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ORIGINAL ARTICLE

The role of howler monkeys (*Alouatta caraya*) in the primary succession of the Paraná flooded forest (Argentina)

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Abstract

In disturbed forests, Atelidae primates, such as howler monkeys, are known to play a key role in the dynamics of secondary succession. However, little is known about their role in primary succession. Thus, the aim of the present study was to evaluate the role of the howler monkey *Alouatta caraya* in the primary succession dynamics of the Paraná flooded forest, in northeastern Argentina. This was achieved by studying the recruitment of saplings in the latrines of *A. caraya* groups inhabiting the forest in the first stages of succession and the distribution of plant species in relation to the age of the forest. The results showed that: (a) young forest areas were dominated by tree species dispersed by water, wind, birds, bats and fishes, whereas older forest areas were dominated by species dispersed by *A. caraya*, with individuals of some species present in young forests; (b) the floristic composition of saplings growing in *A. caraya* latrines of young forest areas was similar to that of old forest areas; and (c) saplings growing in young forest areas were heavily associated with *A. caraya* latrines and corresponded to species from older forest areas. The results allow the conclusion that *A. caraya* plays a role in the last phase of primary succession of the Paraná flooded forest, as well as in contributing to an increase in the structural complexity and species diversity in the young areas of the Paraná islands.

Abstract in Spanish is available with online material.

KEYWORDS
Eugenia punicifolia, *Ocotea diospyrifolia*, sapling recruitment, seed dispersal

1 | INTRODUCTION

In tropical forests, the mechanism of seed dispersal affects the spatial distribution patterns of tree species, evidencing its relevance in the long-term community structure of these forests (Seidler & Plotkin, 2006). In particular, seed dispersal by frugivores plays a relevant role in their natural dynamics, affecting their structure, diversity and composition (Chaves et al., 2018; Stevenson, 2011). In both intact and degraded forests of Asia, Corlett (2017) determined that seed dispersal by vertebrate frugivores is crucially important because it helps to maintain links across the fragmented landscape and to recover abandoned agricultural lands. In tropical forests of Africa, Clarck et al. (2001) identified two different functional groups of seed dispersers and found that they disperse plants of different canopy strata, exhibiting low overlap in the species they disseminate. These authors concluded that small changes in vertebrate composition within forests can potentially affect forest structure. In neotropical forests of South America, Dugger et al. (2019) observed that seed dispersal networks are more specialized and diverse than in Africa, and thus are more vulnerable to the loss or decrease of any frugivore population. Regarding seed dispersal by primates, in forests of South America, Stevenson (2011) showed that a decrease in Ateline

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monkey populations can alter plant diversity patterns. This author observed that, when Ateline monkey populations decrease, plant species dispersed by them (i.e. those with medium seed sizes and endozoochory syndromes) become less abundant, whereas species not dispersed by them are not affected (Stevenson, 2011).

Ateline monkeys, in particular monkeys of the genus *Alouatta*, have been found to play a key role in the dynamics of secondary succession when forests are either disturbed (Muscarella & Fleming, 2007; Rodrigues da Silva & Matos, 2006; Simoes & Marques, 2007) or fragmented (Boyle et al., 2013; Santamaría Gómez, 2004). *Alouatta pigra*, for example, plays a relevant role in maintaining forest regeneration dynamics in agro-ecosystems of low impact, such as those under the canopy of cocoa plantations (Zárate et al., 2018). *Alouatta guariba clamitans*, on the other hand, can act as a seed disperser of most fleshy-fruited species in small Atlantic forest fragments (Chaves et al., 2018). This is because this monkey has a very flexible fruit diet and can thus adapt to limited and variable fruit resources available in small fragments (Chaves et al., 2018). In the Amazon, *Alouatta macconnelli* helps in the conservation and recovery of the forest by moving seeds between continuous forest and small forest fragments (Santamaría Gómez, 2004). Finally, in the Paraná flooded forest in northeastern Argentina, *Alouatta caraya* disperses many fleshy-fruited species and saplings of several of these species recruit only in its latrines (Bravo, 2012a). Although all these studies show that *Alouatta* spp. monkeys play a main role in secondary succession, little is known about their role in primary succession, i.e. the succession that starts on a new surface with no previous vegetation (Walker & Moral, 2003).

The Paraná flooded forest in northeastern Argentina shows a process of accretion of sand bars on the islands of the Paraná River, thus offering new surfaces for plant colonization (Pereira, 2016). Here, colonization starts by grasses and two or three dry-fruited tree species, which make up the pioneer forest. Colonization later continues with the appearance of fleshy-fruited species, which allows the forest to change to a pluri-specific mature forest (Zambiasio et al., 2018). On these islands, periodic floods favor vegetation with high recovery rates (Eskuche & Fontana, 1996). These first stages of succession are characterized by the germination and recruitment of willows (*Salix humboldtiana*) and alders (*Tessaria integrifolia*) (Marchetti et al., 2013), which are trees that, as adults, can be used by *A. caraya* as support, a fact that allows this species to start inhabiting the area. In fact, besides birds, *A. caraya* is the only frugivorous species with large and stable populations on islands of Paraná River (Neiff, 2001). *A. caraya* thus plays a relevant role in the regeneration of mature forests of the Paraná flooded forest, mainly, but not only, of the dominant species *Ocotea diospyrifolia*, *Eugenia punicifolia*, and *Psychotria carthagenensis*, and in general of species with large seeds (more than 5 mm in length) (Bravo, 2012a; Bravo & Cueto, 2020).

The Paraná flooded forest thus offers a great possibility to study the role of *A. caraya* in the early stages of primary succession. Therefore, the aim of the present study was to evaluate the role of *A. caraya* in the primary succession dynamics of this forest. This was achieved by studying the sapling composition in latrines of *A. caraya* groups inhabiting the forest during the first stages of succession (biogeomorphic stage) and comparing it with the sapling composition in latrines of *A. caraya* groups inhabiting the oldest stage of succession (ecological stage). To determine the role of other frugivores in primary succession, the composition of saplings growing out of latrines in young forest areas was also determined. The main hypothesis was that *A. caraya* is the main animal responsible for the arrival of fleshy-fruited species to the pioneer forest. Based on this, the predictions were: (a) that the floristic composition of adult trees in young (<50 years) and old areas (>150 years) of the forest will be different, whereas the floristic composition of saplings growing in latrines located in young and old areas will be similar because *A. caraya* disperses only fleshy-fruited species characteristic of old forests; and (b) that the saplings of fleshy-fruited species in young forest areas will be strongly associated with *A. caraya* latrines.

2 | METHODS

2.1 | Study site

The study was carried out on Brasilera Island, an island located at the confluence of the Paraná and Paraguay rivers, in Chaco, Argentina (27°30′S, 58°41′W). The climate is subtropical, with an annual average temperature of 21°C and annual thermal amplitude of 12°C. Annual precipitation is approximately 1500 mm. Although precipitation decreases during the winter, there is no marked dry season because evapotranspiration is low during this period.

Like other flooded forests associated with large rivers (such as the Pantanal in the Paraguay River or the Várzea in the Amazon), the flooded forests of the Paraná River islands are both geomorphologically and biogeographically influenced by fluvial dynamics (Daly & Mitchell, 2000; Pereira, 2016). Islands increase their areas by the accretion of sand bars, and, as a consequence, plants have new surfaces to colonize (Pereira, 2016). As in other fluvial systems, these Paraná islands present four succession stages (i.e. the geomorphic, pioneer, biogeomorphic and ecological stages) (Brumnich et al., 2019; Corenblit et al., 2007). Along the four stages, the importance of the physical and abiotic factors that control the succession decreases, whereas that of biotic factors increases, and, as indicated above, the biogeomorphic stage starts with the germination of *T. integrifolia* and *S. humboldtiana* (Brumnich et al., 2019). These pioneer tree species act as traps for sediments, a fact that in turn allows an increase in the elevation of sand bars, and next allows the germination and recruitment of other plant species (Brumnich et al., 2019). Consequently, the forest types and relative abundance of plant species on islands are defined by topographic, edaphic and age factors (Casco & Neiff, 2013; Daly & Mitchell, 2000; Daly & Prance, 1989). The Brasilera Island is 292 ha in size, 153 ha of which are covered by flooded forests and 24.3 ha of which are covered by young forests (biogeomorphic stage) growing in young areas (González et al., 2002). The complexity of the geomorphology, with bars of different ages covered by grasslands and different kinds of forests and the

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presence of lagoons, is characteristic of islands older than 100 years (Brumnich et al., 2019).

Within the distribution of the genus *Alouatta*, which ranges from Mexico to Argentina, the Paraná River islands have the greatest density (Crockett, 1998). However, the density and group size of *A. caraya* on these islands depend on the forest type. On Brasilera Island, their density ranges between 0.88 individuals/ha and 4.25 individuals/ha and group size ranges between 3 and 25 individuals in young and old areas respectively (Kowalewski, 2007). Small groups settled in young areas frequently have a small portion of their territory within old nearby forest areas or make incursions to older forest areas to take some food resources (personal observations).

In the study site, *A. caraya* latrines are very abundant and can be identified easily when walking through the forest, without having to perform any behavioral observations of the *A. caraya* groups (Bravo, 2012a). Latrines are approximately 5 m in diameter, feces are accumulated on the ground, and saplings of different sizes are growing in them (Bravo, 2012a).

Alouatta caraya monkeys defecate in latrines at the end of a resting period and before or after a territorial encounter with another group (Bravo, 2009). The *A. caraya* groups I have observed during 10 years of study in the area have always used the same latrines. This behavior of making latrines has been related to avoidance of parasite infestation (Kowalewski & Zunino, 2005).

2.2 | Vegetation surveys

To test prediction (a), the species composition of the forest was evaluated in both young and old areas of the island. Twenty-five plots of 20 × 20 m were located at random in the forest of the young areas of the island (characterized by presence of *T. integrifolia* and *S. humboltiana* (Brumnich et al., 2019; Marchetti et al., 2013)), whereas the other 25 were located in the central and southern bars of the island to sample old forests. All trees with more than 10 cm of diameter at breast height were recorded. To find latrines, three transects of 500 m long were used in the old forests and one in the young area. Eighteen latrines were found in the old forests and ten in the young area. All saplings, small individuals with less than a third diameter than adult trees, higher than 25 cm growing in them were recorded. In addition, to test prediction (b), a 1-ha grid with 20-m intervals was established in the young area, and all the saplings of fleshy-fruited species higher than 1 m were identified and categorized as being located either in or outside a latrine and species of adult trees that composed the canopy and sub-canopy were recorded. Saplings smaller than one meter were not included because of the extension of the area sampled.

Because the data were not normally distributed, forest plots and tree species were ordered by Non-metric Multidimensional Scaling (NMDS), using the Bray–Curtis index of dissimilarity and Wisconsin double standardization. Two convergent solutions were found after 50 tries. Scores based on forest plots were compared between old and young areas with Kruskal–Wallis test. Latrines were ordered by two principal component analyses (PCA) using a correlation matrix for latrines. Species present in <30% of them were excluded. Retained components were determined following the broken-stick model and the scree-plot (Jackson, 1993). Scores based on latrines were compared between old and young areas with a Kruskal–Wallis test. The number of species (richness), number of individuals, and number of individuals per species (abundance) between latrines of old and young areas were compared by the *t* test. Finally, the relationship between richness, number of individuals in a latrine, and location of each latrine was evaluated by analysis of covariance (ANCOVA), with the number of individuals as a covariable and the type of area (young/old) as a group variable. Statistical analyses were carried out in R 3.5.2 (R Core, 2018).

3 | RESULTS

Related to prediction (a), the NMDS allowed the grouping of forest plots into two categories, which corresponded to forests of new and old areas (Figure 1, stress = 0.11). Only the first axis (NMDS 1) was related to differences between young and old forest areas on the island (Table S1, Figure 1; Kruskal–Wallis test, $k = 2$, $N = 50$; NMDS 1: $H = 36.53$, $p < .0001$; NMDS 2: $H = 2.56$, $p = .1$). Young forest areas were characterized by *Tessaria integrifolia*, *Salix humboldtiana*, *Albizia inundata*, *Croton urucurana*, and *Sapium haematospermum*, all species with dry fruits (the last one with dry fruit and ariled seeds), whereas old forest areas were dominated by *Ocotea diospyrifolia*, *Eugenia punicifolia*, *E. burkartiana*, and *Psychotria carthagenensis*, all fleshy-fruited species (Table S1, Figure 1). In addition, axis two (NMDS 2) was related to the presence of the fleshy-fruited species

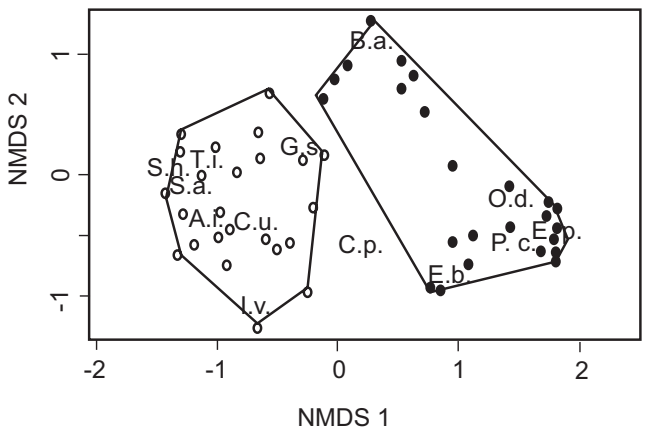


FIGURE 1 Forest plots ordered by the NMDS. Open circles represent plots located in young areas of the Brasilera Island in the Paraná flooded forest (northeastern Argentina). Black circles represent plots located in old areas of the Island. A.i.: *Albizia inundata*, B.a.: *Banara arguta*, C.u.: *Croton urucurana*, C.p.: *Cecropia pachystachya*, E.b.: *Eugenia burkartiana*, E.p.: *E. punicifolia*, G.e.: *Geoffroea striata*, I.v.: *Inga vera*, O.d.: *Ocotea diospyrifolia*, P.c.: *Psychotria carthagenensis*, S.a.: *Sapium haematospermum*, S.h.: *Salix humboldtiana*, T.i.: *Tessaria integrifolia*

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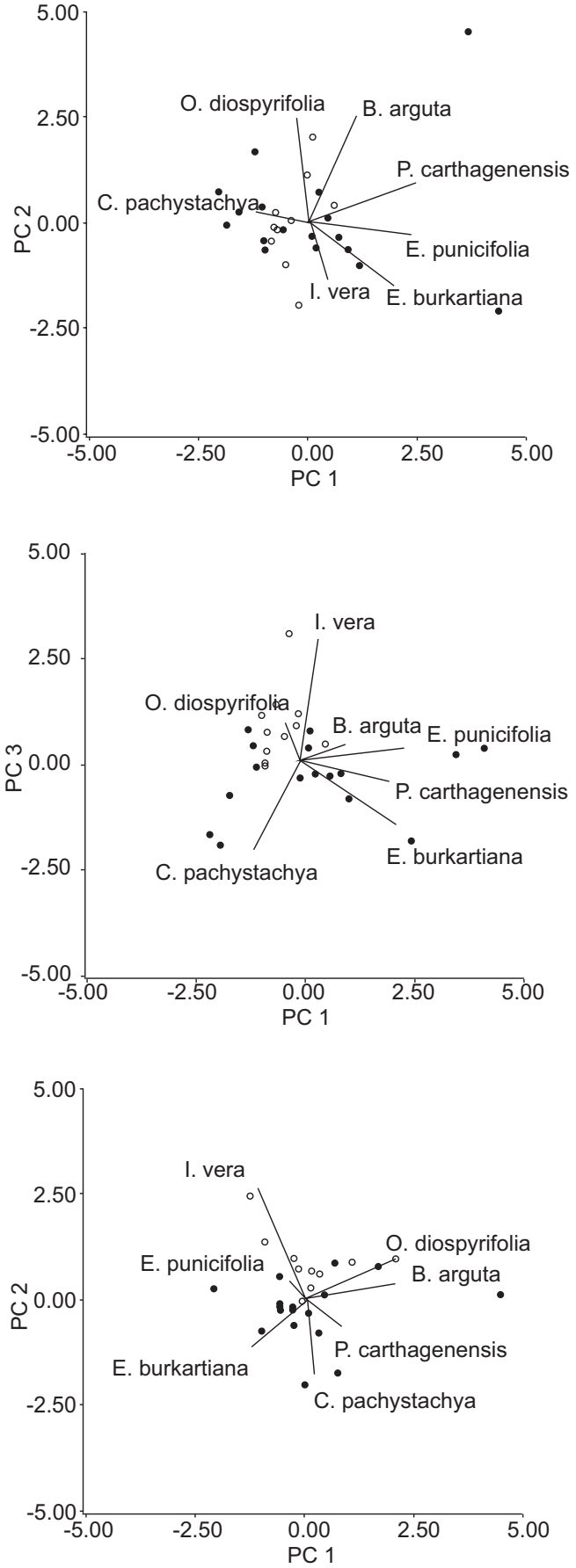


FIGURE 2 Census of saplings in latrines ordered by the first three axes of the Principal Component Analysis. Open circles represent *A. caraya* latrines located in young areas of the Brasilera Island (Argentina). Black circles represent latrines located in old forest areas. Vectors represent species with highest loadings

Banara arguta and *Inga vera*, and showed small differences in the forest of old areas (Table S1, Figure 1).

The first three components of the other PCA were retained and explained more than 70% of the total variability in the floristic composition in latrines (Table S2). However, the order obtained by the PCA was not related to the location of latrines in young or old areas (Figure 2, Kruskal–Wallis test, $k = 2$, $N = 27$; PC1: $H = -0.73$, $p < .99$; PC2: $H = -1.16$, $p = .99$; PC3: $H = 3.18$, $p = .07$).

The saplings found in latrines of young areas represented species recorded previously in the diet of *A. caraya* (Table S3), and were species with large seeds, except for *B. arguta* and *Cecropia pachystachya* (Table S3). These species were a subsample of the species present in forests and latrines of old areas (Table S3). The mean richness of latrines located in young and old areas was similar (Young areas: 4.2 ± 1.7, Old areas: 3.7 ± 1.6; $t = 0.7$, $df = 18.4$, $p = .45$), but in latrines of young areas species were at low abundance (Young areas: 4.1 ± 2.4 ind/sp, Old areas: 6.9 ± 3.0 ind/sp; $t = -2.56$, $df = 22.14$, $p = .009$). The number of saplings and location of latrines explained 43% of the variability in the richness ($F_{2, 22} = 8.79$, $p = .001$). In general, latrines with more saplings showed higher species richness than latrines with few saplings. However, young areas have a higher species richness when abundance is taken into account (Table 1, Figure S4).

Related to prediction (b), a total of 77 saplings higher than 1 m were recorded in the hectare of young area sampled. Only one sapling of *O. diospyrifolia* was not in a latrine and no saplings or latrines were found in areas dominated by *T. integrifolia* (Figure S5). About 78% of the saplings were *O. diospyrifolia*, 12% *E. punicifolia*, and 10% *Inga vera*. No adult trees of *O. diospyrifolia* or *E. punicifolia* were found. Twenty-eight of the saplings taller than 1 m (seven *E. punicifolia* and 21 *O. diospyrifolia*) were located in two large latrines located under the crown of two *B. arguta* trees (Figure S5).

4 | DISCUSSION

In agreement with the first prediction, the floristic composition of saplings in *A. caraya* latrines in the Paraná flooded forest was similar to that of older forests, even for latrines located in young areas. As predicted, in young areas, saplings of fleshy-fruited species were strongly associated with *A. caraya* latrines: only one out of 77 saplings was found outside a latrine. These results suggest that *A. caraya* plays a relevant role in the primary succession dynamics of the Paraná flooded forest. The role of *A. caraya* seems to be similar to that of *A. macconnelli* in the secondary succession of the Amazon. *Alouatta macconnelli* moves seeds between continuous forest and

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TABLE 1 Analysis of covariance (ANCOVA) summary table to determine the effect of the number of individuals and type of area (young/old) on the richness of saplings growing in latrines of *A. caraya*

Source of variation	SS	*Df*	MS	*F*	*P*
Number of individuals (covariable)	23.49	1	23.49	15.39	.0007
Type of area (group)	7.57	1	7.57	4.9	.03
Error	33.58	22	1.53		

Abbreviations: *df*, degrees of freedom; MS, mean squares; SS, square sum.

fragments of the Amazon forest (Santamaría Gómez, 2004), whereas *A. caraya* moves seeds between mature forests of old areas and young forests in young areas of islands in the Paraná River.

Alouata caraya groups inhabiting young areas of Paraná flooded forest are several times smaller than those inhabiting old areas (Kowalewski, 2007). The groups are cohesive and all the individuals of a group eat on the same food item each time they feed (Bravo & Sallenave, 2003; Kowalewski, 2007). So, a large group will transport a much higher number of seeds from trees to latrines than a small group. Assuming a similar probability to germinate and survive, the only way to find a similar number of saplings in latrines of large and small groups is that the latrine of the small group is used with a higher frequency than the latrine of a large group. Frequency of use of a latrine will involve an increase in the number of species arriving because the species consumed when a small group re-uses the latrine will be different. So, the pattern reported in the present study, that is, latrines with similar number of saplings but high richness, will be observed. Of course, probability to germinate and survive would be not similar because competition and predation in latrines of small groups can be low. Although both factors can contribute to increasing the number of saplings in those latrines, neither of them would impact on richness and would explain the pattern observed. Thus, integrating results, the floristic composition of latrines of *A. caraya* located in young and old areas was similar, and in turn similar to that of forests of old areas. However, latrines showed dissimilar species abundance. This difference may be a consequence of *A. caraya* behavior and social organization.

Seed dispersal by *A. caraya* in the Paraná flooded forest has been intensively studied (Bravo, 2008, 2009; Bravo, 2012a,b; Bravo & Cueto, 2020). Results have shown that *A. caraya* ingestion have a positive effect on *O. diospyrifolia* and *E. punicifolia* germination (Bravo, 2008, 2009). Digestion of seeds by *A. caraya* increases germination speed and cleans seeds of larvae, decreasing the percentage of seeds predated by arthropods (Bravo, 2008). Latrines provide a suitable environment for the growth of these species due to nitrogen availability (Bravo & Cueto, 2020). Results have also shown that latrines represent important areas of sapling recruitment of different tree species in the forest of old areas of the islands (Bravo, 2012a). In addition, the results of the present study suggest that the incorporation of *O. diospyrifolia*, *E. punicifolia*, and the other fleshy-fruited species to the forest community in young areas of the Paraná flooded forest is also a consequence of *A. caraya* seed dispersal mutualism.

Medium- and large-seeded species are dispersed by large vertebrates, being primates one of the most relevant groups (Fuzessy et al., 2018). However, few other taxa such as oilbirds, umbrella birds, and imperial pigeons can also disperse medium- and large-seeded species (Stevenson et al., 2021). The medium- and large-seeded species dispersed by *A. caraya* in the Paraná flooded forest have a low chance to be dispersed by other agents because most large vertebrates fail to establish populations in this habitat, and *A. caraya* is the only exception (Neiff, 2001). Three species that were present in latrines: *I. vera*, and the small seeded species *C. pachystachya* and *B. arguta*, could be dispersed by other agents. Two of these species are small-seeded (*C. pachystachya* and *B. argute*), and birds, bats, and fishes are frequent disperser agents of them (Araujo et al., 2019; Costa-Pereira et al., 2011; Gonçalves et al., 2007; Luque & Pinilla, 2019; Teixeira et al., 2009). In the case of *I. vera*, 95% of its seeds can germinate in the fruit so it is a viviparous species that can be dispersed by water (Faria, 2006). In the case of *Cecropia* spp., these are common species of secondary and primary successions (large gaps, human disturbed habitats, newly exposed sand in rivers) (Foster et al., 1986; Laurance et al., 2006; Muscarella & Fleming, 2007; Uhl et al., 1988), and *B. arguta* is a common species of lower zones of the Pantanal (Araujo et al., 2019; González et al., 2002; Teixeira et al., 2009). Although *A. caraya* disperses viable seeds of these three species, the presence of other dispersal agents (e.g., bats and birds) means that the adult trees of these species within the young forest might not all be attributable to *A. caraya*.

In the Paraná flooded forest in northeastern Argentina, sand banks are first colonized by grasses during the pioneer stage of succession (Brumnich et al., 2019; Corenblit et al., 2007; Zambiasio et al., 2018). The germination of the dry fruit species *T. integrifolia* and *S. humboldtiana*, which help us to stabilize and elevate the banks, starts the biogeomorphic stage (Brumnich et al., 2019; Pereira, 2016). The seeds of these species are dispersed by water, wind, and fishes. The banks are later colonized by seeds of *S. haematospermum*, *B. arguta*, *C. pachystachya*, and *I. vera*, which are species dispersed by autochory, water, fishes, birds, and bats (Araujo et al., 2019; Costa-Pereira et al., 2011; Gonçalves et al., 2007; Luque & Pinilla, 2019; Teixeira et al., 2009). Later, according to the results of the present study, the banks are colonized by the fleshy-fruited species (trees, shrubs and lianas) that have large seeds and dominate the old forest. The results allow the conclusion that *A. caraya* monkeys are the main animal responsible for this introduction in the young areas of the Paraná flooded forest in northeastern Argentina. The recruitment of saplings in *A. caraya* latrines starts the last phase of succession (ecological stage), allowing the formation of a pluri-specific forest and an increase in structural complexity and species diversity in these young areas.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.r2280gbdw (Bravo, 2021).

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