Biological Conservation 313 (2026) 111510

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Replacing the natural savanna matrix with eucalyptus plantations and soybean fields changes the seed rain promoted by bats in Amazonian savannas☆

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ARTICLE INFO

Keywords:
Bat-plant network
Fruit-eating bat
Land use
Mutualism
Neotropical savannas
Open ecosystems

ABSTRACT

The advance of plantations and croplands into natural areas has catalysed the loss of species and ecosystem functions worldwide. This loss appears to be more intense in tropical regions and may strongly impact groups essential for maintaining forests, such as bats. We evaluated the consequences of land-use changes on seed dispersal carried out by bats in the Savannas of Amapá, northeast of the Brazilian Amazon. More specifically, we compared the metrics of seed dispersal networks of the natural savanna matrix in relation to soybean or eucalyptus matrix, as well as between forest patches inserted in the natural savanna matrix in relation to forest patches inserted in soybean or eucalyptus matrix. Replacing the natural savanna matrix with croplands and plantations in the Savannas of Amapá causes the near disappearance of seed dispersal interactions and a collapse of the network structure in croplands. In addition, the seed dispersal networks in cultivated landscapes were more centered on a few, more abundant and generalist dispersers, which were more linked to pioneer plant species. Our results show that changes in the natural savanna matrix have drastic consequences on the seed rain promoted by bats, which can directly impact the ecological dynamics of the different habitats that comprise this Amazonian ecosystem. Maintaining natural habitats, such as forest and savanna, in cultivated landscapes is crucial and would reduce this negative impact. Savanna remnants can help maintain the original dynamics of bat communities in the landscape and the integrity and robustness of seed dispersal networks promoted by bats.

☆ This article is part of a Special issue entitled: 'Species interactions' published in Biological Conservation.

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https://doi.org/10.1016/j.biocon.2025.111510
Received 30 April 2025; Received in revised form 24 August 2025; Accepted 16 September 2025

1. Introduction

Changes in land use, such as those caused by the establishment of plantations and croplands, are among the greatest threats to Neotropical ecosystems (Antonelli, 2022). This change affects different aspects of biodiversity, including interactions between organisms, and can directly alter the ecosystem services promoted by different species in an area (Valiente-Banuet et al., 2015). Bats, for example, show varied responses to habitat changes among the different key species in interaction networks (Meyer et al., 2016; Williams-Guillén et al., 2016; Mendes and Srbek-Araujo, 2021). Therefore, the ecosystem services they promote can also be altered whether due to anthropogenic or environmental factors (Laurindo et al., 2019; Castillo-Figueroa, 2020a; Carlos et al., 2025). One of the most studied ecosystem services promoted by bats is seed dispersal (Castillo-Figueroa, 2020a; Regolin et al., 2020; Ramírez-Fráncel et al., 2022). Fruit-eating bats are among the most important seed dispersers across the tropics, and together with birds, are responsible for 80 % of the seeds dispersed in some areas of Neotropical forests and savannas (Galindo-González et al., 2000). Therefore, environmental changes that impact how they perform this ecological service can have major cascading impacts on ecosystems (Regolin et al., 2020).

In the Neotropics, fruit-eating bats (family Phyllostomidae) occur in high abundance in natural forest patches (Montiel et al., 2006; Loayza and Loiselle, 2009; Carvalho et al., 2018, 2021) or in forest fragments within landscapes that have been fragmented by anthropogenic activities (Meyer and Kalko, 2008; Rocha et al., 2017; Brändel et al., 2020). The establishment and permanence of these bats in different types of landscapes depend on the availability of resources, such as shelter and food, which are found mainly in forest patches or fragments (Loayza and Loiselle, 2009; Carvalho et al., 2023; Kinap et al., 2024). Furthermore, fruit-eating bats appear to be less influenced by the size of the forest patches than by their isolation (Montiel et al., 2006; Meyer and Kalko, 2008). In this way, the quality and permeability of the matrix are important for these bats, as it can increase connectivity between fragments and thus ensure the persistence of different species of fruit-eating bats in these landscapes (Montiel et al., 2006; Brändel et al., 2020; Carvalho et al., 2020). These dynamics can also be applied to species that occur in the Amazonian savannas (e.g., Carvalho et al., 2021; Kinap et al., 2024; Xavier et al., 2025). The Amazonian savannas are a natural mosaic, consisting of a landscape dominated by an open vegetation natural matrix (shrub or herbaceous, with scattered trees), with patches of forest, flooded areas, or *buritizais* (buriti palm formations dominated by *Mauritia flexuosa* - Mustin et al., 2017). This savanna natural matrix is being rapidly converted into eucalyptus and soybean monocultures (Carvalho and Mustin, 2017). Different species of fruit-eating bats that occur in the Amazon savannas primarily utilise the natural savanna matrix to move between forest patches, which serve as sources of food resources and shelter (Loayza and Loiselle, 2009; Carvalho et al., 2021; Kinap et al., 2024). Recent studies have shown that changes in this savanna matrix have altered the dynamics of its use by bats, resulting in a consequent decrease in the dimensions of diversity (Carvalho et al., 2020; Xavier et al., 2025). Thus, although there is no decrease in the amount of forest in the landscape, the reduction of connectivity between patches due to the replacement of the natural matrix by cultivated landscape may reduce the movement of bats across this landscape and consequently reduce seed dispersal (Montiel et al., 2006; Xavier et al., 2025).

The consumption of fruits by bats in a community forms interaction networks, where interactions can be described by links between consumer species and their resource plants (Bascompte and Jordano, 2007). Variation of the structure of such networks has been linked to the structure and stability of communities (Thébault and Fontaine, 2010). Establishing agricultural systems can not only influence the species composition of bats assemblages, but also the quantity, diversity and accessibility of fruits for bats, thus affecting the structure of these networks (e.g., Laurindo et al., 2019; Mello et al., 2019; Pinheiro et al., 2019). For example, communities with more heterogeneity of trophic resources allow more specialized interactions and, thus, favour the emergence of modules in networks, i.e., subsets of highly connected species within the community (Pinheiro et al., 2019). Communities with more homogeneity of trophic resources lead to sharing the same resource by many species, favouring nested topologies, i.e., when more specialized species interact with a subset of the partners of more generalist species, with no interactions between specialist species (Pinheiro et al., 2019). Furthermore, the richness and composition of species interacting in networks can be altered in landscapes with plantations and croplands due to filtering of functional traits that influence their permanence of bat species in the modified landscapes (e.g., degree of frugivory, body size), and can affect number of interactions and the way bats interact with other nodes (i.e., roles of bats) in these seed dispersal networks (Bascompte and Jordano, 2007; Acevedo-Quintero et al., 2020). In this way, there may be a change in the quantity and identity of species with more central roles within the structure of these networks, that is, those that have greater relative importance, affecting a greater number of nodes directly or indirectly (Mello et al., 2015).

Functional traits that affect bat movement, such as body size and wing morphology, may define the roles of bats in seed dispersal networks in landscapes where agricultural systems have replaced natural habitats (Laurindo et al., 2019; Castillo-Figueroa and Pérez-Torres, 2021). In dense vegetation such as forest habitats, bats with lower body size and higher maneuverability (lower wing loading) are expected to move more efficiently, while in open habitats, bats with greater body size and longer and narrower wings (i.e. greater wing aspect) move more efficiently (Norberg, 1994; Marinello and Bernard, 2014; Castillo-Figueroa, 2020b). Therefore, depending on these functional traits and the type of habitat, bats can access a wider diversity of fruit species and, thus, exhibit preferences that favour specialization, reducing the number of connections and thus their centrality, in seed dispersal networks (Laurindo et al., 2020). Functional traits that allow bats to feed on fruits can also affect seed dispersal networks (Mello et al., 2015). These traits lead to different degrees of frugivory, being related to bat dependence on fruits (Laurindo et al., 2020). Bats with a higher degree of frugivory (i.e., dependence on fruits, Laurindo et al., 2020) tend to be more generalists and assume more central roles in networks than bats with a lower degree of frugivory (Mello et al., 2015).

In addition to functional traits, the presence of plantations and croplands in the landscape also affects abundance, and consequently may also affect the roles of species in networks (Bascompte and Jordano, 2007; Vázquez et al., 2009) as more abundant species tend to engage in more interactions (Bascompte and Jordano, 2007; Vázquez et al., 2009). Therefore, a combination of abundance and functional traits with the type of agricultural systems in the landscape can determine the centrality of bats in seed dispersal networks. However, whether (and the extent) that seed dispersal by bats are affected by replacement of natural vegetation by plantations or croplands has been poorly investigated (see Xavier et al., 2023) which limits the capacity of anticipating and mitigating the impacts on these ecosystem services as well as designing effective management recommendations.

Here, our objective was to evaluate the consequences of land-use changes on seed dispersal carried out by bats in the Savannas of Amapá, an Amazonian savanna located in the northeast of the Brazilian Amazon. More specifically, we investigated how the conversion of the savanna matrix into eucalyptus and soybean monocultures affected the seed dispersal networks promoted by bats. Forest patches in natural landscapes, where the matrix is still savanna, were compared with forest patches where eucalyptus plantations and soybean fields replaced the natural savanna matrix. Furthermore, we also compared seed dispersal networks between the natural savanna matrix and cultivated matrix (eucalyptus plantation and soybean fields). We tested whether the cultivated matrix affected (1) the pattern of seed dispersal interactions carried out by bats; (2) the contribution of bat species to network connectivity and cohesion; and (3) on the relationships between functional traits and abundance with the roles of bats in seed dispersal networks.

We expected that the conversion of the natural savanna matrix into soybean fields would reduce the quantity of fruits and the structural complexity of vegetation of the matrix, thus reducing the movement of bats across the landscape (mainly for those that have greater flight efficiency in obstructed environments), therefore increasing isolation in forest patches (Xavier et al., 2025). This isolation will also decrease the bats' ability to explore the landscape in search of food, and, consequently, the diversity of fruits available to bats in the landscape will decrease (Montiel et al., 2006; Meyer and Kalko, 2008; Brändel et al., 2020; Xavier et al., 2025). The conversion of the natural savanna matrix into eucalyptus plantation will increase the structural complexity of the matrix vegetation and availability of fruits of pioneer plants in the matrix and forest patches (Pina et al., 2013; Carvalho et al., 2020; Xavier et al., 2025), causing bats to consume more frequently fruits of highly abundant pioneer plants and, thus, the diversity of fruits consumed by these bats will be less heterogeneous. As a result, the lower heterogeneity of fruits consumed by bats in cultivated landscapes is expected to affect the structure of seed dispersal networks, increasing nestedness and decreasing modularity (Pinheiro et al., 2019). Due to the changes in

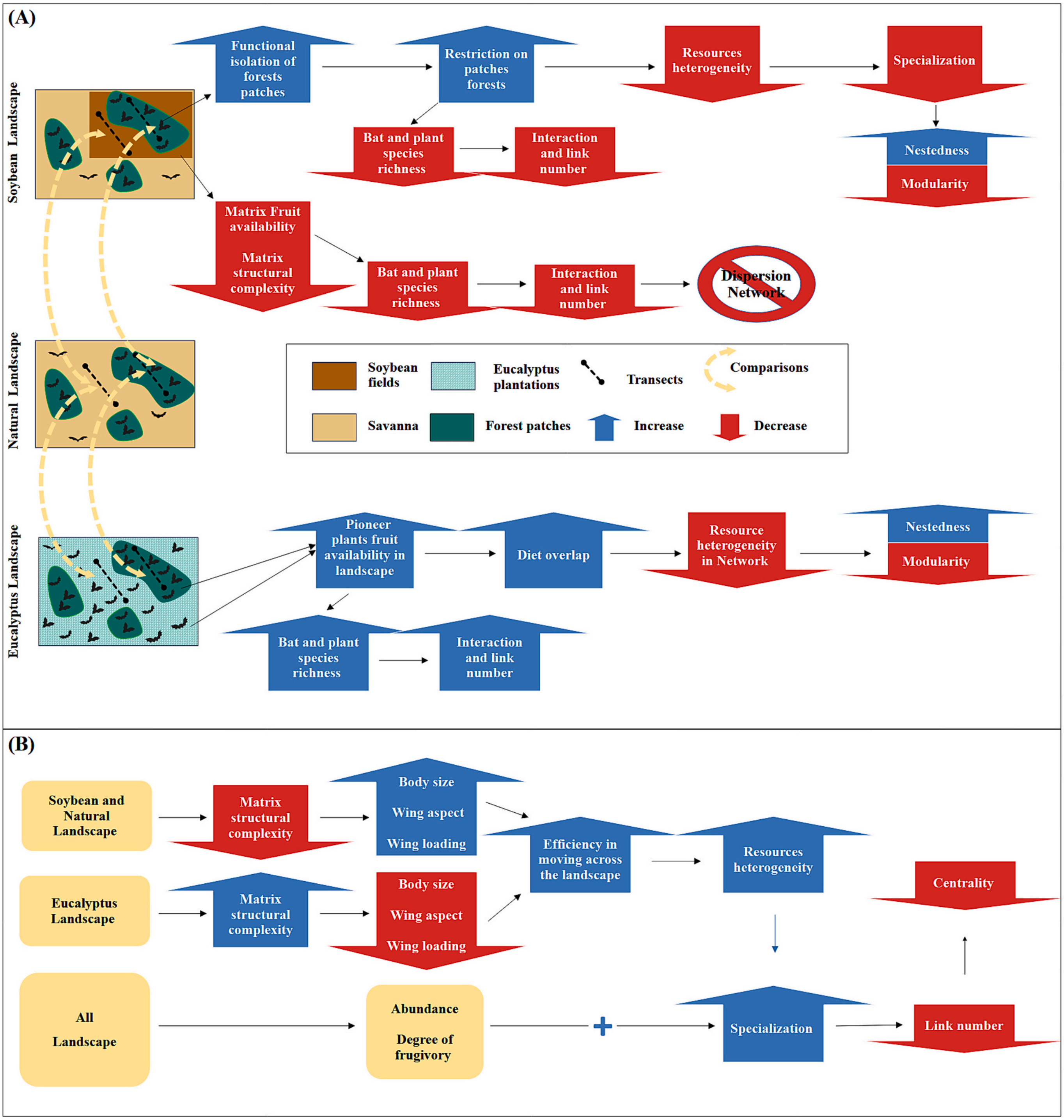

Fig. 1. Prediction of the effects of conversion of natural savanna matrix to eucalyptus plantations or soybeans fields on seed dispersal network structure (A) and relation of the functional traits and abundance with roles of bat in these networks (B) in Savannas of Amapá, Brazil.

the availability of fruits, we also expected an increase in the species richness of bats, plants, and the number of links (distinct pairs of species interacting) and interactions (sum of the number of times each pairwise interaction occurs) in landscapes with eucalyptus plantations (matrix and forest patches); and a decrease in these last parameters in forest patches surrounded by soybean fields. We do not expect to find interactions in soybean fields. Such a scenario is also expected to modify the primary ecological correlates associated with a species' role. We expect that bats that can move more efficiently across the landscape will be able to access a greater heterogeneity of resources and thus specialize (Estrada and Coates-Estrada, 2001; Bianconi et al., 2006). Therefore, bats with greater body size, greater wing aspect ratio, and wing loading would be more specialists, and thus, reduce the number of links in natural landscapes and in soybean fields, where it is necessary to cross a more open matrix to explore different forest patches (Norberg, 1994; Marinello and Bernard, 2014; Laurindo et al., 2020). In landscapes with eucalyptus plantations, where the matrix is more obstructed, we expect an opposite relationship. We expect that in all landscapes, there will be a positive relationship between abundance and degree of frugivory with the number of links (Bascompte and Jordano, 2007; Vázquez et al., 2009; Mello et al., 2015). Finally, we expect that bats with a greater number of links in the network will have greater centrality in the networks (becoming keystone species), since they make a greater number of connections (Mello et al., 2015). This would also modify species roles in these networks, leading to a shift in the identity of keystone species in dispersal networks between cultivated landscapes and natural landscapes (Bascompte and Jordano, 2007; Mello et al., 2015). Our hypotheses are summarized in Fig. 1.

2. Methods

2.1. Study area

We carried out this study in the Savannas of Amapá. This block of Amazonian savanna extends from north to south in the eastern part of the state of Amapá, located in the northeast of the Brazilian Amazon (Fig. 2). In the last 50 years, much of the natural savanna matrix has been converted into eucalyptus monocultures and, more recently (10–15 years), into soybean monocultures (Mustin et al., 2017; Carvalho et al., 2019a). The climate in this area is classified as a tropical monsoon climate (Am - climate classification of Köppen). The rainy season is characterized by rainfall above 100 mm and the dry season below 60 mm per month (Souza and Cunha, 2010). The temperature varies little throughout the year, with an average of around 27 °C (Tavares, 2014).

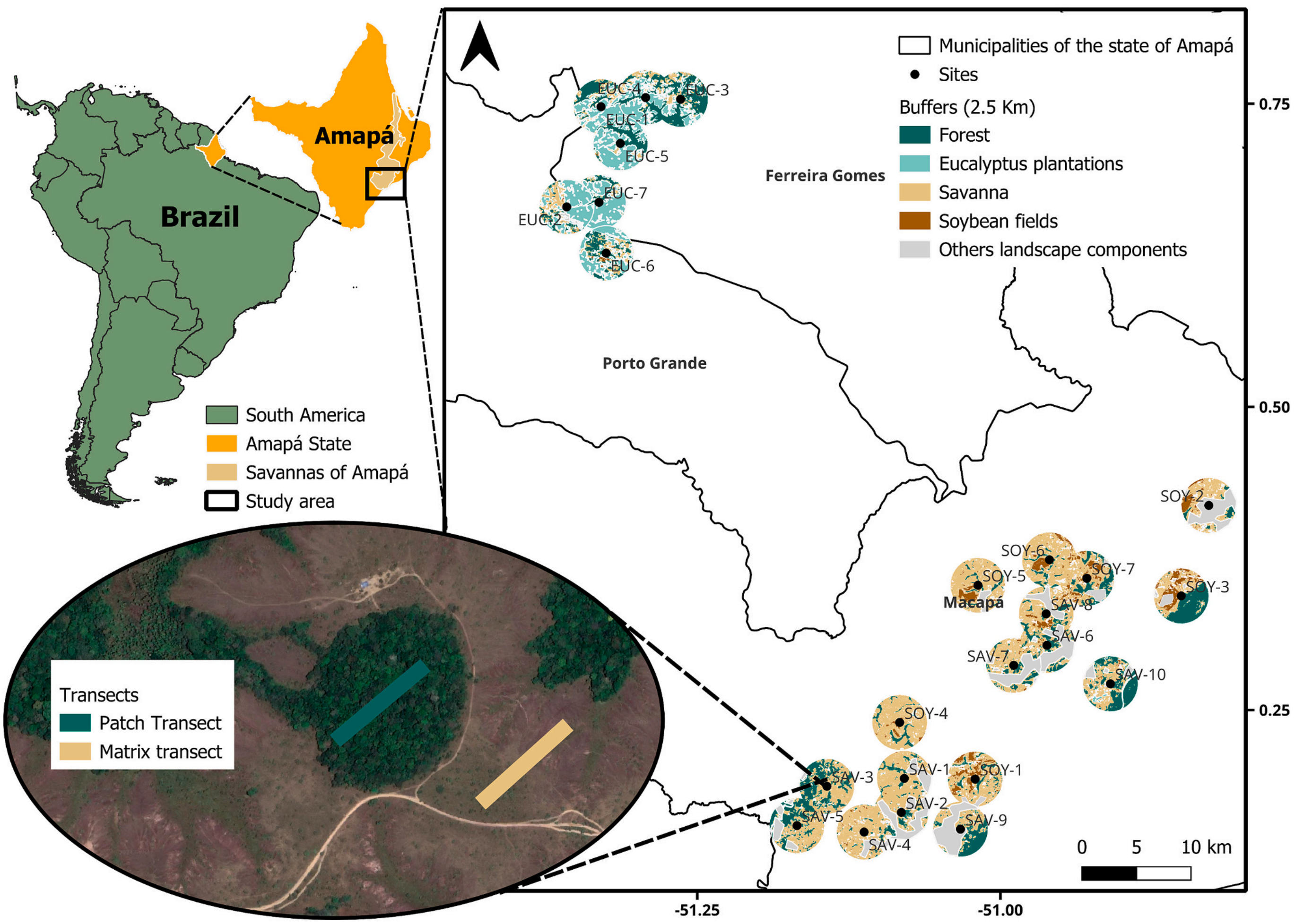

Fig. 2. Study area in Amapá, Brazil. In the upper left corner, location of the state of Amapá, in orange, on the map of South America and distribution of the Savannas of Amapá (light brown) in the state of Amapá, highlighting the study area delimited by a black rectangle. On the right side, distribution of the 24 sampling sites, showing the presence of forest, savanna, soybean fields, and eucalyptus plantation in buffers with a radius of 2.5 km. In the lower left corner, close up of a sampling site illustrating the placement of pairs of mist net transects in a forest patch, and adjacent matrix. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Satellite image obtained from Map data ©2015 Google.

2.2. Sample design

We sampled Phyllostomid bats in 24 sites located in three types of landscapes: 10 sites in landscapes with natural vegetation, where the savanna matrix was not replaced by agricultural systems (hereafter referred to as the natural landscapes), seven sites where the savanna matrix was converted into eucalyptus plantations (hereafter referred to as eucalyptus landscapes), and seven where part of the savanna matrix was converted to soybean fields (hereafter referred to as soybean landscapes; Fig. 2). We selected sites at least 2.5 km away from each other to maintain spatial independence between them (e.g., Carvalho et al., 2023). This is the average distance that larger bats (such as *Artibeus* spp.) move per night in Amazonian savannas (see Bernard and Fenton, 2003). One transect per habitat (forest in natural, eucalyptus and soybean landscapes, and natural savanna matrix, eucalyptus plantations and soybean field) was sampled at each site, resulting in one transect pair per site. In the sites sampled in natural landscapes, one of the transects was in the forest patch (hereinafter referred to as forest patches in natural landscape), and the other in the natural savanna matrix (hereinafter referred to as savanna matrix). In sites with eucalyptus plantations, one transect was located in the forest patch (hereinafter referred to as forest patches in eucalyptus landscape) and the other in the eucalyptus plantation. At sites in soybean field landscapes, one transect was located in the forest patch (hereafter referred to as forest patches in soybean landscape) and the other in the soybean field, totalling 48 transects (Fig. 2). Each transect had approximately 110 m of mist nets and was positioned at least 30 m from the patch/matrix edge. In the case of the forest patches, a 30 m distance from the edge was deemed sufficient to represent the interior of the patches, as the smallest patches were approximately 100 m wide (Carvalho et al., 2023). For more details on the sampled habitats, see the text in Appendix A and Fig. S1.

2.3. Bat data collection

Transects were sampled between February 2019 and February 2022. Each pair of transects simultaneously was sampled for four nights (two consecutive nights in the dry season and two consecutive nights in the rainy season) at each site, from ~20 min before sunset and for approximately 6 h (until 0:00). For this, we set up nine mist nets (dimensions: 12 × 3 m, mesh size 13 mm) in a single line along the ~110 m of each transect. The nets were checked every 15–20 min, or 5–10 min on nights with greater bat activity (Moura et al., 2023). The sampling effort, following Straube and Bianconi (2002), was 7776 $m^2 \times h$ per transect, totalling an effort of 155,520 $m^2 \times h$ in transects located in natural landscapes and 108,864 $m^2 \times h$ in transects in each of the landscapes with eucalyptus plantations and soybean fields. On the second night of sampling at each site, the line of mist nets was moved at least 50 m, thus avoiding a likely decrease in the capture rate due to bats learning the location of the nets (see Marques et al., 2013). Captured bats were identified according to Lim and Engstrom (2001), Reis et al. (2017) and López-Baucells et al. (2018). The nomenclature for bats follows Garbino et al. (2024). The fieldwork follows the guidelines of the American Society of Mammalogists (Sikes et al., 2016). The captured bats were kept in clean cotton bags for a maximum of 2 h to collect faeces, which were then stored in glassine paper envelopes. Adult bats weighing more than 5 g were individually marked with plastic collars, each coded according to Esbérard and Daemon (1999). To mark juveniles and adults of species which have a body mass equal to or less than 5 g, "punch-marking" (small holes made in the dactylopatagium) was used (see Bonaccorso and Smythe, 1972). Recaptures from the same night were not considered in the analysis. Subsequently, the seeds present in the faeces were identified based on the key in Lobova et al. (2009), on the descriptions of Bredt et al. (2012), and by comparisons with seeds collected in the field and from plants deposited in the *Herbário Amapaense, Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá* (IEPA), Macapá, Brazil. Seeds were identified to the lowest taxonomic level possible and were kept as "morphospecies" when we were unable to identify them (Table S1). The amount of seeds of pioneer species found in the diet of bats from each habitat at each site was quantified. This value corresponded to the sum of the occurrences of species and morphotypes of pioneer plant seeds in the faeces of each individual bat from each habitat at each site (Table S2).

2.4. Forests cover in the landscape

Forest cover was quantified within 2.5 km radius buffers around each sampling site following Carvalho et al. (2023). The buffer of each sampled transect, whether in the matrix or in the forest, was centered at the midpoint of each transect. To quantify each component of the landscape, we used a 2020 landcover map of the study area produced by the MapBiomas project (https://mapbiomas.org/en). This raster map was vectorised using the QGIS 3.38.2 (QGIS Development Team, 2024). The vector file was corrected considering the wetland classification provided by Global Wetlands (https://www2.cifor.org/global-wetlands/ - e.g., Carvalho et al., 2023). From the corrected vector file, the forest formation cover was quantified in km^2. As we had to move the transect in the second night of sampling, in each habitat of each site, the forest formation values corresponded to the average of the values quantified for the two buffers drawn for each transect present in the habitat (Table S2).

2.5. Species functional traits and bat abundance

To analyze the role of bat functional traits in the dispersal of seeds in the three types of landscapes we used traits that may influence the movement of bats and their food preferences: wing morphology, body size and degree of frugivory. Wing morphology was represented by wing aspect (squared wingspan divided by wing area) and wing loading (ratio between body mass and wing area). The wing aspect expresses how narrow the wing is (Norberg and Rayner, 1987; Norberg, 1994). Wing loading expresses the weight that bats carry per unit area of their wings (Norberg and Rayner, 1987; Norberg, 1994). These traits positively correlate with flight efficiency and speed and, inversely, with flight maneuverability (Norberg and Rayner, 1987; Norberg, 1994). Thus, species that fly in open areas tend to have greater wing aspect and wing loading, while bats that use obstructed spaces tend to have lower wing aspect and wing loading (Norberg, 1994; Marinello and Bernard, 2014). Wing aspect and loading were obtained from Tavares (2013) and Marinello and Bernard (2014). Body size was represented by body mass and forearm length. Body mass and forearm length values for each individual were obtained in the field, and the average for each species was calculated based on data from adult males, as females may be pregnant but with the fetus not yet palpable, which may bias the value of body mass (Carvalho et al., 2019b). The degree of frugivory for each bat species was assigned according to Mello et al. (2015). Thus, bats classified as obligate frugivores received a grade of three, bats that use fruits as a secondary item in their diet received a grade of two and bats that occasionally use fruits in their diet received a grade of one. The functional traits can be consulted in Table S3. As a proxy for abundance we used the number of captures of each species in the transect (Pineda-Lizano and Chaverri, 2022).

2.6. Network structure and species roles

Networks – To evaluate differences in the patterns of plant-bat interactions across habitat types, we built a binary bipartite network for each sampling site. A network consists of a matrix where each row represents a bat species i and each column represents a plant species j, and intersections aij indicate presence (1) or absence (0) of seeds of plant j in the faeces of bat species i.

Network metrics – We then calculated six complementary metrics to describe the network structure for each habitat of each sampling site:

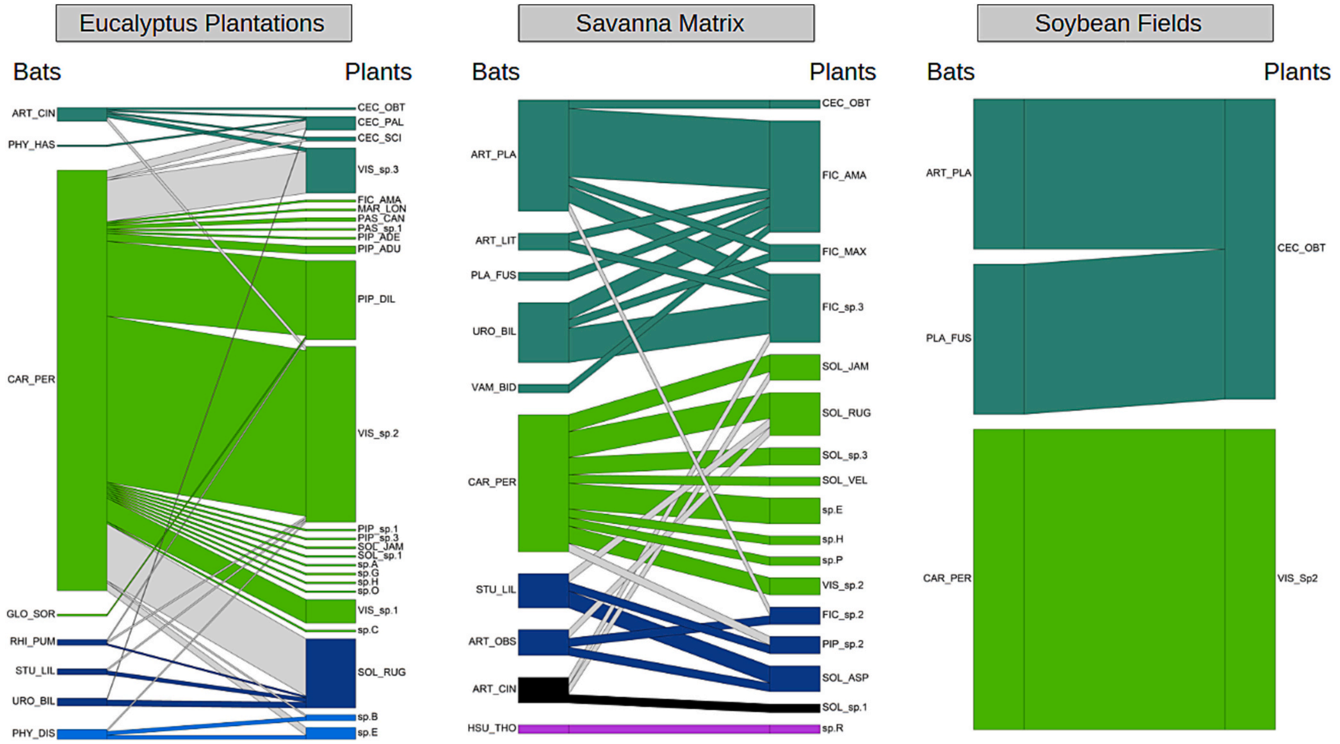

Fig. 3. Seed dispersal networks of eucalyptus plantations, natural savanna and soybean fields matrix in Savannas of Amapá, Brazil. The colors indicate the formation of different modules. These networks are only representative of our results, since the networks analyzed were those corresponding to each sample site (see Figs. S2–S4). Abbreviations for plant and bat species and morphospecies can be found in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

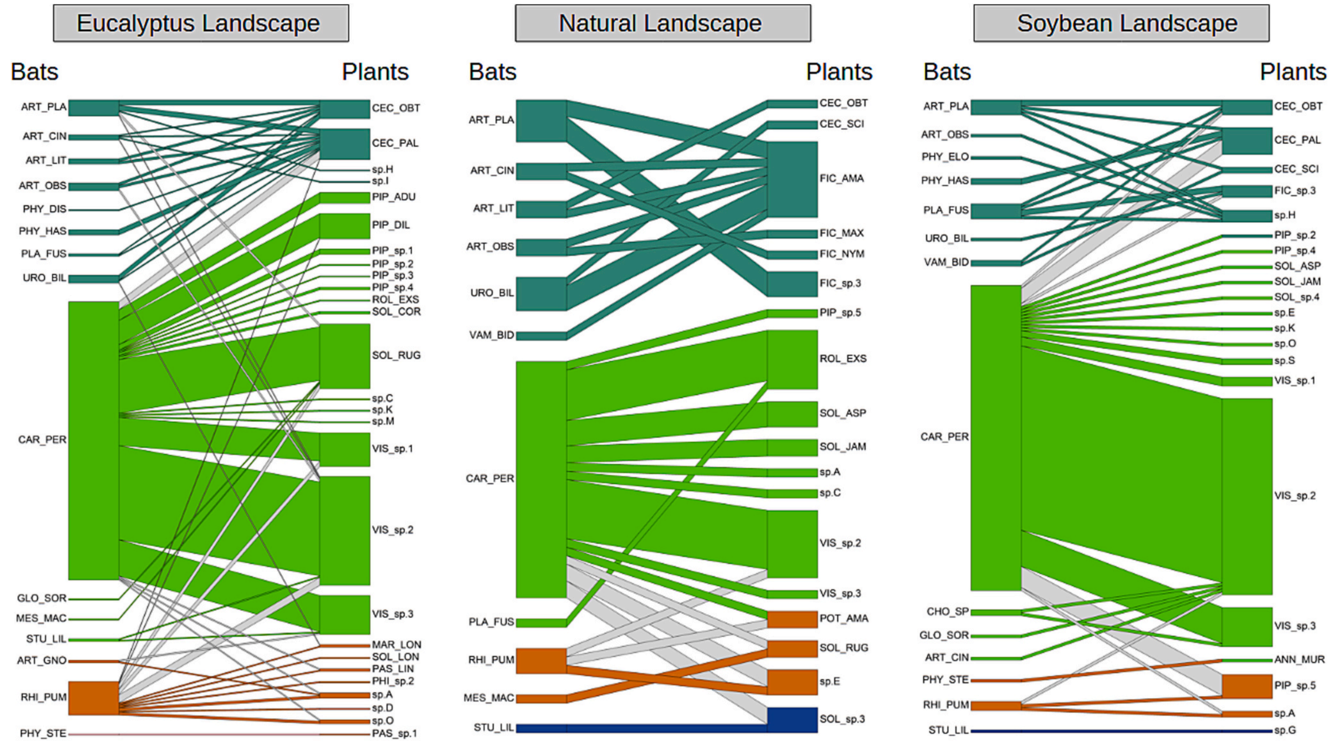

Fig. 4. Seed dispersal networks of forest patches in eucalyptus plantations, natural savanna and soybean fields landscape in Savannas of Amapá, Brazil. The colors indicate the formation of different modules. These networks are only representative of our results, since the networks analyzed were those corresponding to each sample site (see Figs. S5–S7). Abbreviations for plant and bat species and morphospecies can be found in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

number of bat species with seeds in faeces, number of plant species whose seeds were found in bat faeces, number of links (distinct pairs of species interacting), number of interaction events (sum of the number of times each pairwise interaction occurs), nestedness and modularity. Nestedness was calculated using the NODF metric, which calculates non-overlap and decreasing fill of binary matrices (Almeida-Neto et al., 2008). In a nested matrix, species that interact with few partners (specialists) interact with subsets of resources used by more connected species (generalists). NODF values range from zero (non-nested) to 100 (perfectly nested). Modularity (Q) was estimated using the optimisation DIRTLPAwb+ algorithm (Beckett, 2016). A matrix is modular when subsets of species interact with each other but do not interact with other species in the community, forming modules of highly connected partners. Modularity ranges from zero to one (maximum modularity possible). Differences in network dimensions (i.e. numbers of rows and columns) and sampling effort can influence modularity and nestedness metrics. Because of this, values are often not directly comparable among areas. To account for these differences and improve comparability we used Δ-scores, which are the differences between the observed values (of modularity or nestedness) and the average value obtained by null models, to represent modularity and nestedness in our analyses. Thus, the Δ-score represents how much the observed structure deviates from the structure expected by chance being, thus, a measure of effect size (Dalsgaard et al., 2017). One thousand randomisations of networks were created using the Patefield null model, using the R function *r2dtable*. This null model maintains the number of species at each trophic level and the marginal total of the observed matrix. All network metrics and null models were estimated using the package 'bipartite' (Dormann et al., 2009) and reported in Table S2.

Species-level metrics – For each bat species in each network, we calculated metrics related to number of interactions (Normalised degree) and the way bats interact with other nodes (Betweenness centrality and Closeness centrality) in the network: Normalised degree, which is a simple measure of specialization, calculated as the proportion of the total available partners with which species *i* is interacting. This metric varies from zero (no partner interactions) to one (when the species interacts with all available partners) and was estimated with the function '*normalised degree*'; Betweenness centrality, which describes each species in the network based on its position on the shortest paths between other nodes (species), and was estimated with the function '*betweenness*'; and Closeness centrality, which describes each species based on the reciprocal of the sum of the length of the shortest paths between a species and all other species in the networks. Thus, the more central a species is, the closer it is to all other species in the network, and was estimated with R function '*closeness*'. High values of both centrality metrics and Normalised degree are related to species that play key roles in the network. All species-level metrics were estimated using the package 'bipartite' (Dormann et al., 2009) and reported in Table S3.

For visualization purposes, we use the function '*plotweb*' to construct the total dispersal networks including all sampling sites of each habitat (Figs. 3–4). The function '*plotModulesWeb*' was used to classify interactions into different modules. The scattering networks of each habitat of each sampling site, analyzed networks, were also plotted and can be viewed in the Supplementary material (Figs. S2–S7). These functions are part of the package 'bipartite' (Dormann et al., 2009).

2.7. Data analysis

Variation in network metrics – We used Generalized Linear Models (GLMs) to assess whether network metrics (number of bat species, number of plant species, number of links, number of interactions, nestedness and modularity) differ between natural, eucalyptus, and soybean landscapes. In addition, we also used GLMs to assess whether the amount of pioneer species seeds found in the diet of bats differs between these landscapes. Network metrics and amount of seeds of pioneer species of each habitat of each sampling site were used as response variables, while the type of landscape was used as an explanatory variable. Since bats are forest-dependent in the study area (see Carvalho et al., 2021, 2023) and the forest cover can vary in each sampled landscape, forest cover in the 2.5 km buffer was used in all models as a covariate to account for its effect. We separately compared the savanna matrix with the eucalyptus and soybean matrix, as well as the forest in a natural landscape with forests in a eucalyptus and soybean landscape. It was impossible to compare nestedness and modularity between savanna and soybean fields, as the small number of interactions in the soybean fields (three links and four interactions in soybean fields) did not allow the calculation of these metrics. Responses with $p < 0.05$ were considered significant. The models can be consulted in Table S4.

Variation in species-level metrics – To assess whether the role of bats changed between landscapes, we used Pearson's correlation coefficient, following Castaño et al. (2020), between pairs (natural and cultivated landscapes) of each metric (Normalised degree, Betweenness centrality and Closeness centrality) of each species calculated from the networks of each habitat of each sampling site (Table 1). When there was a significant ($p < 0.05$) positive and strong correlation ($r > 0.75$), it was considered that the role of the species did not change from the natural landscape to the eucalyptus or soybean landscapes. It was impossible to compare the savanna with the soybean fields due to the small number of interactions in the soybean fields. It was also not possible to compare Betweenness centrality between habitat pairs, as no bat assumed the role of intermediation in the seed dispersal networks of natural landscapes.

Bat species' roles in seed dispersal networks in relation to species functional traits and abundances – We used Generalized Linear Mixed Models (GLMMs) to verify whether the role of species in networks is related to their abundances and functional traits (wing loading, wing aspect, frugivory degree, body mass and forearm length). In these models, species metrics (Normalised degree, Betweenness centrality and Closeness centrality) calculated for each habitat of each sampling site were included as response variables, whereas abundance in the habitat of each sampling site and the functional traits were included as explanatory variables. The forest cover in the 2.5 km buffer was also used as a covariate to account for its effect. Furthermore, bat species identities were used as a random variable. Abundance, non-categorical functional traits and forest cover were standardized, by subtracting their mean and dividing the result by their standard deviation. Each model's variance inflation factor (VIF) was checked, and predictor variables with VIF > 3 were excluded to avoid multicollinearity between the predictor variables. The degree of frugivory was not used as a predictor for any of the three metrics in the savanna and forest in natural landscapes as all bats in the networks of these habitats had a degree of frugivory equal to three (obligate frugivores). A model was used for each species metric for each habitat (forest in natural, eucalyptus and soybean landscapes, and natural savanna matrix and eucalyptus plantations). Here, it was also impossible to analyze the metrics of the soybean field species due to the

Table 1

Pearson correlation coefficients and statistical significance of the roles of Phyllostomid bats (ND: Normalised degree; and CC: Closeness centrality) in seed dispersal networks of an Amazonian Savanna (Amapá, Brazil) between cultivated landscapes (forest patches and cultivated matrices) and natural landscapes (forest patches and savanna matrix).

Habitats	Variable response	r	p
Forest patches in eucalyptus vs natural landscape	ND	0.83	<0.001
Forest patches in eucalyptus vs natural landscape	CC	0.02	0.87
Forest patches in soybean vs natural landscape	ND	0.84	<0.001
Forest patches in soybean vs natural landscape	CC	−0.04	0.79
Eucalyptus plantations vs natural matrix	ND	0.36	0.02
Eucalyptus plantations vs natural matrix	CC	−0.15	0.36

low number of interactions found. Due to data variation, it was also impossible to assess whether Betweenness centrality varies with abundance and functional traits in savannas and forests in natural landscapes and soybean landscapes. For GLMMs, responses with $p < 0.05$ were considered significant. The models can be consulted in Table S4.

The function *cor.test* of package 'stats' (R Core Team, 2023) was used to assess the correlation between the roles of bats in different landscapes. The function *glmmTMB* of package 'glmmTMB' (Brooks et al., 2017) was used to run the GLMs and GLMMs. This package allows to tune models that contain more zeros than expected from the error distribution (zero-inflated model). Additionally, the package 'DHARMa' (Hartig, 2017) was used to diagnose the models regarding their distributions and assumptions and the possibility of having spatial autocorrelation and more zeros than expected for their distribution (Table S4). All mentioned packages were loaded into the R program, version 4.3.0 (R Core Team, 2023).

3. Results

3.1. General results

On each habitat of each sampling site, seed dispersal networks presented between one and seven bat species, one and thirteen plant species, one and 22 distinct links, and one and 93 interaction events (Figs. 3–4; S2–S7; Table S2). Furthermore, the networks presented low nestedness (mean = 24.52, sd = 16.49) and moderate modularity (mean = 0.49, sd = 0.11). Bat species had a Normalised degree ranging from 0.08 to 1 (mean = 0.31, sd = 0.24), Closeness centrality ranging from 0 to 0.5 (mean = 0.22, sd = 0.16), and Betweenness centrality ranging from 0 to 1 (mean = 0.09, sd = 0.25; Table S3).

3.2. Comparing natural, eucalyptus and soybean landscapes

When the different landscapes were compared, in both the eucalyptus matrix and forest patches in the eucalyptus landscape, nestedness, plant species richness, number of links, number of interactions and abundance of pioneer plant seeds present in the bats' diet increased (Fig. 5, Table S4). Conversely, modularity decreased compared both to savanna matrix and to their forest patches (Fig. 5, Table S4). Bat richness did not differ significantly in eucalyptus matrix compared to natural savanna matrix (Fig. 5A, Table S4), but increased in forests surrounded by eucalyptus matrix compared to forests surrounded by natural landscapes (Fig. 5B, Table S4).

When the savanna and soybean matrices were compared, interaction networks in soybean had lower plant richness, number of links and interactions, while bat richness and abundance of pioneer plant seeds present in the bats' diet did not differ significantly (Fig. 5A, Table S4). It was not possible to calculate nestedness and modularity of the soybean matrix networks as few bat individuals were captured in these croplands and, consequently, only three links and four interactions were found: one interaction between *Platyrrhinus fusciventris* and *Cecropia obtusa*, one between *Artibeus planirostris* and *Cecropia obtusa*, and two between *Carollia perspicillata* and *Vismia* sp.2. In the case of forest patches, the networks of forests in soybean landscape showed higher nestedness and abundance of pioneer plant seeds present in the bats' diet and lower modularity than those of natural landscapes (Fig. 5B, Table S4). The other network metrics did not differ between the forests of these two landscapes (Table S4).

3.3. Role of species in the seed dispersal network

The Normalised degree of bats from the savanna and eucalyptus matrices were positively correlated (Table 1), but this correlation was not considered because $r < 0.75$. The Normalised degree of bats of forest patches in natural, eucalyptus, and soybean landscapes was positively correlated (Table 1). Closeness centrality in savanna and eucalyptus plantations matrices was not significantly correlated, as well as Closeness centrality of forest patches in natural, eucalyptus, and soybean landscapes (Table 1). As no bat in the seed dispersal networks of natural landscapes (forests patches and savanna matrix) showed Betweenness centrality, it was impossible to test this metric's correlation between natural and cultivated landscapes (Table S3). One species of bat in eucalyptus plantation matrix, two species in forests in soybean landscape and eight species in forests in eucalyptus landscape showed some degree of Betweenness centrality (Table S3).

3.4. Roles of bat species in seed dispersal networks in relation to their functional traits and abundance

Abundance, wing loading and body mass were related to the roles of bats in seed dispersal networks (Fig. 6, Table S4). Abundance was positively related to Normalised degree and Closeness centrality in the eucalyptus plantation matrix (Fig. 6A, Table S4) and positively related to Normalised degree in the forests in eucalyptus landscape (Fig. 6B, Table S4). Wing loading was negatively related to Normalised degree in savannas matrix (Fig. 6A, Table S4), and body mass was negatively related to Normalised degree in the forest patches of eucalyptus landscape (Fig. 6B, Table S4).

4. Discussion

Our results showed that replacing the natural savanna matrix with eucalyptus plantations and soybean fields in the Savannas of Amapá causes the near disappearance of seed dispersal interactions and a collapse of the network structure at soybean fields. It also makes seed dispersal networks of eucalyptus plantation matrix and forest patches in cultivated landscapes more centered on few dispersers, likely susceptible to faster propagation of effects and more random, driven mainly by abundance. However, this result should be considered with caution, as some of our networks were small, mainly due to these changes in the landscape. Furthermore, these networks appear to be dependent on the fruiting peak of pioneer plants, found in greater quantities in the diet of bats in cultivated landscapes. This greater availability of trophic resources could have a temporary effect in the forests of the soybean landscape, as the natural savanna matrix is still being replaced (Xavier et al., 2025). As for the eucalyptus plantation matrix, there may be a fluctuation in the availability of fruits every 6–8 years due to its cutting and complete cleaning of the area (Xavier et al., 2025). This result is alarming since all the dynamics in these Amazonian ecosystems, which occur naturally in patches, can be affected more intensely due to the different human interventions over the last few years (Hilário et al., 2017; Mustin et al., 2017).

Studies carried out in other Amazonian savannas throughout South America showed that replacing native vegetation by tree plantations, such as commercial acacia monoculture, reduce bat diversity, as observed in the Lavrados of Roraima, Brazil (Carvalho et al., 2020), and that grazing pressure by cattle disrupts the regeneration of palms, as observed in the Beni savanna, Bolivia (Hordijk et al., 2019). Specifically in the Savannas of Amapá, expanding agricultural areas have promoted the loss of the taxonomic diversity of primates (Calle-Rendón et al., 2020), and of the taxonomic and functional diversity of birds (Pandilha et al., 2021) and bats (Xavier et al., 2025). To the best of our knowledge, we present here the first assessment on how the anthropization of these natural Amazonian landscapes could affect ecological processes intrinsically related to species occurrence. Our results have direct implications for the conservation of Amazonian savannas, from bat species to the recruitment of seedlings in the different natural habitats evaluated, regardless of the type of agricultural system, there are direct impacts on interactions between bats and plants.

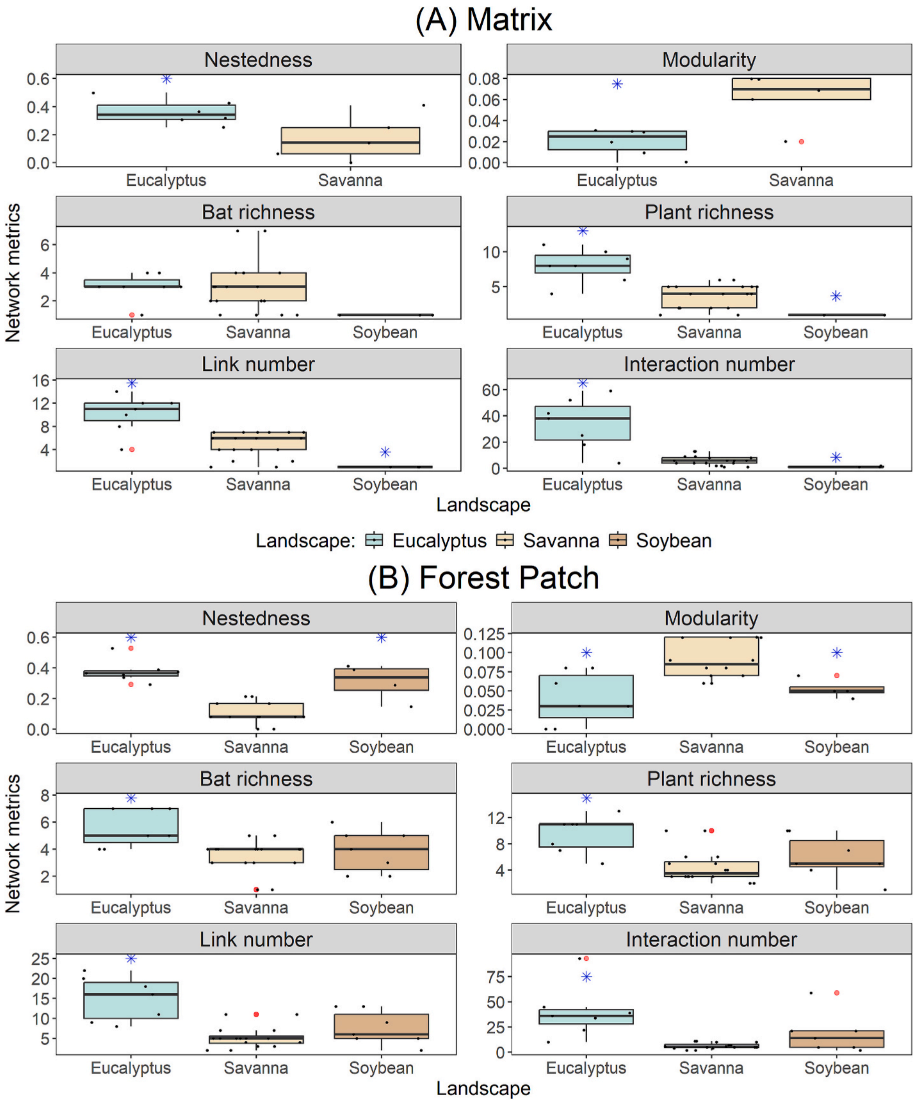

Fig. 5. Changes in the structure of seed dispersal networks carried out by bats (nestedness, modularity, plant and bat richness, number of links and interactions) in the matrix (A) in forest patches (B) due to the replacement of natural savanna matrix by eucalyptus plantations and soybean fields in Savannas of Amapá, Brazil. * Represents significant results ($p < 0.05$) for the conversion of savanna to eucalyptus plantations and soybean fields. The central line corresponds to the median, the lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles), the upper whisker extends from the hinge to the largest value no further than 1.5 * IQR (distance between the first and third quartiles) from the hinge, the lower whisker extends from the hinge to the smallest value at most 1.5 * IQR of the hinge and the red dots correspond to the outlier. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. *Structure of seed dispersal networks*

In the eucalyptus landscape, whether in the matrix or forests patches, our results showed that the conversion of the natural savanna matrix into eucalyptus plantations increased, as we predicted, the consumption of fruits from pioneer plants (*Piper* spp., *Cecropia* spp., *Vismia* spp., and *Solanum* spp.) making the networks more nested and less modular, a pattern that has been interpreted in other mutualistic systems as a consequence of decreasing niche partitioning (Lautenschleger et al., 2021). This change in topology occurs when an environment becomes more homogeneous in trophic resources, restricting opportunities for resource partitioning among bat species which leads to less formation of specialized interaction modules as well as increasing nestedness (Pinheiro et al., 2019; Lautenschleger et al., 2021). Eucalyptus landscapes are not necessarily less diverse in species of fruiting plants that are consumed by bats than natural savanna landscapes. However, the increased availability of fruits from pioneer plants has been observed in other Neotropical savannas (see Pina et al., 2013; Carvalho et al., 2020) and has been recorded in our areas in the same sampling period (Xavier et al., 2025). Bats widely use fruits of pioneer species (Fleming, 1982, 1986; Lobova et al., 2009), its greater availability increases the abundance of obligate frugivorous bats, and attracts secondary and occasional frugivores, such as *Glossophaga soricina*, *Phyllostomus discolor*, and *Phyllostomus hastatus* (Mello et al., 2015), which consume fruits in eucalyptus landscapes. Thus, the fruiting of pioneer plants leads to greater sharing of such resources between poorly connected and less central bat species that feed on the same plant species than highly connected and central bats. This makes the diversity of fruits consumed by bats more homogeneous and contributes to increased nestedness and decreased modularity (Pinheiro et al., 2019). Therefore, this addition of the plant and bat species in the landscape directly increases, as expected, plant richness, number of links and the number of times these links occur (interactions numbers) and change bat species' composition in the seed dispersal networks.

Some of the effects observed in forest patches in eucalyptus landscape also occurred in forests patches when the natural savanna matrix

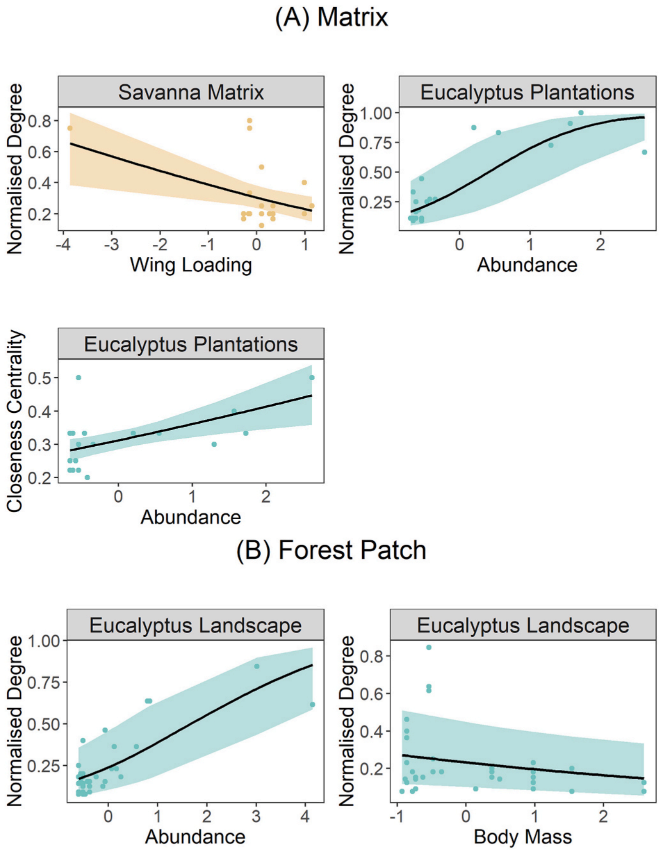

Fig. 6. Relationship between the bats species' roles in seed dispersal networks (Normalised degree and Closeness centrality), abundance and functional traits in the matrix (A) and in forest patches (B) in Savannas of Amapá, Brazil. Only significant effects ($p < 0.05$) were represented. The dots represent the observed data. Solid lines represent the relationship predicted by the models and the shaded area is the 95 % confidence interval in light brown for the natural landscape and light blue for eucalyptus plantations landscape. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

was converted to soybean fields, namely increasing nestedness, decreasing modularity and a change in the composition of bats and seeds in seed dispersal networks. These results are consistent with the increased concentration of bats and pioneer plants in forest patches of these same sampling sites (see Xavier et al., 2025) and with the increased consumption of pioneer plants by bats in these habitats shown in our results. However, contrary to expectations, the plant and bat richness and the number of links and interactions did not differ from the networks of forest patches in natural landscapes. Although soybean fields constitute extremely hostile matrices for bats, as they have not entirely replaced natural savannas, the remnants of this habitat still allow bats to move around this landscape (Bernard and Fenton, 2007; Carvalho et al., 2023), thereby maintaining the dynamics in seed dispersal to some extent. However, savanna areas that are still in soybean landscape may be completely converted, as this is already predicted to occur (Hilário et al., 2017; Mustin et al., 2017), which will result in a decrease in interactions in seed dispersal networks.

In comparisons between natural savanna and soybean matrices, it was possible to observe, as expected, a drastic reduction in plant richness and the number of links and interactions in the latter habitat. However, despite the low use of soybean fields by Phyllostomid bats (Xavier et al., 2025), there was only a tendency towards a decrease in bat richness. Castaño et al. (2020) found a similar response when comparing coffee plantations with continuous forests in the Colombian Andes, where plantation networks had lower plant richness and number of interactions, but similar bat richness. Therefore, it is likely that the few captures in soybean fields, from which we collected faeces, were mostly passing bats that feed in adjacent habitats.

4.2. Bat species' roles in seed dispersal networks across different landscapes

Except for the Normalised degree in forest patches, our results indicate that replacing natural savannas matrix with eucalyptus plantations and soybean fields changes the species roles in seed dispersal networks in the Savannas of Amapá, as expected. Species that are more generalist (i.e., high normalised degree) in natural landscapes, such as *Carollia perspicillata*, tend to retain their generalist role in cultivated landscapes. However, cultivated landscapes exhibit a change in the identity of key species that function as central hubs in the networks, often characterized by higher Closeness centrality, sharing a large part of their diet with other bats that made fewer links (e.g. *Phyllostomus discolor*, *P. hastatus*). The role changes seem to be associated mainly to *C. perspicillata*. In all the habitats analyzed, this species was one of the most generalist (highest Normalised degree) and had the greatest Closeness centrality. *Carollia perspicillata* is the most captured bat in studies carried out in different Neotropical forests (e.g., Muylaert et al., 2017; Martins et al., 2022), Amazonian savannas (e.g., Bernard and Fenton, 2007; Carvalho et al., 2023) and even in habitats degraded by humans (Farneda et al., 2015), such as in eucalyptus and acacia plantations (Pina et al., 2013; Carvalho et al., 2020; Jacomassa et al., 2025). Furthermore, the abundance of this species is greatly influenced by the availability of fruits from pioneer plants, mainly *Piper* spp. (Andrade et al., 2013). However, in natural savannas, this species shares the most central role with other species (such as *Artibeus cinereus*, *A. planirostris*, *A. obscurus*, *Uroderma bilobatum*), while in cultivated landscapes, these roles in seed dispersal networks are centered almost solely on it. Our data show that some species lost their most central roles (e.g., *A. cinereus*, *U. bilobatum*, *A. obscurus*) or no longer occur in some cultivated habitats (e.g., *A. planirostris*). In this way, seed dispersal networks are supported by few species, thus becoming more vulnerable to the loss of dispersers. Furthermore, no bat assumed connector role (i.e., high Betweenness centrality), linking different parts of the dispersion network, in natural landscapes and all habitats that replaced the natural savanna matrix; one or more species assumed this role, with *C. perspicillata* once again being one of the most central species in this role. Thus, in cultivated landscapes, more species exhibit high Betweenness centrality, which shortens the paths between different species or parts of the network. This, in turn, may facilitate the faster propagation of negative effects throughout the seed dispersal network, potentially leading to highest instability in bat-mediated seed dispersal systems (Mello et al., 2019).

4.3. Roles of bat species in seed dispersal networks in relation to their functional traits and abundance

We showed that the relationship between bat abundance and functional traits with their roles in the seed dispersal network varies according to the type of landscape, as expected. However, some of our networks have few bats and plant species and, consequently, few interactions, which may be biasing the results, especially for centrality metrics (Martin and Niemeyer, 2021). In natural landscapes, the efficient flight (high wing loading) was associated with Normalised degree, while in eucalyptus landscape, abundance and body mass was associated with Normalised degree and Closeness centrality. In soybean landscapes, abundance and functional traits were not related to the bats' roles. In natural savannas, the results showed, as expected, bats with greater wing loading made fewer links (lower Normalised degree) within seed dispersal networks. Thus, this better movement across the landscape, due to the greater wing loading for certain species of bats (e.g., *Sturnira lilium*, *Platyrrhinus fusciventris*), which will lead to greater use of the natural matrix to move between forest patches (Carvalho et al., 2021), could lead to a greater opportunity to explore the landscape, making the accessed resources more heterogeneous and thus favouring specialization and decreasing their Normalised degree (Pinheiro et al., 2019). This positive relationship between wing loading and Normalised degree was also expected in landscapes with soybean fields. However, the lack of relationship between these variables in these landscapes may reflect the fact that the replacement of the natural savanna matrix by soybean fields decreased movement through the matrix, making these bats more concentrated in the patches, as already seen for these same areas (Xavier et al., 2025). Thus, these traits lose importance for their roles in seed dispersal networks, since bats will use the open vegetation matrix less.

Additionally, the lower wing loading helps transport fruit, which is crucial for bats crossing the savanna carrying fruit from where they found it to their feeding perch (Heithaus, 1982), which may explain the importance of these traits for the role of bats in savannas, but not in eucalyptus landscapes where the matrix is more permeable to most bat species. However, this result should be considered with caution, since the relationship between wing loading and Normalised degree is mainly influenced by a single observation corresponding to the species *Artibeus cinereus*, which has one of the highest Normalised degree values in the savanna matrix, but disappears in the soybean fields and is less connected (low Normalised degree) in all forest patches and in the eucalyptus plantations.

In eucalyptus landscapes, only body mass and abundance were correlated with bats' roles in the seed dispersal network. The presence of larger bats, supported by the great availability of fruit in this landscape, may explain the relationship of body mass with the number of interactions (Normalised degree) of bats in networks (Acevedo-Quintero et al., 2020). In addition, we expected a positive relationship between body mass and the bats' roles at eucalyptus landscape, as this type of plantation, more obstructed than the natural savanna, would tend to act as a filter for larger bats (Laurindo et al., 2020; Castillo-Figueroa and Pérez-Torres, 2021). However, the negative relationship detected suggests that in eucalyptus landscape the potential constraints to fly may be compensated by the greater food availability (Laurindo et al., 2020). In this landscape type, bats with greater body mass may be concentrating their diet on the most abundant fruits to meet their greater energy demand and, therefore, make fewer links (i.e, lower Normalised degree).

In addition to functional traits, abundance was positively associated with Normalised degree and Closeness centrality in eucalyptus matrix and was positively associated with Normalised degree in forest in eucalyptus landscape. The increased quantity of fruits from pioneer plants would lead to an increase in the abundance of bats (Pina et al., 2013; Meyer et al., 2016; Carvalho et al., 2020; Jacomassa et al., 2025) highlighting the relationships between abundance and the roles of bats in seed dispersal networks in this landscape. The results indicated that bats became more connected to each other as they fed on the same super-abundant fruits, and thus, their Closeness centralities also increased (Mello et al., 2015). The results also indicated that bats tended to carry out more interactions (higher Normalised degree) when they were more abundant. These findings suggest that, although bat species exhibit distinct dietary preferences (e.g., *Carollia* for *Piper*, *Sturnira* for *Solanum*, and *Artibeus* for *Ficus* and *Cecropia* - Andrade et al., 2013), they are nevertheless capable of consuming a broad range of fruit resources (Laurindo et al., 2020). However, abundance-driven interactions can be considered random (Vázquez et al., 2009; Laurindo et al., 2020), as all individuals have the same chance of interacting with fruits. Consequently, the most abundant species will carry out more interactions (Vázquez et al., 2009).

4.4. Conservation implications

Despite appearing to benefit some bats species with abundant trophic resources and low contrast with forest patches, eucalyptus plantations alter seed dispersal networks importantly in regard of its general network structure, patterns of bats species' roles and the traits associated with key roles. Furthermore, interactions in these landscapes also become random, driven mainly by abundance. These dynamics in seed dispersal may be altering seedling recruitment in the understory of forest patches. For example, Xavier et al. (2025) has already shown a significant increase in the abundance of pioneer plants, mainly *Piper* spp., in the understorey of these same forest patches immersed in the eucalyptus matrix, which aligns with the increased consumption by bats of these plants observed in our results. Therefore, the change in seed rain promoted by bats with the increase in the occurrence of pioneer plants could have a cascading consequences, affecting the abundance, establishment, persistence and interactions of other groups of plants and animals (Tabarelli et al., 1999), changing the species composition and structures of the forest patches of our cultivated landscapes. This type of negative change in forests adjacent to agricultural systems is likely to occur in other Neotropical savannas, such as the Brazilian Cerrado, which are subject to similar anthropogenic pressures. For example, other studies have already found a negative impact of agricultural systems on bat diversity in the Brazilian Cerrado (Pina et al., 2013; de Oliveira et al., 2017; Ramos Pereira et al., 2018), and forest loss has negatively impacted the modularity, connectivity and richness of interacting bats in seed dispersal and pollination networks in this biome (Carlos et al., 2025). However, more studies must be conducted to evaluate the long-term effects of changes in seed dispersal resulting from the replacement of natural savannas with agricultural systems on seedling recruitment. These new studies should also consider carry out a greater sampling effort to minimize the impact that network with fewer interactions may have on the expected results (e.g., de Aguiar et al., 2019).

In eucalyptus and soybeans landscapes, obligate fruit bats (e.g., *A. planirostris*) were lost and replaced by secondary and occasional frugivores (e.g., *Glossophaga soricina*, *Phyllostomus discolor*, *Phyllostomus hastatus*) with less centrality in the networks. Therefore, in addition to *C. perspicillata*, the seed dispersal networks of these landscapes were supported by a few others obligate fruit bats (e.g., *U. bilobatum*), which appear to be the most sensitive to habitat change, since the results show their decrease in cultivated landscapes. The fact that paths between different species or parts of networks become shorter in networks of these landscapes facilitates the propagation of negative effects throughout the network, making these networks in these landscapes with altered matrix more unstable and susceptible to the loss of disperser species (Mello et al., 2019). All these aspects become even more concerning when we consider forest patches, as they often represent the only native habitat preserved by most properties to comply with legal reserve requirements in Brazil (Overbeck et al., 2022). Along with the Lavrados of Roraima, the Savannas of Amapá are among Amazonian savannas' most threatened. There are often remnants of savanna in soybeans landscapes, but in eucalyptus landscapes, almost the entire matrix has been converted into plantations. Furthermore, eucalyptus plantations represent an unstable habitat. After cutting for wood extraction, eucalyptus plantation areas would be similar, in structural complexity and abundance of resources, to soybean fields. Thus, they these areas may suffer the same drastic reduction in seed dispersion observed in soybean fields since the tendency is for phyllostomid bats to stop moving through these areas, as there is no spatial reference for this (Schnitzler et al., 2003; Jensen et al., 2005).

Our results show that, despite being structurally not very complex and with little food availability for these bats (Xavier et al., 2025), the natural savanna matrix is extremely important for the flow of frugivorous bats between forest patches and, consequently, for the dispersal of seeds in these landscapes. Therefore, our results, in addition to highlighting the consequences of the presence of different types of agricultural systems for seed dispersal networks carried out by bats, show the importance of maintaining, in addition to forest patches, savanna areas in these cultivated landscapes. This measure, in addition to preserving native habitats, increases the heterogeneity of the landscape, maintaining its permeability for bats and other organisms and ensuring the flow of these animals between forest patches (Brändel et al., 2020). That way, these savanna remnants can help maintain the original dynamics of bat communities in landscape with fields and eucalyptus plantations and buffer the effect of logging in landscape with eucalyptus plantations, thus maintaining the integrity of seed dispersal networks promoted by bats.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111510.

CRediT authorship contribution statement

Bruna S. Xavier: Writing – original draft, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Jeferson Vizentin-Bugoni:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Marcelo M. Ferreira:** Writing – review & editing, Methodology, Data curation. **Tiago M. Marques:** Writing – review & editing, Methodology. **Renato R. Hilário:** Writing – review & editing, Supervision, Methodology, Investigation. **José J. Toledo:** Writing – review & editing, Supervision, Methodology, Investigation. **Isaí J. Castro:** Writing – review & editing, Methodology, Investigation. **Karen Mustin:** Writing – review & editing, Methodology, Investigation. **Jorge M. Palmeirim:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Marcus V. Vieira:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization. **William D. Carvalho:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank AMCEL (Amapá Florestal e Celulose S.A) for the authorisation to work in their area with eucalyptus plantation and for all the logistical support. We thank Cledinaldo Marques, Cremilson Marques, Jackson Souza, Joandro Pandilha, Camila Gama, Angélica Alfonso, Fábio Farneda, Maitê Pastor and Saulo Silvestre for their help in sampling and logistics while carrying out activities in the field. We thank Sr. Juliano, Sr. Leandro, Sr. Adriano, Sr. Udimar, Sr. Adilson, Seu Max, Seu Joel, Sr. Daniel e Seu Sena, Seu Evaldo, Sr. Gilfran, Dona Damiana, Seu Matheus, Seu Zé, Seu Joel, Seu Paredão, Dona Deusa, a comunidade de São Pedro do Bois, Abacate da Pedreira and Curiaú for their permission to access the different sample sites and/or for staying in their homes during field activities. This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior [grant numbers 8888.424975/2019-01], the Rufford Foundation [grant numbers 25585-1], the Bat Conservation International [grant numbers 2434131], the National Geographic Society [grant numbers EC-59186R-19 and NGS-83254R-20], the Neotropical Grassland Conservancy [grant numbers 01098803-5]. BSX is supported by Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro - FAPERJ [grant numbers E-200.273/2025 SEI-RJ 260003/001181/2025 and E-26/200.274/2025 SEI-RJ 260003/001181/2025]. JMP is supported by CE3C (Centre for Ecology, Evolution and Environmental Changes) and CHANGE (Global Changes and Sustainability Institute), funded by Fundação para a Ciência e a Tecnologia - FCT [grant numbers UIDB/00329/2020 and LA/P/0121/2020]. KM is supported by an 'Ayuda Beatriz Galindo', funded by the Spanish Ministry of Universities and the Complutense University of Madrid [grant numbers BG22/00121]. MVV was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq [grant numbers 308.974/2015-8 and 441.589/2016-2], and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro - FAPERJ [grant numbers E-203.045/2017]. WDC was supported by "Ayudas Maria Zambrano", funded by the Spanish Ministry of Universities [grant numbers CA3/RSUE/2021-00197], and by "Ayudas para contratos Ramón y Cajal (RYC) 2023" {RYC2023-045231-I}, financed by MCIU/AEI/doi:10.13039/501100011033 and by the FSE+.

Data availability

Data will be made available on request.

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