-dependent mortality processes [23–25]. Seed dispersal by animals is performed by primary or secondary frugivores. The former consume fruits in the canopy and regurgitate or defecate seeds elsewhere, and the latter eat fallen fruits from the ground or directly interact with lose seeds, such as dung beetles [26] and ants [27]. Seed predators may also play a role in seed dispersal processes through scatter hoarding [28]. Seed predation occurs mainly on ripe fruits and mature seeds in the canopy or on the ground by different taxonomic groups, such as birds (e.g., parrots), mammals (e.g., squirrels, monkeys, rodents), or insects (e.g., Hemiptera, Coleoptera), and can be as high as 95% of the crop (by peccary [29]).

In tropical forests, human disturbances, such as habitat loss and hunting, mainly reduce the components of the zoochoric seed dispersal, i.e., tree visitation, dispersal distance, and seed removal [30]. On the contrary, the direction of the effects of human perturbations on seed predation depends on the preferences of the predators and on their responses to the perturbation [31]. For instance, seed predation by mammals decreased with disturbance [29,32,33], and consequently, seed removal rate also decreases [18].

In this context, we examined how forest loss affects the seed removal rates of two zoochoric tree species, in 17 remnants of Atlantic forest in Brazil. We tested for the relationship with forest cover percentage at different scales, taking into account cofactors known to influence seed removal rates (canopy surface and fruit crop). A decrease in seed dispersers and predators in abundance and diversity were previously recorded in the same landscapes due to habitat loss and decrease in fruit availability [34]. Thus, we predicted that seed removal rates are positively correlated to landscape forest cover.

2. Material and Methods

2.1. Study Area

The study was performed in the municipality of Una (15.2937° S, 39.0743° W), in the southern region of the Bahia State, Brazil. The vegetation in this region is classified as Tropical Lowland Rainforest, and the climate according Köppen system is Af type, hot and moist without a distinct dry season. The mean annual rainfall is 2082 mm, while the average temperature is 24.4 °C, and the area shows few seasonal climatic variations (Instituto National de Meterologia, Brazil). The region harbors high levels of plant and animal species richness and represents one of the three pockets of endemism in the Atlantic Forest [35,36]. However, hunting pressure has significantly reduced the population of

seed dispersers, particularly large mammals, and species such as *Tapirus terrestris* (Linnaeus, 1758) and *Tayassu pecari* (Link, 1795) are locally extinct [37–39].

2.2. Sites and Forest Cover

The amount of landscape-scale forest cover is considered a meaningful proxy for habitat loss [40–43], and it is an easy to access metric due to the advance in remote sensing and image analysis methods. In addition, other human pressures, logging, wildfires, or hunting in general occur in synergy and concomitantly with forest loss [1], and thus the amount of landscape forest cover may integrate them. We conducted samplings in pre-selected landscapes of a large network project (SISBIOTA-Functionality), which uses satellites images to identify landscapes with different forest amount, considering only native forest. Each sample site was based around a central point allocated within a forest area, and the proportion of forest cover surrounding that central point was recorded. In this study, we considered each focal tree as the central point to calculate forest cover amount, and we adopted the patch-landscape approach [44] (for details see [45,46]). We considered the percentage of forest cover in different buffers, with a radius of 200 m to 2000 m. The shortest distance between sites was 1 km, while the average distance was 13.7 km (Figure 1).
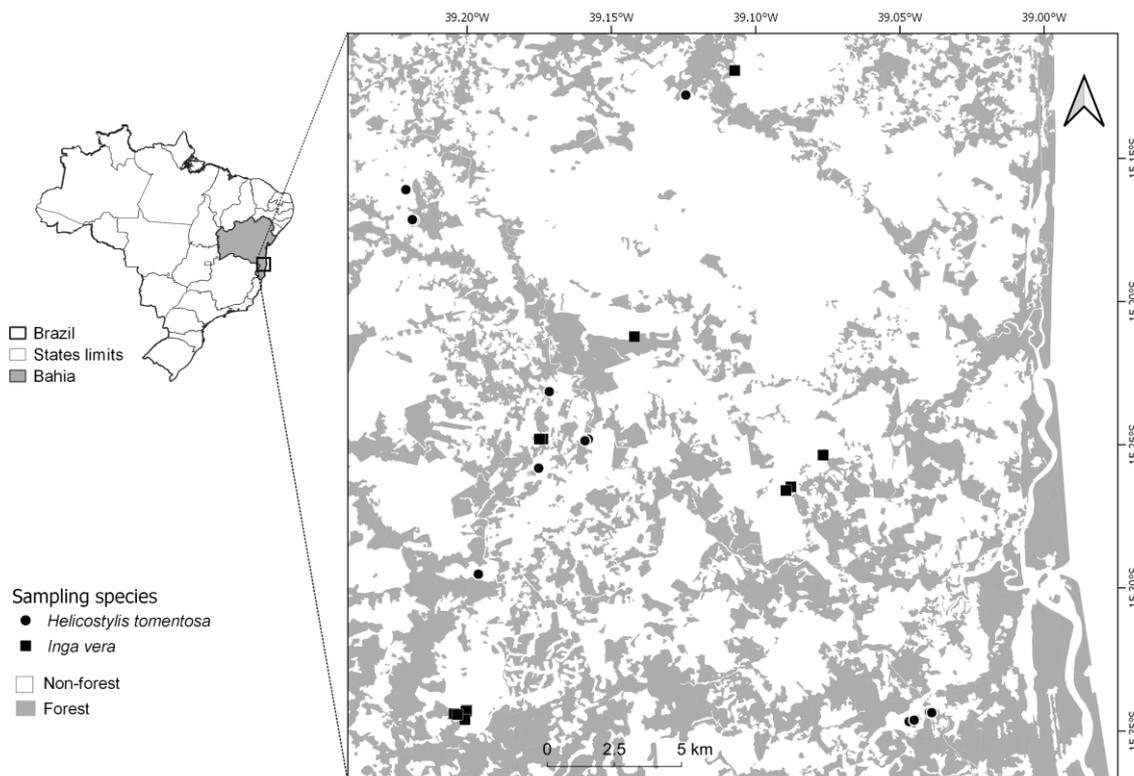

Figure 1. Map depicting all individuals sampled (19 *Helicostylis tomentosa* and 15 *Inga vera*; some points are overlapping on the map, due to its large scale) which were used for the seed removal rate estimates and for calculating the amount of Brazilian Atlantic forest (Bahia, Brazil).

2.3. Study Species

Helicostylis tomentosa (Poepp. and Endl.) J. F. Macbr. is an evergreen species belonging to the Moraceae family. It is a shade-tolerant species, in which the young stages need shade, but trees grow in full sun. The species is present in greater abundance in more conserved Atlantic Forest areas, however, it is also present in areas that have suffered medium to high anthropic disturbances such as slash-and-burn or logging [36,47]. It generally reaches 15 and 30 m in height, with a diameter at breast height of 40 to 70 cm, and crown up to 12 m in diameter [48]. The infructescence have around

7 g and 3 cm in diameter, and it is composed by four to ten fruits, with a single seed of about 0.73 cm diameter in a light-yellow pulp [48,49]. The fruits are consumed by primates [50–52], and according to [53], five or six primate species interact with *H. tomentosa.* However, only *Leontopithecus chrysomelas* (Kuhl, 1820) and *Sapajus xanthosternos* ((Wied-Neuwied, 1826) inhabit the study area. Infructescence with ripe fruits that are not consumed entirely in the treetops are easily found on the ground, and may be intact, partially consumed, or sometimes broken due to the impact upon reaching the ground. It seems there are more terrestrial animal species interacting with fruits and seeds: Tortoises (*Chelonoidis denticulatus* (Linnaeus, 1766); seed disperser [54]), tapirs (*Tapirus terrestris* seed disperser [55]), peccaries (*Pecari tajacu* (Linnaeus, 1758) and *Tayassu pecari*; seed predator, [56]), grey brockets (*Mazama gouazoubira* (G. Fisher [von Waldheim], 1814); seed disperser and predator [57]), and agoutis (*Dasyprocta* (Illiger, 1811); seed disperser and predator [48]). To the best of our knowledge, *H. tomentosa* was rarely consumed by large frugivorous birds (only sometimes by curassows [52]).

Inga vera Willd. is an evergreen pioneer species belonging to the Fabaceae family. It grows up to 18 m in height, with a diameter at breast height of approximately 60 cm, and 10 to 15 m crown diameter bearing long branches. The fruits are indehiscent legumes with an approximate size of 5.6 cm in length and 2 cm in diameter, and when ripe they are brownish to yellowish and contain approximately 14 seeds of 1.5 cm diameter enveloped in a white, sweetish aril [46,58–60]. The fruits and the seeds are mainly consumed by primate seed dispersers [53], but are also unequivocally a source of food for many different species of birds, e.g., five species of parrots (seed predators [61]) and several species of Passeriformes (seed dispersers [62]) and bats (seed dispersers [63]). Ripe fruits are usually not consumed entirely in the treetops, and fallen fruit usually has marks showing that they were partially consumed and are rarely found intact on the ground. Secondary dispersal or predation in *Inga* genera is accomplished by a variety of animals: Small and large rodents (seed predators), tapirs [64], and peccaries (seed predator [65]).

Considering the fruit characteristics of the tree species used and the fauna of the study site, we consider that it is very unlikely that predation by invertebrates will result in seed removal. Thus, we believe that the predation with removal is carried out only by vertebrates such as lizards, but mainly by mammals. Therefore, the removed seeds may have been dispersed by arboreal frugivores (mainly primates), or predated by arboreal animals (e.g., parrots), and on the ground may have been dispersed or predated by terrestrial animals (such as *Pecari tajacu*; *Mazama gouazoubira*; *Dasyprocta leporina* (Linnaeus, 1758); *Cuniculus paca* (Linnaeus, 1766); *Didelphis albiventris* (Lund, 1840); and *Didelphis. aurita* (Wied-Neuwied, 1826))

2.4. Seed Removal Rates

We visited 32 of the 40 available sites between February and March 2018 to search for fruiting specimens of four initially selected focal tree species. Indeed, the fruiting periods of the species could vary according to climate fluctuations, but have to match with the availability of investigators for field work, and it is also necessary to find enough fruiting specimens to adequately conduct the investigations. This resulted in 34 reproductive individuals marked (19 *Helicostylis tomentosa* and 15 *Inga vera*), which were sampled to estimate seed removal rates. To obtain the seed removal rate, we estimated seed production and seed removal from fallen fruits and fruit remains on the ground [5,17]. We estimated seed production (hereafter crop size) and seed removal by counting in quadrats, the number of intact ripe fruits, ripe fruit scraps (pedicels and peduncles, parts of fruits) and loose seeds. Crop size was obtained by adding the number of intact and ripe fruit scraps on the ground and multiplied by the mean seed number per fruit while removed seeds were the missing seeds in the scraps. The removal rate was computed as the ratio of removed seeds over crop size. The efficiency of the seed removal rate testing depends on the researchers' ability to easily and quickly count seeds. Since fruit production was particularly low for *H. tomentosa*, we considered the entire surface under the crown of each studied tree. For *I. vera*, we first tested if our method was accurate by sampling with three 1 m^2 random quadrats under each focal tree. For this, we sampled three trees, each with

20 random quadrats and obtained the mean squared errors (MSE) by bootstrap. The MSE (0.0156, 0.0148 and 0.0269) were in the range of the values obtained by [17], which guarantees the accuracy of the method. We also determined the canopy surface area of each sample tree using the standard forester method by estimating four random crown radii [66].

2.5. Statistical Analysis

All the analyses were done in R3.6.3. We first tested whether tree seed removal rate was spatially auto-correlated with the Moran's I test while varying the number of neighbors (function 'moransI.v' of the *lctools* R package; [67]). We computed the mean distances between k neighbors with the 'knearneigh' function of the *spdep* R package [68]. We used auto-covariate logistic regression models following [69] to test for the relationships between the seed removal rate (the dependent variable) and a combination of landscape and local variables—forest cover, tree canopy surface (m^2 per tree), seed crop (seed number per m^2), and pairwise interactions of these two variables. The auto-covariate was computed using the 'autocov dist' function of *spdep* following [68]. We included in the analysis the linear and the quadratic effects of the landscape forest cover. We evaluated the scale of forest cover effect by varying the buffer radius (200 m to 2000 m). The analyses were performed separately for each species. We tested all the possible combinations of effects using the function 'bestglm' of the *bestglm* R package [70], comparing the fits of variable combinations with the Bayesian information criterion (BIC) and applying the marginality rule (i.e., when an interaction term is included in a model, the corresponding main effects should be also included). We tested the selected models against a null model with the likelihood ratio test and the spatial auto-correlation in the Pearson residuals as above (dataset and R code available in the Supplementary Materials: Supplementary information.zip file). To plot the model prediction of one factor over the observations, we set the other factors to their mean. As predictive capacity power of landscape forest cover, we calculated the partial Efron's pseudo R-squared of the factor with the function 'rsq.partial of the *rsq* R package [71] and compared the coefficients of the models using their 95% confidence intervals.

3. Results

Landscape-scale forest cover ranged between 36.5% and 100% in radius of 200 m to 2000 m. The seed removal rate was on average 0.56, but varied considerably among trees and between species (Figure 2); for *H. tomentosa*, the mean was 50.1%, and for *I. vera*, 62.4%. The canopy surface of the sampled *H. tomentosa* was 11.1 to 61.4 m^2 (mean = 33.0 m^2) and for *I. vera*, 12.6 to 139.3 m^2 (mean = 64.9 m^2). The crop size of *H. tomentosa* varied between 1 and 13 seeds/m^2 (mean = 6.3 seeds/m^2), and that of *I. vera* between 27 and 227 seeds/m^2 (mean = 94.1 seeds/m^2).
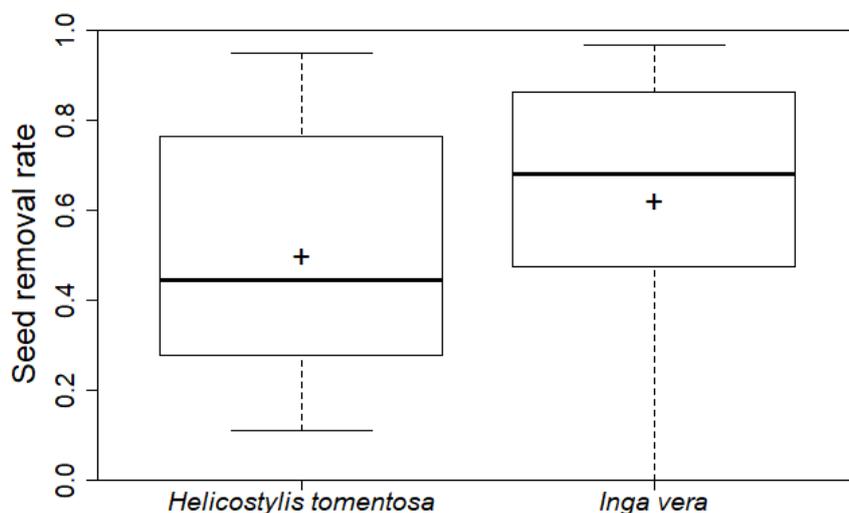

Figure 2. Boxplots of seed removal rates for each species with means (+).

The Moran's I test indicated positive and significant spatial auto-correlation decreasing with distance (number of conspecifics taken into account), which means that seed removal rates were more similar between closer trees. The trend was weaker for *H. tomentosa* than for *I. vera* (Figure 3). It also suggested that, for *I. vera*, spatial auto-correlation extended beyond landscape limits, since the mean number of trees per remnant was only two, while the Moran's I remained significant for distances up to 4 km.
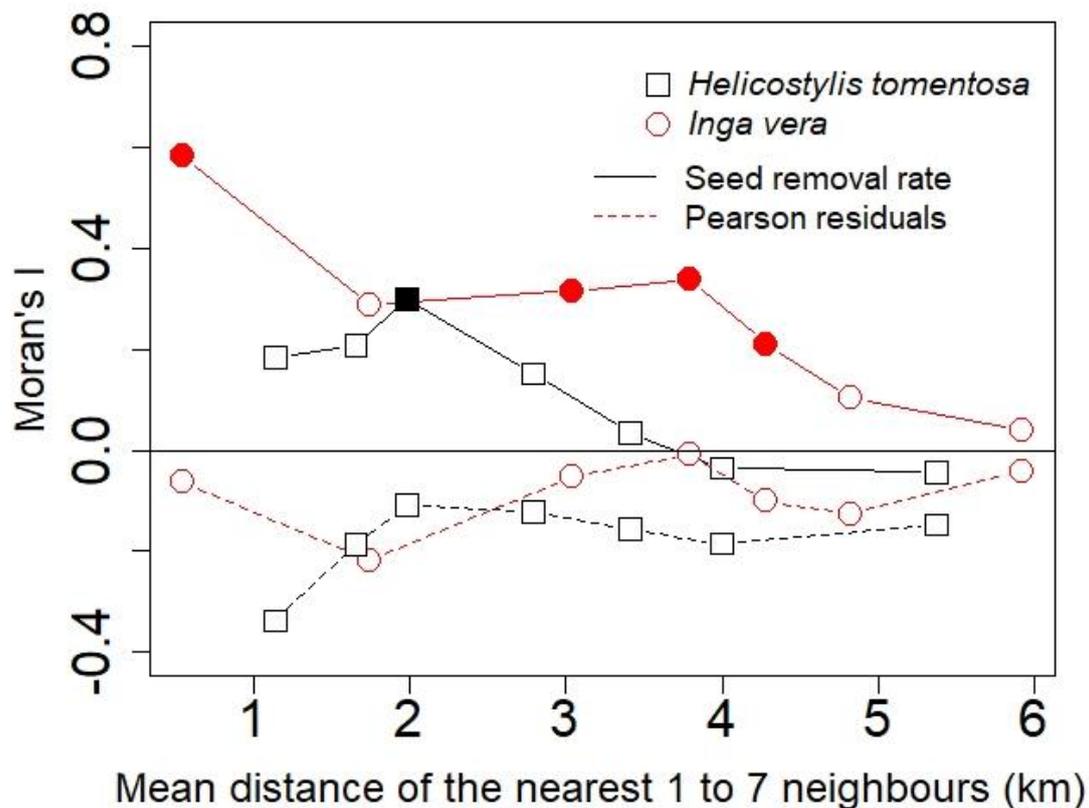

Figure 3. Moran's I for seed removal rates and Pearson residuals of the auto-covariate logistic regression models computed as a function of the number k of neighbors (accounted for k = 1 to 7, from left to right) and expressed as a function of corresponding mean distance. Significant values for $p \leq 0.05$ are in solid symbols and non-significant values in hollow symbols.

Model selection allowed to identify highly significant relationships between seed removal rate and forest cover having a humpbacked shape (Figure 4). The best model of *H. tomentosa* (Table 1) was obtained for landscape forest cover estimated in a radius of 1600 m while for *I. vera*, the best model was obtained for landscape forest cover estimated in a radius of 1400 m (Table 2). For both species, the model also included the canopy surface, the crop, their pairwise interaction, and the auto-covariate. The Pearson residuals were not spatially auto-correlated (Figure 3), which means that the models correctly captured the generating processes. The effects of landscape forest cover were supported by a higher partial pseudo-R squared for *H. tomentosa* than for *I. vera*. Nevertheless, the response of *I. vera* to forest cover was stronger than that of *H. tomentosa* (Figure 4), as also shown by the forest cover coefficients, which were significantly larger. The models selected with the estimations of landscape forest cover in other radii showed the same kind of relationship for forest cover (excepting two of them), i.e., a humpbacked curve, but with lower fit. The responses of the seed removal rate to crop and canopy surface were contrasted and clearly resulted from the interaction between both factors.
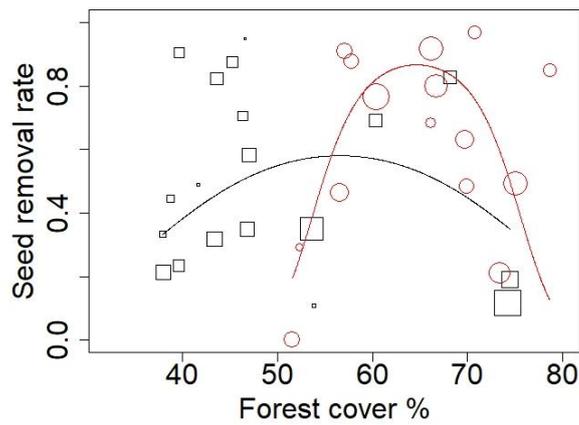
(**a**)
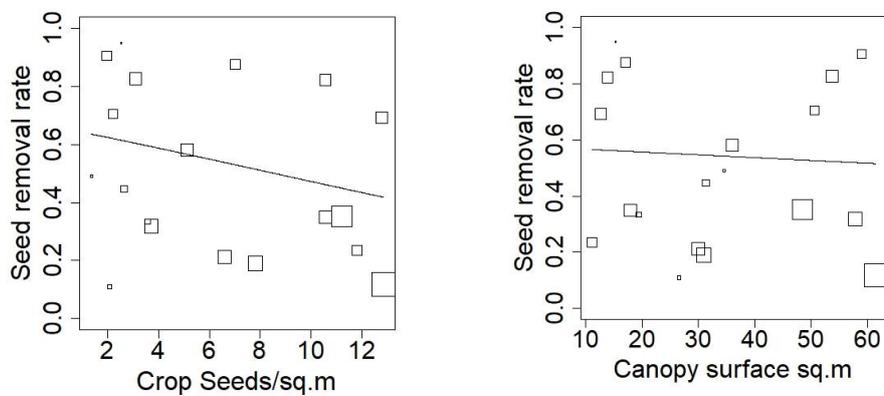
(**b**) *Helicostylis tomentosa*
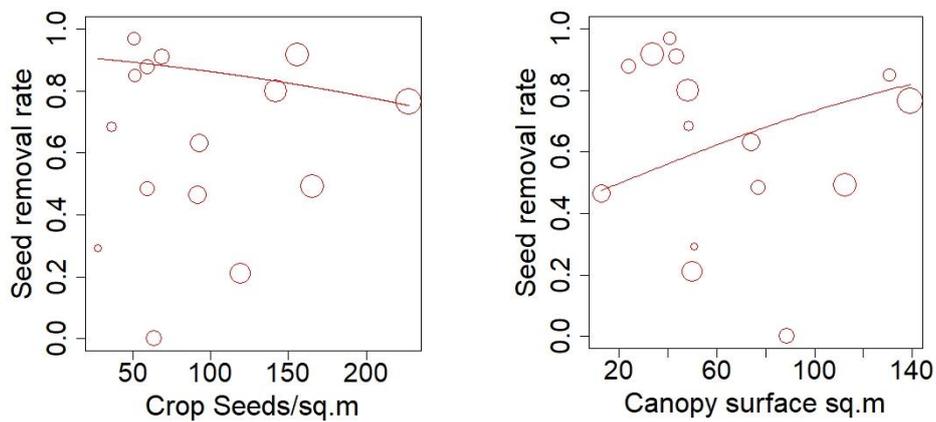
(**c**) *Inga vera*

Figure 4. Results of the logistic regression models. (**a**) Seed removal rates as a function of forest cover around forest remnants (*H. tomentosa*: Observed values in black squares and black prediction line, forest cover estimated in a landscapes of 1600 m radius, *I. vera*: Observed values in red circles and red dashed prediction line, forest cover estimated in landscapes of 1400 m radius); (**b**,**c**) seed removal rate as a function of crop size, and canopy surface (symbol size is a log function of total number of seeds taken into account for each tree).

Table 1. Selected auto-covariate logistic regression models of seed removal rate with Efron's pseudo R-squared and likelihood ratio tests. *Helicostylis tomentosa*, sample size = 19.

Coefficients	Estimates	Standard Errors	Z-Values	*p*-Values
Intercept	−9.76	1.041	−9.374	<0.0001
Forest cover (1600 m radius)	0.333	0.041	8.207	<0.0001
Forest cover^2	−0.0029	0.0003	−8.453	<0.0001
Canopy surface	0.035	0.0060	5.904	<0.0001
Crop size	0.130	0.0307	4.227	<0.0001
Crop x Canopy surface	−0.006	0.0006	−9.824	<0.0001
Scaled auto-covariate	−0.210	0.0569	−3.760	0.0002

95% confidence interval of coefficients; Forest cover: 0.2633–0.4122, Forest cover^2: −0.00363––0.00226; Efron's pseudo R-squared = 0.5878; Partial Efron's pseudo R-squared for forest cover effects = 0.5204; Likelihood ratio test deviance = 645.4, ddl = 6, *p*-value < 0.0001.

Table 2. Selected auto-covariate logistic regression models of seed removal rate with Efron's pseudo R-squared and likelihood ratio tests. *Inga vera*, sample size = 15.

Coefficients	Estimates	Standard Errors	Z-Values	*p*-Values
Intercept	−79.38	5.799	−13.69	<0.0001
Forest cover (1400 m radius)	2.493	0.1820	13.69	<0.0001
Forest cover^2	−0.0193	0.0014	−13.64	<0.0001
Canopy surface	0.0195	0.0037	5.329	<0.0001
Crop size	−0.0009	0.0021	−0.466	0.6415
Crop x Canopy surface	−0.00007	0.00002	−3.483	0.0005
Scaled auto-covariate	−0.1873	0.0635	−2.823	0.0048

95% confidence interval of coefficients; Forest cover: 2.136–2.850, Forest cover^2: −0.0221––0.0165; Efron's pseudo R-squared 0.3867; Partial Efron's pseudo R-squared for forest cover effects 0.1247; Likelihood ratio test deviance = 464.63, ddl = 6, *p*-value < 0.0001.

4. Discussion

The amount of forest cover affects seed removal rates of two plant species in the Atlantic Forest from southern Bahia. However, the effect of forest loss was humpbacked shaped and not linear as expected. Local factors were also important determinants of seed removal rates, depending on the tree species, such as fruit crop and the canopy surface. Thus, our study showed that the response of seed removal rate to forest cover is species-specific. More importantly, the seed removal rate results showed that plant–animal interaction is occurring in all fragments, but it was low in forested landscapes, an indication that they are also defaunated since it is established that the seed removal rate responds to defaunation [18].

The variation of spatial autocorrelation of the seed removal rate with number of neighbors indicated that the *H. tomentosa* seed removal was limited to each forest remnant and landscape, while for *I. vera*, it extended beyond landscape limits. Both species are known to be dispersed by primates, however, *I. vera* is also dispersed by several species of birds and bats, while *H. tomentosa* was only rarely observed being dispersed by curassows [52], which also has a low population in the region. Thus, *I. vera* probably has a more mobile animal community that interacts with seeds than those of *H. tomentosa*—this fact probably favors a higher rate of seed removal for this species, as observed in this work. Seed removal is probably occurring even in the most deforested fragments by some primates that may be relatively little affected or even favored by forest loss [72]. The primate *Leontopithecus chrysomelas*, an important seed disperser in our study area, as well as other tamarins such as *Callithrix penicillata* (E. Geoffroy Saint-Hilaire, 1812) and *Callithrix jacchus* (Linnaeus, 1758), are able to use degraded areas, such as cocoa-shaded plantations, degraded forests, or rubber plantations [73–75]. The seed dispersal by birds and bats may be also important, but only for *I. vera*.

Seed removal rates for both species were higher in fragments immersed in landscapes with intermediate amounts of forest. Seed removal rates must be related to the amount of food resources

offered and diversity of seed dispersers and predators in the region. In forests immersed in more deforested landscapes there is a smaller amount of fruits being offered [46], however, the rate of defaunation is higher, so there are few animals (dispersers and predators) to remove the seeds [76–78] resulting in low seed removal rates. On the other hand, in more forested landscapes, there is a greater supply of fruits and more animals due a lower rate of defaunation, also resulting in low seed removal rates. However, in landscapes with an intermediate forest cover amount, a better balance between supply and demand of fruits is expected, leading to higher seed removal rates and explaining the humpback shape. The forests of this region have a high defaunation rate, in which the population of medium and large mammals has suffered a great decrease or even local extinction, such as the tapir [37,38]. In the same landscapes, it has been shown that deforestation leads to reduced seed predation by small mammals [77]. In this way, small and some species of medium mammals (such as agoutis, pacas, and peccaries) should play the main role in removing fruits on the ground (predation or secondary dispersal). However, it is noteworthy that the forest cover gradient evaluated comprises only 36 to 80% of forest cover in the selected buffers, and it is not possible to infer about fragments in more deforested landscapes due to the fact that fruiting individuals of these species were not found.

The mean seed removal rate was 0.56, but varied considerably among individuals and species. It was lower to *Helicostylis tomentosa*, a shade-tolerant species with more nutritive fruits than *Inga vera*, a shade-intolerant species with poor fruits [46]. However, both species showed individuals with high removal rates (maximum 0.95 for *H. tomentosa* and 0.97 for *I. vera*). In undisturbed fragments, with limited hunting pressure, previous studies showed that seed removal rates could be close to 1 [5,16,17], but this also depends on plant species [18]. The seed removal rate in a well-preserved area was 77%, and 47% in an area with a history of logging and high hunting pressure [18]. The fact that in our study region, there is high hunting pressure, with a decrease in or local extinction of medium and large mammals, [37,38,79], could explain the low rates of seed removal even in the most forested landscapes, even if precise information of these threats on each landscape is lacking.

Seed removal rates can be determined not only by forest amount or diversity of frugivores, but also by individual tree features, such as crown surface area and crop size, but these features interact with the animal communities. Plant size generally correlates with crop size (this is also the case in this study), and larger crops may attract more frugivores. Indeed, crop size is suggested as a key trait for conspicuousness [80], thus, increasing fruit removal. A recent review on the role of fruit crops provided evidence to support the hypothesis that crop size represents a conspicuous signal for the amount of reward for birds [81]. However, faster satiation of disturbed animal communities could occur with larger crops [82] or when important frugivorous species have been extirpated [83]. The larger trees may attract more animals but those trees may produce crops so large that only a smaller proportion of the seeds may finally be removed by dispersers or predators.

5. Conclusions

Seed removal rates in forest remnants were sensitive to forest loss in the landscape, but the responses were species specific. In the limited scope of our study, we did not register the animal communities and their responses to forest loss while it would have helped to strengthen our conclusions. Nevertheless, our analysis highlighted a humpbacked response peaking at intermediate values of landscape forest cover. Below those values, the conditions for the seed dispersers and seed predators probably unduly worsen and the seed removal rate strictly decline. Methodological difficulties are constituted by selecting appropriate species (i.e., species characterized by ripe fruits falling on the ground and fruits leaving traces after consumption) and by finding many individuals with enough ripe fruits of the same species in different landscapes. However, the method is not restricted to threatened tree species or to tropical climate ecosystems. A greater ability to generalize may allow us to deduce a pertinent indicator of forest functionality, and thus of forest health. Thus, the seed removal rate showed that animal–plant interaction occurs in all fragments, however, their health is already compromised since even fragments immersed in highly forested landscapes showed low seed removal rates.

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