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ORIGINAL ARTICLE

Discreet but diverse and specific: Determining plant-herbivore interactions across a species-rich plant family in a tropical rain forest

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Abstract

Studying plant–herbivore interactions within tropical rain forests is fundamental to understanding their ecology and evolution. An important aspect of plant–herbivore dynamics is the role of temporal and taxonomic variables in determining associations between herbivores and their host. Using the diverse and chemically rich plant family Annonaceae (Magnoliales), we conducted a year-long study in Ecuador's Yasuní National Park in lowland Amazonia. We focused on nine understory tree species across a broad phylogenetic range within Annonaceae. For these species, we investigated patterns of herbivory, identified herbivores through DNA barcoding, and documented unique ant–butterfly associations. In general, leaf damage ranged from 0.09% to 25%, with significant temporal fluctuations for three species. Notably, *Anaxagorea brevipes* and *Unonopsis veneficiorum* faced higher herbivore pressure when compared to the other studied species. We document a discreet but diverse herbivore community, with 40 larvae from 12 Lepidoptera families collected throughout the year. Our findings identify, for the first time across a phylogenetically diverse sampling of Annonaceae, the specialization of herbivores on our focal species. Overall, our data provide valuable information on herbivory patterns at the local scale for this important rain forest plant family. Furthermore, these findings contribute to our understanding of the ecological processes that influence plant species diversity in tropical rain forests.

Abstract in Spanish is available with online material.

KEYWORDS
Annonaceae, ant-tending homopterans, *Crematogaster*, herbivory, host specificity, Yasuní

1 | INTRODUCTION

Tropical rain forests (TRF) are widely recognized as the most biodiverse terrestrial ecosystems on Earth, with over 40% of global plant diversity thought to occur within them (Eiserhardt et al., 2017). Recent estimates suggest that tropical forests may harbor up to 53,000 tree species (Slik et al., 2015), with the Amazon basin alone containing between 15,000 and 16,000 tree species (Antonelli et al., 2018; Ter Steege et al., 2020). Since Wallace 1878), the origins of TRF diversity have puzzled scientists, and many hypotheses have been proposed to explain it (Hill & Hill, 2001). One increasingly accepted hypothesis suggests that diversification in TRF is related to the interactions between plants and their insect herbivores (Cogni et al., 2022; Connell., 1971; Ehrlich & Raven, 1964; Janzen, 1970).

To date, most studies on plant–herbivore interactions in TRF have focused on single, generally species-rich genera of tropical plant families, including *Protium* (Burseraceae) (Fine et al., 2004), *Inga* (Fabaceae) (Endara et al., 2021; Forrister et al., 2023), *Piper* (Piperaceae) (Dyer et al., 2010), and *Psychotria* (Rubiaceae). Although these studies have provided fundamental insights into the evolution of plant diversity and community assembly in the Amazon (Fine et al., 2004; Forrister et al., 2023; Kursar et al., 2009), most of them are restricted to closely related species within a single genus. Few studies have looked into these interactions at broader taxonomic and phylogenetic scales across a plant family (Lamarre et al., 2012; Novotny et al., 2002). Thus, our understanding of plant–herbivore interactions across entire dominant tropical plant families and/or related genera remains limited.

With around 2500 species belonging to 108 genera, the pantropical plant family Annonaceae (Magnoliales; The Angiosperm Phylogeny Group et al., 2016) is a major component of TRF worldwide (Couvreur et al., 2011), and in particular of the Amazon region (Ter Steege et al., 2013). Indeed, Annonaceae is ranked as the sixth most diverse tree family of the Amazon flora (Ter Steege et al., 2013). In addition, based on molecular dating estimates, Annonaceae is estimated to have originated around 100 million years ago (Couvreur et al., 2011; Pirie & Doyle, 2012), that is, at the onset of modern TRF assemblages (Eiserhardt et al., 2017). Interestingly, Annonaceae species are known for their high chemical diversity, especially in secondary metabolites (Liaw et al., 2016; Menezes et al., 2021). This diversity suggests a potential important role of the evolutionary interplay between herbivores and the members of this family. For these reasons, Annonaceae could serve as a model family to unravel the impact of plant–herbivore evolution in rain forests at deeper temporal, taxonomic, and phylogenetic scales than previously undertaken.

Nevertheless, we still lack a basic understanding of how plant species interact with their insect herbivores in this family. To date, just a handful of studies have described herbivore diversity and leaf damage in Annonaceae, mainly in South America. Based on a literature review and personal observations on the diverse *Annona* genus (including *Rollinia*), Maas et al. (1992) noted that, in general, only a few herbivores were regularly found feeding on *Annona* species, with a tendency of showing high host specialization. Nascimento et al. (2011) studied herbivory in *Xylopia sericea* in the Mata Atlântica of Brazil (in planted *Eucalyptus* forest and a forest fringe), also detecting few herbivores feeding on its leaves. This study also noted leaf damage on several other Annonaceae at their site, finding greater leaf damage on gap-colonizing species compared to shade-tolerant ones (Coley, 1983; Kursar & Coley, 2003).

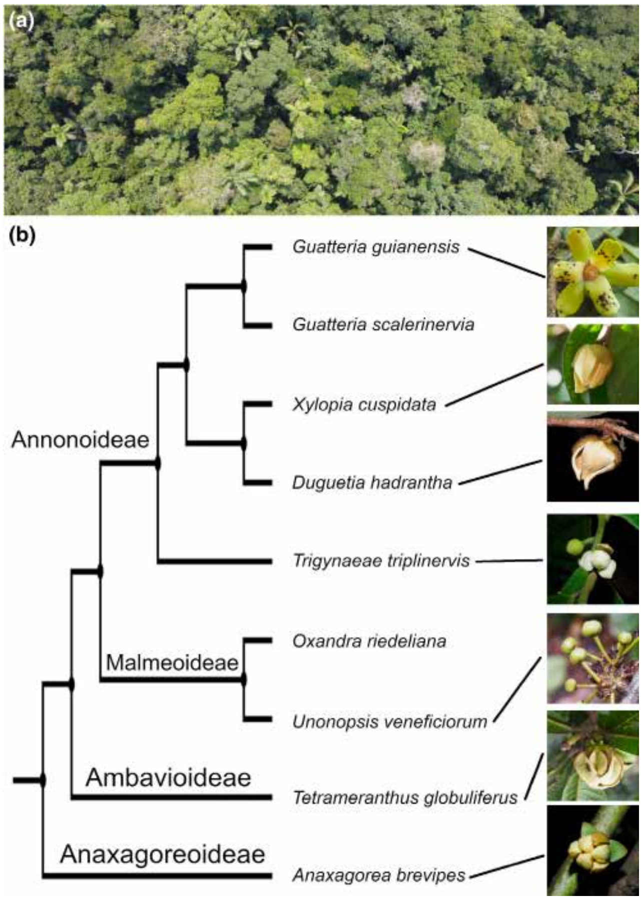

FIGURE 1 Study site and phylogenetic relationships between the focal species of Annonaceae. (a) Drone shot of the Yasuní 50 ha Dynamic Plot where our study was carried out. (b) Summary cladogram illustrating the phylogenetic relationships between the four Annonaceae subfamilies (following Chatrou et al., 2012) and flower photos of some of the species studied here (Photos Thomas L.P. Couvreur).

In this context, we undertook a year-long study of Annonaceae–insect interactions focusing on nine species within a 50-ha plot in the Yasuní National Park in the Ecuadorian Amazon. Yasuní is regarded as one of the most diverse TRF on Earth (Perez et al., 2014; Valencia et al., 2004) and is characterized by constant climatic conditions throughout the year; thus, it is considered an aseasonal forest (Garwood et al., 2023). Within this 50-ha *terra firme* forest plot, these nine species of Annonaceae cover all four recognized subfamilies (Figure 1), a relatively unique situation at this very local scale. Thus, the Yasuní plot provides a great opportunity to study herbivory across a phylogenetically diverse sample for a major tropical plant lineage.

In this study, the first of its kind to our knowledge, we examine the intraspecific patterns of herbivory and host association across sympatric species coexisting within a single site. Specifically, we ask: Are species across this phylogenetically diverse sample of Annonaceae impacted in the same way by herbivory? Is there a relationship between climate and leaf damage, that is, can we identify a season where leaf damage or herbivory presence increases and is this consistent across species? Are Annonaceae herbivores species-specific or are they shared (monophagous herbivores) across this assemblage?

2 | METHODOLOGY

2.1 | Study site

Our research was conducted within the 50-ha Yasuni Forest Dynamics Plot (YFDP) located next to the Yasuní Research Station of the Pontificia Universidad Católica del Ecuador (Valencia et al., 2004). The plot is located in the Yasuní National Park (YNP) which together with the Waorani Ethnic Reserve belongs to the UNESCO Man and the Biosphere Reserve (Bass et al., 2010) and is the largest protected area in Amazonian Ecuador (Perez et al., 2014). YNP is an evergreen lowland wet forest ranging in elevation from 200 to 300 m above sea level (Bass et al., 2010). It has a 15–30 m canopy with some emergent trees reaching 50 m (Perez et al., 2014). Rainfall and temperatures are aseasonal, with a mean annual rainfall of 2500–3200 mm, and no month averages <100 mm of rain; the mean annual temperature is 25–27°C (Garwood et al., 2023). In this plot, each tree with a diameter greater than 1 cm at breast height (DBH, measured at 1.3 m) was tagged, mapped, measured, and identified (Valencia et al., 2004).

2.2 | Studied species

Annonaceae comprises four subfamilies (Figure 1): Anaxagoreoideae, Ambavioideae, Annonoideae, and Malmeoideae (Chaowasku, 2020; Chatrou et al., 2012; Guo et al., 2017). Together, the subfamilies Annonoideae and Malmeoideae contain most (2386 out of ca. 2500) of the species diversity in the family (Couvreur et al., 2019).

We focused on understory species (i.e., species reaching maturity—flowering—in the understory) to allow ease of access to leaves and herbivores. We sampled between seven and thirteen individuals ≥5 cm DBH per species. Because we wanted to study herbivory and host association for herbivores across the whole family, our sampling strategy focused on nine species in the YFDP covering the phylogenetic breadth of Annonaceae, including species from all four subfamilies (Table 1, Figure 1). In addition, we selected two species within the same genus, two species within the same tribe but different genera, and finally two species from two different tribes within both major subfamilies (Annonoideae and Malmeoideae).

The species *Guatteria guianensis* was identified as *G. multivenia* in the Yasuní plot data. However, both names are now synonymized, and we follow this taxonomy here (Maas et al., 2015). Finally, one of the studied species, *Tetrameranthus globuliferus*, was absent from within the plot, but a small population was located on the Chorongo trail, a 2-km terra-firme forest path surrounding the plot and located at the north of the plot entrance. In order to facilitate an improved comprehension of the principal characteristics of the species included in this study, we have provided a detailed description of each in Table 2.

2.3 | Leaf herbivory estimation

Leaf herbivory was measured following Coley (1983). For each individual tree, five or six mature leaves (recently expanded) were randomly selected across all available branches. For each leaf, we visually estimated the percentage of tissue removal (i.e., potentially eaten by the herbivore) from the total surface of the leaf. Destructive sampling in the Yasuní 50 ha plot is highly restricted, and visual estimation is the only method we can use. A recent study showed that visual estimation of leaf damage can be

TABLE 1 Systematics (subfamily and tribe), abundance, and max DBH (diameter at breast height) of the nine focal species of Annonaceae in or near* the Yasuní forest dynamics plot.

Subfamily	Tribe	Genus	Species	Code	$N_{1–10}$	N_{10}	DBH_{max}	N_{sample}
Ambavioideae		*Tetrameranthus*	*globuliferus*[a] Westra	YTG	0	0	10	11
Anaxagoreoideae		*Anaxagorea*	*brevipes* Benth	YAB	42	0	67	11
Annonoideae	Duguetieae	*Duguetia*	*hadrantha* (Diels) R.E.Fr.	YDH	333	12	92	8
	Guatterieae	*Guatteria*	*guianensis* (Aubl.) R.E.Fr. (syn.: *G. multivenia* Diels)	YGM	193	10	97	12
		Guatteria	*scalarinervia* D.R. Simpson	YGS	328	23	112	11
	Bocageae	*Trigynaea*	*triplinervis* D.M. Johnson & N.A. Murray	YTT	149	1	76	7
	Xylopieae	*Xylopia*	*cuspidata* Diels	YXC	315	0	27	13
Malmeoideae	Malmeae	*Oxandra*	*riedeliana* R.E.Fr.	YOR	56	7	137	8
	Malmeae	*Unonopsis*	*veneficiorum* (Mart.) R.E.Fr.	YUV	1128	1	54	13

Abbreviations: Code, 3-letter species code; N_{10}, number of trees >10 cm DBH in the plot; DBH_{max}, 95 percentile of maximum adult stature (mm) of trees on the plot; N_{sample}, number of trees sampled in this study; $N_{1–10}$, number of trees 1–10 cm DBH in the 25 ha plot.

[a] Individuals of *Tetrameranthus globuliferus* were sampled outside the plot, less than 1 km away from the plot. DBH of *T. globuliferus* was taken from (Westra & Maas, 2012).

TABLE 2 The following section provides a detailed description of the nine species of Annonaceae that are the focus of this research project.

Species	Height	Indument in adult leaves	Flowers	Petals	Disposition	Leaf length (cm)	Monocarp shape	#Seeds
Anaxagorea brevipes (Benth)	Small understory tree (10 m)	Glabrous	Cauliflorous or brachyflorous	Yellow to cream	Alternate	8–27	Apocarpous, dehiscent clubbed shaped, stipitate	11
Xylopia cuspidata Diels	Understroy tree (6 m)	Simple	Cauliflorous or brachyflorous	Cream	Alternate	to 15	Apocarpous, indehiscent, lumpy and ridged, subsessile	4–5
Guatteria guianensis (Aubl.) R.E.Fr. (*Guatteria multivenia* Diels)	Understory to subcanopy tree (20 m)	Glabrous	Brachyflorous	Green to light yellow	Alternate	to 60	Apocarpous, indehiscent, ellipsoid to rounded, subsessile	1
Guatteria scalarinervia D.R. Simpson	Understory to subcanopy tree (25 m)	Glabrous	Cauliflorous	Green to yellow or cream	Alternate	to 25	Apocarpous, indehiscent, ellipsoid, spititate	1
Tetrameranthus globuliferus, Westra	Medium sized understory tree (10–15 m)	Stellate or star-shaped	Brachyflorous	Cream-yellow	Spiral	to 37	Apocarpous, indehiscent, globose, sessile	1–2
Oxandra riedeliana R.E.Fr.	Canopy tree (30 m)	Glabrous	Brachyflorous	White to yellow	Alternate	to 17	Apocarpous, indehiscent, rounded, stipitate	1
Trigynaea triplinervis D. M. Johnson & N. A. Murray	Understory tree (6–15 m)	Glabrous	Brachyflorous	Bright white	Alternate	to 25	Apocarpous, indehiscent, pear-shaped, subsessile	6–8
Unonopsis veneficiorum (Mart.) R.E.Fr.	Understory tree (7 m)	Glabrous	Cauliflorous or brachyflorous	Cream to white or yellow	Alternate	to 30	Apocarpous, indehiscent, globose, stipitate	1
Duguetia hadrantha (Diels) R.E.Fr.	Understory tree (15 m)	Scale-like	Brachyflorous	Cream white to light yellow	Alternate	to 24	Pseudosyncarpus, indehiscent, pyramidal, sessile	1

both accurate and precise when compared to digital estimations (Johnson et al., 2016).

Mean herbivory was estimated for each individual plant. Our sampling unit was, therefore, the individual tree. This process was repeated, observing all tagged individuals in April, September, and November 2021 and January, March, and May 2022.

2.4 | Climate data

To identify the driest and rainiest months at the study site, we extracted average monthly rainfall for the years 2000–2018 from the data collected by Garwood et al. (2023). On average, August and September have the least rain and April to July the most rain. The details of the average of all the months studied are in Table S1.

2.5 | Herbivores

Any larvae found feeding on the leaves (young and mature) were collected and preserved in 90% alcohol for further identification. Each collection received a unique code associated with its respective host plant. Species were identified using barcodes. We sequenced the short fragment of the mitochondrial cytochrome c oxidase (COI) subunit gene (Jin et al., 2018; Wilson et al., 2018).

We performed DNA extraction using two different protocols depending on the size of the specimens. For specimens measuring less than 0.5 cm, the modified 5% Chelex protocol (Lienhard & Schäffer, 2019) was employed. For larger samples, the CTAB reagent extraction protocol was used (Lavinia et al., 2017; Patzold et al., 2020).

Two sets of primers were used for PCR amplification. Universal primers for the Cytochrome c oxidase 1 gene, namely LCO1490 (5′-GGTCAACAAATCATAAAGATATTATTGG) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA), were adopted from Folmer et al. (1994). In addition, modified primers for lepidopteran species, LepF1 (5′-ATTCAACCAACCAATCATCATAAABATATTATTGG) and LepR1 (5′TAAACTTCTGGATGGATGTCCAAAAAAATCA), were used as suggested by Hebert et al. (2003).

The extraction and identification work were carried out at the Endara lab in Universidad de las Américas, and the morphospecies were sequenced by Macrogen, Inc. (Seoul, South Korea). We used the Geneious Prime bioinformatics software (Kearse et al., 2012) to edit and analyze the COI sequences.

All sequences were assigned to molecular operational taxonomic units (MOTUs) (Blaxter et al., 2005), considering the distance/similarity-based sequence clusters (Ryberg, 2015). For the assignment of MOTUs, divergence in COI sequences was estimated using the ASAP (Assemble Species by Automatic Partitioning) program (Puillandre et al., 2021), using the default parameters for clustering. Taxonomic identification of herbivores down to the family level was performed by BLASTing each consensus sequence on the NCBI BLAST website (Obando., 2022). Some of the results provided by NCBI ranged from order to species level; in all cases, choosing the closest match value to 98%.

2.6 | Ants

During monitoring, we recorded any ants patrolling the leaves. Ants were collected and preserved in 90% alcohol for identification (Table S2). Each collection received a code associated with its respective host plant. The specimens were identified by the specialist Adrián Troya and deposited in the Gustavo Orcés V. Natural History Museum of the Escuela Politécnica Nacional, Ecuador.

2.7 | Data analysis

We examined inter and intraspecific variation in standing herbivory over time by estimating leaf area lost from 5 to 6 leaves per tree per census, as described above. Because these data are not normal (i.e., they are continuous percentage data, bounded by 0 and 100), we analyzed the data using beta regression modeling, which is more appropriate than ANOVA and simple linear regression and better than applying a transformation such as arcsine, on rescaled ($0 > x < 1$) herbivory data (Douma & Weedon, 2019). We calculated a mixed-effects beta regression model of rescaled herbivory as a function of species, with census as a random effect. We also calculated simple beta regression models of herbivory as a function of species, as well as herbivory as a function of census for all species pooled and for each species separately. For the significant fixed effects in these models, we calculated all post-hoc pairwise comparisons of species or census intervals.

Finally, to examine and visualize interactions between Annonaceae and its herbivores, we constructed a network diagram, scoring each focal Annonaceae with the number and taxon of the herbivore.

We ran all analyses in the statistical software environment R 1.7.0 (R Core Team, 2022). We calculated the generalized mixed effects models using the package lme4 (Bates et al., 2015), beta regressions using the glmmTMB package (Brooks et al., 2017), and we tested pairwise comparisons using the package emmeans 1.8.6. (Lenth et al., 2023). We constructed the network diagram using the package bipartite (Dormann et al., 2008).

3 | RESULTS

3.1 | Herbivore damage in Annonaceae

Throughout the census period, we measured herbivore damage in over 3000 leaves across all species, with an average of 36 observations per species. We found that all species experienced some level of herbivore damage (Table 3). Our pairwise comparisons showed that *Anaxagorea brevipes* had statistically the highest herbivory on average (p value <.0001) followed by *Unonopsis veneficiorum* and *Trigynaea triplinervis* (Table 4). Significant intraspecific variation in herbivory between censuses was only detected for *Xylopia cuspidata* and *Trigynaea triplinervis* (Table 5, Figure 2).

Although herbivore damage patterns were broadly consistent across most species throughout the year (Table 4), three pairwise comparisons (Table 6) suggested a significant difference in herbivory between sampling months (April–September; April–November 2021; September 2021 and March 2022). None of these months is the wettest on average (September is often one of the driest).

3.2 | Diversity of herbivores

Throughout the 11-month census, over a thousand herbivore observations were carried out for all species. A total of 40 larvae were collected across all species over our study period. Using DNA barcoding together with morphological identification, we identified 32

TABLE 3 Average percentage of herbivory in Annonaceae species per month.

Species	Apr 21 (%)	Sep 21 (%)	Nov 21 (%)	Jan 22 (%)	Mar 22 (%)	May 22 (%)
Tetrameranthus globuliferus (YTG)	na	1.59	2.57	10.89	2.63	4.39
Unonopsis veneficiorum (YUV)	8.49	8.4	9.65	9.5	13.69	11.33
Anaxagorea brevipes (YAB)	21.17	10.30	14.36	23.30	19.68	24.56
Xylopia cuspidata (YXC)	10.13	3.46	3.94	3.64	7.50	2.32
Duguetia hadrantha (YDH)	7.15	0.13	5.48	4.32	7.17	1.25
Oxandra riedeliana (YOR)	9.27	0.5	5.81	6.04	0.61	4.35
Trigynaea triplinervis (YTT)	17.17	3.81	6.25	10.06	5.81	4.48
Guatteria scalarinervia (YGS)	3.71	0.09	1.82	3.71	4.55	1.55
Guatteria guianensis (YGM)	6.74	0.62	5.79	2.17	3.07	2.70

TABLE 4 Standing herbivory, with census as a random effect.

Species comparison	Estimate	SE	Df	Z ratio	*p* Value
YAB – YDH	1.36	0.18	Inf	7.75	**<.0001**
YAB – YGM	1.48	0.16	Inf	9.49	**<.0001**
YAB – YGS	1.62	0.16	Inf	10.05	**<.0001**
YAB – YOR	1.36	0.18	Inf	7.79	**<.0001**
YAB – YTG	1.46	0.17	Inf	8.58	**<.0001**
YAB – YTT	0.81	0.18	Inf	4.63	**.0001**
YAB – YUV	0.67	0.15	Inf	4.63	**.0001**
YAB – YXC	1.16	0.15	Inf	7.75	**<.0001**
YDH – YGM	0.13	0.18	Inf	0.7	.9988
YDH – YGS	0.26	0.19	Inf	1.42	.8916
YDH – YOR	0.01	0.20	Inf	0.04	1.0000
YDH – YTG	0.10	0.19	Inf	0.51	.9999
YDH – YTT	−0.55	0.20	Inf	−2.73	.1365
YDH – YUV	−0.68	0.18	Inf	−3.91	**.0030**
YDH – YXC	−0.19	0.18	Inf	−1.08	.9766
YGM – YGS	0.14	0.17	Inf	0.81	.9967
YGM – YOR	−0.12	0.18	Inf	−0.66	.9992
YGM – YTG	−0.03	0.18	Inf	−0.17	1.0000
YGM – YTT	−0.68	0.18	Inf	−3.67	**.0076**
YGM – YUV	−0.81	0.16	Inf	−5.2	**<.0001**
YGM – YXC	−0.32	0.16	Inf	−2.02	.5306
YGS – YOR	−0.26	0.19	Inf	−1.37	.9080
YGS – YTG	−0.16	0.18	Inf	−0.91	.9926
YGS – YTT	−0.81	0.19	Inf	−4.3	**.0006**
YGS – YUV	−0.95	0.16	Inf	−5.9	**<.0001**
YGS – YXC	−0.46	0.16	Inf	−2.79	.1184
YOR – YTG	0.09	0.19	Inf	0.47	.9999
YOR – YTT	−0.55	0.20	Inf	−2.77	.1249
YOR – YUV	−0.69	0.18	Inf	−3.94	**.0026**
YOR – YXC	−0.20	0.18	Inf	−1.13	.9706
YTG – YTT	−0.65	0.20	Inf	−3.32	**.0256**
YTG – YUV	−0.78	0.17	Inf	−4.58	**.0002**
YTG – YXC	−0.29	0.17	Inf	−1.69	.7502
YTT – YUV	−0.14	0.18	Inf	−0.77	.9975
YTT – YXC	0.35	0.18	Inf	1.98	.5573
YUV – YXC	0.49	0.15	Inf	3.26	**.0305**

Note: Values in bold correspond to values that have statistical significance.

See Table 1 for the codes of the species.

lepidopteran herbivores. Eight herbivores could not be analyzed because DNA extraction or sequencing failed, and morphological identification was impossible.

All larvae collected and identified belonged to the order Lepidoptera and were distributed in 12 families and 17 species (Table 7, Figure 3). The moth families Erebidae and Geometridae were the most diverse; the remaining families had two or one species only (Table 7). Although our sample size was small, we were able to detect a pattern in the interactions of herbivores with the different Annonaceae species in the plot. We found that most herbivores were present in the drier months, that is, March 2022, followed by September 2021, February, and April 2022 (Figure 4).

We found several species within the Erebidae family: *Gonodonta fulvangula* actively feeding on the leaves of *Trigynaea triplinervis*; *Cosmosoma orathidia* feeding on *Anaxagorea brevipes* (Table 7, Figure 3); and for the first time, the moth *Viviennea* sp. on *Guatteria scalarinervia*. We also discovered *Cocytius* sp. larvae from the Sphingidae family, known to feed on Annonaceae genera such as *Annona* and *Rollinia* (Peña & Bennett, 1995) feeding on *Xylopia cuspidata* in this study.

Furthermore, we identified individuals from the microlepidoptera genera *Choristoneura* and *Clepsis* (Tortricidae) feeding on certain genera of Annonaceae, known for a broader affiliation with Annonaceae and other plant families (Gilligan & Brown, 2018). Gelechiidae moth species were also found feeding on *Duguetia hadrantha* and *Xylopia cuspidata*.

Depressariidae larvae, belonging to the superfamily Gelechioidea, were observed feeding on *Oxandra riedeliana* and *Tetrameranthus globuliferus*. Additionally, we noticed interactions with families such as Saturniidae, Geometridae, Urodidae, Crambidae, and Noctuidae, with some species of the Annonaceae family.

We also described an interaction between the larvae of the butterfly genus *Nymphidium* sp. (Riodinidae; tribe Nymphidiini) and ants living on two Annonaceae species, *Unonopsis veneficiorum* (429 observations) and *Oxandra riedeliana* (one observation). Although the sample size was small, we observed a consistent association between these larvae and ants belonging to the genus *Crematogaster*. During the monitoring period, we observed that the larvae of the family in question approached the part of the caterpillar's head where there was a specialized apparatus for feeding the ants with a sugary substance. The ants, meanwhile, remained in the vicinity of the larvae, which prevented other insects and predators from approaching.

The network of interactions between the herbivores (lepidopteran larvae) and the nine focal Annonaceae species resulted in a total of 21 interactions (Figure 5).

TABLE 5 The two focal species that showed significant differences in herbivory between censuses.

Species	Comparison	SE	Df	Z ratio	*p* Value
Xylopia cuspidata	Apr 21 – Nov 21	0.359	Inf	3.041	.0285
Trigynaea triplinervis	Apr 21 – Jan 22	0.429	Inf	3.127	.0218
	Apr 21 – Nov 21	0.444	Inf	3.656	.0035
	Apr 21 – Sep 21	0.459	Inf	4.284	.0003

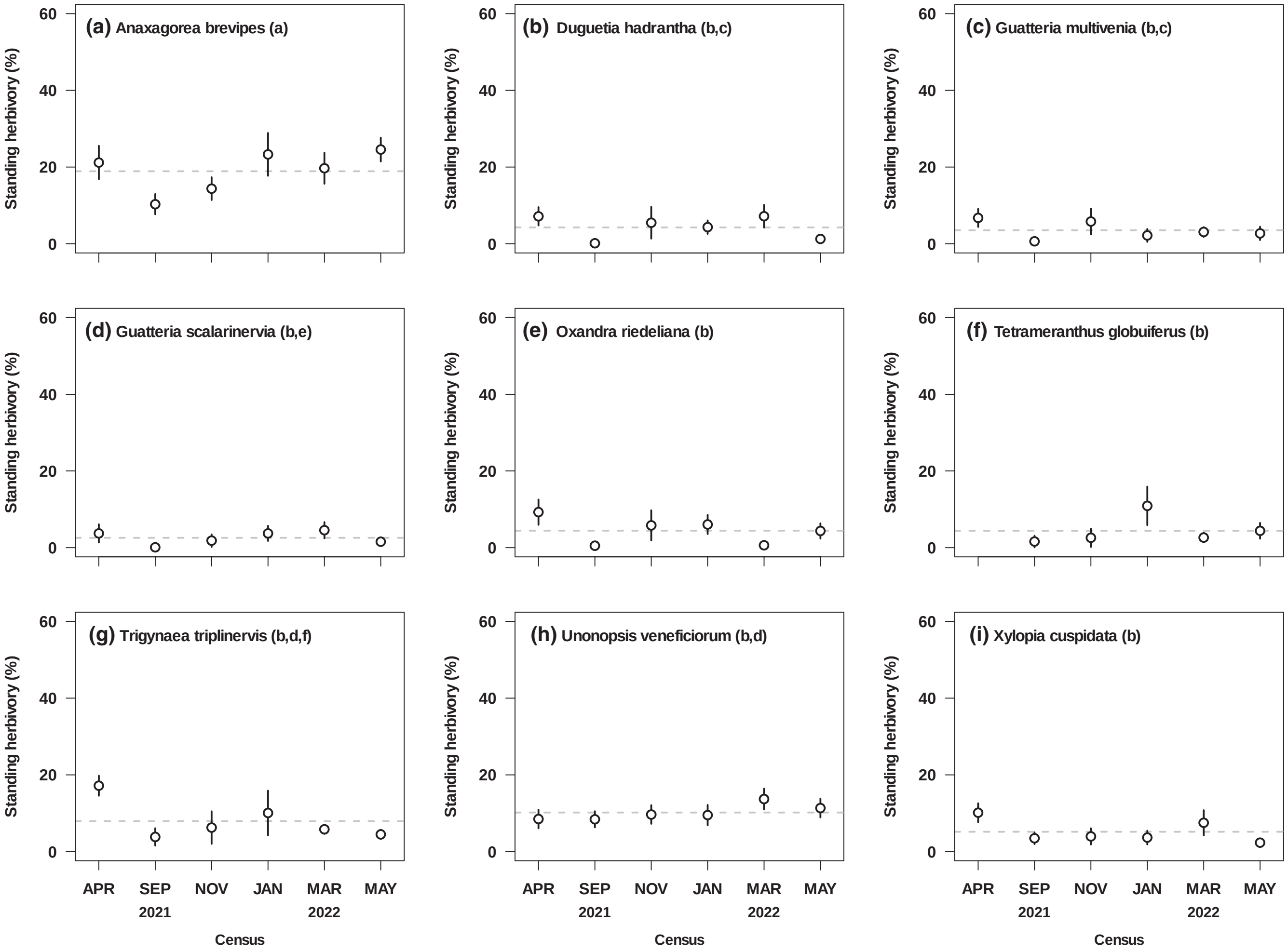

FIGURE 2 Variation in leaf herbivory damage among nine species of Annoncaceae within the Yasuni lowland rain forest dynamics plot over 1 year (2021–2022). Seven to 13 trees were sampled each month per species. Gray circles indicate samples from individual trees; black points with white fill indicate means for that census and species; error bars indicate 1 SE; a horizontal dashed line indicates overall species-mean herbivory; different letters in parentheses after the species name indicate significant differences between overall species-means (Table 6).

3.3 | Interactions of ants with Annonaceae

Interestingly, ants were only observed on two species in our study site: *Unonopsis veneficiorum* and *Oxandra riedeliana*. In this study, six different ant taxa were collected belonging to several different ant genera. One species of ants were documented per individual. These were identified as *Crematogaster* cf. *tenuicola*, *Pheidole* sp. ecu2121, *Camponotus* sp. ecu2144, *Megalomyrmex foreli*, *Cephalotes opacus*, and *Dolichoderus inpai* and *D. decollatus* (Figure 6). On *Oxandra riedeliana*, we recorded only one *Crematogaster* cf. *tenuicola* (Figure 6).

4 | DISCUSSION

To our knowledge, this is the first study to describe local inter- and intraspecific patterns of herbivory and associated insects (herbivores) across a phylogenetically diverse assemblage of co-existing Annonaceae species (Figure 1; Table 1). The range of standing herbivory observed in this study (Table 3) is similar to that reported for other tropical rain forest species (0.09%–30%) (Cárdenas et al., 2014; Coley & Barone, 1996; Mendes et al., 2021; Nascimento et al., 2019; Varanda et al., 2008). Interestingly, low percentages of leaf herbivory (average of 5.2%) were also reported across a large array of vascular plants (Turcotte et al., 2014). Likewise, the average of herbivory for 31 Magnoliid species reported by Turcotte et al. (2014) is consistent with our findings.

4.1 | Variation in herbivory in co-existing Annonaceae across ecological and evolutionary time

Our results show that for co-existing Annonaceae, herbivore damage varied across species. *Anaxagorea brevipes*, which belongs to the sister genus to the rest of the family (Chatrou et al., 2012; Couvreur et al., 2019), bore significantly higher leaf damage when compared to

TABLE 6 Monthly herbivory pairwise comparisons.

Comparison	SE	Df	Z ratio	*p* Value
Apr 21 – Sep 21	0.148	Inf	4.435	**.0001**
Apr 21 – Nov 21	0.147	Inf	3.099	**.0238**
Apr 21 – Jan 22	0.146	Inf	2.092	.2913
Apr 21 – Mar 22	0.146	Inf	1.078	.8902
Apr 21 – May 22	0.146	Inf	1.909	.3962
Sep 21 – Nov 21	0.145	Inf	−1.380	.7389
Sep 21 – Jan 22	0.145	Inf	−2.420	.1492
Sep 21 – Mar 22	0.144	Inf	−3.465	**.0070**
Sep 21 – May 22	0.144	Inf	−2.608	.0952
Nov 21 – Jan 22	0.144	Inf	−1.040	.9044
Nov 21 – Mar 22	0.143	Inf	−2.086	.2945
Nov 21 – May 22	0.144	Inf	−1.229	.8229
Jan 22 – Mar 22	0.143	Inf	−1.046	.9021
Jan 22 – May 22	0.143	Inf	−0.189	1.0
Mar 22 – May 22	0.142	Inf	0.858	.9563

Note: Values in bold correspond to values that have statistical significance.

the other Annonaceae species studied in the plot (Table 3; Figure 2). Classical theory of plant–herbivore coevolution suggests that in response to the pressure exerted by herbivores, plants present a pattern of cumulative defense evolution over evolutionary time (Agrawal & Fishbein, 2008; Becerra et al., 2009; Ehrlich & Raven, 1964). Thus, herbivory attack would be expected to be reduced during the diversification process of a lineage. Our results agree with this expectation, since this early diverging Annonaceae lineage exhibited higher herbivory attach than extant lineages co-existing in our study site. Similarly, *Unonopsis veneficiorum* and *Trigynaea triplinervis* exhibited higher herbivory, suggesting potential vulnerability compared with other species.

Temporal patterns of plant and animal activity, such as herbivory, are hypothesized to be driven by seasonal climatic variation. However, such temporal patterns are less well understood in equatorial forests, where climatic conditions remain nearly constant throughout the year. In our study site, we found little variation in average herbivory across the year. This contrasts with previous studies in other tropical areas where changes in herbivory levels across the plant community have been observed throughout the year. For instance, Coley and Barone (1996) working in Panama found lower herbivory in dry periods compared to rainy periods, mainly due to lower herbivore abundance in the dry season. We hypothesized that the observed lack of intra-annual variation in herbivory might be due to the fact that the Yasuni forest is much less seasonal than many tropical forests (Cárdenas et al., 2014; Garwood et al., 2023). There is no pronounced regular dry season with an expected <100 mm rainfall per month. Even though there are significant annual cycles of rainfall and irradiance (Garwood et al., 2023), this variation may not be as pronounced as to affect the presence or abundance of herbivores over the year. An alternative explanation is that we monitored expanded mature leaves for leaf damage, which are known for being less preferred by herbivores than young expanding leaves (Coley & Barone, 1996; Endara et al., 2017; Nascimento et al., 2019). Interestingly, although most herbivory damage occurs on young leaves, it is also present on mature leaves, stems, and even flowers.

4.2 | Herbivore community associated with co-existing Annonaceae species

In terms of the insect herbivores associated with Annonaceae, we found a community of mostly specialized Lepidoptera larvae (Table 7, Figure 3). Even though we were looking for all insect herbivores associated with Annonaceae, we only found larvae of Lepidoptera on the leaves. Overall, these results are congruent with previous observations in Annonaceae, suggesting a discreet but diverse herbivore community (Maas et al., 1992). Few Lepidoptera species, however, were shared among Annonaceae despite the local scale of our study (Figure 5). For example, no herbivores were shared between the two closely related species of the genus *Guatteria* sampled in our study (Figure 3). While some studies have suggested low host specificity in TRFs in general (Godfray et al., 1999; Novotny et al., 2002), our study emphasizes the significance of considering the chosen plant family host and its implications for understanding the diet breadth of herbivores. In this context, our study supports the idea that, in the tropics, there are more specialized insects and a thin tail of generalist insects (Dyer et al., 2007; Forister et al., 2015). However, our sample size remains low, and our observations should be confirmed over longer time scales.

Our observation records of Annonaceae–herbivore associations agree with studies in other tropical forests. For example, we found *Gonodonta fulvangula* (Erebidae) actively feeding on leaves of *Trigynaea triplinervis*. This herbivore–plant interaction was also found in Brazil, where larvae of *Gonodonta* sp. were feeding on *Annona squamosa* L. (Braga Sobrinho, 2014) and *Gonodonta fulvangula* on *Annona muricata* L, defoliating these trees. We also documented the species *Cosmosoma orathidia* (Erebidae) feeding on *Anaxagorea brevipes*. Interestingly, this same species was reported in Costa Rica feeding on *Anaxagorea crassipetala* Hemsl. (Carmona, 2020). On the other hand, *Cocytius* sp., from the Sphingidae family, known to feed on Annonaceae genera like *Annona*, including ex-*Rollinia* (Peña & Bennett, 1995), was also found on *Xylopia cuspidata* in this study. This finding aligns with the observations of Maas et al. (1992) and suggests chemical similarities across these genera. However, the Sphingidae family's polyphagous nature across Solanaceae, Euphorbiaceae, Caricaceae, and Annonaceae (Bustos, 2008) indicates potential specialization within herbivore genera for certain host plants. We also found other interactions with families of moths such as Saturniidae, Geometridae, Urodidae, Crambidae, and Noctuidae, which are considered polyphagous herbivores feeding on a wide variety of families (Bodner et al., 2010; Heppner, 2005; Kitching & Kitching, 1984; Léger et al., 2021; Sohn, 2013).

TABLE 7 Species of Lepidoptera found on leaves of the nine studied species of Annonaceae during regular surveys in 2020–2021.

Subfamily	Tribe	Genus	Species	Moths families	Butterflies families
Ambavioideae		*Tetrameranthus*	*globuliferus*[a]	Depresariidae (*Antaeotricha* sp2.) **14** Urodidae (unknown genus)**18** Geometridae (*Perigramma* sp.) Taxonomic id.	
Anaxagoreoideae		*Anaxagorea*	*brevipes*	Erebidae (*Cosmosoma orathidia*) **11**	
Annonoideae	Duguetieae	*Duguetia*	*hadrantha*	Gelechiidae (Taxonomic id) Tortricidae (*Choristoneura* sp.) **8** Tortricidae (*Choristoneura* sp1.) **9**	
	Guatterieae	*Guatteria*	*guianensis*	Geometridae (*Physocleora* sp.) **12** Geometridae (*Physocleora* sp.) **15** Tortricidae (*Clepsis persicana*) **19**	Hesperiidae (*Quadrus* sp.) **21**
		Guatteria	*scalarinervia*	Erebidae (*Viviennea* sp.) **4** Erebidae (unknown genus) **10**	
	Bocageae	*Trigynaea*	*triplinervis*	Erebidae (*Gonodonta fulvangula*) **3** Noctuidae (*Eriopinae* sp.) **7** Noctuidae (unknown genus) **5** Geometridae (*Epimecis* sp.) **9** Geometridae (unknown genus) **16** Braconidae (*Glyptapanteles*) **6**	
	Xylopieae	*Xylopia*	*cuspidata*	Gelechiidae (*Dichomeris acuminatus*) **2** Geometridae (*Semiothisa pallidata*) **2** Saturniidae (Taxonomic id.) Sphingidae (*Cocytius* sp.) **17** Crambidae (*Piletocera chlorura*) Taxonomic id.	Hesperiidae (*Pythonides pteras*) **1**
Malmeoideae	Malmeae	*Oxandra*	*riedeliana*	Depresariidae (*Antaeotricha* sp1.) **13**	Riodinidae (*Nymphidium* sp.) **20**
	Malmeae	*Unonopsis*	*veneficiorum*	Tortricidae (*Choristoneura* sp.) Taxonomic id.	Riodinidae (*Nymphidium* sp.) Taxonomic id.

Note: Numbers in bold after each insect taxa correspond to the numbers of molecular operational taxonomic units (MOTUs). Taxonomic ID: Not sequenced, but identified based on morphology.

Overall, our findings underline the importance of studying herbivore diversity and their host-plant relationships, as these interactions provide valuable insights into the intricate ecological networks in natural ecosystems. Some families of butterflies and moths have a high degree of specialization in their host plants (Janz et al., 2001). For example, the caterpillars of the butterfly tribe Leptocircini feed exclusively on the leaves of the genus *Annona* and potentially Annonaceae in general (Allio et al., 2020). This specialization could be attributed to the diversity of secondary metabolites produced by Annonaceae species (Menezes et al., 2021) providing rich chemical cues for herbivores to detect and adapt to.

4.3 | Interactions between herbivores, ants and Annonaceae

Interactions with ants are considered one of the most effective defenses for plants, with >100 plant families reported to have evolved structures to recruit ants (Weber & Agrawal, 2014). Notably, among all the nine species of Annonaceae studied in the plot, only two species showed association with ants. *Unonopsis veneficiorum* and *Oxandra riedeliana* were found to be visited by a total of six ant genera (see Section 3; Figure 6), with most genera associated with the former host species. All these ant taxa are known to harvest plant exudates (Davidson et al., 2003). Ants might choose their trophobiotic partners based on different factors, including dietary requirements, behavioral patterns, or host tree characteristics. The diversity of ants observed on *U. veneficiorum* might be related to the presence of secretory cells. Indeed, the leaves of 30% of species in *Unonopsis* are reported to have secretory cells (Maas et al., 2007). However, to date, it remains unclear if *Unonopsis veneficiorum* has such structures. In any case, we observed a high percentage of leaf damage in *Unonopsis veneficiorum* (Table 3) in relation to the other studied Annonaceae species, suggesting that ants are not providing the protection observed in species that have interactions with ants (Kursar et al., 2009; Pereira et al., 2020; Souza et al., 2024).

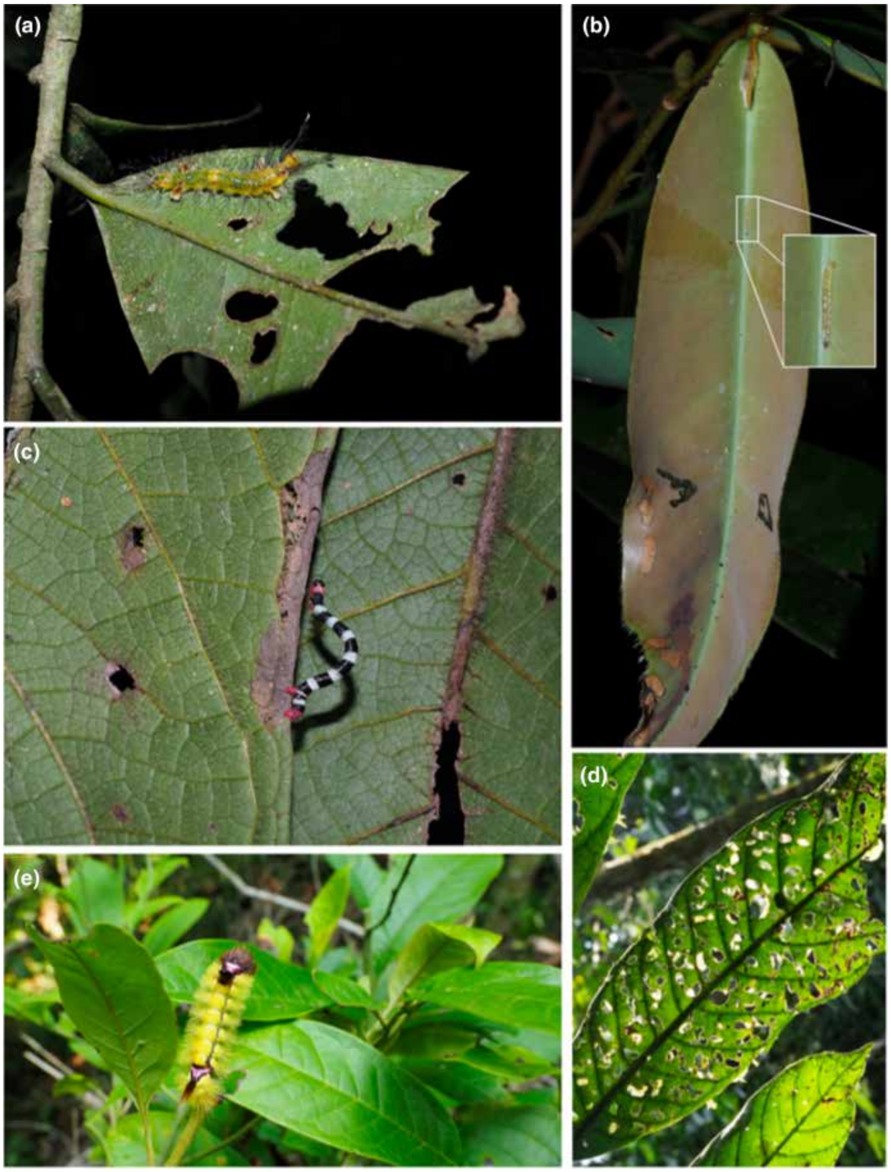

FIGURE 3 Photos of four herbivores found on Annonaceae plants. (a) *Cosmosoma orathidia* on *Anaxagorea brevipes*; (b) *Dichomeris acuminatus* on *Xylopia cuspidata*; (c) *Perigramma* sp. on *Tetrameranthus globuliferus*; (d) Example of leaf herbivory in *Unonopsis veneficiorum* probably caused by beetles; (e) *Viviennea* sp. on *Guatteria scalarinervia*. Photo credit: Thomas L.P. Couvreur.

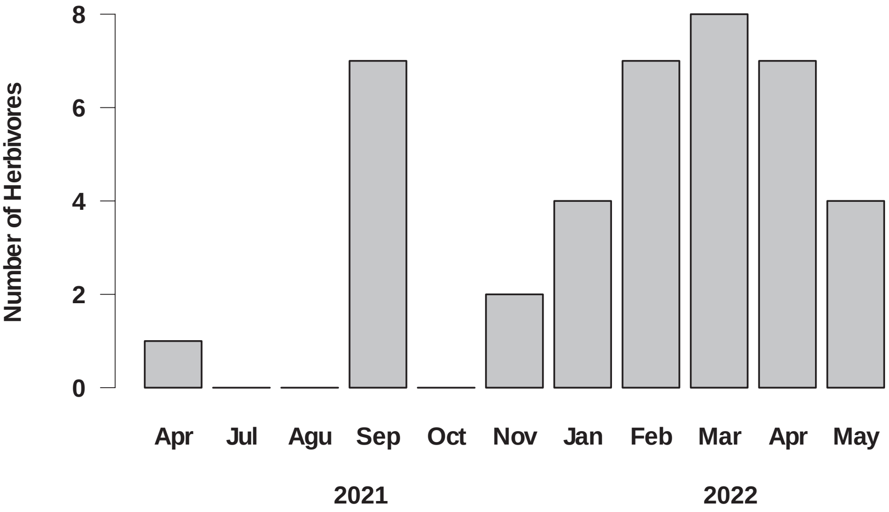

FIGURE 4 The total number of herbivores collected each month for all nine species of Annonaceae within the Yasuní lowland rain forest 50 ha dynamics plot over a period of 1 year (2021–2022). For each species, 7–13 individuals were sampled each month.

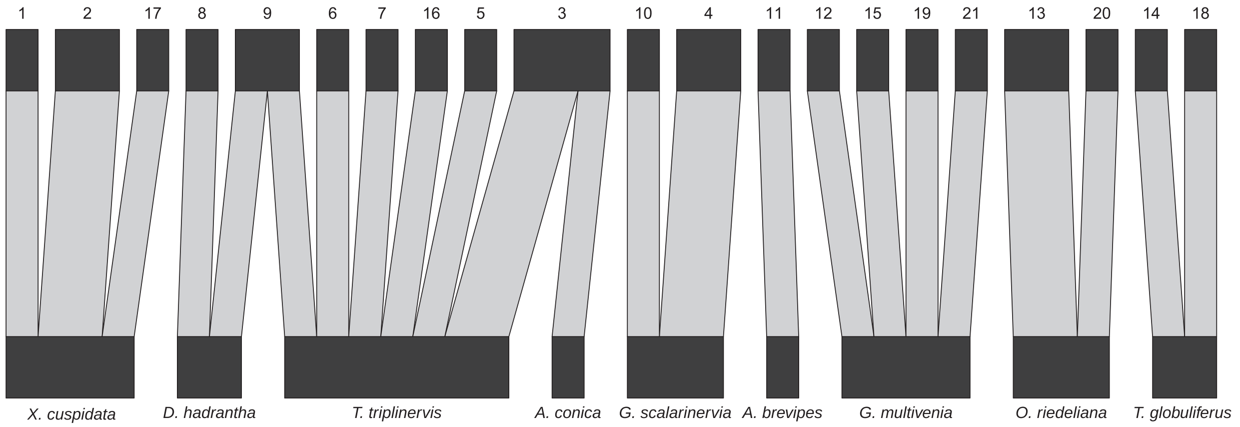

FIGURE 5 Interaction network of the nine Annonaceae species (bottom) and their associated insect herbivores (top). The thickness of the lines represents the abundance of herbivores feeding on each species of the Annonaceae family. The numbers on the top are the numbers of the MOTUs (see Table 5 for correspondence). *Guatteria multivenia* is a synonym of *G.guianensis*. 1: Hesperiidae (*Pythonides pteras*) 2: Gelechiidae (*Dichomeris acuminatus*); 2: Geometridae (*Semiothisa pallidata*); 3: Erebidae (*Gonodonta fulvangula*); 4: Erebidae (*Viviennea* sp.); 5: Noctuidae (unknown genus); 6: Braconidae (*Glyptapanteles*); 7: Noctuidae (*Eriopinae* sp.); 8: Tortricidae (*Choristoneura* sp.); 9: Tortricidae (*Choristoneura* sp1.); 9: Geometridae (*Epimecis* sp.); 10: Erebidae (unknown genus); 11: Erebidae (*Cosmosoma orathidia*); 12: Geometridae (*Physocleora* sp.); 13: Depresariidae (*Antaeotricha* sp1.); 14: Depresariidae (*Antaeotricha* sp2.); 15: Geometridae (*Physocleora* sp.); 16: Geometridae (unknown genus); 17: Sphingidae (*Cocytius* sp.); 18: Urodidae (unknown genus); 19: Tortricidae (*Clepsis persicana*); 20: Riodinidae (*Nymphidium* sp.); 21: Hesperiidae (*Quadrus* sp.).

Alternatively, the presence of ants could be related to the lepidopteran herbivore found feeding on both *Unonopsis veneficiorum* and *Oxandra riedeliana*.

We report the first observation of a potential mutualism between *Nymphidium* sp. butterfly larvae (Riodinidae; Nymphidiini), being tended by *Crematogaster* ants on *Unonopsis veneficiorum* (multiple observations) and *Oxandra riedeliana* (one observation). This association aligns with the documented myrmecophily of *Hallonympha paucipunta* (Riodinidae) in the Brazilian cerrado on ten different host plants (families) (Kaminski, 2008), suggesting a broader potential for ant–butterfly interactions within the Nymphidiini tribe.

The riodinids were tended by ants despite being in their third and subsequent instars. Although ants typically surround these caterpillars, there is a shift in the caterpillars' feeding behavior as they mature. The timing of the caterpillars' feeding on the extrafloral nectaries is coordinated with their transition to feeding on the leaves (Devries & Baker, 1989). The younger instars are often found near the nectaries, while adult caterpillars feed only at night (Devries & Baker, 1989). In our study, neither *Unonopsis* nor *Oxandra* exhibited extrafloral nectaries, which presents an opportunity for further investigation into this relationship (Pierce & Dankowicz, 2022).

Finally, we also observed ant-tended homopterans occurring on *Unonopsis veneficiorum*. Such ant–homoptera associations have been reported (Blüthgen et al., 2000) in several canopy Annonaceae species (*Guatteria schomburgkiana* Mart. and four species of *Xylopia*) from the lowland TRF of Venezuela (Orinoco region, state of Amazonas). Furthermore, Blüthgen et al. (2004) mentioned specialized associations between ants and specific host plants, such as the case of *Dolichoderus bispinosus* and *Gerridius scutellatus* on plants of *Xylopia*. In our study, we did not observe ant-tended homopterans on *Xylopia cuspidata* or the two *Guatteria* species. To date, the interactions between ants and Annonaceae remain little explored, and more observations in the field will be needed to confirm their role.

5 | CONCLUSION

Our research in the highly diverse lowland rain forests of the Yasuní National Park provides new insights into plant–herbivore interactions within the chemically diverse Annonaceae plant family. We show, for the first time in the family and across a broad phylogenetic sampling of species, that despite co-occurring locally and being exposed to the same community of herbivores, all nine species appear to have a few but species-specific community of herbivores, even between closely related species. Herbivory was similar to that documented in other tropical plants and showed little variation across the year, as expected given the lack of seasonality for these forests. Finally, we also uncovered unique ecological associations for ants and Annonaceae.

These findings provide the first steps towards documenting the intricate relationship between Annonaceae and their herbivores across the family and to untangle the evolutionary dynamics that could help explain the diversity of this family from local to more regional scales. In addition, our results will participate in ongoing conservation efforts in Yasuní as they reveal the factors that influence patterns of herbivory, such as temporal fluctuations and insect specialization on specific Annonaceae species. This information is vital for developing targeted conservation strategies that address the specific threats faced by these plants. Ultimately, our research contributes to the broader goal of preserving the rich biodiversity of the Yasuní rain forest.

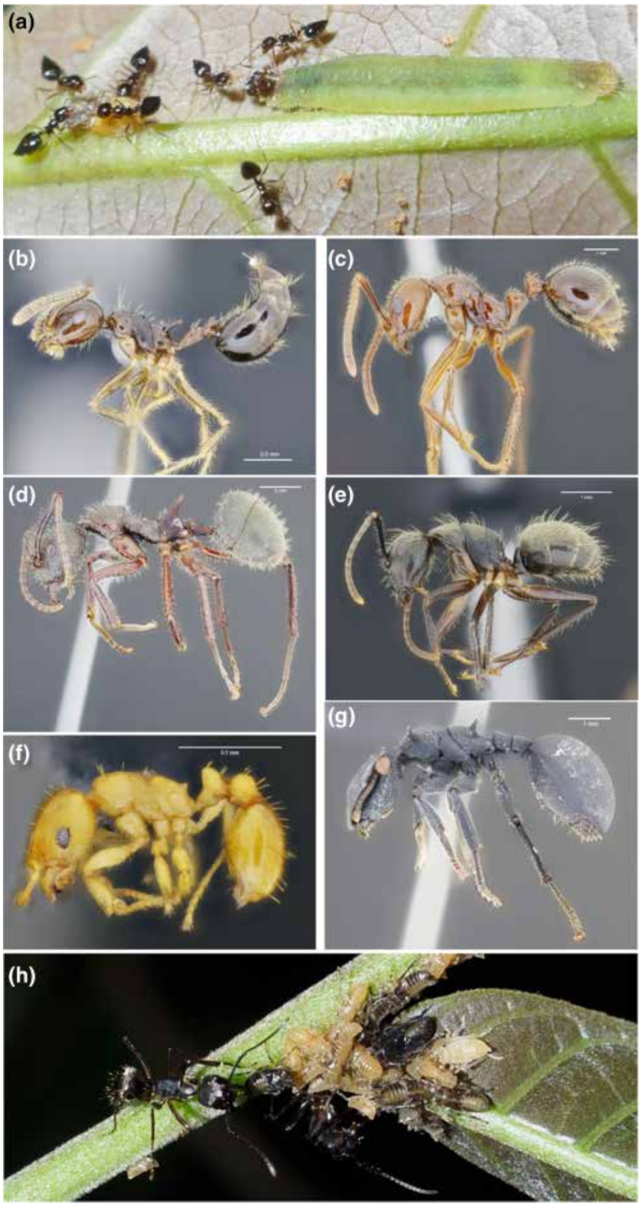

FIGURE 6 Photos of ant species found on Annonaceae. (a) Interaction between *Crematogaster* sp. and *Nymphidium* sp. larva; (b) *Crematogaster* cf. *tenuicola*; (c) *Megalomyrmex foreli*; (d) *Dolichoderus decollatus*; (e) *Camponotus* (*Myrmobrachys*); (f) *Pheidole*; (g) *Cephalotes opacus*; (h) Interaction between *Dolichoderus* sp. ants and aphids. Photo Credits: Paola Santacruz (a); Adrián Troya (b–g); Thomas L.P. Couvreur (h).

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CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.jdfn2z3m7.

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