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Article

Traits of the host trees, not community diversity, drive epiphytes abundance in tropical seasonal forests

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Abstract: Epiphytes are considered indicators of forest ecological integrity, but the factors that explain their abundance are still not well understood. We here evaluated tree colonization by epiphytes in old-growth monospecific reforestation stands of *Astronium urundeuva* (M.Allemão) Engl. (Anacardiaceae) and *Eucalyptus saligna* Sm. (Myrtaceae), in comparison to a neighbor seasonal tropical forest fragment under similar environmental conditions. In each forest type, we identified and measured all trees (planted and colonizers) from 5-cm stem diameter in five 200 m² plots and quantified all vascular epiphytes per tree. Tree species were categorized by bark roughness, canopy deciduousness and growth rate. The abundance of epiphytes and the frequency of host trees were higher in the *A. urundeuva* plantation than in the native forest, with the *E. saligna* stand in an intermediate position. Also, we found that host traits influenced the abundance of epiphytes in their trunks. Host trees had average stem perimeter and height both higher than non-hosts, which indicates that colonization is more likely to occur in older trees. The average abundance of epiphytes per tree was higher in species with rough bark, but no relationship was found with canopy deciduousness or tree growth rate. We evidenced, therefore, that forest plantations, even if monospecific, can provide habitat for epiphytes. However, at community level, colonization success, either in native or restored forest, depends on the relative abundance of species whose bark type favors epiphytes establishment.

Keywords: *Non-Tree Life Forms; Forest Restoration; Tropical Seasonal Forest; Epiphytism; Host Preference.*

Atributos das árvores hospedeiras, e não a diversidade da comunidade, conduzem a abundância de epífitas em florestas tropicais sazonais

Resumo: Epífitas são consideradas indicadores de integridade ecológica em florestas, mas os fatores que explicam sua abundância ainda não são bem compreendidos. Neste estudo, avaliamos a colonização por epífitas em antigos talhões monoespecíficos de *Astronium urundeuva* (M.Allemão) Engl. (Anacardiaceae) e *Eucalyptus saligna* Sm. (Myrtaceae), em comparação com um fragmento vizinho de floresta estacional semidecidual sob condições ambientais semelhantes. Em cada tipologia florestal, identificamos e medimos todas as árvores (plantadas e que colonizaram os locais) a partir de 5 cm de diâmetro à altura padrão, em cinco parcelas de 200 m². Nelas, também quantificamos todas as epífitas vasculares por árvore. Em busca de uma explicação funcional para as diferenças entre espécies, utilizamos rugosidade da casca, deciduidade da copa e taxa de crescimento como atributos potencialmente relevantes. A abundância das epífitas e a frequência de forófitos foi maior no talhão de *A. urundeuva* do que na floresta nativa, com o talhão de *E. saligna* ocupando uma posição intermediária. Encontramos evidências, também, de que os atributos dos forófitos influenciaram a abundância de epífitas em seus troncos. Os forófitos apresentaram maior perímetro médio e altura que as árvores não hospedeiras, o que indica que a colonização é mais provável de ocorrer em árvores mais velhas. A abundância média de epífitas por árvore foi maior em espécies com casca rugosa, mas nem a deciduidade da copa, nem a velocidade de crescimento exerceram efeito neste aspecto. Evidenciamos, portanto que, plantações florestais, ainda que monoespecíficas, podem prover habitat para epífitas. Contudo, em nível de comunidade, o sucesso da colonização, seja em florestas nativas ou restauradas, depende da abundância relativa de espécies cujo tipo de casca favorece o estabelecimento de epífitas.

Palavras-chave: *Formas de Vida Não-Arbóreas; Restauração Florestal; Epifitismo; Preferência de Hospedeiro.*

Introduction

When tropical forests recover from disturbances (either naturally or via active restoration), it is well known that epiphytes are the latest plant group to colonize and re-establish in that ecosystem (Lisboa et al., 1991, Kanowski et al., 2003, Martin et al., 2013, Novais et al., 2020, Parra-Sanchez & Banks-Leite 2020). Intrinsic characteristics of the group, such as slow growth and requirements for specific substrate and humidity in the canopy (Zotz 1995, Hietz 1999), besides dispersal limitations due to low landscape permeability, affect their arrival and establishment (Reid et al., 2016). For these reasons, epiphytes presence may be a good indicator of forest ecosystem health (Hietz 1999) and thus to assess forest restoration success or guiding adaptive management interventions.

Studies have shown low abundance of epiphytes in secondary and restored tropical forests (Suganuma & Durigan 2015, Garcia et al., 2016), and the viability of increasing epiphyte presence in forest ecosystems undergoing restoration has been recently investigated. Different attempts to restore epiphyte community include reintroducing them on planted trees (Duarte & Gandolfi 2017, Domene 2018, Benavides et al., 2023, Sasamori et al., 2023) or stimulating natural colonization by tree planting in different spatial arrangements (Reid et al., 2016). Despite limited evidence of success provided by those studies, re-introduction of these plants in forest restoration projects has been recommended, whenever budget restrictions allow (Duarte & Gandolfi 2017). Little scientific research has been done, however, to evaluate whether spontaneous colonization of planted trees by epiphytes could be enhanced by the selection of a particular group of tree species. Host tree characteristics that favor the colonization and perpetuation of epiphytes might be crucial to assist in planning and decision-making of forest restoration projects, since species' conservation is utterly dependent on environmental recovery (Reid et al., 2016).

Epiphytes are plants which use other plants (phorophytes or hosts) as support in some part of their life cycle, with no soil connection nor using nutrients from the hosts directly (Madison 1977, Kress 1986). Epiphytes form a synusiae whose abundance can be related to microclimatic conditions and successional stage, with higher abundance being expected in wetter habitats and mature forests (Richards 1996, Novais et al., 2020). There is scientific evidence for epiphyte preference for certain species of phorophytes (Kersten 2010, Couto et al., 2022), which indicates a relationship between colonization success and traits of host trees. Bark roughness of the host tree has been considered a relevant trait (Kernan & Fowler 1995, Carlsen 2000, Callaway et al., 2002, Hernandez-Garcia 2021), as it determines water retention capacity, which is important in the epiphyte establishment phase (Kersten 2010). However, a recent review at global scale (Tay et al., 2023) showed that it is not just about bark roughness, with how an epiphyte attaches itself to the substrate being a crucial issue.

In this study, we assessed three distinct types of forests located in similar environmental conditions: one homogeneous forest plantation of an exotic species (*Eucalyptus saligna* Sm., Myrtaceae), another of a Brazilian native species (*Astronium urundeuva* (M.Allemão) Engl., Anacardiaceae), and a native tropical seasonal forest fragment with no evidence of recent disturbance. We aimed at verifying whether epiphyte abundance differs between forest types and between host species as related to their traits. At community level, we expected that epiphyte abundance would be higher in the native forest, given previous studies showing low abundance in monospecific plantations (Hietz 2005; Boelter et al., 2011). Our hypothesis was that tree species diversity permits a higher diversity of organisms that depend on them (Barthlott et al., 2001, Thomsen et al., 2018, Wagner & Zots 2020). To investigate whether the success of epiphyte colonization can be explained by the traits of the host tree, we explored size (height and stem perimeter), growth rate, canopy deciduousness, and bark roughness as predictors of epiphytes' presence and abundance. We expected to find a positive relationship of epiphyte colonization with host tree size (Malizia 2003, Burns & Dawson 2005, Hirata et al., 2008), because it is a proxy for the substrate surface to be colonized. By favouring epiphyte fixation and water retention, bark roughness (Malizia 2003, Wagner et al., 2021) should have a positive effect. Moreover, we expected more epiphytes on slow-growing trees, provided that fast growth could hamper epiphytes' fixation on the stems (Hirata et al., 2008). Because hosts with seasonal deciduous canopy due to seasonal droughts have been reported to have less colonization by epiphytes (Einzmann et al., 2015), we expected that deciduous trees would have lower epiphyte abundance in the studied forests.

Material and Methods

1. Study site

The three forest types studied form a continuous patch of about 8 ha, located around the stream of a small tributary of the Paranapanema river, between the municipalities of Assis and Tarumã (São Paulo, Brazil), at an average elevation of 520 meters above sea level (Figure 1). Regional climate is Köppen's Cfa, which is humid subtropical with hot summer (Alvares et al., 2013). The average annual rainfall is 1450 mm, concentrated during summer (December to March), with an average annual temperature of 21.8°C (Durigan & Leitão-Filho 1995). Soil type is a clayish and fertile Haplic Lixisol according to WRB (2006) (Durigan & Leitão-Filho 1995). The original vegetation of the region is Seasonal Semideciduous Forest (IBGE 2012).

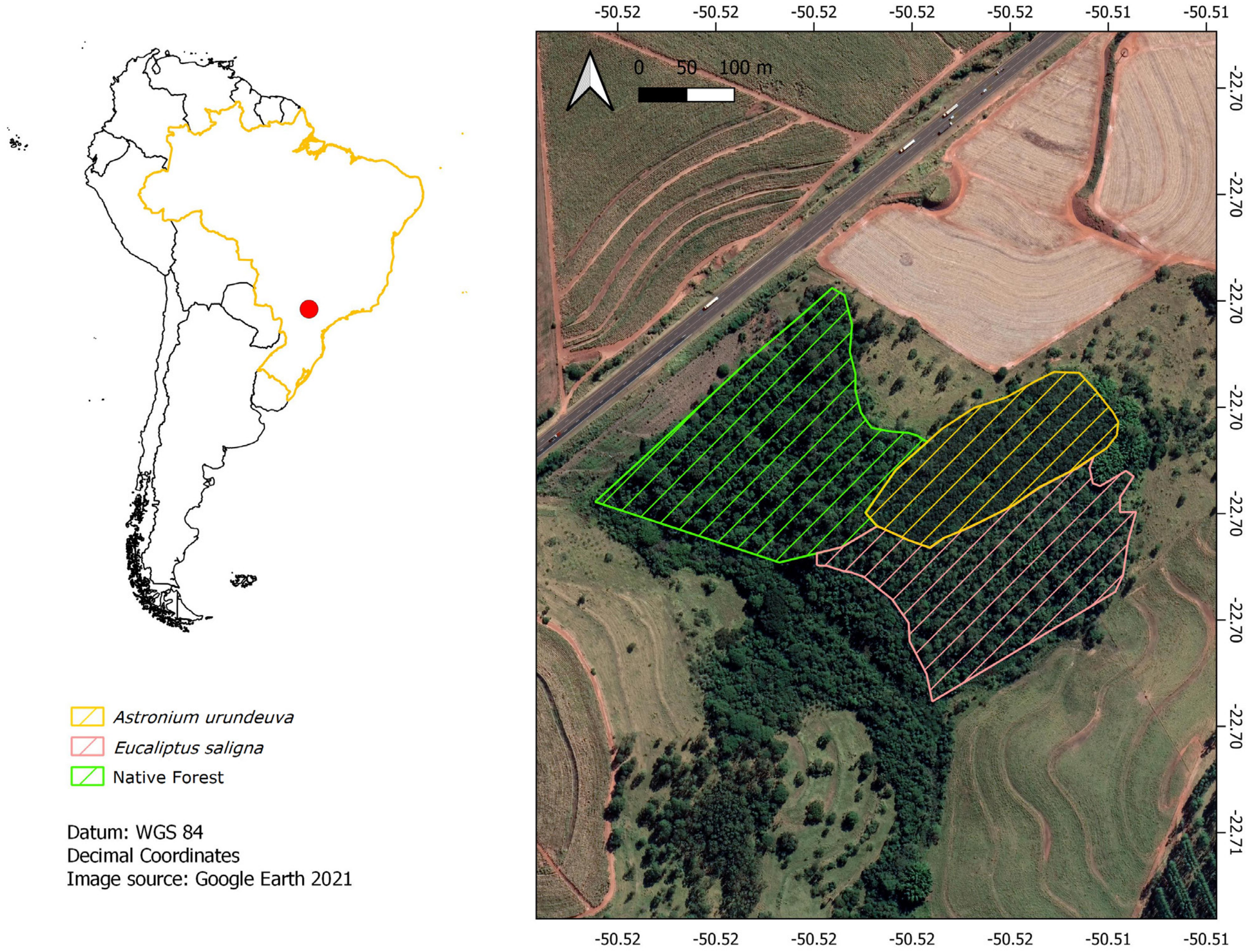

Figure 1. Location of the study site in Brazil, and position of the three forest stands studied, forming a continuous forest fragment, between Assis and Tarumã municipalities.

The forest types assessed were: (i) a monospecific plantation of aroeira (*Astronium urundeuva*), with an area of 2.5 ha (central coordinates 22º42’05”S and 50º30’54”W), with native plants colonizing the understory; (ii) a monospecific plantation of eucalyptus (*Eucalyptus saligna*) with an approximate area of 2.5 ha (central coordinates 22º42’10”S and 50º30’53”W), with abundant regeneration of native plants in its understory; (iii) an old-growth forest remnant, with an area of 3.0 ha (central coordinates 22º42’05”S and 50º31’04”W). *E. saligna* (henceforth *Eucalyptus*) is an exotic species widely cultivated in Brazil. *A. urundeuva* (henceforth *Astronium*), despite native in the seasonal Atlantic Forest (Souza et al., 2019), has not been recorded in the study region (Durigan et al., 2004).

The precise age of the planted stands could not be rescued, but both were planted simultaneously more than 40 years before sampling. No anthropogenic disturbances have been recorded in the native remnant at least for the last 40 years (Figure 2).

2. *Sampling design and data collection*

In each forest type, we sampled five plots of 25 × 8 m (200 m²), 20 m apart from each other, at least 50 m away from the stream margin. In each plot, we identified and measured the stem diameter of all tree individuals with diameter at breast height (DBH) ≥ 5 cm and visually estimated the total height. We measured each stem individually and, to represent tree size in the analyses, we decided to convert the measure of stem diameter into perimeter, summing up them in cases of multi-stemmed trees. Epiphytes rely on bark surface available to be colonized. Therefore, we considered that perimeter would be a more suitable predictor variable to represent substrate surface than the mean diameter, the squared diameter, or the basal area. Should we have used basal area as predictor, for example, we could have risked underestimating available colonizing surface in multi-stemmed trees with similar basal area to single-stemmed trees. Within each forest type we considered all sampled trees as potential hosts, including native species that colonized the understory of the monospecific plantations.

The tree species recorded were functionally classified according to three traits: i) bark roughness (smooth or rough); ii) leaf phenology (deciduous or evergreen), and iii) growth rhythm (fast, moderate, or slow). For bark roughness we used the images from Ramos et al., (2015); for leaf phenology, we consulted Backes and Irgang (2002) and the database from Universidade Estadual do Centro Oeste – Unicentro (https://sites.unicentro.br/wp/manejoflorestal/). To categorize the native species by growth rate, we used data taken from the permanent

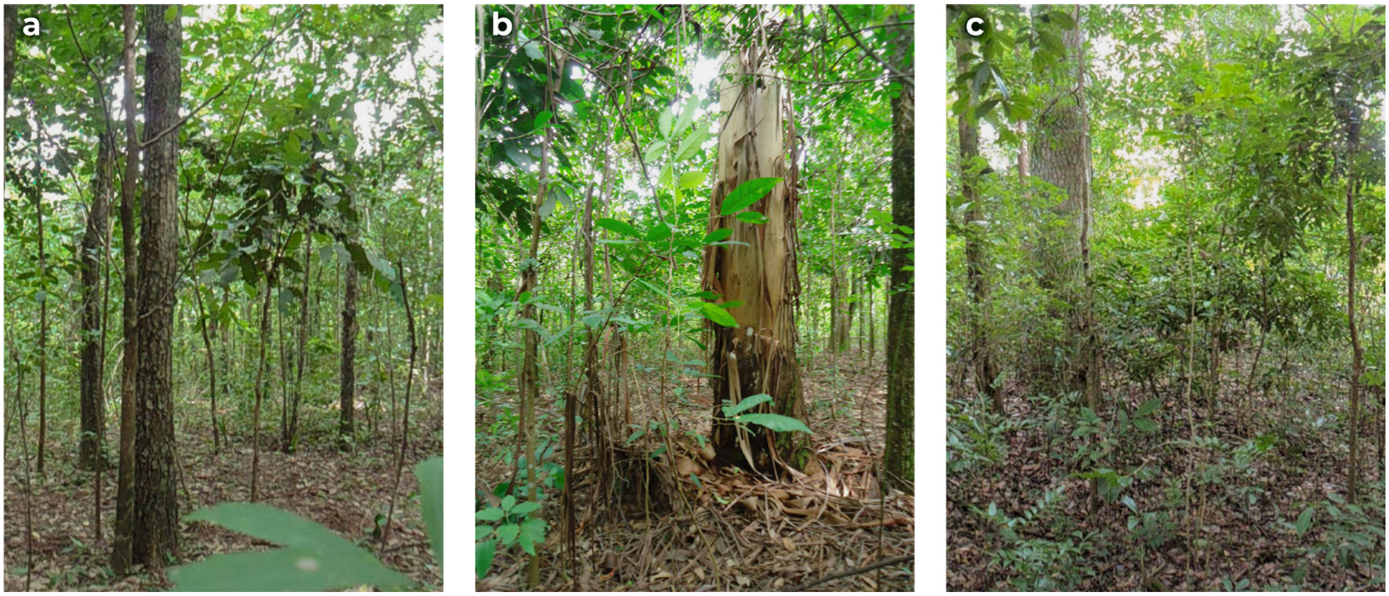

Figure 2. The three forest types studied: (a) Planted stand of aroeira (*Astronium urundeuva*); (b) Planted stand of eucalypt (*Eucalyptus saligna*); (c) Native Forest.

plot network installed since 1992 in the sampled native forest fragment (Giampietro 2005, data available at the BioTime data base Dornelas et al., 2018). For *Eucalyptus* and *Astronium*, we estimated the mean annual increase in diameter from data obtained in the sampling plots and the approximate age of the stands. Based on the distribution of values among species, we established the categories as: slow growth = annual diameter increment <1.5 mm/yr; moderate growth = 1.5–2.5 mm/yr; and fast growth ≥2.5 mm/yr.

For each sampled tree, we recorded the presence or absence of epiphytes to obtain the percentage of host trees in each forest type. In each host tree, we counted all individuals of established vascular epiphytes. To properly separate individual epiphytes growing in clusters, we considered any clearly delimited group as one single individual, following previous studies (Sanford 1968, Wagner & Zots 2020). When analyzing rhizomatous epiphyte species (creeping habit), rhizome interruption was used as criterium to differentiate individuals. Although we aimed at epiphytes abundance and not composition, we roughly categorized the species in taxonomic groups, to provide an overall characterization of the epiphyte community present in the study areas. As in other studies (Wagner et al., 2015), all Pteridophyte species were considered as a single group and the other groups refer to the families recorded.

3. *Data analysis*

For each forest type, we calculated the mean values of basal area, host tree density and epiphyte density per hectare. We calculated the frequency (%) of host trees in relation to the total number of individuals sampled in each plot. To compare these variables among forest types, we used analysis of variance (ANOVA), followed by Tukey test.

To explore the relationships between epiphytes and traits of individual trees, we also performed analysis of variance (ANOVA) followed by Tukey test. Data were log-transformed for specific models to meet normality assumptions and to reduce the influence of outliers, the variables transformed were: tree height, stem perimeter and number of epiphytes per tree. For the models assessing the tree height and stem perimeter (response variables) of host and non-host trees (predictor variable) we performed only the log transformation (Quinn & Keough 2002). For the bark roughness model, we applied log+1 transformation in the response variable number of epiphytes per tree, due to the presence of zero values. To verify whether the abundance of epiphytes was associated with host tree traits, we carried out the analyses of variance (ANOVA) at host species level, to avoid bias due to the large differences in number of host individuals among species. We thus obtained the average number of epiphytes per tree for each host species. We then compared the epiphytes abundance between trait groups as follows: i) slow vs. moderate vs. fast growing, vi) deciduous vs. evergreen, and vii) rough vs. smooth bark.

We checked the assumptions for all models by graphical analyses and performed Levene's test for homogeneity of variance across groups from car package (Fox & Weisberg 2019). All analyses were performed using the R program version 4.1.1 (R Core Team 2021), for the Tukey post-hoc test we used the agricolae package (Mendiburu 2021).

Results

In the whole area sampled, we recorded a total of 469 trees, from 56 species. Out of these, 197 trees (104 planted and 23 native colonizing species) were sampled in the *Astronium* stand, 187 trees (43 planted 25 native colonizing species) in the *Eucalyptus* stand, and 85 trees (31 species) in the native forest. Among the sampled trees, 254 (54%) were hosts, with a total of 3,394 epiphytes counted (see Table 1).

When the forest stands were compared, we found no differences in basal area [Figure 3(a), P = 0.12, with an average of 47.61 m^2 ha^{-1} in the native forest, 35.57 m^2 ha^{-1} in the *Astronium* stand, and 24.70 m^2 ha^{-1} in the *Eucalyptus* stand. However, we found differences in epiphyte occurrence. Frequency [Figure 3(b), P = 0.0123], and density [Figure 3(c), P = 0.0059] of trees with epiphytes were both higher in the *Astronium* stand than in the native forest, not differing from the *Eucalyptus* stand,

Table 1. Tree species, traits, and average number of epiphytes found in all three forest stands.

Species	Growth rhythm of the species	Deciduousness	Bark texture	Average epiphythes/tree	Bromeliaceae	Pteridophyta	Cactaceae	Piperaceae	Orchidaceae	Araceae	Total epiphytes
Aegiphila integrifolia (Jacq.) Moldenke	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Albizia niopoides (Spruce ex Benth) Burkart	Fast	Deciduous	Smooth	0.0	0	0	0	0	0	0	0
Alchornea glandulosa Poepp. & Endl.	Fast	Evergreen	Smooth	1.8	12	8	0	0	0	0	20
Aloysia virgata Ruiz & Pav.) Juss.	Moderate	Deciduous	Rough	8.0	2	6	0	0	0	0	8
Annona cacans Warm.	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Annona sylvatica A.St.-Hil.	Fast	Evergreen	Smooth	0.5	0	1	0	0	0	0	1
Aspidosperma polyneuron Müll.Arg.	Moderate	Evergreen	Rough	0.0	0	0	0	0	0	0	0
Astronium graveolens Jacq.	Moderate	Deciduous	Smooth	6.0	0	0	6	0	0	0	6
Astronium urundeuva (M.Allemão) Engl.	Slow	Deciduous	Rough	20.4	1569	537	8	2	1	0	2117
Campomanesia xanthocarpa (Mart.) O.Berg	Slow	Evergreen	Rough	0.5	0	0	0	1	0	0	1
Casearia gossypiosperma Briq.	Fast	Deciduous	Smooth	5.0	25	0	0	0	0	0	25
Casearia sylvestris Sw.	Moderate	Evergreen	Rough	64.0	2	62	0	0	0	0	64
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Colubrina glandulosa Perkins	Moderate	Deciduous	Rough	1.5	0	0	5	1	0	0	6
Cordia superba Cham.	Fast	Deciduous	Rough	3.0	0	0	2	1	0	0	3
Croton floribundus Spreng.	Fast	Evergreen	Smooth	2.0	2	0	0	0	0	0	2
Cupania vernalis Cambess.	Fast	Evergreen	Rough	1.7	1	4	0	0	0	0	5
Cytharexylum myrianthum Cham.	Fast	Deciduous	Rough	7.5	1	29	0	0	0	0	30
Eucalyptus saligna Smith	Fast	Evergreen	Smooth	2.0	80	3	1	0	0	0	84
Eugenia blastanta (O.Berg) D.Legrand	Slow	Evergreen	Rough	3.0	0	0	5	1	0	0	6
Eugenia uniflora L.	Slow	Evergreen	Smooth	3.0	3	0	0	0	0	0	3
Ficus eximia Schott.	Fast	Deciduous	Smooth	3.5	1	4	2	0	0	0	7
Gallesia integrifolia Spreng. Harms	Moderate	Evergreen	Smooth	0.6	0	0	1	2	0	0	3
Guarea guidonia (L.) Sleumer	Fast	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Guarea kunthiana A.Juss.	Moderate	Evergreen	Smooth	3.9	17	86	0	2	0	0	105
Inga vera Willd.	Fast	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Jacaranda micrantha Cham.	Moderate	Deciduous	Rough	4.0	0	4	0	0	0	0	4
Lacistema hasslerianum Chodat	Moderate	Evergreen	Smooth	2.5	3	2	0	0	0	0	5
Machaerium paraguariense Hassl.	Fast	Deciduous	Smooth	2.0	0	0	2	0	0	0	2
Margaritaria nobilis L.f.	Moderate	Deciduous	Smooth	2.0	0	2	0	0	0	0	2

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Species	Growth rhythm of the species	Deciduousness	Bark texture	Average epiphythes/tree	Bromeliaceae	Pteridophyta	Cactaceae	Piperaceae	Orchidaceae	Araceae	Total epiphytes
Metrodorea nigra A.St.-Hil.	Slow	Evergreen	Smooth	0.3	0	1	0	1	0	0	2
Moquiniastrum polymorphum (Less.) G.Sancho	Fast	Evergreen	Rough	11.0	9	13	0	0	0	0	22
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Fast	Evergreen	Smooth	1.3	26	0	0	0	0	0	26
Myrsine umbellata Mart.	Moderate	Evergreen	Smooth	5.0	161	17	0	1	0	0	179
Nectandra cuspidata Nees	Fast	Evergreen	Smooth	0.1	2	0	0	0	0	0	2
Nectandra megapotamica (Spreng.) Mez	Fast	Evergreen	Smooth	0.7	0	3	0	1	0	0	4
Nectandra oppositifolia Nees & Mart.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Ocotea diospyrifolia (Meisn.) Mez	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Ocotea indecora (Schott) Mez	Moderate	Evergreen	Smooth	1.4	0	12	2	0	0	0	14
Ocotea puberula (Rich.) Nees	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Peltophorum dubium (Spreng.) Taub.	Fast	Deciduous	Rough	0.0	0	0	0	0	0	0	0
Picramnia ramiflora Planch.	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fast	Deciduous	Rough	1.0	0	0	0	1	0	0	1
Prockia crucis P.Browne ex L.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Prunus myrtifolia (L.) Urb.	Slow	Evergreen	Smooth	10.0	5	35	0	0	0	0	40
Psidium guajava L.	Slow	Evergreen	Smooth	2.1	19	0	0	0	0	0	19
*Sapium glandulosum (*L.) Morong	Fast	Deciduous	Smooth	0.0	0	0	0	0	0	0	0
Siparuna guianensis Aubl.	Moderate	Evergreen	Smooth	2.7	19	24	0	0	0	0	43
Sorocea bonplandii (Baill.) W.C.Burger et al.	Slow	Evergreen	Smooth	0.3	0	0	0	1	0	0	1
Syagrus romanzoffiana (Cham.) Glassman	Slow	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Tabernaemontana catharinensis A.DC.	Fast	Deciduous	Smooth	11.3	38	6	0	0	0	1	45
Terminalia glabrescens Mart.	Moderate	Deciduous	Rough	46.0	25	21	0	0	0	0	46
Trichilia catigua A.Juss.	Moderate	Evergreen	Smooth	0.0	0	0	0	0	0	0	0
Trichilia clausseni C.DC.	Fast	Deciduous	Smooth	0.7	0	0	0	8	0	0	8
Trichilia pallida Sw.	Moderate	Evergreen	Smooth	6.8	93	326	0	3	0	0	422
Zanthoxylum caribaeum Lam.	Fast	Deciduous	Smooth	5.5	5	6	0	0	0	0	11

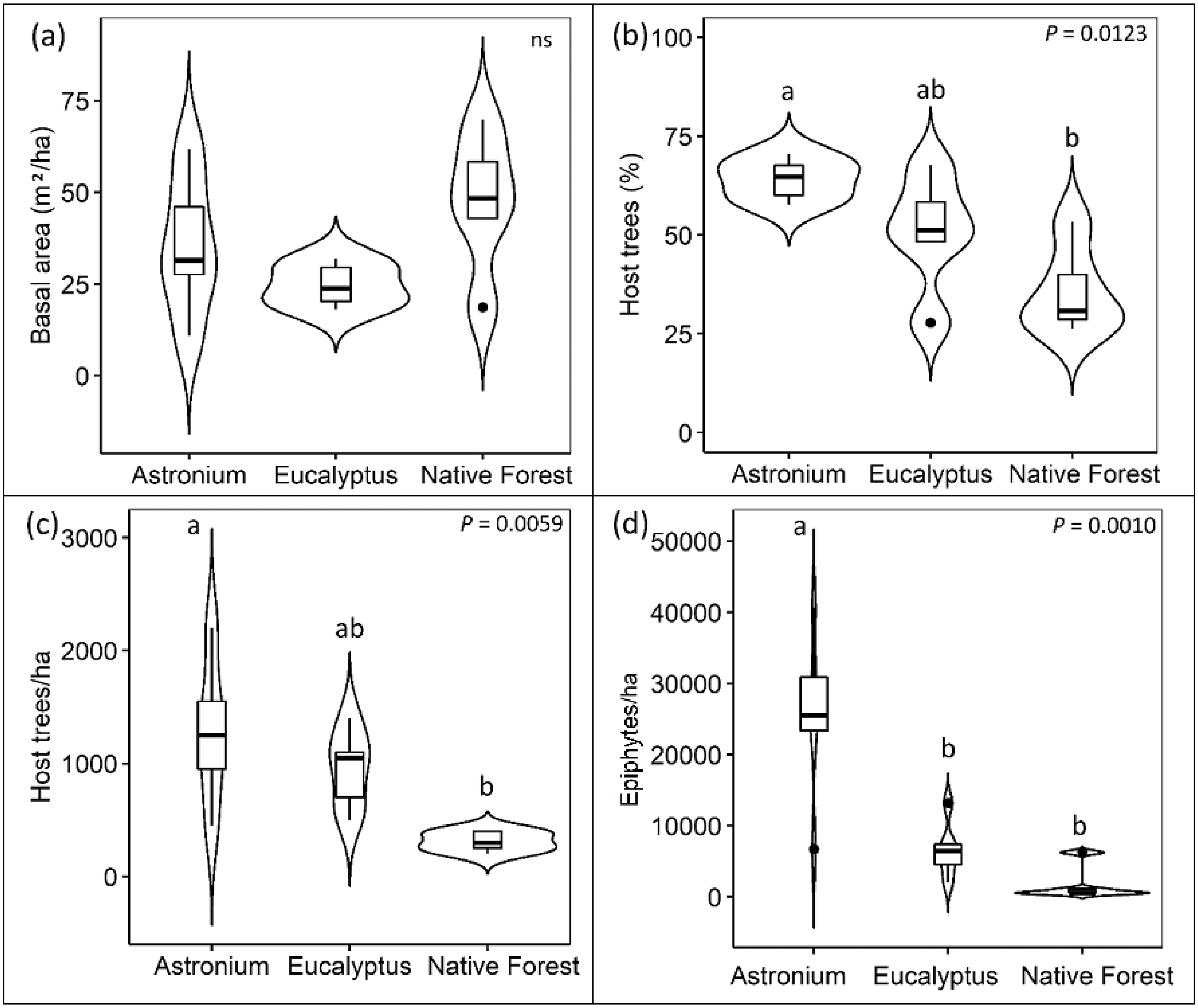

Figure 3. Comparison between forest types (stand of *Astronium urundeuva*, *Eucalyptus saligna* and native forest) based on tree basal area (a), frequency of host trees per hectare (b), density of host trees (c), and epiphyte density (number of epiphytes per hectare) (d). Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves). The same letter on top of the shapes indicates the values do not differ by Tukey's test (P values are <0.05; α = 0.05); ns: non-significant differences.

which stayed in an intermediate position. The average abundance of epiphytes per hectare in the *Astronium* stand was higher than in the other two forest types, which did not differ [Figure 3(d), P = 0.0010].

When host and non-host trees were compared (Figure 4), we found significant differences in their size. Average stem perimeter of host trees (51 cm), as a proxy for the substrate area to be colonized, was 46% greater than that of non-host trees (35 cm) [Figure 4(a), P < 0.0001]. Host trees, with average height of 15.2 m, were 50% taller than non-host trees (10.1 m) [Figure 4(b), P < 0.0001].

When we compared the abundance of epiphytes between groups of host species by their traits (Figure 5), we found differences only related to bark roughness. While species with rough bark had an average of 17 epiphytes per tree, those with smooth bark had only 3 epiphytes per tree [Figure 5(a)]. No significant differences were found related to leaf phenology [Figure 5(b), P = 0.67] or growth rhythm [Figure 5(c), P = 1.44] of the host species.

As a rough characterization of the epiphyte community composition, we found, in decreasing order of frequency: Bromeliaceae (in 42% of trees, recorded in all forest types), Pteridophytes (in 34% of trees, in all forest types), Piperaceae (4% of trees, absent in the *Eucalyptus* stand), Cactaceae (3% of trees, all forest types), and, at last, Orchidaceae and Araceae, both recorded only in the *Astronium* stand, each one in a single tree sampled (Table 1).

Discussion

Epiphytes presence has been considered a good indicator of forest ecosystem health worldwide (Benzing 1998, Hietz 1999), but whether

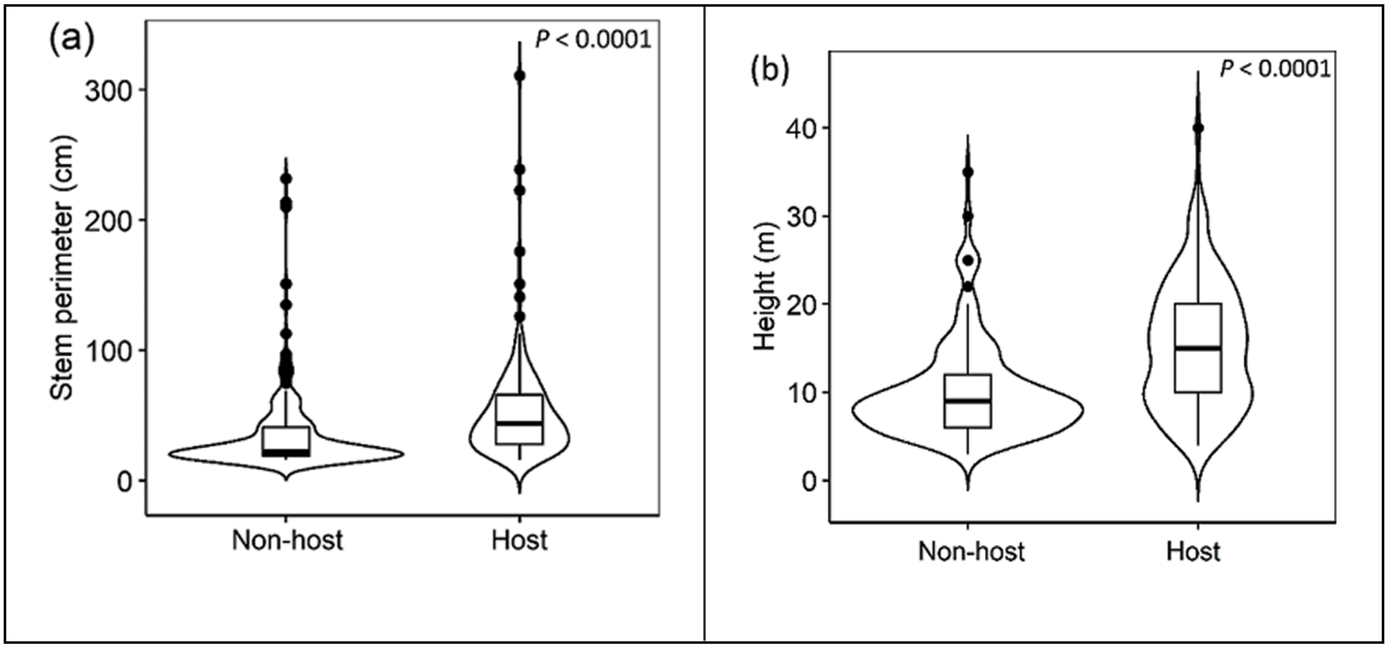

Figure 4. Comparison of tree size between host (n = 254) and non-host (n = 215) trees, by average values of (a) Stem Perimeter, and (b) Tree height. Box plots showing the median and quartiles, combined with violin plots showing the shape of data distribution. Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves).

epiphyte abundance depends on the host tree traits, and therefore on community composition, is still controversial (Tay et al., 2023). Besides the importance of this issue for plant community ecology, it has practical implications for the real world, since restoring forests became a global challenge (Verdone & Seidl 2017). By exploring the epiphyte abundance in a native undisturbed forest in comparison with planted forest stands, our study contributes to the debate within the restoration context. The species diversity to be reintroduced has been an issue in forest restoration for a long time, considered by researchers to be essential for the success of restoration (Ruiz-Jaen & Aide 2005, Rodrigues et al., 2009, Rodrigues et al., 2011). From our results we can infer that selecting the tree species matters, because different species provide different contributions in triggering colonization by epiphytes. Planting a high number of tree species, however, may not assure epiphyte abundance, if the species planted do not have the right traits to be a welcoming host.

1. *Can monospecific forest plantations catalyze colonization by epiphytes?*

Several studies have shown that monospecific plantations catalyse colonization by tree species from the regional pool (Parrota et al., 1997, Brockerhoff et al., 2008, Viani et al., 2010, Guerin et al., 2021), partially corroborating the Field of Dreams hypothesis (Palmer et al., 1997, Suganuma & Durigan 2021). However, this issue has not been explored for life forms other than trees. The only known study for the Atlantic Forest region addressing this issue concluded that monospecific plantations do not favor epiphyte colonization, and monospecific plantations with exotic species tend to be even worse as catalysts for epiphyte colonization (Boelter et al., 2011).However, we achieved very different results from those found by the cited author. . Refuting our first hypothesis, we found lower frequency of trees with epiphytes and lower abundance of epiphytes per host tree or per hectare in the native forest remnant compared to *Astronium* plantation (native species). The *Eucalyptus* stand (exotic species) did not differ from the native forest. We therefore concluded that monospecific stands can be as efficient or even more than the diverse native forest in catalysing epiphytes colonization. The low tree diversity of planted stands, which even after 40 years have lower tree species richness than the native forest, did not result in the expected low abundance of epiphytes. We did not assess epiphyte diversity, however, which could have been affected by tree species richness (Barthlott et al., 2001).

2. *Does host tree size matter?*

Our results support the positive correlation between epiphyte abundance and host size, as found by Malizia (2003), Burns & Dawson (2005), (Laube & Zots 2006), Hirata et al., (2008), and Shen et al., (2022). However, other studies have failed to prove this relationship (Bennet 1986; Zimmerman & Olmstead 1992, Vergara-Torres et al., 2010).When comparing the average size between host and non-host trees, we found a large difference, with an advantage for trees with epiphytes both in height (50% larger) and in stem perimeter (46% larger). We used the stem perimeter as the predictor variable because it is more directly correlated to substrate surface than stem diameter or basal area, especially in the cases of multi-stemmed trees. Our result can be explained, therefore, simply by the greater surface available for colonization or by taller trees providing higher light incidence on their trunks (Sillet 1999). However, it can also be indirectly associated with the age of the trees, as larger trees tend to be older within a population, so they had more chances of being colonized, as they were exposed to the colonization process for a longer time. In our study, however, all trees planted within a stand were the same age, restricting this explanation to hosts in the native forest or to those growing in the understory of planted stands, for which differences in size could be related to differences in age.

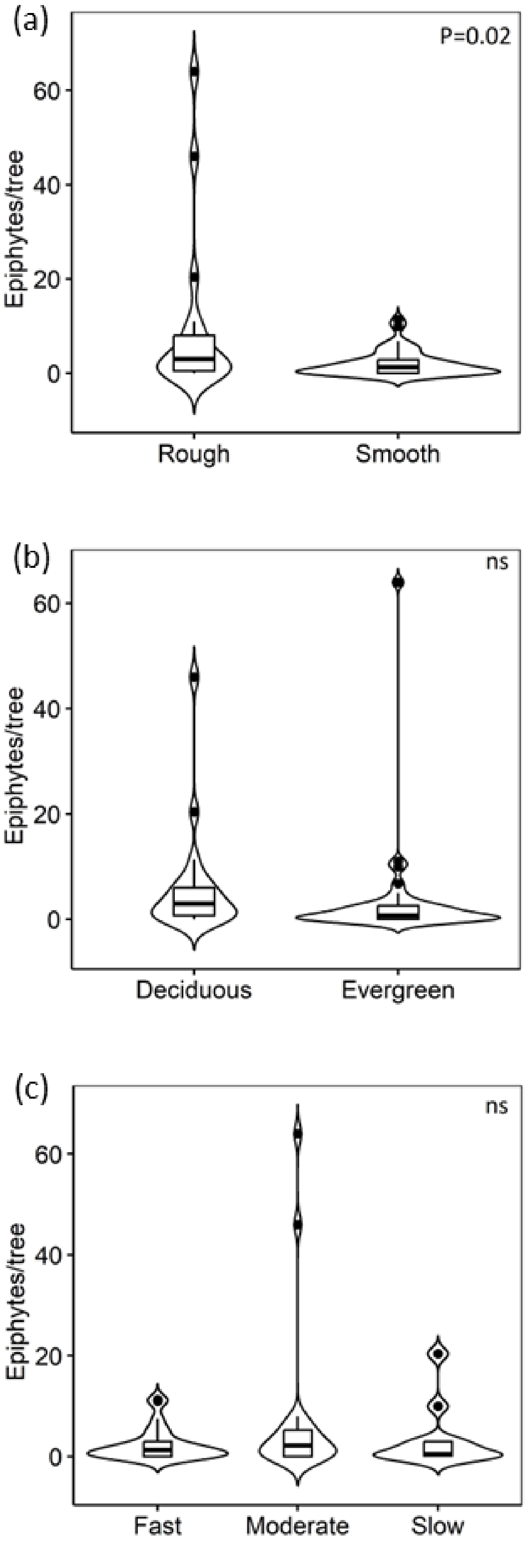

Figure 5. Comparison of epiphytes abundance (average number of epiphytes per tree) between host species, grouped by their traits. (a) Rough (n = 17) vs. Smooth bark (n = 39); (b) Deciduous (n = 21) vs. Evergreen (n = 35); and (c) Fast (n = 25) vs. Moderate (n = 20) vs. Slow growth (n = 11). Box plots show median and quartiles from the raw data. Violin plots show the data distribution (density curves).

3. *Are there traits of the host tree favoring epiphytes colonization?*

Studies have shown the existence of "functional specificity" (Malizia 2003, Wagner et al., 2021, Couto et al., 2022), with certain traits of the host tree species turning them into preferred or limiting hosts (Hernandez-Perez et al., 2018). In studies addressing plant-plant interactions, it is not uncommon that host specificity is not proven at the species level, but that hosts show some functional pattern related to the demands of plants that depend on them (Norton & Carpenter 1998, Campos et al., 2021). Our study supports the existence of traits favoring epiphytes colonization, with bark roughness standing out, as previously demonstrated by Benzing (1990), Malizia (2003), and Wagner et al., (2021). The tridimensional structures in rough bark can give the species a better performance as host (Benzing 1990, Brown 1990, Kersten et al., 2009, Sáyago et al., 2013). Water retention by rough, porous bark favors the anchorage of bromeliad seeds, promoting their survival and protecting them from drought at early stages (Reyes-Garcia et al., 2008, Hietz & Hietz-Seifert 1995, Castro-Hernandez et al., 1999, Wolf & Konings 2001, Winkler et al., 2005, Geraldino et al., 2010). Bark traits, therefore, explain the high abundance of epiphytes in the *Astronium* stand, because this planted species, with its rough bark, corresponds to more than half the trees in the community.

Contrary to our expectations, however, neither tree growth rate nor leaf phenology explained differences in epiphytes abundance among host species. Rasmussem & Rasmussem (2018), in a review about epiphyte habitat, suggested that these plants face the challenge of adapting to a constantly changing environment, so that slow growth could be favorable, but this was also not proven by Hirata et al., (2008). Deciduous canopy is reported to exert a negative influence due to exposing epiphytes to drought conditions in seasonal climates, impairing their establishment and growth (Einzmann et al., 2015). Despite the long dry season in our study sites, deciduousness seemed not to be a relevant trait, since the fully deciduous *A. urundeuva* was among the most favorable host species.

Conclusion

Comparing old monospecific plantations and an old-growth forest in the same landscape, under the same soil and climate conditions, provided us a unique opportunity to investigate the relationship between epiphyte abundance and the tree community diversity and composition, which are, ultimately, driven by the size and traits of individual trees. We concluded that the abundance of epiphytes per tree in the studied forests is primarily determined by the bark traits, with rough bark favoring colonization by epiphytes, supporting the hypothesis of "functional specificity". Since bark roughness is an evolutionary trait of the species, it is the proportion of species with smooth or rough bark in the community that will determine the abundance of epiphytes in the forest. The attribute is especially advantageous in seasonal forests, where there is water restriction for part of the year. This finding has relevant implications for management interventions or ecological restoration, in cases where restoring epiphyte populations is among the project's goals. The expected negative influence of deciduousness on epiphyte abundance was not confirmed in our study, although it may occur in other forests under more stressful climatic conditions.

Although we found a positive correlation between tree size and the number of epiphytes, this correlation is likely more related to the age of the phorophyte than to the intrinsic growth rate of the species, because the abundance of epiphytes per host tree did not differ between slow, moderate, or fast-growing species. It is reasonable to expect, therefore, that the abundance of epiphytes within a forest, whether secondary or restored, will increase over time, until it reaches levels compatible with old-growth forests under similar climatic conditions, with higher abundance being expected in wetter habitats.

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Author Contributions

Dimitrio Fernandes Schievenin: collected and analyzed the data, and led the writing of the manuscript.

Camila Alonso Santos: collected the data, contributed to the draft and gave final approval for publication.

Karina de Lima: collected the data, contributed to the draft and gave final approval for publication.

Antônio Carlos Galvão de Melo: designed the methodology, contributed to the draft and gave final approval for publication.

Vera Lex Engel: designed the methodology, contributed to the draft and gave final approval for publication.

Giselda Durigan: conceived the idea, designed the methodology, and contributed to the draft and final version of the manuscript.

Conflicts of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data Availability

All data collected and used to base our analysis, and therefore, this study, are available in the Dataverse at https://doi.org/10.48331/scielodata.5E2RBE.

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