



How an invasive tree reshapes the forest floor and alters amphibian occupancy through direct and indirect effects

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Abstract Biological invasions can alter forest ecosystems, reshaping microhabitats and disrupting the interactions that sustain native communities. Among these invaders, the jackfruit (*Artocarpus heterophyllus*) has spread widely across the Atlantic Forest, where its ecological impacts remain poorly understood. We investigated how jackfruit density influences forest-floor structure and the occupancy of three leaf-litter amphibian species. Using generalized linear mixed models, occupancy modelling, and structural equation models (SEM), we evaluated both direct and indirect pathways linking invasion intensity to key habitat attributes, including leaf-litter depth, arthropod density and diversity, and amphibian occurrence. Jackfruit density had strong negative effects on litter depth and arthropod density, indicating habitat

simplification and resource loss. Occupancy models revealed contrasting responses among species, with generalists more tolerant to invaded conditions and forest specialists negatively affected by invasion intensity or dependent on litter-mediated pathways. The SEM confirmed that invasion effects propagate through structural and trophic mechanisms, altering microhabitat structure and prey availability. Our results demonstrate that invasive trees can restructure forest-floor ecosystems through cascading physical and biological changes. These invasion-driven filters promote biotic homogenization by favoring disturbance-tolerant species while disadvantaging microhabitat specialists. Recognizing and mitigating these indirect pathways is critical for conserving amphibian diversity and maintaining the ecological resilience of tropical forests under increasing invasion pressure.

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Introduction

Invasive alien plants represent one of the major threats to biodiversity worldwide, significantly altering species composition, ecosystem structure and functioning (Ehrenfeld 2003; Vilà et al. 2011; Wilcove et al. 1998; Simberloff et al. 2013). They can also alter forest floor food webs, indirectly affecting

fauna that depend on these habitats (DeVore 2011). A key factor behind the success of many invasive plants is their ability to escape natural enemies, allowing them to dominate new habitats and outcompete native species (Schirmel et al. 2016). One mechanism that can enhance their competitive success is the production of allelopathic compounds, which are common among many plant species but may be particularly influential in facilitating invasion (Callaway and Aschehoug 2000; Bais et al. 2003). The effects of allelopathy are particularly evident in woody invaders, such as the jackfruit tree (*Artocarpus heterophyllus* Lam.), which has been shown to alter habitat conditions by affecting the structure and composition of the leaf litter layer (Bais et al. 2003; Perdomo and Magalhães 2007), a critical component for many forest-dwelling species, including amphibians. These disruptions can have cascading effects on resident fauna by changing food availability and microhabitat quality, as well as influencing biotic interactions (Levine et al. 2004). Thus, understanding the role of invasive species in reshaping habitats is crucial for predicting their impact on local biodiversity and ecosystem functions.

Invasive vegetation can alter habitat structure, herbivory and predator–prey interactions, and the reproductive success of many species of the herpetofauna community (Martin and Murray 2011; Burrow and Maerz 2022). In particular, the effects of invasive plants on amphibian ecology and diversity are increasingly studied, with most research to date has focused on aquatic environments (see Bucciarelli et al. 2014). Early studies highlighted that non-native flora could alter the survival and development of amphibian larvae by changing the quality and availability of resources in their habitats. For instance, plant species that have become invasive outside their native ranges, such as *Lonicera maackii* and *Phragmites australis*, have been shown to influence amphibian development through changes in microclimate, altered nutrient composition of detritus, and secondary metabolite release that can impair physiological processes (Maerz et al. 2005; Watling et al. 2011). Similarly, the expansion of *Phragmites australis* in North American wetlands has led to long-term population declines in *Anaxyrus fowleri* by reducing breeding-site availability and altering wetland connectivity (Greenberg and Green 2013). Although most research has focused on aquatic systems, recent

studies have shown that invasive plants can also affect terrestrial amphibians through multiple, often interacting mechanisms. For example, *Ligustrum lucidum*, which is invasive in South American subtropical forests, forms dense evergreen canopies that reduce light availability and soil moisture, driving local declines and community shifts in native anurans (Segura et al. 2021). Likewise, the presence of exotic grasses such as *Microstegium vimineum* in eastern North America can lead to increased predation pressure on juvenile toads through structurally mediated effects on intraguild predators (Devore and Maerz 2014). In forested environments, exotic trees and shrubs can alter the decomposition rate and chemical properties of the leaf litter, reshaping microflora and arthropod assemblages that support forest-floor food webs (Woodworth et al. 2020; Landsman et al. 2021). Beyond structural and trophic effects, invasive vegetation can also affect amphibian physiology and health; for instance, Giant reed (*Arundo donax*), invasive in riparian systems of the western United States, modifies the microclimate and reduces the diversity of beneficial skin bacteria, leading to poorer body condition (Hernández-Gómez et al. 2020). Collectively, these studies reveal that invasive plants can influence amphibians not only through changes in resource availability or larval habitats, but also by altering the structure, chemistry, and microclimatic stability of terrestrial environments on which many species depend.

Jackfruit, a tree native to India, is recognized as a significant invasive species in Brazil, particularly within the Atlantic Forest (Fabricante et al. 2012; Bergallo et al. 2016). Its introduction dates to the colonial period in 1683, with further propagation encouraged by royal decrees in the nineteenth century, which promoted the planting of economically valuable non-native species (Pereira and Kaplan 2013). The Atlantic Forest's favorable climatic conditions, similar to those found in its native habitat, facilitated its spread, while human use and animal consumption further contributed to increase propagule pressure (Bergallo et al. 2016). Jackfruit's presence, both in native and invasive range, has been shown to negatively impact native plant diversity, either through direct competition or by allelopathic actions that inhibit the growth of native seedlings, leading to significant habitat structure changes (Kumar et al. 2006; Perdomo and

Magalhães 2007). Its invasion success is evident also in protected areas where jackfruit trees form dense stands, altering vegetation composition and consequently forest-floor composition, and this may result in both direct and indirect consequences for forest community assemblages, challenging conservation efforts aimed at preserving native biodiversity.

In the Atlantic Forest, studies have indicated that jackfruit trees can have both positive and negative effects on small mammal communities. For example, frugivorous species may benefit from jackfruit as a food source, while insectivorous species might be negatively impacted due to habitat alterations caused by the high density of these trees (Gama-Matos et al. 2020). However, no data are currently available regarding the influence of jackfruit density on amphibian communities. Considering this gap, the present study aimed to evaluate the influence of jackfruit density on the occupancy of leaf-litter amphibians in a protected area of the Atlantic Forest and to explore how local habitat changes driven by an invasive tree affect species with different ecological requirements. Here, we focused on three leaf-litter amphibian species characterized by contrasting ecologies and habitat-use strategies. Leaf-litter amphibians are ideal focal species for assessing such effects because they depend on the structure and moisture of the forest floor for foraging, thermoregulation, and reproduction, making them highly responsive to changes in microhabitat quality and litter dynamics (Van Sluys et al. 2007; Oliveira et al. 2013). Specifically, we addressed the following questions: (I) To what extent is jackfruit tree density related to key habitat characteristics such as leaf-litter depth and arthropod communities? (II) How does jackfruit density affect amphibian occupancy in the Atlantic Forest? (III) Do species differ in their responses to jackfruit invasion, and can these relationships be explained by indirect pathways involving habitat structure and resource availability? By integrating occupancy modelling and structural equation modelling, we aim to disentangle direct and indirect effects of an invasive tree on terrestrial amphibians, contributing to a broader understanding of how plant invasions reshape forest-floor ecosystems and biodiversity in tropical forests.

Material and methods

Study area

The Duas Bocas Biological Reserve (DBBR) is located in the rural municipality of Cariacica, Espírito Santo, Southeastern Brazil (20°14'04" to 20°18'30" S; 40°28'01" to 40°32'07" W). Covering an area of approximately 2910 ha, the reserve constitutes a legally protected fragment of the Atlantic Forest, characterized as Submontane Dense Ombrophylous Forest (Novelli 2010). The elevation within the DBBR ranges from 200 to 738 m above sea level, harbouring a high diversity of flora and fauna, including rare and endemic species, and a rich amphibian community (Cozer et al. 2020; Gama-Matos et al. 2020; Linause et al. 2020; Pereira-Ribeiro et al. 2020b). Approximately 80% of the reserve is covered by native forest, while the remaining 20% consists of secondary forest, streams, a dam, and riparian zones, with about 50 years of regeneration since being previously occupied by coffee and jackfruit plantations (Azevedo and Santos 2000; Boni et al. 2009). The reserve lies on the watershed divide between the Santa Maria da Vitória and Jucu river basins, both draining eastward to the Atlantic Ocean. Within the reserve, several perennial and temporary streams originate, including the headwaters of the Duas Bocas River and its main tributaries, such as Pau Amarelo and Naia Assu creeks. These watercourses traverse both pristine and regenerating forest, forming a dense drainage network that maintains high humidity conditions and breeding site availability for amphibians year-round. This hydrological system also sustains the Duas Bocas reservoir, a key water source for the region.

The climate in the DBBR is classified as humid tropical, with average annual temperatures ranging from 19 °C in winter to 25.5 °C in summer, and an average annual rainfall of approximately 1500–1600 mm. Rainfall is relatively well-distributed throughout the year, with higher precipitation occurring in the summer months (Bastos et al. 2015).

The DBBR contains ten official trails managed for research and patrol activities. For this study, we used three of them—Represa Velha, Alto Alegre, and Córrego do Pilão—which provided access to the sampling sites (Fig. 1). The Represa Velha trail (3.5 km) crosses secondary forest interspersed with banana,

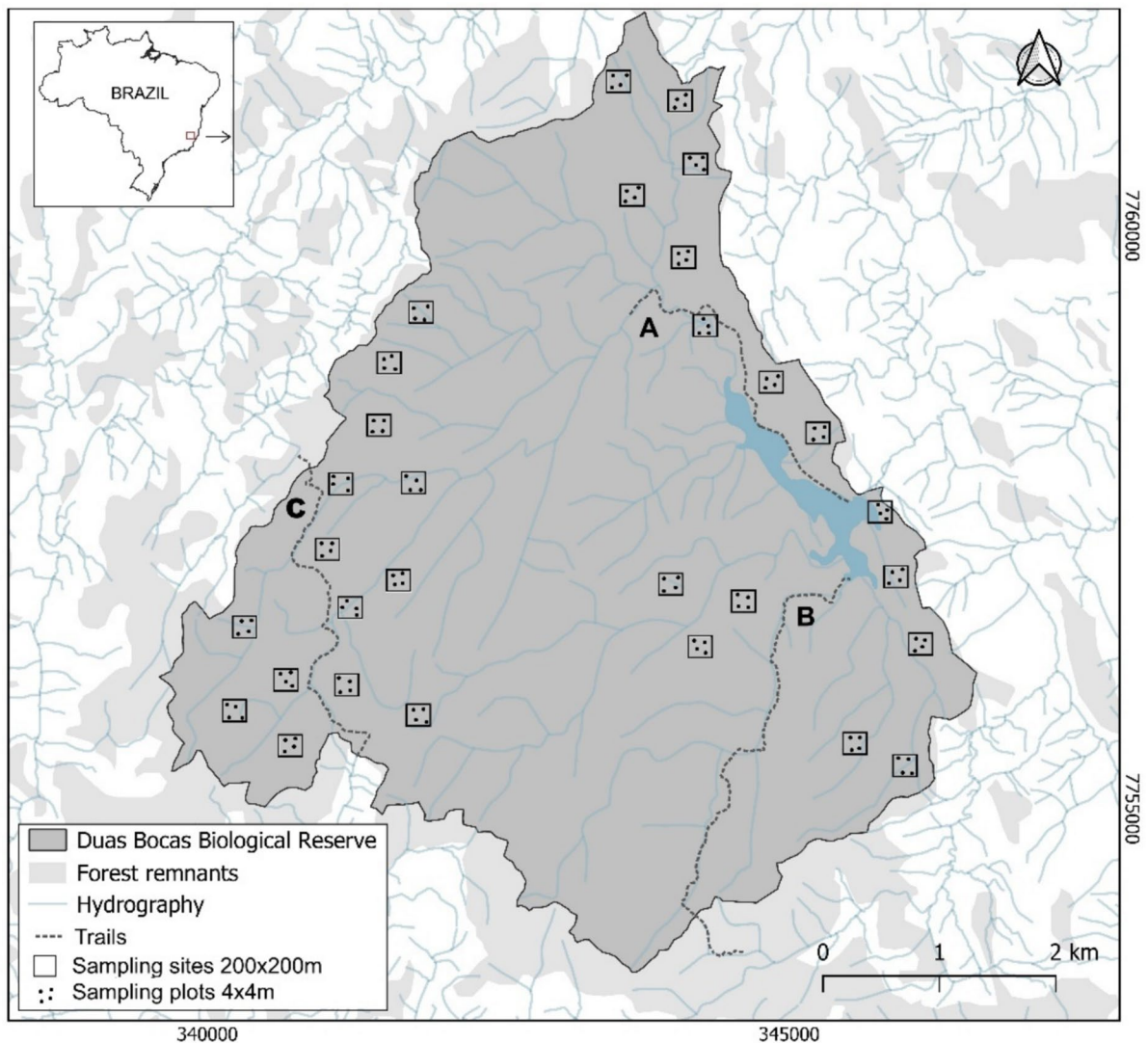


Fig. 1 Map of the Duas Bocas Biological Reserve, showing trails, the local hydrographic network, and 30 sampling sites (200×200 m), each containing four 4×4 m plots (black dots)

used for amphibian and habitat surveys. A=Represa Velha trail; B=Córrego do Pilão trail; C=Alto Alegre trail

coffee, and pasture areas, showing the highest density of jackfruit trees (Boni et al. 2009; Novelli 2010). In contrast, the Alto Alegre trail (4 km) runs through well-preserved forest with a dense canopy and deep leaf litter. The Córrego do Pilão trail (approximately 5 km) represents a transition between these two conditions, traversing mixed vegetation with intermediate disturbance levels. These three trails together form a gradient of habitat structure and jackfruit density across the reserve, encompassing both regenerating and old-growth forest areas.

The DBBR plays a crucial role in the conservation of biodiversity of the region, constituting part of one of the major ecological corridors in the Espírito Santo state and being fundamental for the water supply to the local population.

Amphibian species under study

Leaf-litter amphibians are species that spend most of their life cycle within the forest floor layer, relying on the litter microhabitat for shelter, foraging, and

reproduction (Pontes and Rocha 2011). This study focused on three species commonly found in the Duas Bocas Biological Reserve: *Rhinella crucifer*, *Haddadus binotatus*, and *Proceratophrys schirchi* (Fig. 2). All these species are endemic to the Atlantic Forest (Haddad et al. 2013) and represent distinct ecological

strategies and reproductive modes, providing complementary insights into how habitat alterations influence terrestrial anurans.

Rhinella crucifer (Wied-Neuwied, 1821) has a wide distribution throughout the Atlantic Forest, ranging from the state of Rio de Janeiro to Ceará,



Fig. 2 Visual representation of contrasting habitats and focal amphibian species sampled in the Duas Bocas Biological Reserve, Espírito Santo, Brazil. **A** Area dominated by high jackfruit (*Artocarpus heterophyllus*) density, characterized by reduced understory vegetation and shallower leaf-litter layer. **B** Example of a native forest site without jackfruit trees, showing

higher vegetation complexity. **C** *Rhinella crucifer*, a generalist species tolerant of disturbed habitats. **D** *Haddadus binotatus*, a direct-developing terrestrial frog dependent on humid microhabitats. **E** *Proceratophrys schirchi*, a cryptic litter-dwelling ambush predator associated with well-preserved forest interiors

including northeastern Minas Gerais (Baldissera et al. 2004; Frost 2023). This species is known for its explosive breeding behavior, displaying opportunistic mating strategies where males alternate between calling, territorial behavior, and inactivity periods (De Oliveira et al. 2014). This species accounts for nearly 70% of the total anuran biomass and is the most abundant within the leaf-litter amphibian community of the reserve (see Vagmaker et al. 2020).

Haddadus binotatus is found in the leaf litter of Atlantic Forest remnants and has a broad geographical range from Bahia to Rio Grande do Sul (Sluys and Rocha 2008). This species is characterized by the direct development of its terrestrial eggs, which are deposited on fallen logs (Izecksohn and Carvalho-e-Silva 2001), thus having its life cycle strictly dependent on leaf litter.

Proceratophrys schirchi inhabits moist leaf-litter microhabitats of well-preserved Atlantic Forest areas (Haddad et al. 2013; Vagmaker et al. 2020). Although less abundant and scarcely studied than the other two species (Vagmaker et al. 2020), it is typically associated with shaded forest interiors and relies on small streams for reproduction, where eggs are deposited in flowing water (Haddad et al. 2013).

Amphibian sampling and microhabitat characterization

We conducted monthly surveys between October 2017 and January 2019 across 30 sampling sites within the Duas Bocas Biological Reserve. Sampling sites were randomly selected among accessible grid cells from a 200×200 m grid covering the reserve, maintaining a minimum distance of 200 m between sites to ensure spatial independence. Within each site, we established four secondary plots (4×4 m each; Fig. 1), placed at least 50 m apart to avoid spatial overlap (Allmon 1991; Rocha et al. 2000). Each secondary plot was georeferenced and enclosed with a 1 m-high plastic mesh, inserted a few centimeters into the soil to prevent anurans from escaping beneath it.

We installed the plots in the afternoon (2:00–3:00 pm) and measured habitat variables before nightfall. We measured leaf-litter depth (mm) at the four corners of each plot, and the mean value was used for analyses. To estimate arthropod density, we collected 25×25 cm leaf-litter samples from the same corners and sorted them in the laboratory to

the taxonomic level of order. Unidentified remains were classified as “Unidentified Arthropod Remains” (U.A.R.). The total litter-sampling area per plot was 0.25 m² (four samples of 25×25 cm), and arthropod density was expressed as the number of individuals per 100 m² based on the mean of the four sub-samples. Around each 4×4 m plot, we delimited an additional 100 m² area (plots of 10×10 m), including the central plot, to count jackfruit trees with diameter at breast height (DBH) > 5 mm. Jackfruit density was expressed as individuals per 100 m².

Amphibian monitoring was conducted after sunset (6:00–10:00 p.m.), and temperature (°C) and relative humidity (%) were recorded at the beginning of each sampling session using a thermo-hygrometer. We sampled amphibians with four observers systematically searching the leaf litter on hands and knees using headlamps and flashlights. We spent 20–30 min per plot depending on vegetation density and litter depth. We placed each captured individual in breathable plastic bags to prevent recapture during the same sampling session. At the end of each session, all individuals were identified to species and released at the point of capture within the same plot. In addition to the three focal species, a small number of individuals belonging to other amphibian species were occasionally recorded at very low frequencies (typically 1–5 individuals per species), which precluded their inclusion in the occupancy analyses (Table A2.S7; Vagmaker et al. 2020). For each individual, we recorded the site, plot, time, and observer. Each 4×4 m plot represented one sampling session, resulting in four sampling sessions per site, and the four plots within a site were generally surveyed on different nights within the same month, with a maximum interval of one month between sessions.

Data analysis

Habitat variables (litter depth, arthropod density and jackfruit density) were averaged across the four secondary plots to obtain representative values for each site, which were subsequently used in occupancy and SEM analyses.

To evaluate how jackfruit density affected key habitat attributes and arthropod communities, we fitted a series of generalized linear mixed models (GLMMs) using the *glmmTMB* package in R (Brooks et al. 2017), based on data from 120 secondary plots

(4×4 m) nested within 30 sites (Table A1.S1). Site was included as a random intercept to account for non-independence among plots within the same sampling area. We modeled leaf litter depth and arthropod density as continuous positive responses using Tweedie distributions with a log link, and arthropod diversity (number of taxonomic orders) with a COM-Poisson model to account for underdispersion in the count data. All predictors were standardized (mean=0, SD=1). We selected the best-fitting models using Akaike's Information Criterion (AIC) and evaluated residuals with the *DHARMA* package. Effect sizes were expressed as incidence rate ratios ($IRR = e^{\beta}$), representing proportional changes in the response variable for each one-standard-deviation increase in jackfruit density (or arthropod density for the diversity model).

We estimated occupancy (Ψ) and detection probability (p) with single-season occupancy models in R (v4.1.2) using the unmarked package (Fiske and Chandler 2015). In this notation, $\Psi(\sim \dots)$ specifies the linear predictor for the state process (occupancy) and $p(\sim \dots)$ specifies the linear predictor for the observation process (detection). For each species, we used observation-level covariates of relative humidity and temperature (measured at each nightly survey) for detection, and site-level covariates of jackfruit density (individuals/100 m²), leaf-litter depth (mm), arthropod density (individuals/100 m²) and arthropod diversity (number of taxonomic orders) for occupancy. Before modelling, we screened covariates for pairwise collinearity and retained all predictors $|r| < 0.60$. Canopy cover was initially considered as a candidate predictor due to its known influence on forest microclimate and litter dynamics. However, exploratory analyses indicated limited spatial variation in canopy cover across sampling plots (approximately 67–91%, with most plots presenting values above 75%), reflecting a predominantly closed-canopy system. In preliminary models, canopy cover did not improve model fit and increased model complexity without altering inference. Therefore, canopy cover was excluded from the final analyses to maintain model parsimony.

For each species, we implemented a two-step model-selection workflow:

Step 1—detection: We compared candidate detection structures $p(\sim 1)$, $p(\sim \text{humidity})$, $p(\sim \text{temperature})$ and $p(\sim \text{humidity} + \text{temperature})$ while holding a simple working occupancy term $\Psi(\sim 1)$ to

select the detection model. We ranked candidates by AICc and retained the best-supported structure.

Step 2—occupancy: With p fixed to the selected detection structure, we compared biologically motivated occupancy formulas combining jackfruit density, litter depth, arthropod density and arthropod diversity. We ranked candidates by AICc, treated $\Delta\text{AICc} < 2$ as substantial support, and based inference on the top model (Burnham et al. 2011). Although selection proceeded in two steps, unmarked jointly estimates Ψ and p for any specified pair of formulas.

Our sampling design provided four repeated surveys per site within the same month (one 4×4 m plot per occasion on different nights), which we treated as temporal replicates under a single-season framework. We assumed closure (constant occupancy state within the monthly window), allowed detection to vary among visits via the observation covariates, and estimated Ψ at the site scale (MacKenzie et al. 2002; Bailey et al. 2014).

We assessed goodness-of-fit of the top occupancy model for each species using the MacKenzie–Bailey parametric bootstrap (1000–2000 simulations) to compute the overdispersion parameter $\hat{c}$. Models with $\Delta\text{AICc} < 2$ were regarded as having a high level of support (Burnham et al. 2011). Full model selection tables (AICc, ΔAICc , weights) are provided in supplementary material (Tables A1.S2 and A1.S3).

After occupancy modelling, we used a piecewise Structural Equation Model (SEM) to disentangle direct and indirect pathways linking jackfruit trees to amphibian occupancy (Grace 2006; Kline 2016). For each species, we first obtained site-level occupancy predictions ($\hat{\psi}$) from the best single-season occupancy model. We then specified a species-specific SEM with jackfruit density as the exogenous driver and leaf-litter depth, arthropod density, and arthropod diversity as mediators, linking these to $\hat{\psi}$. Concretely, we fitted the following linear component models:

(1) $\text{litter_z} \sim \text{jackfruit_z}$; (2) $\text{arthropod_density_z} \sim \text{jackfruit_z}$; (3) $\text{arthropod_diversity_z} \sim \text{jackfruit_z}$; and (4) $\hat{\psi} \sim \text{jackfruit_z} + \text{litter_z} + \text{arthropod_density_z} + \text{arthropod_diversity_z}$.

Before SEM, we standardized all site-level covariates (z-scores). We fitted the piecewise models with the piecewiseSEM package (Lefcheck 2016), summarized standardized path coefficients, and assessed

global fit using Fisher's C and d-separation tests ($\alpha=0.05$).

Full results of the GLMMs, occupancy models, detection models, and structural equation models are provided in Appendix 1. Raw field data, including detection histories, environmental covariates, and records of additional amphibian species, are available in Appendix 2.

Results

Effects of Jackfruit density on microhabitat and arthropod communities

We recorded jackfruit trees in 12 out of 30 sampling sites, with a mean density of 3.2 ± 4.7 individuals/100 m² across all sites (or 8.0 ± 3.9 individuals/100 m² when only invaded sites are considered). We identified 12 arthropod orders in the leaf-litter samples, with Isopoda (352 individuals), Araneae (233), and Hymenoptera (190) being the most abundant groups. Other taxa included Blattodea (57), Chilopoda (52), Orthoptera (50), Opiliones (22), Coleoptera (17), Diptera (7), Pseudoscorpiones (4), Phasmatodea (2), and Acari (2), in addition to 90 individuals classified as unidentified arthropod remains (U.A.R.).

Generalized linear mixed models revealed that jackfruit density had negative effects on leaf litter depth (Tweedie GLMM, $\beta = -0.54 \pm 0.09$ SE, $p < 0.001$) and on arthropod density (Tweedie GLMM, $\beta = -0.17 \pm 0.07$ SE, $p = 0.021$). In contrast, arthropod diversity (number of orders) was positively related to arthropod density (COM-Poisson GLMM, $\beta = 0.25 \pm 0.03$ SE, $p < 0.001$), while the direct effect of jackfruit density was not significant (COM-Poisson GLMM, $\beta = -0.07 \pm 0.05$, $p = 0.15$) (Table A1.S1).

Occupancy and detection models by species

Rhinella crucifer

The estimated probability of occupancy for *R. crucifer* was 43% (0.43 ± 0.09), with a detection probability of 67% (0.67 ± 0.06). The best-supported detection model for *Rhinella crucifer* included both humidity and temperature (Table A1.S2), with the

lowest AICc value (95.65) and a model weight of 0.87. Detection probability increased slightly with humidity ($\beta = 0.17 \pm 0.11$ SE) and showed a near-zero effect of temperature ($\beta = 0.04 \pm 0.28$ SE), although confidence intervals slightly overlapped zero, indicating weak but consistent trends. For occupancy, the best-fitting model included only the continuous effect of jackfruit tree density (Table 1). The coefficient for jackfruit density was positive ($\beta = 0.59 \pm 0.42$ SE), showing a tendency toward higher occupancy in areas with higher jackfruit density (Fig. 3).

Haddadus binotatus

The occupancy probability for *H. binotatus* was estimated at 72% (0.72 ± 0.18), with a detection probability of 25% (0.25 ± 0.07). Detection probability was best described by the null model, indicating no strong climatic effects on detectability (Table A1.S2). Occupancy of *H. binotatus* was negatively associated with jackfruit density ($\beta = -0.39 \pm 0.17$ SE), showing lower occupancy probabilities in areas of high jackfruit density (Fig. 4).

Proceratophrys schirchi

The estimated occupancy probability for *P. schirchi* was 30% (0.30 ± 0.12), with a detection probability of 29% (0.29 ± 0.11). Detection probability showed weak variation among climatic models, indicating minimal influence of temperature or humidity (Table A1.S2). Occupancy was positively related to leaf-litter depth ($\beta = 0.68 \pm 0.42$ SE) and arthropod diversity ($\beta = 2.47 \pm 1.61$ SE), though both effects were estimated with moderate uncertainty (Table 1, Fig. 5).

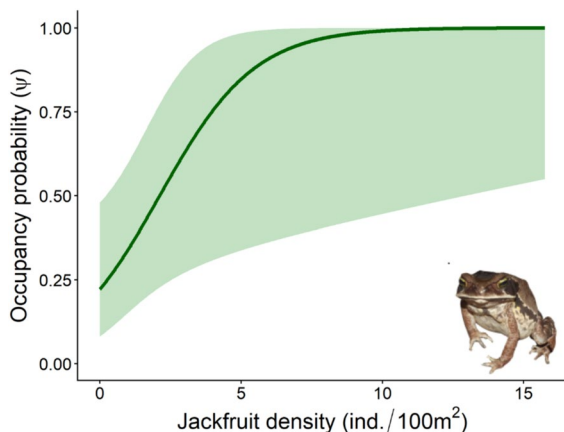
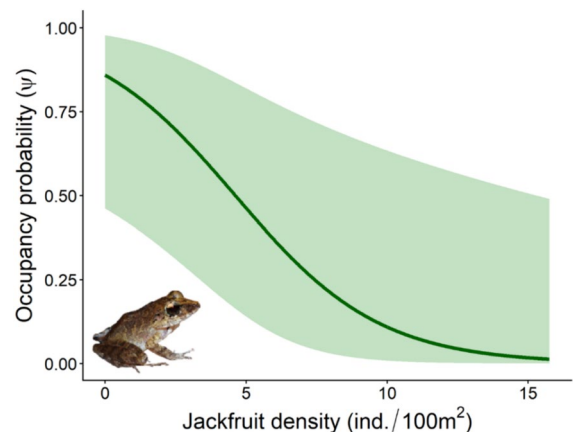
Structural equation model (SEM)

The structural equation models revealed consistent environmental pathways linking jackfruit tree density to habitat structure and invertebrate communities (Table A1.S4, Fig. 6). Across all species, jackfruit density had strong negative effects on leaf-litter depth ($\beta = -0.56$, $p = 0.001$) and arthropod density ($\beta = -0.49$, $p = 0.006$), and no detectable effect on arthropod diversity ($\beta = -0.11$, $p = 0.57$).

Table 1 Five best-ranked single-species, single-season occupancy models for three amphibian species—*Rhinella crucifer*, *Haddadus binotatus*, and *Proceratophrys schirchi*—in the Duas Bocas Biological Reserve, Brazil.

Model	K	AICc	Δ AICc	AICcw
<i>Rhinella crucifer</i>				
Ψ (jackfruit), p (humid + temp)	5	95.655	0.000	0.482
Ψ (jackfruit + dens_art), p (humid + temp)	6	97.890	2.236	0.158
Ψ (jackfruit + div_art), p (humid + temp)	6	98.048	2.394	0.146
Ψ (jackfruit + litter), p (humid + temp)	6	98.730	3.075	0.104
Ψ (jackfruit + div_art + dens_art), p (humid + temp)	7	100.638	4.983	0.040
<i>Haddadus binotatus</i>				
Ψ (jackfruit), p (.)	3	111.280	0.000	0.402
Ψ (jackfruit + litter + div_art), p (.)	5	111.471	0.191	0.366
Ψ (jackfruit + div_art), p (.)	4	113.394	2.114	0.140
Ψ (jackfruit + litter), p (.)	4	114.982	3.701	0.063
Ψ (.), p (.)	2	117.482	6.202	0.018
<i>Proceratophrys schirchi</i>				
Ψ (litter + div_art), p (.)	4	56.787	0.000	0.646
Ψ (jackfruit + litter + div_art), p (.)	5	59.183	2.396	0.195
Ψ (litter), p (.)	3	60.091	3.305	0.124
Ψ (jackfruit + div_art), p (.)	4	64.029	7.243	0.017
Ψ (jackfruit + litter + dens_art), p (.)	5	65.215	8.428	0.010

Covariates include jackfruit density (*Artocarpus heterophyllus*; ind/100 m²; 'jackfruit'), litter depth (mm; 'litter'), arthropod diversity (number of orders; 'div_art'), and arthropod density (ind/100 m²; 'dens_art'). Ψ =occupancy, p=detectability, AIC=Akaike information criterion, AICcw=Akaike weight, K=number of parameters. 'Humid' refers to air relative humidity and 'temp' to air temperature, included only in detection models for *R. crucifer*, where they improved model fit. Detection for the other two species followed the null model. "(.)" indicates that no covariate was included in that component of the model

**Fig. 3** Probability of occupancy of *Rhinella crucifer* in relation to jackfruit density (ind/100 m²) in the Duas Bocas Biological Reserve, Brazil**Fig. 4** Probability of occupancy of *Haddadus binotatus* in relation to jackfruit density (ind/100m²) in the Duas Bocas Biological Reserve, Brazil

These effects represent the environmental alterations induced by jackfruit invasion and were identical across the three species-specific models.

Species differed, however, in how these habitat changes influenced occupancy (ψ): *Rhinella crucifer* showed a positive direct effect of jackfruit density

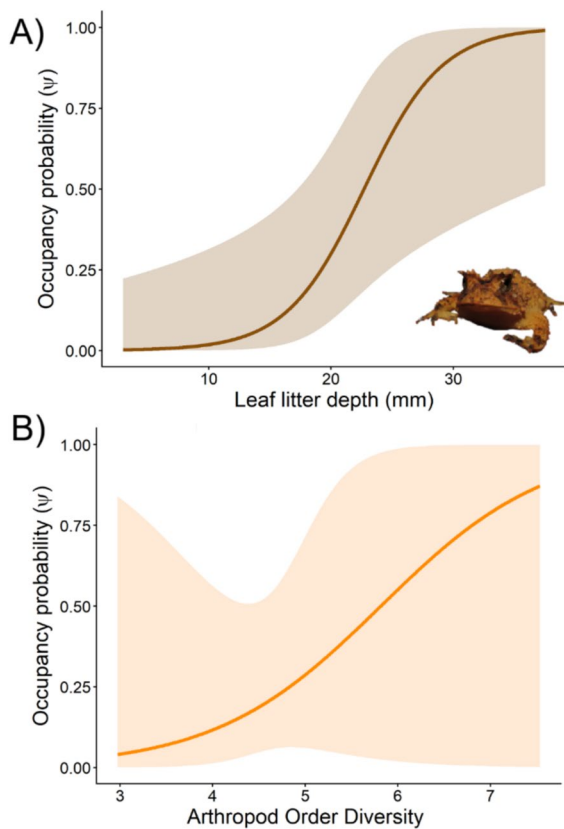


Fig. 5 Probability of occupancy of *Proceratophrys schirchi* in relation to litter depth **A** and arthropod diversity **B** in the Duas Bocas Biological Reserve, Brazil

on occupancy ($\beta=0.84$, $p<0.001$), while indirect effects through leaf litter and arthropods were weak and non-significant. *Haddadus binotatus* displayed a negative direct effect of jackfruit density on occupancy ($\beta=-0.93$, $p<0.001$), with small and non-significant indirect effects. *Proceratophrys schirchi* did not exhibit a direct effect of jackfruit density on occupancy; instead, its occupancy was positively influenced by leaf-litter depth ($\beta=0.74$, $p<0.001$) and arthropod diversity ($\beta=0.34$, $p=0.002$).

Discussion

The leaf litter layer plays a critical role in forest ecosystems, providing habitat and food for a wide range of organisms while buffering against fluctuations in humidity and temperature (Sayer 2006; Dias et al. 2017). This layer is essential for maintaining nutrient

cycling, soil formation, and the structural complexity that supports numerous microhabitat specialists (Sayer 2006; Dias et al. 2017). However, the spread of exotic plant species can significantly disrupt these fundamental processes, impacting both the organisms that inhabit the litter layer and the ecosystem functioning of invaded areas (Callaway and Aschehoug 2000; Schirmel et al. 2016). Across tropical and temperate forests alike, invasive woody plants have been shown to alter soil chemistry, decomposition rates, and litter accumulation, thereby reshaping the physical and biological structure of the forest floor (Levine et al. 2004; Pyšek et al. 2012; Woodworth et al. 2020; Landsman et al. 2021; Segura et al. 2021). Beyond these structural effects, invasive trees with allelopathic potential can further intensify these impacts by releasing phytochemicals that modify soil and litter chemistry, influencing microbial activity and nutrient cycling, and potentially affecting fauna that depend on this layer, including amphibians (Burrow and Maerz 2022). Although most evidence of such chemical interference comes from aquatic systems (Perez et al. 2013; Bucciarelli et al. 2014; Burrow and Maerz 2022), similar mechanisms can also occur in terrestrial environments, particularly for organisms chronically exposed to decomposing litter, a possibility that remains largely unexplored in forest ecosystems.

Our findings revealed that jackfruit density negatively influenced both litter depth and arthropod density, indicating that the invasive tree simplifies forest-floor structure and reduces available resources for leaf-litter fauna. Such effects are consistent with those reported for other invasive trees that can suppress native vegetation through shading, root competition, or allelopathic interference, and can accelerate decomposition through changes in litter chemistry (Bais et al. 2003; Kumar et al. 2006; Perdomo and Magalhães 2007; Gama-Matos et al. 2020; Segura et al. 2021). By reducing leaf litter accumulation, the jackfruit tree may decrease habitat complexity and microclimatic stability, limiting the abundance of litter-dwelling arthropods that form the trophic base for forest-floor food webs (Cole et al. 2016; Woodworth et al. 2020; Landsman et al. 2021). These results confirm that invasive woody plants can exert cascading effects through both structural and trophic pathways and highlights a broader concern about how chemical and physical alterations by invasive flora impact essential microhabitats for invertebrates

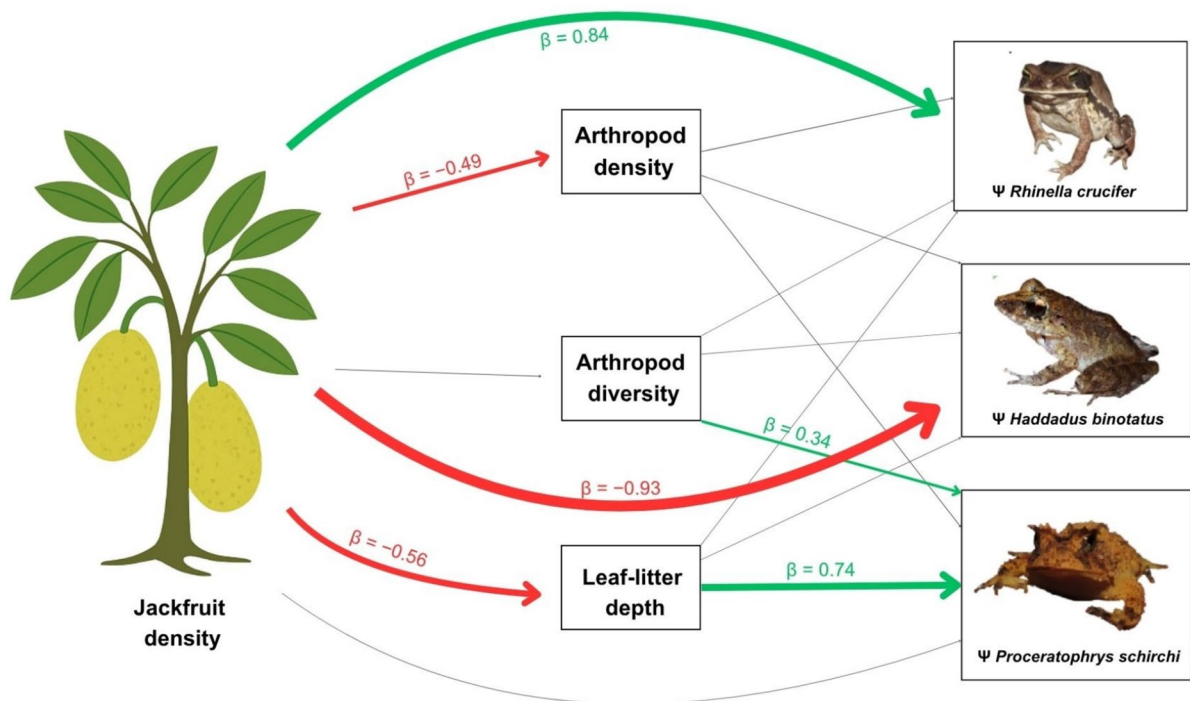


Fig. 6 Piecewise structural equation model (SEM) showing the direct and indirect effects of jackfruit density on micro-habitat structure, arthropod communities, and amphibian occupancy (Ψ) in the Duas Bocas Biological Reserve. SEMs were fitted separately for each amphibian species, although they are displayed together for clarity. Red and green arrows represent

significant negative and positive pathways, respectively, with arrow thickness proportional to standardized path coefficients (β). Thin grey lines indicate non-significant paths. Effects of jackfruit density on leaf-litter depth and arthropod density were estimated using the same model structure and parameterization across all species-specific SEMs

and amphibians, a pattern documented across multiple regions (e.g. Richardson et al. 2000; Nunes et al. 2019; Falaschi et al. 2020).

The three amphibian species responded in contrasting ways to the environmental changes induced by jackfruit invasion. For *Rhinella crucifer*, representative of the *R. crucifer* species group, we observed a positive direct effect of jackfruit density on occupancy, consistent with the generalist behavior and high ecological tolerance described for this clade (Baldissera et al. 2004; Pereyra et al. 2021). Species within the *R. crucifer* group are widely distributed across the Atlantic Forest and commonly occur in secondary forests, forest edges, disturbed fragments, and even agricultural landscapes, where their tolerance to warmer, drier, and more open microhabitats reflects a remarkable ecological plasticity and ability to exploit simplified environments (e.g. Baldissera et al. 2004; D'Anunção et al. 2013; Pereira-Ribeiro et al. 2020a; Vagmaker et al. 2020). This generalist profile

suggests that such species can benefit from environmental simplification, at least in the short term. Similar trends have been observed for other generalist vertebrates in the same region, such as small mammals that also thrive in jackfruit-dominated areas (Gama-Matos et al. 2020). In addition to any direct benefits, the reduced suitability of jackfruit-altered habitats for more specialized species may further favor generalists by lowering interspecific competition in disturbed contexts. Together, these patterns indicate that the invasive tree may favor adaptable, disturbance-tolerant species while indirectly disadvantaging habitat specialists, contributing to biotic homogenization processes driven by plant invasions.

In contrast, *Haddadus binotatus* showed a strong negative direct effect of jackfruit density on occupancy, consistent with its association with less disturbed forest habitats and its high abundance in continuous forest areas reported in previous studies (e.g. Almeida-Gomes et al. 2016). As a direct-developing

species that deposits terrestrial eggs on decaying logs or within the leaf litter, *H. binotatus* is highly dependent on humid microhabitats and stable litter conditions (Izecksohn and Carvalho-e-Silva 2001). The absence of significant indirect effects via litter depth or arthropod variables in the SEM suggests that the invasive tree influences this species primarily through direct environmental alterations rather than mediated habitat changes. This direct effect may arise from unmeasured microenvironmental factors, such as reduced litter moisture, altered decomposition dynamics, or the presence of phytochemicals released during jackfruit leaf decay, that could compromise survival of adults or more fragile life stages, such as eggs and juveniles (Stephens et al. 2013; Stoler and Relyea 2013; Haggerty et al. 2019). Similar declines in litter-dwelling amphibians have been reported in disturbed tropical forests, where species with narrow ecological niches tend to decline due to habitat alteration (Scheffers et al. 2013; Nowakowski et al. 2018; Hoffmann et al. 2021).

Proceratophrys schirchi did not exhibit a direct relationship with jackfruit density, but its occupancy increased with deeper leaf litter and greater arthropod diversity. This species is a nocturnal, cryptic ambush predator that relies on dense litter and moist soils for camouflage and foraging, and it is often associated with well-preserved forest interiors (Almeida et al. 2011; Ferreira et al. 2019; Rodder et al. 2007; Vagmaker et al. 2020). Its positive response to litter depth and arthropod diversity indicates a dependence on microhabitat quality rather than tree composition per se. These findings support the growing evidence that microstructural habitat complexity and prey availability are key drivers of occupancy for forest-floor amphibians, even in the absence of direct vegetation effects.

The structural equation models provided a mechanistic framework linking these patterns. Across all species, jackfruit density consistently reduced leaf-litter depth and arthropod density, confirming its role as a driver of habitat simplification. However, the strength and direction of subsequent effects on amphibian occupancy varied according to species traits. While *R. crucifer* and *H. binotatus* responded directly to invasion intensity, *P. schirchi* responded to the secondary habitat modifications mediated by variation in forest litter and arthropod community. This divergence supports a trait-based filtering process,

whereby invasive plants restructure communities not only through habitat loss but by selecting for functional attributes such as tolerance to desiccation, reproductive mode, feeding habits, and microhabitat use (Greenberg and Green 2013; Devore and Maerz 2014; Segura et al. 2021). Our SEM framework thus highlights multiple causal pathways—structural, trophic, and physiological—through which invasive trees can reshape amphibian assemblages.

Although our study provides strong evidence for how the invasive jackfruit tree alters habitat structure and amphibian occupancy, some methodological aspects warrant consideration for future research. First, we did not explicitly include proximity to water bodies as a predictor variable, which can influence species with aquatic larvae. However, in our study area, the hydrographic network is dense and well distributed, with most of our study sites located within short distances of perennial or temporary streams. Because of this high and relatively homogeneous water availability and given that one of the three focal species have terrestrial reproductive modes, we expect this factor to have had little influence on our results. Nevertheless, future studies conducted in landscapes with greater hydrological variability should consider including measures of water proximity or breeding-site availability to test for potential interactions with invasive vegetation. Second, our sampling design spanned 15 months, but each site was surveyed within a single month, minimizing within-site seasonal variability under a single-season occupancy framework. In this humid tropical region, rainfall is relatively well distributed throughout the year; however, we further evaluated whether microclimatic conditions measured during surveys exhibited meaningful temporal variation. Across all sampling occasions, air temperature ranged from 18.3 to 27.8 °C, but most occasions were characterized by similar temperatures, with within-occasion variation typically $\leq 2\text{--}3$ °C. Likewise, relative humidity remained predominantly high throughout the monitoring period, with most values concentrated between approximately 65 and 80%, and only a few isolated measurements outside this range. No clear temporal segregation among sampling occasions or study areas was observed for either variable (Table A2.S5 and A2.S6). Together, these patterns indicate that microclimatic variation during the study period was largely short-term and episodic rather than seasonally

structured. Therefore, broad seasonal effects are unlikely to have biased occupancy estimates beyond fluctuations already captured by the temperature and humidity covariates included in detection models. Still, in ecosystems with stronger rainfall seasonality, multi-season occupancy models could provide a valuable extension to assess temporal dynamics in colonization and extinction probabilities. Third, we focused on three well-detected species to ensure model stability and reliable estimation of detection and occupancy parameters. While this species-specific approach allowed us to identify distinct mechanisms of response to invasion, future research should expand this framework to multi-species occupancy or community models, which can capture covariance in species responses and reveal broader functional shifts in assemblage structure. In addition, applying similar approaches to threatened or Data Deficient amphibian species could help identify whether invasive plants impose comparable constraints on the most vulnerable components of amphibian communities across different ecological contexts. Finally, our inferences are limited to a single protected Atlantic Forest reserve, and the extent to which these mechanisms apply to other invaded forests remains to be tested. Future studies conducted across multiple regions and invasion contexts could help determine whether the direct and indirect pathways observed here represent generalizable patterns of invasion impacts on tropical amphibian assemblages.

Our findings demonstrate that the invasive jackfruit tree plays a major role in reshaping forest-floor ecosystems, substantially altering habitat structure and the occupancy of leaf-litter amphibians in the Atlantic Forest. While the effects of jackfruit density on amphibian species are complex, our results reveal a clear ecological filtering process, where more tolerant and generalist species such as *Rhinella crucifer* are favored by invasion, whereas specialists such as *Haddadus binotatus* and *Proceratophrys schirchi* are negatively affected through habitat degradation and resource alteration. This pattern reflects how invasive plants can promote biological homogenization by simplifying habitat structure, reducing leaf-litter depth, and altering invertebrate assemblages that sustain the forest-floor food web. These cascading effects emphasize the need to preserve and restore microhabitat complexity, particularly the quantity and quality of leaf litter that support stable trophic and thermal conditions for forest-floor

amphibians. Effective conservation planning should therefore combine invasive species control with habitat restoration actions that maintain the fine-scale structural conditions essential for native communities to persist. Given the exceptional vulnerability of amphibians to habitat disturbances, our results reinforce the urgent need for invasive species management in protected areas, ensuring that both the direct and indirect impacts on biodiversity are addressed. Amphibians are experiencing unprecedented global declines driven by multiple, interacting threats—including disease, habitat loss, biological invasions, and climate change—and the terrestrial alterations caused by invasive plants represent an often-overlooked yet growing component of this crisis (Stuart et al. 2004; Bellard et al. 2012). Recognizing and mitigating these indirect invasion pathways is therefore critical for safeguarding amphibian diversity and maintaining the ecological resilience of tropical forests under changing climates.

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Declarations

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