

Phytotelmata in native and exotic plants and their mosquito (Diptera: Culicidae) assemblages: Diversity and first records of plant-mosquito associations in a subtropical region of Argentina

CARLA N. ALVAREZ^{1,2,✉}; RAÚL E. CAMPOS^{1,2,3} & MARINA STEIN^{1,2}

¹ Universidad Nacional del Nordeste (UNNE), Instituto de Medicina Regional, Área de Entomología. Resistencia, Chaco, Argentina. ² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Ciudad Autónoma de Buenos Aires, Argentina. ³ Instituto de Limnología "Dr. Raúl A. Ringuelet" (Universidad Nacional de La Plata-CONICET). La Plata, Buenos Aires, Argentina.

ABSTRACT. Phytotelma refers to the water accumulated in certain plant structures that constitute the main natural microhabitats for the development of mosquitoes. This study aimed to identify native and exotic plants with phytotelmata and their mosquito fauna (Diptera, Culicidae) in a subtropical area of northeastern Argentina, looking for new records of plant-mosquito associations. The samples were collected bimonthly during 2015-2017 at two sites in each of three localities in the Formosa, Corrientes and Chaco provinces. Species of Apiaceae, Araceae, Arecaceae, Bromeliaceae, Fabaceae, Poaceae and Strelitziaceae were identified as having phytotelmata and all except the latter harbored mosquitoes. Most woody phytotelmata were found in native bamboo *Guadua chacoensis* (Poaceae), which harbored six culicid species mainly of the Sabethini tribe. The herbaceous phytotelmata with the highest abundance were found in native *Aechmea distichantha* (Bromeliaceae), which harbored four culicid species, most of the Culicini tribe. New records of culicids that inhabit native phytotelmata in Argentina include *Haemagogus spegazzinii* in *Prosopis nigra* and *Culex coronator* in *Acrocomia aculeata*, and in exotic phytotelmata include *Wyeomyia codiocampa* and *Toxorhynchites theobaldi* in *Bambusa vulgaris*. Furthermore, two species of the *Microculex* subgenus were found in *Alocasia macrorrhiza* and one in *Aechmea miniata*. The diversity of native plant species with phytotelmata is an important factor in supporting a diverse assemblage of Culicidae, playing a relevant role in the conservation of mosquito diversity.

[Keywords: microhabitat, herbaceous phytotelmata, woody phytotelmata, *Aechmea distichantha*, *Guadua chacoensis*]

RESUMEN. Las fitotelmata y sus ensambles de mosquitos: Diversidad y primeros registros de asociaciones planta-mosquito en una región subtropical de la Argentina. Las fitotelmata se refieren al agua acumulada en ciertas estructuras vegetales que constituyen los principales microhábitats naturales para el desarrollo de los mosquitos. Este estudio tuvo como objetivo identificar plantas con fitotelmata y su fauna de mosquitos (Diptera, Culicidae) en una zona subtropical del nordeste de la Argentina, buscando posibles nuevos registros de asociaciones planta-mosquito. En tres localidades de la zona (una, en la provincia de Formosa; otra, en la de Corrientes, y la tercera, en la de Chaco) se eligieron dos sitios/localidades y se recolectaron muestras cada dos meses entre 2015 y 2017. Se identificaron especies de Apiaceae, Araceae, Arecaceae, Bromeliaceae, Fabaceae, Poaceae y Strelitziaceae que tenían fitotelmata, y todas —excepto esta última— albergaban mosquitos. La mayoría de las fitotelmata leñosas se encontraron en el bambú nativo *Guadua chacoensis* (Poaceae), que albergaba seis especies de culícidos, principalmente de la tribu Sabethini. Las fitotelmata herbáceas con mayor abundancia de mosquitos se encontraron en la nativa *Aechmea distichantha* (Bromeliaceae), que albergaba cuatro especies de culícidos, principalmente de la tribu Culicini. El primer hallazgo de culícidos habitando fitotelmata nativas en la Argentina incluye a *Haemagogus spegazzinii* en *Prosopis nigra* y *Culex coronator* en *Acrocomia aculeata*, y en fitotelmata exóticos a *Wyeomyia codiocampa* y *Toxorhynchites theobaldi* en *Bambusa vulgaris*. Además, se encontraron dos especies del subgénero *Microculex* en *Alocasia macrorrhiza* y una en *Aechmea miniata*. La diversidad de especies de plantas nativas con fitotelmata es un factor importante para sostener un ensamblaje diverso de Culicidae, desempeñando un papel relevante en la conservación de la diversidad de mosquitos.

[Palabras clave: microhábitat, fitotelmata herbácea, fitotelmata leñosa, *Aechmea distichantha*, *Guadua chacoensis*]

INTRODUCTION

Phytotelma refers to the water accumulated in several plant structures (Frank 1983). They can be classified according to different criteria such as the type of plant that originates them (i.e., herbaceous or woody phytotelmata) or according to the structure of the plant on which the water accumulates (e.g., leaf axils, modified leaves, hollows in tree trunks, bamboo stalks, flowers and fruits and pods) (Campos and Gleiser 2016). Phytotelmata are known to harbor around 70 families in 11 orders of insects, including more than 400 species of mosquitoes, some of them vectors of pathogens (Fish 1983; Harbach 2023; WRBU 2023). For this reason, phytotelmata are considered important habitats for mosquitoes of medical interest (O'Meara et al. 1995; Greeney 2001), contributing to the increase of their local diversity and abundance (Lounibos 1979; Machado-Allison et al. 1986; Derraik 2009).

A close association between the host plant and its inhabiting insect community has been early recognized (Frank 1983). For example, *Microculex* Theobald and *Phoniomyia* Theobald mosquitoes are the most frequent subgenera in the axils of plants of the family Bromeliaceae (Müller and Marcondes 2006; Stein et al. 2011; Cardoso et al. 2015), while mosquitoes of the Sabethini tribe are the most characteristic inhabitants of bamboo internodes (Louton et al. 1996; Lozovei 2001; Campos et al. 2011). There are also more specific associations, such as those observed for mosquitoes of the subgenus *Phytotelmatomyia* Rossi and Harbach, which inhabit exclusively the axils of *Eryngium* (Apiaceae) plants (Balseiro 1983; Campos and Lounibos 1999). The association and specificity between native mosquito species and host plants suggests close coevolutionary processes between them (Delgado-Petrocelli and Machado-Allison 2006), although plants that grow outside their natural range have also become suitable habitats for some native mosquito species (Delgado-Petrocelli and Machado-Allison 2006; Lounibos and Frank 2009).

In Argentina, the first investigations of mosquitoes in phytotelmata date from the late '50s and '60s. These research projects were carried out in temperate zones and reported on species identities, including the original descriptions of their immature stages, mentioning their host plants (Martínez et al. 1959; Casal and García 1966, 1967a,b; Casal et al. 1966; García and Casal 1967, 1968a,b).

Following these initial investigations, some ecological studies were developed using different types of larval habitats, including phytotelmata (Stein et al. 2011, 2012, 2016), while others were exclusively focused on phytotelmata (Torales et al. 1972; Balseiro 1983; Campos and Lounibos 1999; Marti et al. 2007; Campos 2010, 2013, 2015a,b; Albicocco et al. 2011; Campos et al. 2011; Junges et al. 2016). In the last twenty years, only a few ecological studies have focused on the mosquito species (Diptera: Culicidae) that inhabit phytotelmata in the subtropical region of Argentina (Rossi et al. 1999; Campos et al. 2011; Campos 2013, 2015a; Stein et al. 2018). The objective of the present study was to identify phytotelmata in native and exotic plant species that can harbor Culicidae in the northeast of Argentina, exploring the specificity of their associations and searching for new unreported records.

MATERIALS AND METHODS

Study area

The study was carried out in three localities in the Chacoan biogeographic subregion of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). Both Herradura (26°29'44.68" S - 58°18'23.28" W) and San Cayetano (27°34'11.99" S - 58°43'48.75" W) are located within the floodplain of the Paraná and the Paraguay rivers, whereas Colonia Benítez (27°20'7.15" S - 58°58'3.60" W) is within an area with estuaries, bamboo forests and riparian forests (Ministerio de Desarrollo Social y Medio Ambiente 1999) (Figure 1). Their climate corresponds to a humid-subhumid regime, characterized by a dry-subhumid period. The climate is notably more humid-subhumid in areas closer to the Paraguay river (CIRN-INTA 1982; APN 2023). The average annual temperature is 23 °C and the average annual rainfall is 1280 mm. In summer (December-February), the average temperature reaches 27 °C, with a maximum that may exceed 43 °C, whereas in winter (July-September), the average temperature is 15 °C. The rainy season occurs between November and April, with peaks in spring (November) and autumn (March-April) (Bruniard 1978).

Sampling sites

Two sites with native and exotic plants were sampled at each locality. Herradura (Formosa):

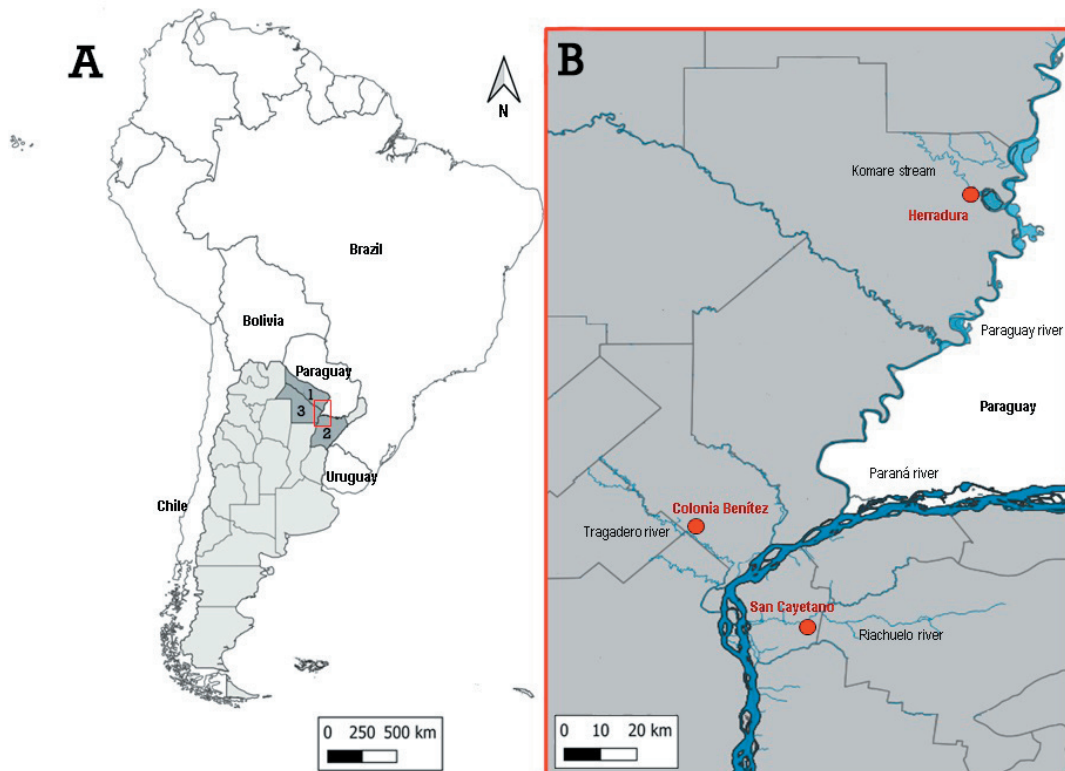


Figure 1. A) Location of Argentina in South America and details of the three provinces studied. 1) Formosa province. 2) Corrientes province. 3) Chaco province. B) Sampling sites in the three mentioned provinces: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province).

Figura 1. A) Ubicación de la Argentina en Sudamérica y detalle de las tres provincias de estudio. 1) Provincia de Formosa. 2) Provincia de Corrientes. 3) Provincia del Chaco. B) Sitios de muestreo en las tres provincias mencionadas: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco).

1) A commercial plant nursery ($26^{\circ}29'30.82''$ S - $58^{\circ}18'22.79''$ W) with a wide variety of native and exotic plants in an 8-ha property bordering a lagoon; 2) La Florencia ranch ($26^{\circ}29'2.50''$ S - $58^{\circ}18'12.90''$ W), a 3-ha property bordered by El Salado stream, which conserves a riverside ecosystem of exuberant native flora composed mainly of *Handroanthus impetiginosus* (Mart. ex DC.) Mattos (Bignoniaceae), *Enterolobium contortisiliquum* (Vell.) Morong, *Erythrina crista-galli* L. and *Libidibia paraguariensis* (D. Parodi) Burkart (Fabaceae) (Gobierno de la Provincia de Formosa 2023). San Cayetano (Corrientes): 1) Fields surrounding the San Cayetano Provincial Park ($27^{\circ}33'11.18''$ S - $58^{\circ}40'30.96''$ W), characterized by grasslands, palm groves and cattle grazing; 2) A 2-ha private property (Casa del Médico) ($27^{\circ}34'0.65''$ S - $58^{\circ}42'57.92''$ W), crossed by a small arm of the Riachuelo river, with *Guadua chacoensis* (Rojas) Londoño and P.M. Peterson cane fields, lemon trees, palm trees and some specimens of ornamental exotic plants such as *Alpinia* Roxb. (Zingiberaceae), *Dracaena fragrans* (L.) Ker Gawl. (Asparagaceae), *Cordyline rubra*

(Otto and A. Dietr.) Kuntze (Agavaceae) and *Philodendron* Schott (Araceae). Colonia Benítez (Chaco): 1) Los Chagueros Natural Reserve ($27^{\circ}20'5.91''$ S - $58^{\circ}58'2.26''$ W), with 19-ha of native forest in a gallery jungle mainly formed by *E. contortisiliquum*, *Handroanthus* Mattos and *Peltophorum dubium* (Spreng.) Taub. (Fabaceae), with estuaries, ravines and lagoons associated with the Tragadero river (APN 2023); 2) A private property (Small Property) ($27^{\circ}34'0.65''$ S - $58^{\circ}42'57.92''$ W) near the natural reserve, crossed by a small arm of the Tragadero river, with the presence of native flora such as *Aechmea distichantha* Lem. (Bromeliaceae) and *Prosopis* L. (Fabaceae), as well as ornamental exotic flora such as *Alocasia macrorrhiza* (L.) G. Don. (Araceae), a patch of bamboo cane and some lemon trees.

Mosquito sampling and identification

Mosquitoes were sampled bimonthly from February 2015 to July 2017. Culicidae larvae were searched in bamboo internodes, axils of Bromeliaceae, tree holes, fallen palm bracts

and any other plant structure presumed able to collect water.

The water and specimens contained in all phytotelmata were extracted by means of a suction bottle. In bamboos, holes were opened with a drill at the upper end of each internode to access to the accumulated water and washed and re-extracted several times to collect the existing specimens. Culicidae larvae were collected per phytotelma, recording the date of collection, the site and the type and species of hosting plant, and transported to the laboratory to be reared to adult stage in tubes with water from their microhabitats; if up to five individuals in Polystyrene tubes (5 mL, Khan type), and when more, in plastic containers (100 mL, Greyton type). Culicidae species were identified based on available dichotomous keys (Lane 1953; Correa and Ramalho 1956; Darsie 1985) and original descriptions (Lynch Arribáizaga 1891; Coquillett 1906; Dyar and Knab 1907a,b; Casal and García 1967a,b; Augier et al. 2003; Rossi and Harbach 2008).

Plant species with phytotelmata were preliminary identified at field based on their morphological characteristics, particularly those of their reproductive structures. When possible, the reproductive structures of the plant species were carefully collected and/or photographed in the field and their identification was further supported by consulting local experts of the Instituto de Botánica del Nordeste (IBONE) at the Facultad de Ciencias Agrarias, Universidad Nacional del Nordeste, Corrientes. Keys of Martínez (2005) and Lizarazu (2013) were used in the laboratory work to identify the species of Apiaceae and Poaceae, respectively. Vegetation present in Los Chaguares Natural Reserve had already been identified by its professional staff.

Minimum sample size

To establish a minimum sample size, the quality of exploratory samplings was assessed by adjusting the Clench equation (Jiménez-Valverde and Hortal 2003) to their species accumulation curves. The Clench equation allows modeling the relationship between sampling effort and the number of species found, and provided a good fit with various arthropod taxa (Soberón and Llorente 1993; Moreno and Halfpeter 2000). A slope <0.1 at the curve's end indicates a fairly complete

and highly reliable inventory (Soberón and Llorente 1993).

The quality of exploratory inventories was evaluated for culicids inhabiting bromeliad axils in Colonia Benítez (4 mosquito species recorded in 26 bromeliads) and San Cayetano (4 species in 7 bromeliads). Both cases resulted in a fairly complete and reliable record of the culicid fauna ($R^2 > 0.88$; slopes < 0.1 ; recorded fauna $> 90\%$), indicating a minimum of 8 bromeliads in San Cayetano and 20 bromeliads in Colonia Benítez required to achieve a 95% record of culicids breeding in bromeliad axils (Table 3). The same procedure for culicids inhabiting bamboo internodes in Herradura (3 species in 14 internodes) and San Cayetano (3 species in 13 internodes) indicated a minimum of 21 and 7 internodes, respectively ($R^2 > 0.9$; slopes < 0.1 ; recorded fauna $> 95\%$) (Table 4).

Based on the analysis and prior studies in the area (Stein et al. 2011; Campos 2015b), minimum sample sizes were established for bamboo internodes in San Cayetano and Herradura ($N=80$), and for bromeliads in Colonia Benítez and San Cayetano ($N=25$). In Herradura, available bromeliads limited the sample size to $N=6$. For less abundant or occasional phytotelmata (e.g., tree holes, palm bracts and fallen leaves), all those with immature culicid stages were considered in the sample size.

Data analysis

We classified plants into those with herbaceous or woody phytotelmata and associated each species (or group of species) with its culicid fauna. Because not all types of phytotelmata were represented at each site, descriptors of the mosquito assemblages (i.e., abundance, richness, diversity, dominance) were calculated per locality (2 sites), aggregating all bimonthly samples. The Margalef index (Mg) was used to estimate species richness, which can range from a minimum value of zero (indicating one species) to a maximum close to 5 indicating high diversity (Margalef 1995; Manzoor et al. 2020). The Shannon-Wiener index (H) was used to estimate diversity, which takes values between zero when there is a single species and a maximum of $\log(\text{number of species})$ (Magurran 1988). The Berger-Parker index (D) was used to quantify dominance within the 0-1 range, with higher values indicating greater dominance and lower diversity (Magurran

1988). Ecological indices were calculated using the vegan package (Oksanen et al. 2018) in the R statistical platform (R Core Team 2023) within the RStudio integrated development environment (RStudio Team 2023, version 2023.6.2.561).

RESULTS

Phytotelmata recorded

A total of 17 species of plants with phytotelmata, both native and exotic, were recorded during the study (Table 1). San

Table 1. Plants with phytotelmata recorded in two focal sites at each of three localities of northeastern Argentina (Herradura [Formosa province], San Cayetano [Corrientes province] and Colonia Benítez [Chaco province]) between 2015 and 2017. The structure that accumulates water is specified, together with the general habitat and the geographical distribution of the species in South America (countries) and Argentina (provinces). In bold, records from the present study that documented these plants as phytotelmata in the specified locations.

Tabla 1. Plantas con fitotelmata registradas en dos sitios focales en cada una de las tres localidades del noreste de Argentina (Herradura [provincia de Formosa], San Cayetano [provincia de Corrientes] y Colonia Benítez [provincia de Chaco]) entre 2015 y 2017. Se especifica la estructura que acumula agua junto con el hábitat general y la distribución geográfica de las especies en América del Sur (países) y la Argentina (provincias). En negrita, los registros del presente estudio que documentaron estas plantas como fitotelmata en las ubicaciones especificadas.

Family and species (type)	Structure	Distribution	Habitat	Geographical distribution
Apiaceae (herbaceous)				
<i>Eryngium</i> sp.	Leaf axils	Native	Terrestrial	Argentina: Corrientes
<i>Eryngium stenophyllum</i> Urb.	Leaf axils	Native	Terrestrial	Brazil; Paraguay; Uruguay; Argentina: Chaco, Corrientes, Misiones, Santa Fe (Calviño and Martínez 2007).
Araceae (herbaceous)				
<i>Alocasia macrorrhiza</i> (L.) G. Don	Leaf axils	Exotic	Terrestrial	Argentina: Chaco
Arecaceae (woody)				
<i>Acrocomia aculeata</i> (Jacq.) Lodd. ex Mart.	Palm bracts	Native	Terrestrial	Brazil; Paraguay; Argentina: Chaco, Corrientes, Misiones, Formosa, Salta (Instituto de Botánica Darwinion 2023).
<i>Roystonea regia</i> (Kunth) O.F.Cook	Palm bracts	Exotic	Terrestrial	Argentina: Formosa
Bromeliaceae (herbaceous)				
<i>Aechmea distichantha</i> Lem.	Leaf axils	Native	Terrestrial/epiphytic	Brazil; Bolivia; Paraguay; Uruguay; Argentina: Misiones, Corrientes, Chaco, Formosa, Santa Fe, Jujuy, Salta, Catamarca, Tucumán (Smith and Downs 1979; Barberis et al. 2014).
<i>Aechmea miniata</i> var. <i>discolor</i> Beer ex Baker.	Leaf axils	Exotic	Terrestrial/epiphytic	Argentina: Formosa
<i>Aechmea</i> Morphospecies 1	Leaf axils	Unknown	Terrestrial/epiphytic	Argentina: Formosa
<i>Aechmea</i> Morphospecies 2	Leaf axils	Unknown	Epiphytic	Argentina: Formosa
<i>Aechmea</i> Morphospecies 3	Leaf axils	Unknown	Terrestrial	Argentina: Corrientes
Fabaceae (woody)				
<i>Prosopis nigra</i> Griseb.	Holes in trunks and branches	Native	Terrestrial	Brazil; Bolivia; Paraguay; Uruguay; Argentina: Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, La Pampa, La Rioja, San Luis, Santa Fe, Salta, Santiago del Estero, San Juan, San Luis, Tucumán (Gimenez et al. 2003; Fagúndez Pachón 2015)
Poaceae (woody)				
<i>Bambusa tuldoidea</i> Munro	Internodes/Stumps	Exotic	Terrestrial	Argentina: Chaco
<i>Bambusa vulgaris</i> var. <i>vittata</i> Rivière and C. Rivière	Internodes/Stumps	Exotic	Terrestrial	Argentina: Chaco, Formosa
<i>Guadua chacoensis</i> (Rojas) Londoño and P.M. Peterson	Internodes/Stumps	Native	Terrestrial	Brazil; Bolivia; Paraguay; Uruguay; Argentina: Buenos Aires, Chaco, Corrientes, Formosa, Misiones Tucumán (Lizarazu 2013).
Strelitziaceae (woody)				
<i>Ravenela madagascariensis</i> Sonn.	Leaf axils	Exotic	Terrestrial	Argentina: Formosa
Unidentified trees (woody)				
	Holes in trunks and branches	Unknown	Terrestrial	Argentina: Formosa
Unidentified fallen leaves				
	Leaf blade	Unknown	Terrestrial	Argentina: Formosa

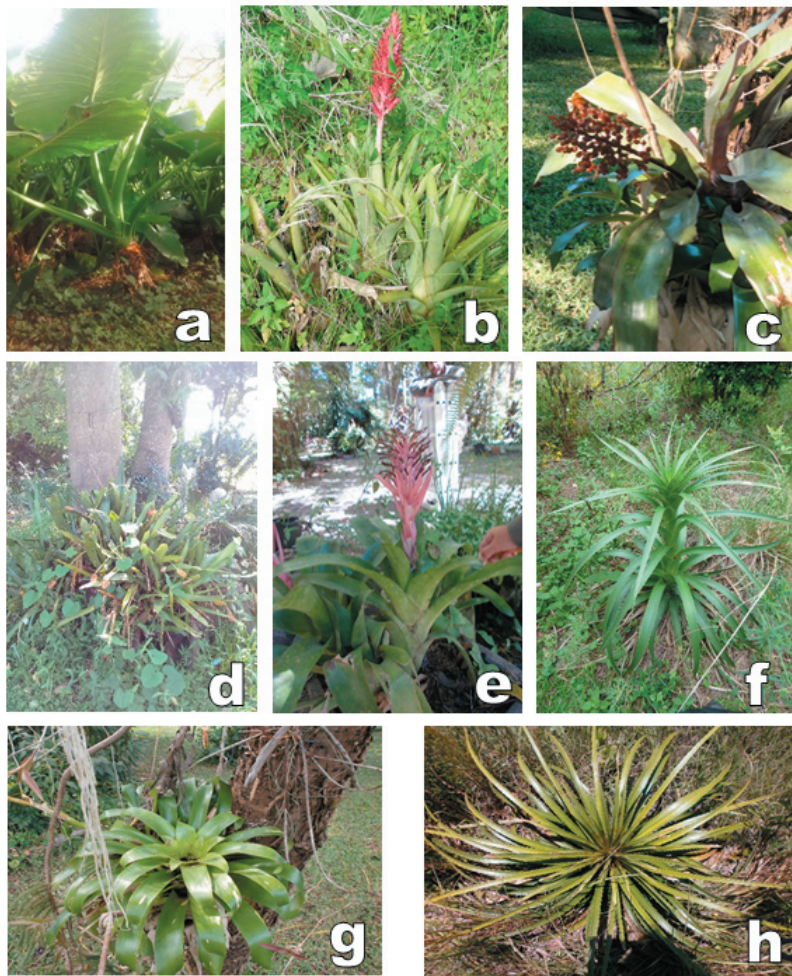


Figure 2. Herbaceous plants with phytotelmata recorded between 2015 and 2017 in three localities of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). a) *Alocasia macrorrhiza*. b) *Aechmea distichantha*. c) *Aechmea miniata* var. *discolor*. d) Bromeliad morphospecies 1. e) Bromeliad morphospecies 2. f) *Eryngium* sp. g) Bromeliad morphospecies 3. h) *Eryngium stenophyllum*.

Figura 2. Plantas herbáceas con fitotelmata registradas entre 2015 y 2017 en tres localidades del noreste argentino: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco). a) *Alocasia macrorrhiza*. b) *Aechmea distichantha*. c) *Aechmea miniata* var. *discolor*. d) *Aechmea* morfoespecies 1. e) *Aechmea* morfoespecies 2. f) *Eryngium* sp. g) *Aechmea* morfoespecies 3. h) *Eryngium stenophyllum*.

Cayetano had the highest proportion of phytotelmata formed in native plants (80% native, 20% unknown), followed by Colonia Benítez (50% native, 50% exotic) and Herradura (11% native, 44.5% exotic, 44.5% unknown). Eleven of the 17 plants with phytotelmata were identified at the species level; the rest only to the genus or family level. Eight of them were herbaceous, including the native *Aechmea distichantha* Lem. and the exotic *Aechmea miniata* var. *discolor* Beer ex Baker bromeliads (Bromeliaceae). Additionally, phytotelmata were found in two Apiaceae species, *Eryngium stenophyllum* Urb. and *Eryngium* sp., and in the exotic plant *Alocasia macrorrhiza* (L.) G. Don (Araceae) (Figure 2). Woody phytotelmata, such as bamboo canes, tree hollows, and palm leaf sheaths, were also found (Table 1, Figure 3). The former included canes of the native bamboo *Guadua chacoensis* and of the exotic one *Bambusa vulgaris* var. *vittata* Riviére and C. Riviére. Tree species in which hollows were found could not be identified to the species level, with the exception of *Prosopis*

nigra Griseb due to the absence of observable taxonomic structures (e.g., flowers, fruit), and they were, thus, grouped as unidentified tree holes. Two dried palm leaves containing water were found on the ground: *Roystonea regia* (Kunth) O. F. Cook —an exotic species cultivated for ornamental purposes— and the native species *Acrocomia aculeata* (Jacq.) Lodd. Mart (Arecaceae) (Figure 3).

Culicidae in phytotelmata

Most culicids inhabited one (*Tx. bambusicola*, *Sa. identicus*, *Sa. undosus*, *Wyeomyia* spp., *Wy. muehlensi* and *Cx. renatoi*) or two species of phytotelmata (*Tx. guadeloupensis*, *Tx. h. sepatarus*, *Tx. theobaldi*, *Wy. codiocampa*, *Cx. castroi* and *Hg. spegazzinii*). Only a few species inhabited three (*Cx. imitator*) or up to 4 (*Cx. davisii*) different types of phytotelmata (Table 2).

A total of 6761 immature Culicidae were collected, with the highest percentages found in Bromeliaceae (73.1%), Poaceae (21.9%) and

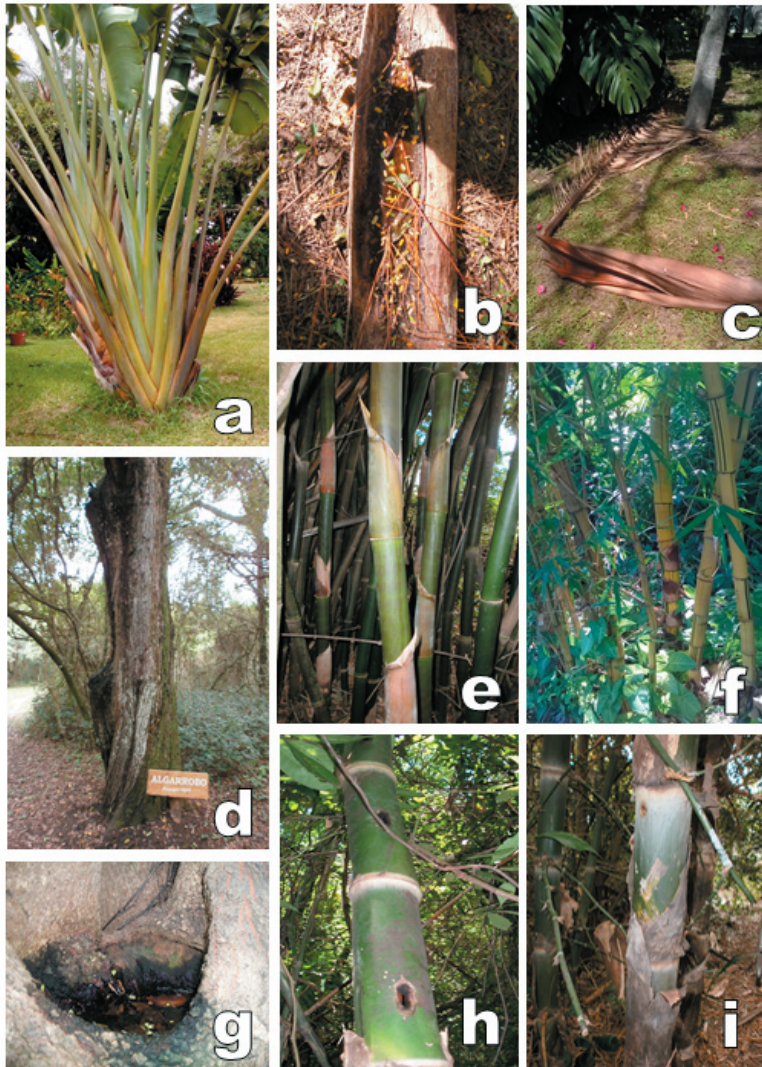


Figure 3. Woody plants with phytotelmata recorded between 2015 and 2017 in three localities of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). a) *Ravenela madagascariensis*. b) *Acrocomia aculeata* leaf sheaths. c) *Roystonea regia* leaf sheaths. d) *Prosopis nigra*. e) *Bambusa tuldooides*. f) *Bambusa vulgaris* var. *vittata*. g) Hole in trunk of an unidentified tree. h) *Guadua chacoensis* in Herradura. i) *Guadua chacoensis* in San Cayetano.

Figura 3. Plantas leñosas con fitotelmata registradas entre 2015 y 2017 en tres localidades del noreste de la Argentina: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco). a) *Ravenela madagascariensis*. b) Vainas de hojas de *Acrocomia aculeata*. c) Vainas de hojas de *Roystonea regia*. d) *Prosopis nigra*. e) *Bambusa tuldooides*. f) *Bambusa vulgaris* var. *vittata*. g) Agujero en el tronco de un árbol no identificado. h) *Guadua chacoensis* en Herradura. i) *Guadua chacoensis* en San Cayetano.

Apiaceae (4.5%); less than 1% were from other plant families. *Aechmea distichantha* harbored the largest number of Culicidae larvae (N=4904), corresponding to five species of the tribes Culicini (two species), Toxorhynchitini (two species) and Sabethini (one species) (Table 3). The tribe Culicini was the most abundant (N=4004), with 85.9% of the specimens belonging to *Culex (Microculex) imitator* Theobald (Table 4). Only one larva of *Culex (Microculex) davisi* Kumm was collected from *A. miniata* var. *discolor*, whereas 40 specimens were collected from *Aechmea* morphospecies 1. Among Poaceae, the native woody bamboo *G. chacoensis* showed the highest mosquito species richness and abundance, with a total of 1460 individual belonging to 6 species of Culicidae, represented by 2 tribes: Sabethini (four species) and Toxorhynchitini (two species) (Table 3). About 88.8% of the collected

individuals were identified as *Wyeomyia (Miamiya) codiocampa* Dyar and Knab. Conversely, 20 specimens were collected in the exotic bamboo *B. vulgaris* var. *vittata*, with 17 corresponding to *Wy. codiocampa*, two to *Toxorhynchuites guadeloupensis* and one to *Toxorhynchuites theobaldi*. In Apiaceae, *Culex (Phytotelmatomyia) castroi* Casal and García was the most abundant culicid found in the axils of both *Eryngium* species (N=304), whereas only one specimen of *Culex (Phytotelmatomyia) renatoi* Lane and Ramalho was found in *Eryngium* sp. In Araceae, *A. macrorrhiza* was found harboring two culicid species: *Cx. imitator* (N=1) and *Cx. davisi* (N=10) (Table 3). *Haemagogus spegazzinii* Bréthes (N=2) was the only mosquito species collected from tree holes (in *P. nigra*), whereas *Culex (Culex) coronator* Dyar and Knab (N=18) was collected from fallen leaves of *A. aculeata*.

Table 2. Culicidae fauna and its host plants recorded between 2015 and 2017 in three localities of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). Host plant species in bold are first records in Argentina. Previous records referenced within parentheses.
Table 2. Fauna de Culicidae y sus plantas hospedadas registradas entre 2015 y 2017 en tres localidades del noreste de Argentina: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco). Los registros previos a este estudio son citados entre parentesis.

Tribe	Species	Host plant	Previously cited
Aedini	<i>Haemagogus (Haemagogus) spegazzinii</i> Brèthes	<i>Prosopis nigra</i>	Unidentified tree (Stein et al. 2012; Campos and Gleiser 2016)
	<i>Culex (Culex) coronator</i> Dyar and Knab	Unidentified tree	<i>Prosopis pallida</i> (Obholz et al. 2020)
Culicini	<i>Culex (Microculex) davisi</i> Kumm	<i>Acrocomia aculeata</i>	Artificial containers
	<i>Culex (Microculex) imitator</i> Theobald	<i>Aechmea distichantha</i>	<i>Aechmea distichantha</i> (Torales et al. 1972; Campos et al. 2011; Stein et al. 2013)
Culex (<i>Phytotelmatomyia</i>)	<i>castroi</i> Casal and García	<i>Aechmea miniata</i>	
		Morpho-species 1	
Culex (<i>Phytotelmatomyia</i>)	<i>renatoi</i> Lane and Ramalho	<i>Alocasia macrorrhiza</i>	<i>Aechmea distichantha</i> (Torales et al. 1972; Campos et al. 2011; Stein et al. 2011, 2013)
		<i>Aechmea distichantha</i>	<i>Vriesea friburgensis</i> Mez (Campos et al. 2011)
Culex (<i>Phytotelmatomyia</i>)	<i>renatoi</i> Lane and Ramalho	Morpho-species 1	
		<i>Alocasia macrorrhiza</i>	
Culex (<i>Phytotelmatomyia</i>)	<i>renatoi</i> Lane and Ramalho	<i>Eryngium</i> sp.	<i>Eryngium</i> sp. (Campos et al. 2011)
		<i>Eryngium stenophyllum</i>	<i>Eryngium cabreriae</i> Pontiroli (Campos and Lounibos 1999)
Culex (<i>Phytotelmatomyia</i>)	<i>renatoi</i> Lane and Ramalho	<i>Eryngium</i> sp.	<i>Eryngium eburneum</i> Decne (Albicocco et al. 2011)
		<i>Eryngium stenophyllum</i>	<i>Eryngium horridum</i> Malne (Campos 2010, 2015b)
Culex (<i>Phytotelmatomyia</i>)	<i>renatoi</i> Lane and Ramalho	<i>Eryngium</i> sp.	<i>Eryngium pandanifolium</i> Cham. and Schltidl. (Campos and Lounibos 1999; Albicocco et al. 2011; Junges et al. 2016)
		<i>Eryngium stenophyllum</i>	<i>Eryngium serra</i> Cham. and Schltidl. (Albicocco et al. 2011)
Sabethini	<i>Sabethes (Peytonulus) identicus</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Sagittaria montioidensis</i> Cham. and Schltidl. (Albicocco et al. 2011)
	<i>Sabethes (Peytonulus) undosus</i> Coquillett	<i>Guadua chacoensis</i>	<i>Eryngium cabreriae</i> (Campos and Lounibos 1999)
Wyeomyia	<i>Wyeomyia (Miamiya) codiocampa</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Eryngium eburneum</i> (Albicocco et al. 2011; Campos 2015b)
		<i>Bambusa vulgaris</i> var. <i>vittata</i>	<i>Eryngium elegans</i> (Campos 2010)
Wyeomyia	<i>Wyeomyia</i> sp1	<i>Guadua chacoensis</i>	<i>Eryngium horridum</i> (Campos 2010, 2015b)
		<i>Aechmea distichantha</i>	<i>Eryngium pandanifolium</i> Cham. and Schltidl. (Campos and Lounibos 1999; Albicocco et al. 2011; Junges et al. 2016)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) bambusicola</i> Lutz and Neiva	<i>Aechmea distichantha</i>	<i>Eryngium serra</i> (Campos 2010, 2015b; Albicocco et al. 2011)
		<i>Aechmea distichantha</i>	<i>Eryngium stenophyllum</i> Urb., (Campos 2010, 2015b)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) guadeloupensis</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Guadua</i> sp. (Campos et al. 2011; Campos 2015a; Stein et al. 2018)
		<i>Bambusa vulgaris</i> var. <i>vittata</i>	<i>Guadua</i> sp. (Campos et al. 2011; Campos 2015a; Stein et al. 2018)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) haemorrhoidalis separatus</i> Lynch Arribalzaga	<i>Bambusa vulgaris</i> var. <i>vittata</i>	<i>Guadua trinii</i> (Campos et al. 2011)
		<i>Guadua chacoensis</i>	<i>Aechmea distichantha</i> (Torales et al. 1972; Campos 2011; Stein et al. 2011)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Eutypus egulis</i> Martius (Campos et al. 2011)
		<i>Aechmea distichantha</i>	<i>Aechmea distichantha</i> L. (Campos et al. 2011)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	Unidentified Bamboo (García and Casal 1968b; Campos et al. 2011)
		<i>Aechmea distichantha</i>	<i>Guadua chacoensis</i> (Kojas) Londrigo and P.M. Peterson (Campos et al. 2011)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Guadua chacoensis</i> (Campos et al. 2011; Campos 2015a; Kossí and Lestani 2014)
		<i>Aechmea distichantha</i>	Unidentified tree (Mangudo et al. 2015)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Aechmea distichantha</i> (Campos et al. 2011)
		<i>Aechmea distichantha</i>	<i>Ligustrum lucidum</i> Ait. (Campos 1994)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	<i>Guadua</i> sp. (Stein et al. 2018)
		<i>Aechmea distichantha</i>	<i>Acer negundo</i> L. (Campos 1994)
Toxorhynchitini	<i>Toxorhynchites (Lynchella) theobaldi</i> Dyar and Knab	<i>Guadua chacoensis</i>	Unidentified tree (Mangudo et al. 2015)
		<i>Aechmea distichantha</i>	

Table 3. Abundance of Culicidae larvae found in each host plant species along bimonthly samples between 2015 and 2017 in two focal sites at each of the three localities of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). Plant origin is indicated at each locality it was detected.

Tabla 3. Abundancia de larvas de Culicidae encontradas en cada especie de planta huésped durante muestreos bimestrales entre 2015 y 2017 en dos sitios focales de cada una de las tres localidades del noreste de la Argentina: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco). El origen de las plantas se indica en las localidades en que fueron encontradas.

Species	<i>Aechmea distichantha</i>	<i>Aechmea miniata</i>	<i>Aechmea</i> sp.	<i>Alocacia macrorrhiza</i>	<i>Eryngium</i> sp.	<i>Eryngium stenophyllum</i>	<i>Guaadua chacoensis</i>	<i>Bambusa vulgaris</i> var. <i>vittata</i>	<i>Acrocomia aculeata</i>	<i>Prosopis nigra</i>	ND tree
<i>Culex (Culex) coronator</i>	0	0	0	0	0	0	0	0	18	0	0
<i>Culex (Microculex) davisi</i>	565	1	4	10	0	0	0	0	0	0	0
<i>Culex (Microculex) imitator</i>	3439	0	32	1	0	0	0	0	0	0	0
<i>Culex (Phytotelmatomyia) castroi</i>	0	0	0	0	279	25	0	0	0	0	0
<i>Culex (Phytotelmatomyia) renatoi</i>	0	0	0	0	1	0	0	0	0	0	0
<i>Haemagogus (Haemagogus) spegazzinii</i>	0	0	0	0	0	0	0	0	0	1	1
<i>Sabethes (Peytonolus) identicus</i>	0	0	0	0	0	0	34	0	0	0	0
<i>Sabethes (Peytonolus) undosus</i>	0	0	0	0	0	0	17	0	0	0	0
<i>Toxorhynchuites (Lynchiella) bambusicola</i>	2	0	0	0	0	0	0	0	0	0	0
<i>Toxorhynchuites (Lynchiella) guadeloupensis</i>	0	0	0	0	0	0	77	2	0	0	0
<i>Toxorhynchuites (Lynchiella) h. separatus</i>	157	0	4	0	0	0	0	0	0	0	0
<i>Toxorhynchuites (Lynchiella) theobaldi</i>	0	0	0	0	0	0	33	1	0	0	0
<i>Wyeomyia (Miamiya) codiocampa</i>	0	0	0	0	0	0	1297	17	0	0	0
<i>Wyeomyia (Phoniomyia) muelhensi</i>	741	0	0	0	0	0	0	0	0	0	0
<i>Wyeomyia (Wyeomyia.) spp.</i>	0	0	0	0	0	0	2	0	0	0	0
Herradura		Exo	Unk				Nat	Exo			Unk
Colonia Benítez	Nat			Exo		Nat		Exo		Nat	
San Cayetano	Nat				Nat				Nat		

Nat: Native; Exo: Exotic; Unk: Unknown

Five of the plant species with phytotelmata found in the present study were recorded harboring mosquitoes for the first time in Argentina: *B. vulgaris* var. *vittata*, which hosted mosquito species from the Sabethini and Toxorhynchitini tribes; *P. nigra*, which hosted mosquito species from the Aedini tribe, and *A. miniata* var. *discolor* and *A. macrorrhiza*, which hosted species from the Culicini tribe. Additionally, the temporary phytotelma *A. aculeata* hosted one species from the Culicini tribe (Table 2).

Native plants harbored the highest abundance of Culicidae larvae (N=6688) (Table 3). Furthermore, *A. distichantha* harbored up to four culicid species inhabiting the same plant, while *A. miniata* var. *discolor* showed only one species. *A. aculeata* hosted one mosquito species, whereas *R. regia* did not support any mosquito species. Interestingly, up to three mosquito species were found cohabiting the same internode of both *G. chacoensis* and *B. vulgaris* var. *vittata*, although the native

bamboo hosted more Culicidae than the exotic bamboo.

Variations in the Culicidae assemblage were observed among the three localities. San Cayetano exhibited the highest mosquito diversity, characterized by the highest species richness and lower dominance (Mg=1.666; H=1.62; D=0.4771). In contrast, Colonia Benítez showed lower richness with intermediate diversity and dominance (Mg=0.618; H=0.9139; D=0.6971) (Table 4). Herradura, with a higher variety of phytotelmata, displayed intermediate richness and dominance.

DISCUSSION

Plant communities and their associated phytotelmata, as well as the culicid species that they host, vary depending on the climatic region. For instance, Campos et al. (2011) found that in the Paraná Forest (a biogeographic province in the Chacoan biogeographic subregion of northeastern Argentina), most

Table 4. Abundance of Culicidae larvae of each species collected along bimonthly samplings between 2015 and 2017 in two focal sites at each of three localities of northeastern Argentina: Herradura (Formosa province), San Cayetano (Corrientes province) and Colonia Benítez (Chaco province). Mg: Margalef index of species richness. H: Shannon-Wiener diversity index. D: Berger-Parker dominance index.

Tabla 4. Abundancia de larvas de Culicidae de cada especie recolectadas durante muestreos bimensuales entre 2015 y 2017 en dos sitios focales de cada una de las tres localidades del noreste de la Argentina: Herradura (provincia de Formosa), San Cayetano (provincia de Corrientes) y Colonia Benítez (provincia de Chaco). Mg: Índice de Margalef de riqueza de especies. H: Índice de diversidad de Shannon-Wiener. D: Índice de dominancia de Berger-Parker.

Species	Herradura	Colonia Benítez	San Cayetano
<i>Culex (Culex) coronator</i>	0	0	18
<i>Culex (Microculex) davisi</i>	5	511	64
<i>Culex (Microculex.) imitator</i>	32	2274	1166
<i>Culex (Phytotelmatomyia) castroi</i>	0	25	279
<i>Culex (Phytotelmatomyia) renatoi</i>	0	0	1
<i>Haemagogus (Haemagogus) spegazzinii</i>	1	1	0
<i>Sabethes (Peytonulus) identicus</i>	0	0	34
<i>Sabethes (Peytonulus) undosus</i>	0	0	17
<i>Toxorhynchites (Lynchiella) bambusicola</i>	0	0	2
<i>Toxorhynchites (Lynchiella) guadeloupensis</i>	46	0	33
<i>Toxorhynchites (Lynchiella) h. separatus</i>	4	68	89
<i>Toxorhynchites (Lynchiella) theobaldi</i>	17	0	17
<i>Wyeomyia (Wyeomyia) codiocampa</i>	950	0	364
<i>Wyeomyia (Phoniomyia) muehlensi</i>	0	383	358
<i>Wyeomyia (Wyeomyia) sp.1</i>	0	0	2
N	1055	3262	2444
Type of phytotelmata	9	5	6
Mg	0.8619	0.618	1.666
H	0.4566	0.9139	1.62
D	0.9005	0.6971	0.4771

phytotelmata are associated with the families Poaceae (three plant species harboring a total of 15 culicid species), Bromeliaceae (two plant species harboring six culicid species) and Apiaceae (one plant species harboring three culicid species each). Similarly, in our region of study we found the greatest species richness of Culicidae in Poaceae (two plant species harboring a total of six culicid species), followed by Bromeliaceae (three plant species harboring five culicid species, with the highest abundance) and Apiaceae (two plant species harboring two culicid species). The breeding of species richness in these plants aligns with other studies conducted in this area (in bamboo: Campos 2015a; in bromeliads: Torales et al. 1972). On the contrary, in the Pampean biogeographic province (a temperate region in the center of Argentina), most phytotelmata belonged to the Apiaceae family Apiaceae, with seven plant species hosting only four culicid species (Campos and Lounibos 1999; Campos 2010, 2015b; Albicócco et al. 2011).

Our study found that localities with a higher proportion of phytotelmata formed in native plants exhibited greater mosquito richness. For example, in San Cayetano,

where almost all phytotelmata were in native plants, we detected the highest mosquito richness (Margalef index) with intermediate abundance, probably due to the prevalence of native bromeliads and bamboo species such as *A. distichantha* and *G. chacoensis*, which host a diverse mosquito assemblage in this area (Torales et al. 1972; Campos 2015a). On the contrary, Herradura — with phytotelmata of different origins (mostly exotic) — showed intermediate mosquito richness and the lowest abundance. Specifically, the native plant *G. chacoensis* in Herradura hosted a mosquito assemblage with a high dominance of species, aligning with previous research that characterized the mosquito community in *Guadua* sp. as having high dominance (Campos 2015a). Colonia Benítez had an equal proportion of native and exotic phytotelmata and showed intermediate mosquito richness but the highest abundance of mosquitoes. These findings suggest an association between the origin of the plants that form phytotelmata and greater diversity of mosquitoes, although caution is warranted due to unequal sampling efforts across sites (see Materials and Methods).

Native bamboo *G. chacoensis* served as an important larval habitat that hosted a great diversity of mosquito species, whereas exotic bamboo *B. vulgaris* var. *vittata*, in contrast, supported a much lower diversity. *Bambusa vulgaris*, originally from India, has been cultivated widely spreading in the USA, Central America and the Caribbean, as well as in South America from Colombia and Venezuela to Argentina; we registered it in Colonia Benítez and in Herradura. *Bambusa vulgaris* var. *vittata* harbored mosquitoes only in Herradura, where it was surrounded by *G. chacoensis*, which could have facilitated its colonization. In Colonia Benítez, instead, *B. vulgaris* was surrounded by *B. tuldooides*, another exotic species from which no mosquitoes were collected, and none of them presented perforations on their stems. Fenoglio et al. (2020) also found native plants harboring significantly richer insect communities than exotic plants, presumably due to their greater evolutionary history together. In the Atlantic Forest of Brazil, *B. tuldooides* —also introduced— has been acclimated; thus, the wild fauna interacts with it searching for food or oviposition sites, perforating the culms and turning their internodes into phytotelmata (Müller 2008). The species of Culicidae hosted by this exotic phytotelmata included *Sa. aurescens* Lutz, *Shannoniana fluviatilis* Theobald, *Wy. limai* Lane and Cerqueira, *Tx. bambusicola* and *Tx. theobaldi* —all recorded in Argentina—, and the latter found particularly in the Chaco province (Rossi 2015). No culicid larvae were found in another introduced plant species —*R. madagascariensis* (Strelitzaceae)—, which is endemic to Madagascar and accumulates significant volumes of water (Lehtinen 2002). However, the presence of chemical compounds with larvicidal properties may deter the choice of these phytotelmata as a breeding site by female mosquitoes: leaf extracts from this plant have potential larvicidal effects on the *Culex* vishnui group (Bhattacharya et al. 2014).

Many mosquito species are restricted to reproduce in phytotelmata (Martin-Smith 2004). In northeast Argentina, some of the main larval habitats for mosquitoes of the Sabethini tribe are bamboos (Campos et al. 2011; Campos 2013, 2015a). However, here we report the first finding of the mosquito *Toxorhynchites* (*Lyn.*) *theobaldi* in the internodes of *G. chacoensis* and *B. vulgaris* in Argentina. Larvae of *Tx.* (*Lyn.*) *theobaldi* have previously been found in tree holes (Mangudo et al.

2014) and in the internodes of *Merostachys claussoni* Munro (Poaceae) (Campos et al. 2011). *Toxorhynchites* (*Lyn.*) *guadeloupensis* was also found in bamboo internodes, as in previous studies (Campos et al. 2011; Rossi and Lestani 2014; Campos 2015b); although, in northwestern Argentina it can also occupy axils of bromeliads and tree holes (Stein et al. 2013; Mangudo et al. 2015). *Wyeomyia codiocampa* showed consistently and abundantly in *G. chacoensis* in Herradura and San Cayetano, as previously documented in different localities of Misiones (Campos et al. 2011) and Corrientes (Campos 2015b), suggesting a strong ecological association. Furthermore, *Wy. codiocampa* was also found in *B. vulgaris* in Herradura, being the first record of this species using this exotic bamboo as a larval habitat in Argentina. Similarly to our findings, previous research recorded *Sabethes identicus* Dyar and Knab and *Sa. undosus* Coquillett in the internodes of *Guadua* spp. in the provinces of Misiones (Campos et al. 2011) and Corrientes (Campos 2015a). It should be noted that *Sa. undosus* was collected in bamboo traps in the province of Chaco (Stein et al. 2012), but we did not find it in Colonia Benítez, where bamboo habitats were available. According to previous studies (Campos 2013), no species of the genus *Culex* were recorded in bamboo. In the Misiones province, researchers found this woody phytotelmata colonized by *Cx.* (*Car.*) *secundus* Bonne-Wepster and Bonne, *Cx.* (*Cux.*) *mollis* Dyar and Knab, *Cx.* (*Mcx.*) *neglectus* Lutz and *Cx.* (*Car.*) *soperi* Antunes and Lane (Stein et al. 2018; Rossi and Lestani 2014; Rossi 2015). Furthermore, the last two culicid species were also collected from bamboo internodes in Brazil.

In Argentina, 15 species of Culicidae have been recorded in tree holes, 9 of which were recorded in the northeast of the country (Campos and Gleiser 2016). However, we only found one mosquito species in the tree holes: *Hg. spegazzinii* in *P. nigra*, the first record of this Fabaceae species as a larval habitat for mosquitoes in Argentina (only recently it was also collected from *Prosopis caldenia* L. [Obholz et al. 2020]). *Haemagogus* species are acrodendrophilic (Roberts et al. 1981; Pinto et al. 2009) (i.e., they select the high jungle strata where arboreal animals on which *Haemagogus* females feed are found [mainly monkeys], probably responding to variations in temperature and humidity in the environment) (Marcondes and Alencar 2010). On occasions, specimens of *Haemagogus* have been found in lower strata: *Hg. leucocelaenus*

and *Hg. spegazzinii* in tree holes and ovitraps in the understory in Pampa del Indio Provincial Park, Chaco province, Argentina (Oria et al. 2012; Stein et al. 2012). In addition, the low frequency and abundance of *Haemagogus* mosquitoes in our study may result from the low height of the tree holes inspected (1 m above ground) or the human disturbance of our study sites, given that *Haemagogus* mosquitoes are generally wild and rarely leave the forest (Camargo-Neves et al. 2005).

Tree and palm leaves of different species were scattered on the ground of our sampling sites, but mosquito larvae were found only in the leaves of the native palm *A. aculeata*. These phytotelmata differ in terms of their permanence and frequency compared with on-plant phytotelmata, suggesting that they can be used as larval habitats by generalist species (Greeney 2001). For example, *Culex* (*Cux.*) *coronator* Dyar and Knab is a generalist species that breeds in both artificial containers (Rossi and Almirón 2003) and permanent ground-based larval habitats, such as ponds and lakes (Ronderos et al. 1991; D'Oria et al. 2010). When the leaves fall to the ground, they function as containers, collecting water at their broadened bases. The discovery of *C. coronator* in this habitat may be circumstantial, but it represents the first recorded instance of this mosquito species occupying this type of natural microhabitat. However, temporary phytotelmata from exotic palms (*Roystonea regia*) did not harbor culicids, suggesting that the presence of this culicid species may be influenced by other factors.

Aechmea distichantha, a native bromeliad of the Chacoan understory that formed herbaceous phytotelmata (Barberis et al. 2014), serve as important breeding sites for a diverse assemblage of Culicidae. In accordance with previous studies (Torales et al. 1972; Stein et al. 2011), *Culex* (*Mcx.*) *imitator*, *Cx.* (*Mcx.*) *davisi*, *Wy.* (*Pho.*) *muehlensi* and *Tx.* (*Lyn.*) *h. separatus* were included in its characteristic assemblage of associated culicids. Another two species of *Toxorhynchites* were previously identified breeding on the axils of *A. distichantha*: *Toxorhynchites* (*Lyn.*) *bambusicola* in the northeast of Argentina (provinces of Misiones and Corrientes) (Campos 2011; Campos et al. 2011) and *Tx.* (*Lyn.*) *theobaldi* in the northwest (Jujuy province) (Apumaita et al. 2023). According to Cardoso et al. (2015), the subgenera *Microculex* and *Phoniomyia* are considered generalist mosquitoes, inhabiting a wide range of plants that accumulate water,

although our results only partially support this characterization. *Microculex* was bred in five different phytotelmata, but *Phoniomyia* was exclusively located on the axils of *A. distichantha*. Another finding of culicid breeding in native herbaceous phytotelmata was the presence of species of the subgenus *Phytotelmatomyia* only in *Eryngium* spp., a circumstance already observed in previous studies (Campos and Lounibos 1999; Campos 2010; Campos et al. 2011). Our results in this subtropical area of Argentina show that *Cx. castroi* is the dominant culicid species in this microhabitat, whereas other studies in the temperate region have shown different patterns of abundance of *Cx. castroi*, *Cx. renatoi* and *Cx. hepperi* (Campos and Lounibos 1999; Campos 2010, 2015b; Albicócco et al. 2011; Junges et al. 2016). In the present study, we also found exotic plants that form herbaceous phytotelmata. *Alocasia macrorrhiza* — an Araceae native to southeastern Asia — is cultivated in Argentina for ornamental purposes (Crisci and Katinas 1997). The present study represents the first record of *Microculex* species, *Cx. davisi* and *Cx. imitator*, harbored in this exotic plant. In Venezuela and Brazil, *A. macrorrhiza* supports a high species richness of mosquitoes, being Sabethini the dominant tribe of this community. Furthermore, *Aedes aegypti* L. and *Ae. albopictus* Skuse, two species of medical importance, have been collected from this plant (Delgado-Petrocelli and Machado-Allison 2006; Ferreira-Keppeler et al. 2017). On the other hand, *A. odora* (Lodd.), a subspecies of *A. macrorrhiza* (Crisci and Katinas 1997), was found in the Paraná rainforest of Argentina, although without harboring Culicidae larvae (Campos et al. 2011). *Aechmea miniate*, an ornamental bromeliad species originally from Brazil, is widely cultivated due to the vibrant color of its inflorescence. In the Herradura nursery garden, this bromeliad was found as an epiphyte, on the ground next to the base of some trees, and in pots. We recorded for the first time in Argentina the presence of an individual of *Cx. davisi* in this bromeliad.

Although the presence of a host plant does not imply its use by mosquitoes to breed in, associations of high specificity allow for the prediction of the distribution of some culicid species. Currently, some species of Culicidae that are exclusive inhabitants of phytotelmata have a restricted distribution in Argentina despite the wide distribution of their host plant. This is the case for the four species in the subgenus *Phytotelmatomyia* recorded in only five provinces of Argentina

(from the subtropical to the temperate region: Corrientes, Misiones, Buenos Aires, Entre Ríos and Río Negro) (Rossi 2015; Campos et al. 2023), while the 31 species of its main host *Eryngium* spp. show a much extended distribution in the country (Martínez 2005; Campos and Gleiser 2016). Another case is *Culex davisi*, which we collected exclusively from *A. distichantha* in previous studies (Stein et al. 2018; Campos et al. 2023) and has only been recorded in the Corrientes, Chaco and Formosa provinces (Rossi 2015), while the plant host is present in other six provinces (Misiones, Santa Fe, Jujuy, Salta, Catamarca and Tucumán (Barberis et al. 2014); higher sampling effort in those provinces will probably result in a larger distribution range for the mosquito. In spite of high specificity, mosquitoes may sometimes extend further than their preferred host: *Cx. imitator* has been recorded in 10 provinces, including Buenos Aires, where Ronderos et al. (1991) collected females using CDC light traps, but its host plant *A. distichantha* was not recorded yet (Campos and Gleiser 2016).

In summary, we detected 15 of the 27 species of culicids that exclusively inhabit phytotelmata from northeastern Argentina.

The Toxorhynchitini tribe was the best represented, with four out of five species recorded in the area. Our findings highlight the presence of diverse assemblages of Culicidae in phytotelmata formed by both native and exotic plants. While the contribution of exotic plants with phytotelmata to this assemblage appeared to be lower, this aspect deserves further investigation. The role of phytotelmata in supporting the diversity of Culicidae and its epidemiological implications is underscored by the potential establishment of expanded introduced species such as *Aedes albopictus* (Skuse), which has already been collected from natural microhabitats within the northeastern region of Argentina (province of Misiones) (Alonso 2020).

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