



Climate drivers and novel insect associations shape pre-dispersal predation in *Hancornia speciosa*

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Abstract

Pre-dispersal seed predation reduces the numbers of viable seeds produced by plants and their populations. *Hancornia speciosa* Gomes (Apocynaceae), popularly known as mangabeira, is native to Brazil and widely distributed in savannas, open sandy landscapes, and coastal restinga vegetation formations. Its edible fruits generate income for thousands of families. We recorded attacks by *Asphondylia hancorniae*, a specialist endoparasitic gall midge, on immature *H. speciosa* fruits on trees in the Chapada Diamantina mountains and in the coastal zone, Northeastern Brazil, for 24 months. We also investigated the influence of environmental variables on this process. *Asphondylia hancorniae* attacks cause the withering of immature fruits before seed formation and dispersal. We suggest the use of the Fournier Intensity Index as a quantitative tool to assess the intensity of seed predation and plant disease occurrence in a standardized and comparable manner. Predation intensity reached 47.22% in coastal zone and 35.65% in the inland Chapada Diamantina mountains populations and showed positive correlations with temperature and photoperiod. This approach is especially important for conservation strategies aiming to understand the impact of fruit losses in *H. speciosa* caused by the gall midge *A. hancorniae* and how contrasting climatic factors modulate those plant-insect interactions. The damage caused by *A. hancorniae* on fruits allowed secondary attacks by *Hypothenemus obscurus*, an association not previously reported as involving a Cecidomyiidae fly and a Scolytinae bark beetle. Our results highlighted the greater habitat fragmentation along the coast appears to amplify negative environmental impacts on the fruiting of *H. speciosa*.

Keywords Cecidomyiidae · Environmental variables · Mangaba · Pre-dispersal predation

Introduction

The innumerable interactions between plants and other organisms, ranging from molecular to ecosystem levels, vary from positive mutualistic interactions to antagonistic encounters that drive physiological, ecological, and evolutionary responses (Giron et al. 2018). Classical examples of those interactions include pollination and seed dispersal, which are essential to plant reproductive success, as well as herbivory and parasitism, which have led to the evolution of defense mechanisms that mitigate fitness losses (Lev-Yadun 2021; Giron et al. 2018). Simultaneous and overlapping interactions between plants and multiple organisms can generate cascading effects, producing permanent or temporary consequences that connect diverse life forms in ongoing evolutionary processes (Giron et al. 2018; Van Dam 2009).

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Although plants have evolved constitutive and induced defenses against herbivores (Lev-Yadun 2021), pre-dispersal predators continue to affect individual fitness and population dynamics by reducing the number of viable seeds (Downey et al. 2020; Crawley 2000). Previous studies have shown that pre-dispersal predation can influence recruitment, population growth, phenological patterns, and the selection of evolutionary traits (Miyake et al. 2017; Souza and Fagundes 2016; Kolb et al. 2007a, b). Through coevolution, many pre-dispersal predators become specialized on a limited number of host species and, at the community level, may prevent host overabundance, contributing to the maintenance of tropical biodiversity (Downey et al. 2020; Grip-enberg et al. 2019; Connell 1971; Janzen 1970).

Investigations of periodic events in organism life cycles and their relationships with climate (i.e., phenology) are essential for understanding the effects of climate change on biotic interactions (Hamann et al. 2021; Pedroso et al. 2021; Sánchez et al. 2012; Greenberg et al. 2008). In addition to biotic drivers, abiotic factors such as climatic variables directly influence seed predation intensity (Bogdziewicz et al. 2019; Koundinya et al. 2018; Espelta et al. 2008). Temperature, rainfall, photoperiod, and other environmental factors modulate both host and predator traits, including flowering, pollination, fruit set, fruit nutritional content, insect emergence, body size, voltinism, and oviposition, reflecting the complexity of plant–insect interactions (Zambrano-González et al. 2023; Moreira et al. 2020; Zeuss et al. 2016; Poncet et al. 2008).

Because pre-dispersal predation directly reduces seed production and fruit availability, its effects extend beyond population dynamics to species of socio-economic importance. In plants that are harvested from natural populations, fruit losses caused by specialized predators may compromise both ecological persistence and resource availability for human use. Understanding the drivers of these interactions is therefore particularly relevant for species that simultaneously sustain biodiversity and support traditional livelihoods (Prasanna et al. 2022; Ratnadass et al. 2012).

Hancornia speciosa Gomes (Apocynaceae), popularly known as mangabeira, is native to Brazil, Paraguay, Bolivia, and Peru and occurs primarily in Brazilian savannas and coastal restingas, growing on sandy, well-drained, nutrient-poor soils (Silva Júnior et al. 2017; Pereira et al. 2024, 2025). Although cultivation protocols have been developed (Muniz et al. 2019; Ferreira and Marinho 2007; Léo et al. 2015; Vieira Neto et al. 2002), most fruits are harvested from natural stands managed by traditional communities.

Among the insect groups known to affect fruit production in various plant species, the family Cecidomyiidae (Diptera) comprises phytophagous insects best known for their ability to induce galls (Carneiro et al. 2009). Within

this family, the genus *Asphondylia* Loew includes approximately 320 described species, many of which attack floral structures and can reduce fruit production (Gagné and Jaschhof 2021). In Brazil, 23 species have been formally described (Maia and Oliveira 2021), although many likely remain undescribed (Flor and Maia 2017). Although several insect predators affecting *H. speciosa* have been reported (Silva et al. 2019; Léo et al. 2015; Vieira Neto et al. 2002), attacks by Cecidomyiidae gall midges have not previously been documented.

Abiotic factors, particularly climatic variables, play a central role in modulating plant–herbivore interactions by influencing plant physiology, herbivore performance, and the temporal synchrony between them. In systems involving pre-dispersal seed or fruit predators—especially specialist galling insects—climatic conditions regulate the timing, duration, and magnitude of flowering and fruiting, thereby determining the availability of susceptible reproductive tissues for oviposition and larval development (Fernandes et al. 2025; Gil-Tapetado et al. 2020; Blanche 2001).

Here we describe for the first-time fruit losses in *H. speciosa* caused by the gall midge *Asphondylia hancorniae* (Maia et al. 2023) and evaluate whether predation rates differ between regions and are modulated by climatic factors.

Materials and methods

Host species and study area

Hancornia speciosa is widely distributed on sandy, nutrient-poor and very well-drained soils in savanna formations, coastal Restinga, coastal plains, and Cerrado in Brazil (Flora e Funga do Brasil 2025). It is a pioneer and heliophyte tree or shrub, semideciduous, producing abundant latex and reaching heights of 5–15 m. It produces oblong to elliptic bacoid fruits (“mangaba”) with masses between 9 and 30 g and diameters between 2 and 6 cm, with up to 91% pulp and 3–22 seeds. The fruit pulp has high concentrations of vitamins and minerals, antioxidant properties, and a low caloric value (Flora e Funga do Brasil 2025; Silva et al. 2016; Silva Júnior et al. 2018; Pereira et al. 2016; Lederman et al. 2000).

The present study followed six populations of *H. speciosa* (Supporting Information Table 1) growing in fine, deep, well-drained, sandy white quartz soils in Bahia State, Brazil (Pereira et al. 2024, 2025). Three populations were located on sandy coastal plains (restinga vegetation) within the Atlantic Forest phytogeographic domain (Queiroz et al. 2017) (two in the municipality of Mata de São João and one in the municipality of Salvador). The other three populations were situated in the municipality of Lençóis, within the sandy Capitinga phytophysiology within the Caatinga

domain in the Chapada Diamantina highlands (Funch et al. 2021). The two study zones were selected to represent contrasting climatic contexts within the distribution range of *H. speciosa*, particularly differing in long-term precipitation regime, relative humidity, and oceanic influence.

Predation patterns and gall midge determination

Immature fruits at various developmental stages were collected directly from the trees and examined for the presence of larvae and pupae. Adult insects were obtained by rearing a subset of the collected pupae to emergence.

Insect samples (males, females, pupal exuviae, and third-instar larvae) were prepared following the methodology of Gagné (1994) and deposited in the Entomological Collection of the National Museum/Federal University of Rio de Janeiro (MNRJ). Specimens were identified using the key provided by Gagné (1994). Adult specimens of *Hypothenemus* developing within withered fruits were collected, pinned, and identified. Voucher specimens were deposited in the Museu de Entomologia da FEIS/UNESP (MEFEIS), Ilha Solteira, São Paulo, Brazil.

Predation data

Fruit predation intensity on 108 individuals of *H. speciosa* (54 individuals in each region) was monitored monthly from September/2019 to August/2021. Those observations were performed on marked adult individuals in each study site (individual focal plants separated by approximately 10 m).

To obtain standardized estimates of fruit predation intensity, we adopted the phenological intensity method proposed by Fournier (1974), which has been widely applied in ecological studies to quantify visually perceptible processes in plant canopies. This semiquantitative method classifies intensity levels into discrete percentage-based categories, allowing for consistent comparisons across individuals and populations. In addition to its applicability to reproductive phenophases, this approach can be extended to estimate the intensity of other conspicuous biotic interactions, such as herbivory and foliar diseases caused by fungi, bacteria, and viruses (Fournier 1974; San Martín-Gajardo and Morellato 2003).

The predation intensity estimate is based on a semi-quantitative scale composed of five categories (0–4) at 25% intervals (Fournier 1974), determined by the following formula (San Martín-Gajardo and Morellato 2003):

$$\%Fournier = \frac{\sum Fournier}{4 \cdot N} \cdot 100$$

Where Σ is the sum of Fournier categories and N the number of monitored individuals in each region.

Fruits showing signs of predation were collected from all populations. After collection, they were opened, and any insect larvae and pupae were collected. The pupae were kept in screened containers to allow adult insect emergence; after 48 h, the adults were transferred to 70% alcohol for further taxonomic classification.

Environmental variables

Both study regions are located in tropical climate zones, characterized by warm temperatures throughout the year; as they are located at the same latitude, their photoperiods and global radiation levels are quite similar (For study areas coordinates and environmental details, see Supplementary Information Table 1). However, rainfall and relative humidity differ between the two regions, as the coastal zone is influenced by tropical rainforests with well-distributed rainfall (climate classification Af), while the Chapada Diamantina mountains are located in the semiarid continental interior where drought conditions often prevail (climate classification Aw), following Alvares et al. (2013).

Rainfall, relative humidity, solar radiation, and temperature data were obtained online from the National Institute of Meteorology (<https://portal.inmet.gov.br/dadoshistoricos>); station A401 (Salvador) for the Coastal region and station A425 (Lençóis) for the Chapada Diamantina region. Photoperiod was obtained from the Photoperiod Calculator site (<http://www.internetsv.info/PhotoPeriodC.html>). Environmental data are presented in Fig. 1.

Data analysis

Principal components analysis

Environmental variables across phytophysiognomies were summarized using the axis scores derived from a principal component analysis (PCA) based on the correlation matrix, implemented with the *FactoMineR* package (Husson et al. 2017). All environmental variables were standardized prior to analysis, and correlations between individual variables and PCA axis scores were examined. The first two PCA dimensions were retained to describe the main environmental gradients and their association with predation across phytophysiognomies.

Statistical analysis

Data normality and predation distribution were assessed using the Shapiro–Wilk test and visual inspection of Q–Q (quantile–quantile) plots (Supporting Information Fig. 1).

Fig. 1 Environmental conditions recorded in Chapada Diamantina and coastal populations during the study period



Because the data were not normally distributed, differences in predation between the two phytophysionomies were tested using the Mann–Whitney test (Crawley 2013). Data variability is illustrated using a violin distribution plot.

Generalized linear models

We used generalized linear models (GLMs) to test the effects of environmental variables on fruit predation in *H. speciosa* across phytophysionomies. Residual distributions were evaluated through visual inspection of Q–Q plots and the Shapiro–Wilk test to assess departures from normality. Because the response variable showed overdispersion and did not meet normality assumptions, models were fitted using a negative binomial error distribution (Crawley 2013). Temperature, precipitation, relative humidity, and photoperiod were included as continuous explanatory variables after assessing collinearity using Pearson correlation analysis ($r \geq 0.7$) (Supporting Information Fig. 2). All analyses were conducted in R version 4.0.2 (R Core Team 2020), and graphs were produced using the *ggplot2* package (Wickham 2015).

Results

Gall midge determination and predation patterns

The biological material collected in both regions confirmed that *A. hancorniae*, described by Maia et al. (2023), is responsible for immature fruit predation in *H. speciosa*.

Dry, wrinkled mangaba fruits are easily identified as they are clearly distinct from the shiny, reddish epicarp of healthy ripe fruits (Fig. 2a, b). Oviposition apparently occurs at very early stages of fruit development (likely occurring shortly after pollination) although it was not directly recorded. Fruit withering begins after adult emergence, while the fruit is still at an early developmental stage (approximately 1.5 cm in diameter). Predated fruits reach only one-third to one-half the size of mature healthy fruits. No seeds (damaged or intact) were found in predated fruits. Figure 2c illustrates the stages of fruit withering.

Larvae of *A. hancorniae* (Fig. 3a–b) were observed in stage 1 fruits (Fig. 2c), whereas pupae (Fig. 3c–d) occurred in stages 2 and 3. Pupal exuviae (Fig. 3e) were frequently observed adhered to the external surface of stage 3 fruits, indicating successful adult emergence (Fig. 3f). In addition, adult *Hypothenemus obscurus* (Fabricius) (Supporting



Fig. 2 Aspect of the fruits of *Hancornia speciosa* Gomes. **a** Healthy mature fruit; **b** Predated fruit; **c** Stages of fruit withering. Gray bars: 2 cm

Information Fig. 3) were recorded feeding on the dry mesocarps of fruits in stages 6–8 (Fig. 2c).

Fig. 3 *Asphondylia hancorniae* predation process on *Hancornia speciosa* immature fruits. **a**: Larva inside inner gall; **b**: Larva detail; **c**: Pupae details. **d**: Pupa inside inner gall **e**: Pupal exuvia. **f**: Adult. Gray bars: 5 mm

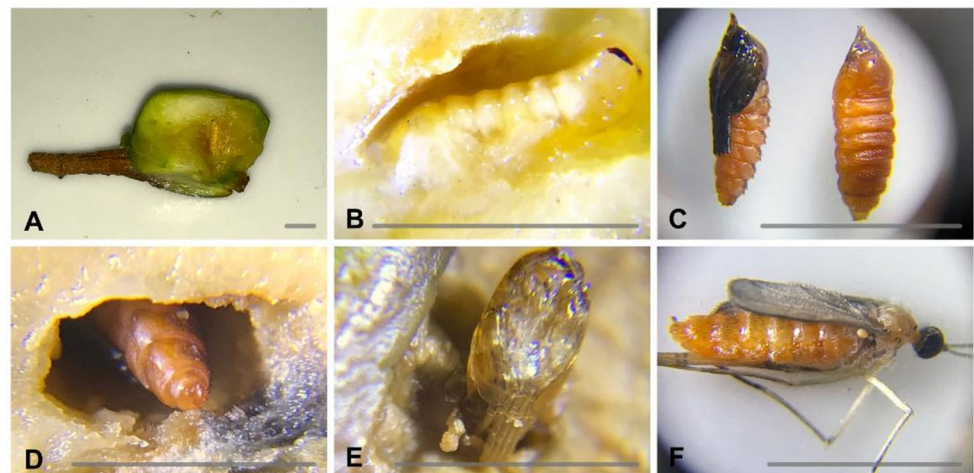
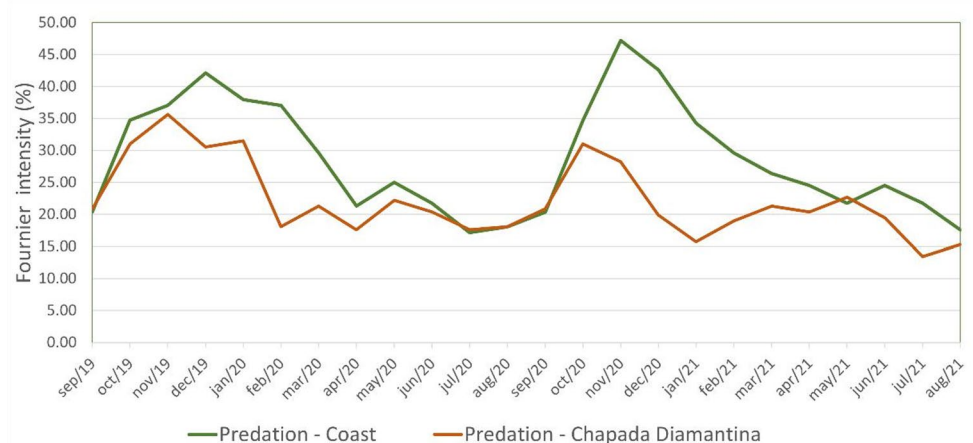


Fig. 4 Temporal fluctuation of fruit predation in both regions from September 2019 to August 2021



Predated fruits were observed on trees throughout the year, with primary peak intensities occurring between October and January—especially pronounced in late 2020 on the coast—and secondary peaks from March to July. Greater amplitude and longer duration of high-intensity periods were recorded in the coastal zone, where high predation levels extended for additional months compared to Chapada Diamantina. (Fig. 4). This temporal pattern is reflected in the overall predation rates, as fruit predation intensity consistently reached higher percentages in the coastal zone (42–47%) than in Chapada Diamantina (31–35%).

Environmental gradient analysis

The first two principal components explained 77.8% of the variation of climatic variables and predation along environments (Fig. 5). The first axis (PCA1) explained 56.6% of the data variation and was positively related to radiation ($R=0.93$, $p<0.05$), temperature ($R=0.72$, $p<0.05$) and photoperiod ($R=0.85$, $p<0.05$), and negatively related to relative humidity ($R=-0.76$, $p<0.0$). The second axis

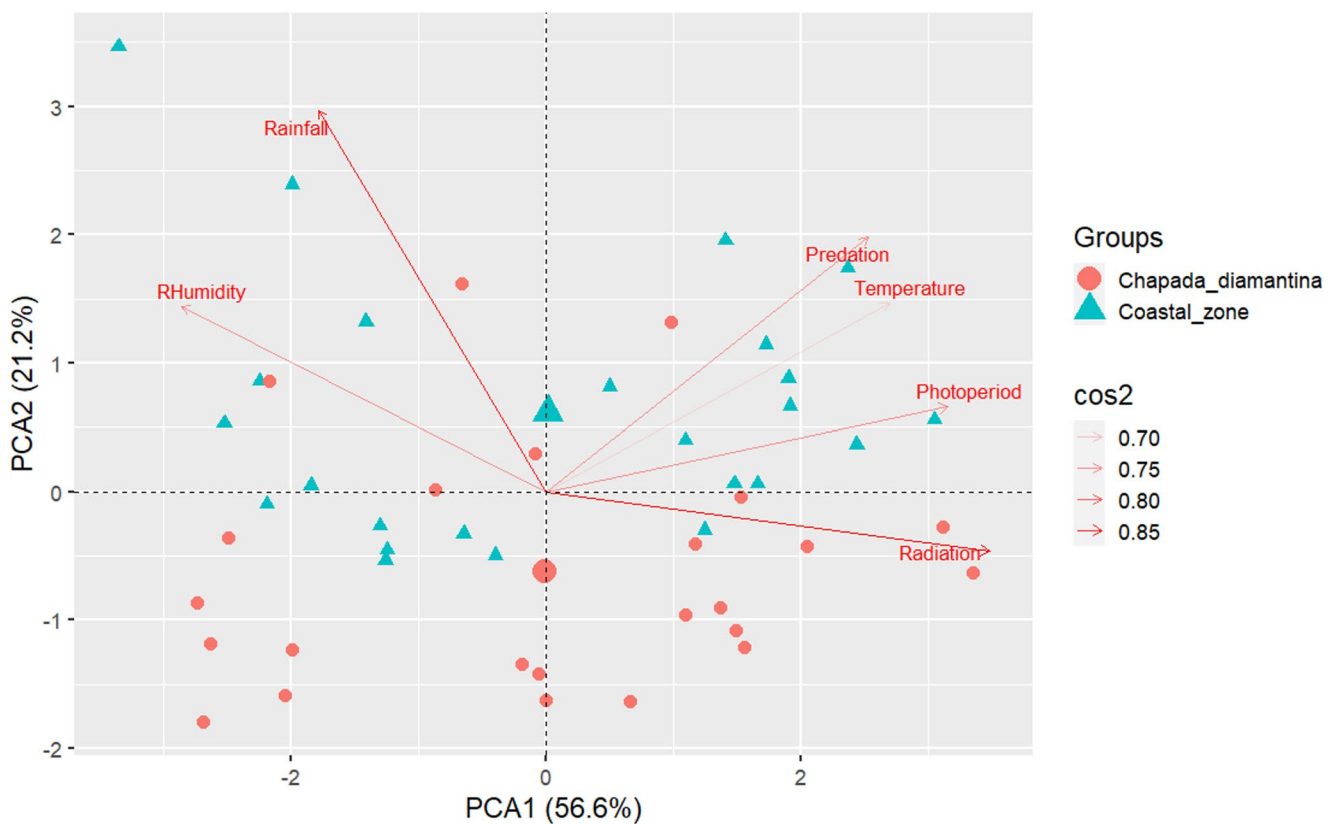


Fig. 5 Principal components analysis (PCA) for predation intensity distribution along phytophysiognomies. For analysis, temperature, relative humidity, photoperiod were included. Significance levels were

based on Pearson correlation coefficients between variables and principal components, and Cos2 means the relative contribution of the variables represented by the vectors

Table 1 Generalized Linear Models (GLM) explaining the relationships between predation (response variable as proportional data), climate (temperature, rainfall, relative humidity and radiation), photoperiod and Region context as predictors

Response variable	Model	Predictors	Estimate	t	p	AIC
Predation	Model 1	~Photoperiod+Temperature	0.081/0.062	4.409/2.966	<0.001	302.3
	Model 2	~Photoperiod	0.11	6.11	<0.001	308.6
	Model 3	~Temperature	0.1	4.89	<0.001	316.5
	Model 4	~Region context	0.26	3.14	<0.01	327.7

(PCA2) explained 21.2% of the data variation and was positively correlated with rainfall ($R=0.80$, $p<0.05$). Predation showed a high positive and significant correlation with both the PCA1 ($R=0.67$, $p<0.05$) and PCA2 ($R=0.53$, $p<0.05$) dimensions, and was associated with the highest values of temperature, radiation, and photoperiod. The positive correlations between predation and both PCA axes therefore suggest that fruit predation responds to the climatic gradient represented by the two phytophysiognomies.

Effects of environmental variables on predation

Generalized linear models with single predictors indicated that variation in fruit predation was primarily associated with temperature, photoperiod, and phytophysiognomic context. When multiple predictors were included, the

interaction between temperature and photoperiod remained the strongest explanatory component of predation dynamics (Table 1). Photoperiod (Fig. 6a; Est. = 0.10, $t=6.11$, $p<0.001$) and temperature (Fig. 6b; Est. = 0.10, $t=4.89$, $p<0.001$) both showed significant positive effects on predation intensity, and their interaction was also significant (Fig. 6c; Est. = 0.081 / 0.062, $t=4.409 / 2.966$, $p<0.001$). In addition, the regional context exerted a significant effect (Fig. 7; Est. = 0.25, $t=3.13$, $p<0.01$), with predation intensity consistently higher in coastal populations. Notably, the main climatic predictors identified in the models—temperature and photoperiod—showed little variation between the two study regions, suggesting that differences in predation intensity may also reflect local ecological or landscape factors.

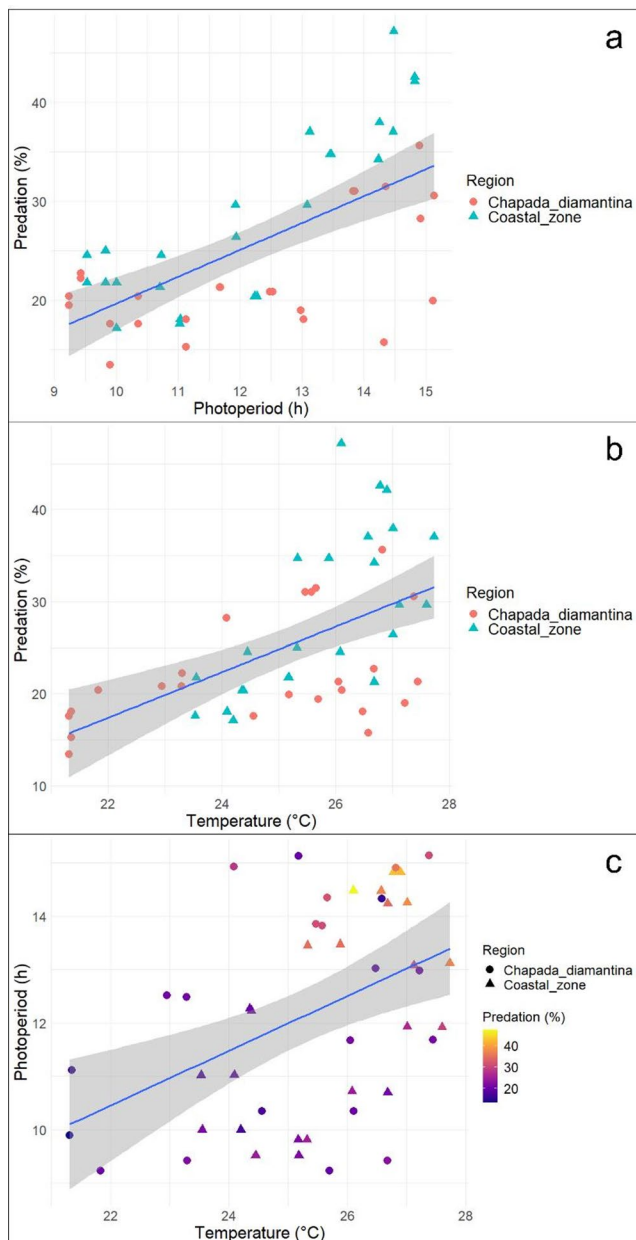


Fig. 6 Relationship between predation and photoperiod across phyto-physiognomies based on the main Generalized Linear Models. Solid lines represent the model-fitted values (predicted) and the shaded polygons the 95% confidence interval associated with the modeled predictions. **a:** Photoperiod. **b:** Temperature. **c:** Photoperiod+Temperature

Discussion

The significance of this study lies in identifying a major cause of fruit loss in *H. speciosa*, namely pre-dispersal predation by the recently described gall midge *A. hancorniae*, and in demonstrating how this process is modulated by environmental variables. This interaction reduces seed availability and may have important consequences for plant recruitment. Furthermore, damage caused by *A. hancorniae*

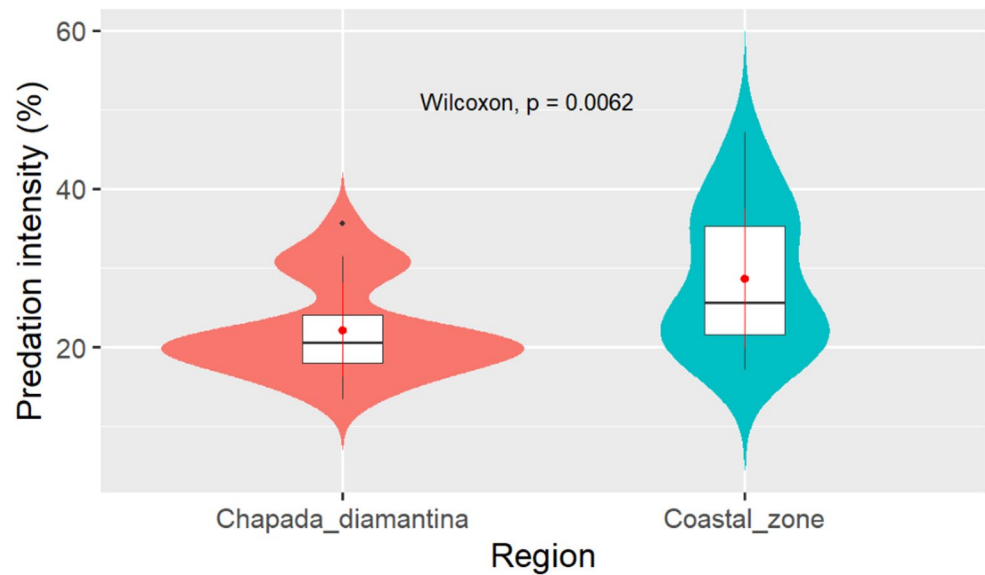
facilitates secondary colonization by dry plant matter–feeding insects such as *H. obscurus*. This observation indicates that fruit exploitation in *H. speciosa* involves multiple insect species acting at distinct developmental stages, revealing a temporally structured and potentially complex pattern of pre-dispersal predation. The sequential attack by *A. hancorniae* and *H. obscurus* represents a particularly noteworthy finding of this study, as this association between a Cecidomyiidae fly and a Scolytinae bark beetle appears to be previously unreported and highlights the potential for cascading biotic interactions affecting fruit fate.

Species of *Asphondylia* are known to maintain symbiotic associations with fungi that line the larval chamber, with larvae feeding primarily on mycelium rather than directly on plant tissues (Bernardo et al. 2021; Zymowska et al. 2020; Park et al. 2019). In *A. hancorniae*, the reduced gall develops centrally within immature fruits, occupying tissues that would otherwise form seeds (Maia et al. 2023). Following adult emergence, the fruit typically withers and desiccates. These structural changes may create conditions that facilitate subsequent colonization by *H. obscurus*, although the role of fungal activity in this process was not evaluated in the present study.

Although *H. obscurus* was recorded only in late-stage, desiccated fruits and therefore appears to act as a strictly secondary colonizer, the species is widely recognized as a tropical scolytine borer associated with several cultivated plants and stored products (Wood 1982; Greco and Wright 2012; Mitchell and Maddox 2010). Its occurrence in *H. speciosa* fruits suggests that predated or aborted fruits may serve as temporary breeding substrates or shelter sites for beetle populations in natural environments. Bark beetles commonly exploit stressed or decomposing plant tissues and can persist in non-crop hosts within surrounding vegetation, which may function as reservoirs in heterogeneous landscapes (Wood 1982; Hulcr and Stelinski 2017). In mosaic landscapes where native vegetation occurs near agricultural systems—particularly coffee plantations and other perennial crops—such substrates could contribute to local population persistence and potential links between natural and managed systems.

This predation pattern resembles that reported for *Asphondylia uvarum* on grapes (Gagné et al. 2018), suggesting functional similarities among congeneric species that exploit fleshy fruits during early developmental stages. In addition, *A. hancorniae* exhibits marked morphological differences from other *Asphondylia* taxa associated with Apocynaceae (Maia et al. 2023), reinforcing its taxonomic distinctiveness and apparent host specificity. Unlike most gall midges, which induce conspicuous and structurally elaborate galls, *A. hancorniae* relies on a highly reduced gall structure limited to a single larval chamber. Such a

Fig. 7 Comparisons of the predation intensity between phytophysiognomies based on Mann-Whitney test ($P < 0.05$). The mean value (red point) is presented for different phytophysiognomies, and the violin shape represents the distribution of predation data variability



strategy likely represents an efficient exploitation of reproductive tissues, minimizing additional structural modification of the host organ while maintaining conditions suitable for insect development.

While pollination can shape plant distribution patterns (Shahbazi et al. 2016), pre-dispersal predation may reduce seed output and potentially influence recruitment dynamics (Kolb et al. 2007a). The strong host specificity of *A. hancorniae* (Maia et al. 2023) suggests that fruit predation on *H. speciosa* could generate localized reductions in reproductive output, similar to patterns documented in other host–galler systems (Kolesik et al. 2010; Yamaguchi and Hayashida 2009). The levels of fruit predation recorded in this study—reaching approximately 31–47% depending on region—indicate that *A. hancorniae* can represent a substantial source of reproductive loss in *H. speciosa*. Because oviposition occurs during early fruit development, infested fruits fail to produce viable seeds, effectively converting a portion of reproductive investment into non-functional structures. Given the high levels of fruit predation recorded in coastal populations, the potential consequences for reproductive output and fruit availability deserve consideration.

The effects are broadly compatible with the density- and distance-dependent framework proposed by Janzen (1970) and Connell (1971), in which host-specific natural enemies contribute to diversity maintenance. Capitinga and coastal restinga are predominantly herbaceous–shrub vegetation types characterized by low tree-species richness and reduced arboreal density, with *H. speciosa* representing the most abundant tree species (Funch et al. 2021; Soares & Junior 2018). Under such conditions, sustained reductions in viable seed production could potentially influence recruitment patterns and local dominance. However, because seedling survival, host density effects, and post-dispersal dynamics

were not assessed, any inference regarding Janzen–Connell mechanisms remains tentative.

Seasonal environmental cues appear to regulate the temporal dynamics of fruit predation in both phytophysiognomies, as temperature and photoperiod emerged as the strongest predictors of predation intensity in our models. Notably, these same variables were previously identified as key drivers of fruiting expression in *H. speciosa* (Pereira et al. 2025). Temperature and photoperiod are major regulators of insect phenology, controlling development rates, diapause, and seasonal activity patterns. Gall-inducing insects, particularly Cecidomyiidae, are typically highly host-specific herbivores whose life cycles are tightly synchronized with host plant phenology (Yukawa and Rohfritsch 2005; Raman et al. 2005; Fernandes and Price 1992; Price et al. 1987). This specialization may account for the consistent association observed here between *A. hancorniae* and *H. speciosa*, as well as the seasonal synchronization between oviposition and early fruit development.

Predation pressure on *H. speciosa* was consistently higher in the coastal restinga than in the inland capitinga site. However, temperature and photoperiod showed little variation between the two regions, indicating that these factors alone cannot account for the higher predation levels observed in coastal populations. Rather than explaining spatial differences, these environmental variables likely act as broad seasonal regulators of insect activity. In this context, temperature and photoperiod may synchronize the timing of insect life cycles and predatory interactions, while local ecological conditions—such as habitat structure, resource availability, or community composition—may also influence the magnitude of predation across sites. This interpretation is consistent with the model selection results, which identified temperature and photoperiod as the strongest

predictors of temporal variation in predation intensity across both phytophysiognomies. More broadly, these findings suggest that climatic cues structure the seasonal dynamics of plant–insect interactions, whereas local ecological context may modulate their intensity across habitats.

Beyond temperature and photoperiod, other ecological factors may interact with seasonal cues to influence pre-dispersal predation dynamics. Host plant density, vegetation structure, elevation, and the availability of alternative hosts can affect resource concentration and predator performance in plant–insect systems (Kula et al. 2014; Von Euler et al. 2014; Kolb et al. 2007b). Interannual variation in seed production and extreme climatic events may further modulate these dynamics by altering flowering synchrony and fruit availability (Vanhellemont et al. 2014; Sánchez et al. 2012; Espelta et al. 2008). Although the capitinga and coastal restinga share broadly similar physiognomic structures, they differ in floristic composition, elevation, oceanic influence, and long-term precipitation variability. Such environmental distinctions likely affect species persistence and the strength of interspecific interactions, potentially contributing to the differences in predation intensity observed among *H. speciosa* populations. Taken together, these results emphasize that pre-dispersal predation is embedded within a complex network of climatic and ecological drivers operating across spatial and temporal scales.

Landscape context may also contribute to the observed differences in predation intensity. Restinga populations occur near anthropized and metropolitan areas, whereas capitinga populations lie within the buffer zone of the Chapada Diamantina National Park. Habitat fragmentation has been associated with altered plant–enemy interactions and increased herbivory rates (Queiroz et al. 2022; Mendes et al. 2015; Garcia & Chacoff 2007). Such differences in surrounding land use could therefore influence local insect dynamics and potentially contribute to the higher predation intensity observed in the coastal zone. However, disentangling landscape effects from climatic drivers would require dedicated landscape-scale analyses.

Reduced plant fecundity can have important consequences for fitness and long-term persistence (Sercu et al. 2020; Gripenberg 2018; Crawley 2000), particularly in species subject to extractive harvesting such as *H. speciosa*. Mangaba fruit collection by human populations constitutes an additional extrinsic driver, with still-uncertain effects on seed dispersal effectiveness and population dynamics. The species also has considerable economic relevance: annual yields exceed 2000 tons, with an estimated market value exceeding US\$1 million (IBGE 2023). Despite the development of local production chains, natural populations are increasingly threatened by habitat loss, particularly on private lands undergoing agricultural expansion and real estate

development (Fajardo et al. 2018; Silva Júnior et al. 2017; Costa et al. 2015). In this context, reductions in viable fruit production caused by pre-dispersal predation could potentially affect plant recruitment and the sustainability of extractive use.

Overall, this study demonstrates that pre-dispersal predation in *H. speciosa* is climate-sensitive, context-dependent, and embedded within broader ecological and anthropogenic gradients. By linking host-specific reproductive predation, environmental drivers, and landscape context, our findings contribute to understanding how insect–plant interactions influence fruit fate and potentially shape recruitment dynamics in heterogeneous tropical systems.

Conclusion

Our findings highlight the ecological significance of pre-dispersal fruit predation in *H. speciosa* mediated by the specialist gall midge *A. hancorniae*. By damaging up to 47% of immature fruits in Bahia, Brazil, this interaction prevents seed development and may constrain plant reproductive output and dispersal. Predation intensity was primarily modulated by temperature and photoperiod, indicating strong climatic control, while environmental context also played an important role, with consistently higher predation levels recorded in the coastal zone compared to Chapada Diamantina.

We also demonstrate that standardized and scalable approaches such as the Fournier Intensity Index can provide a practical framework for quantifying biotic interactions in natural populations. Applied to fruit predation in *H. speciosa*, this approach may support long-term ecological monitoring, facilitate cross-study comparisons, and improve the early detection of emerging threats to plant reproductive success.

Understanding the drivers and magnitude of pre-dispersal fruit predation in tropical fruit trees is therefore essential for anticipating how plant–insect interactions may respond to environmental change and for guiding conservation and management of native fruit resources.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11829-026-10241-w>.

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Author contributions VAMP and LSF contributed to the study's con-

ception and design. Material preparation, data collection and analysis were performed by VAMP and PMV. The first draft of the manuscript was written by VAMP and LSF and all authors commented on previous versions of the manuscript. Predator insects' identification were performed by CAHF and VCM. All authors read and approved the final manuscript.

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Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare no competing interests.

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