

REPRODUCTIVE ECOLOGY IN MEXICAN ANNONACEAE: WHAT DO WE KNOW?

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Abstract

Annonaceae is a family of the order Magnoliales with a high species richness and a characteristic floral structure and composition. This lineage inhabits tropical forests around the world, and its evolutionary history has been addressed through the study of its reproductive mechanisms, mainly in Asian and South American species. In Mexico there are 75 reported species of which about 60 % are endemic, however, there are few studies of the reproductive ecology of these plants. In this review we examine the reproductive ecology of the Mexican Annonaceae, floral morphology and biology, phenology, pollination systems, and seed dispersal mechanisms. In general, Mexican Annonaceae have protogynous flowers, they are pollinated by insects, and few species of the genus *Desmopsis* have reproductive systems by cloning. Herbarium data and publications indicate that they have seasonal flowering patterns linked to rainfall. Beetles, flies, and ants can be the main pollinators, and seed dispersal depends on vertebrates. This review highlights the urgent need for in-depth study of reproductive ecology and specialized reproductive interactions in Mexico's threatened tropical systems.

Keywords: Flower, phenology, pollination, Sapranthinae, seed dispersal.

Resumen

Annonaceae es una familia del orden Magnoliales con una alta riqueza de especies y una estructura y composición floral características. Este linaje habita en bosques tropicales de todo el mundo y su historia evolutiva ha sido abordada a través del estudio de sus mecanismos reproductivos, principalmente en especies asiáticas y sudamericanas. En México se reportan 75 especies, de las cuales alrededor del 60 % son endémicas, sin embargo, existen pocos estudios de la ecología reproductiva de estas plantas. En esta revisión examinamos la ecología reproductiva de las Annonaceae mexicanas, la morfología y biología floral, la fenología, los sistemas de polinización y los mecanismos de dispersión de semillas. En general, las Annonaceae mexicanas tienen flores protóginas, son polinizadas por insectos y algunas especies del género *Desmopsis* tienen sistemas reproductivos por clonación. Las publicaciones y datos de herbario indican que tienen patrones de floración relacionados con la precipitación. Los escarabajos, las moscas y las hormigas son los polinizadores potenciales, y la dispersión de semillas depende de los vertebrados. Esta revisión destaca la urgente necesidad de un estudio profundo de la ecología reproductiva y de las interacciones especializadas en los sistemas tropicales amenazados de México.

Palabras clave: Flor, fenología, polinización, Sapranthinae, dispersión de semillas.

The Annonaceae is a pantropical family that belongs to the order Magnoliales and is the most diverse plant family in this group, with a remarkable diversity of floral architecture. This family has evolved a conserved reproductive system where a significant number of the studied species reproduce sexually, rely on beetle pollination, and exhibit primarily fragrance and food rewards as attraction mechanisms (Gottsberger 1999, Saunders 2020). This cantharophilous, or at least entomophilous, reproductive system is shared among basal angiosperm lineages (Gottsberger 1988). These mutualistic interactions have persisted for approximately 86 % of angiosperm evolutionary history, with their origins extending back to the Early Cretaceous period (Stephens *et al.* 2023).

Fossil evidence indicates that the main groups of pollinating beetles (*e.g.*, Scarabaeoidea, Tenebrionoidea, Curculionoidea, and Chrysomeloidea) diversified before the radiation and floristic dominance of angiosperms, approximately 112-93.6 Mya. (Wang *et al.* 2013). Nevertheless, from this ancestral condition, the Annonaceae have evolved distinct reproductive strategies including specialized features such as pollination chamber, thermogenesis, scents and fleshy food bodies, that distinguish them from other plant groups such as Winteraceae with open flowers with unordered arrangement of sexual whorls (Gottsberger 1988).

Research on reproductive aspects of Annonaceae, such as flower morphology, and anthesis, has been extensive, mainly on species found in South America (*e.g.*, Webber & Gottsberger 1996, Gottsberger 1999, 2012, 2014, 2016, Jürgens *et al.* 2000, Gottsberger & Webber 2018) and Asia (*e.g.*, Pang & Saunders 2014, Lau *et al.* 2017, Xue *et al.* 2020, Saunders 2020).

Existing research has demonstrated that the family is predominantly self-compatible and the outcrossing is promoted by a suite of mechanisms (Pang & Saunders 2014 and references there in). The main strategies include protogynous dichogamy, generalized in the family, and floral cohort synchrony as in *Annona mucosa* (Murray & Johnson 1987). The dichogamy is often combined with petal movements that control access to the floral chamber (*e.g.*, *Xylopia championii*, Ratnayake *et al.* 2007). Less common mechanisms are heterodichogamy for example in *Anaxogorea prinoides* which produces two floral morphs where the male and female phases are active at different complementary moments. When the male phase ends in one morph, the female phase starts in the other, ensuring cross-pollination (Teichert *et al.* 2011) and herkogamy, a physical separation of the gynoecium and androecium, as seen in some *Annona* and *Anaxogorea* (Lora *et al.* 2011, Braun & Gottsberger 2012). Some lineages like *Pseuduvaria* and *Uvariopsis* have unisexual flowers, are dioecious and have evolved functional monoecy through flower synchronization; while *Uvariopsis* individuals are truly monoic (Su & Saunders 2006, Pang *et al.* 2013). Apomixis has only been documented for *Cymbopetalum brasiliense* (Braun *et al.* 2011). Cross pollination is mainly beetle-mediated, with flowers attracting pollinators with sweet or foul scents and offering shelter, food, and thermogenesis. However, other pollinators like flies, thrips, and bees have also been recorded (Silberbauer-Gottsberger *et al.* 2003).

In Mexico Annonaceae diversity is notable with 75 species belonging to 11 genera, one of them, *Tridimeris*, being endemic to the country (Hurtado-Reveles *et al.* 2026). From this diversity, it is possible to find lineages that are morphologically and ecologically distinct across the various regions where they inhabit. The ecological affinities within Mexican Annonaceae range from a generalized preference for the tropical rain forest, as documented for the family, to very contrasting affinities. Examples of this are the genus *Sapranthus*, distributed mainly in tropical dry deciduous forest (Schatz *et al.* 2018b), the endemic *Tridimeris* restricted to cloud forest in mountainous zones (Ortiz-Rodriguez *et al.* 2024) and *Annona*, a genus appreciated for its edible fruits and medicinal properties, which have a long history of use that has resulted in these species having a widespread distribution and no clear biogeographic patterns (Schatz 1987, Hurtado-Reveles *et al.* 2026). Additionally, each genus is defined by a unique set of vegetative and floral traits (Martínez-Velarde & Fonseca 2017, Schatz *et al.* 2018a, 2018b). The morphological variation of flower comprises flower position, merism, size, color and texture, that could influence the reproductive mechanisms (van Heusden 1992, Silberbauer-Gottsberger *et al.* 2003, Saunders 2020). Variations on all these features are represented in Mexican genera, even in a single genus, for example in *Desmopsis* we can find floral variation in color, shape, size and merism (Martínez-Velarde *et al.* 2025). Ecologically, Annonaceae remains a key element of the humid forests in the country's southern region and is represented in dry and cloud forests as well. This ecological diversity makes the Mexican Annonaceae a unique, interesting model to study the evolution and

current dynamics of reproductive strategies. Therefore, understanding the reproductive systems of Annonaceae and their interactions with other ecological factors is essential for comprehending the processes and evolutionary history that take place within these ecosystems.

Based on the above information, we asked the following questions: What aspects of reproductive ecology in Mexican Annonaceae species are currently known? How many studies exist about reproductive ecology on Mexican Annonaceae and on which taxa? What are the main knowledge gaps regarding the reproductive ecology in Mexican Annonaceae?

In this review, we present an analysis of the current knowledge on the reproductive ecology of Annonaceae in Mexico, including the main reproductive characteristics in the family in order to contextualize the Mexican species. Finally, we highlight the most critical aspects that, in our view, require greater attention within this field.

Materials and methods

We made a systematic and exhaustive review of all studies which analyzed or mentioned some aspects of reproductive ecology of Mexican Annonaceae species. From these revised papers, a selection of those that mention genera or species present in Mexico was employed to the subsequent revision.

We searched the Web of Science database in 2025 using the keywords “Annonaceae,” “Mexico,” “flower,” and “ecology” across the entire available time range. Of the 154 articles retrieved, 108 were excluded because, despite containing the keyword “flower,” the focus was not on reproduction or ecology. A complementary search in Google Scholar using the same keywords yielded some additional articles beyond those already present in the Web of Science database.

To supplement this search, we consulted phenological data from taxonomic revisions of genera (*e.g.*, Maas *et al.* 2007, 2015, Schatz *et al.* 2018a, 2018b, Ortiz-Rodriguez *et al.* 2024) as well as Mexican species descriptions. Additionally, we compiled data from MEXU herbarium specimens and gathered records from the GBIF database to examine phenological patterns in the tribe Sapranthinae, which we subsequently analyzed. We selected the Sapranthinae subtribe because it is the best represented lineage in Mexico compared to other Annonaceae species.

Our review is composed by three main topics: the first is a brief yet substantial compendium of the most salient concepts, which serve to contextualize to the reader within the reproductive ecology of Annonaceae in general; the second topic is an analysis of the reproductive ecology studies in Mexican Annonaceae species, emphasizing the most outstanding findings in themes such as pollination, floral phenology, floral anatomy and seed dispersal; finally we highlight areas of future study and summarize our main reflections and conclusion from the studies on the reproductive ecology of Mexican Annonaceae species.

Mexican species contextualization: Key aspects of the reproductive ecology of Annonaceae

Reproductive ecology examines factors that led to offspring production within plant lineages. In the specific case of angiosperms, studies include the determination of floral morphology, floral phenology, reproductive systems, pollination, relative fruit and seed production, as well as fruiting phenology and dispersion.

Floral diversity in Mexican Annonaceae. Annonaceae is a lineage with well-defined and distinctive characteristics and a conserved basic structure displaying hermaphroditic, trimerous flowers with a differentiated perianth, petals arranged in two whorls, laminar stamens, and a whorled arranged apocarpous gynoecium (van Heusden 1992, Endress & Armstrong 2011) ([Figure 1A-C](#)). However, significant variation exists among species reflecting adaptations to biotic interactions (Saunders 2010, Cruz-Durán & Rosas-López 2016). Mexican species are not an exception, exhibiting significant diversity in inflorescence position, axillary being ancestral and cauliflory the derived state (Fries 1948); number of parts per whorl, trimerous, dimerous and tetramerous flowers characterizing different genera; as well as size, shape, color, and texture of perianth, for example *Tridimeris* is a genus with small flowers and light-color

and fleshy petals, while their sister genus *Sapranthus* present big flowers with dark-reddish and membranous petals (Schatz 2018b, Ortiz-Rodriguez *et al.* 2024) (Figure 2; Table 1).

In Mexico the Annonaceae family comprises 75 native species belonging to 11 genera (Hurtado-Reveles *et al.* 2026). These species inhabit mainly lowland tropical forests as well as cloud forests and are distributed in the southern region of Mexico. Such geographical distribution corresponds to the northern part of the Mesoamerican region. The 75 species present in Mexico belong to different clades within the Annonaceae phylogeny (Nge *et al.* 2024, Guo *et al.* 2017), found in three of four subfamilies: *Annona*, *Cymbopetalum*, *Guatteria*, and *Xylopia* are part of Annonoideae subfamily; *Mosannonna*, *Oxandra*, *Unonopsis*, *Desmopsis*, *Tridimeris* and *Sapranthus* belongs to Malmeoideae subfamily and finally, *Anaxagorea* is part of Anaxagoroideae. Such phylogenetic diversity is also a reflection of floral morphological and ecological diversity and therefore of the diversity of reproductive mechanisms at different levels.

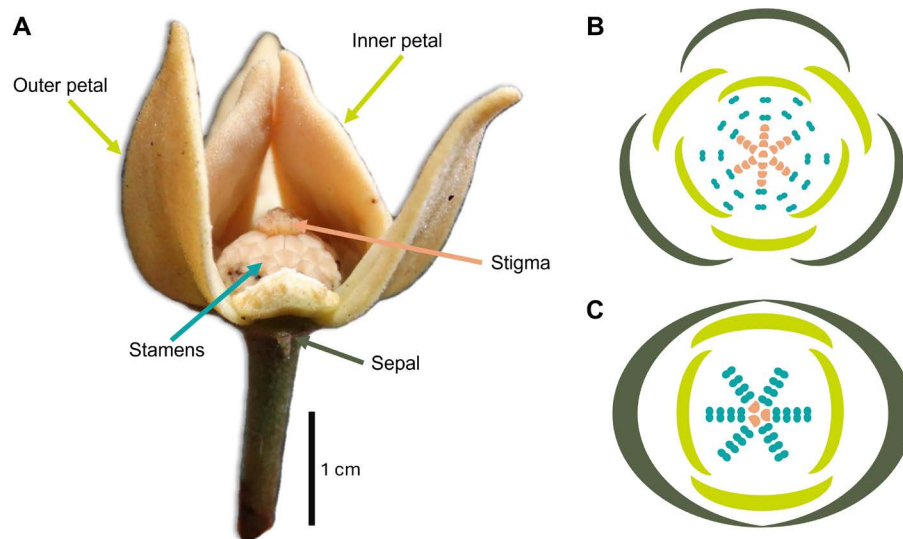


Figure 1. Illustrative schemes of the floral whorls in Mexican Annonaceae species. A. *Desmopsis dubia* flower with labels for each whorl; B. Floral diagram of a trimerous Annonaceae species; C. Floral diagram of a dimerous *Desmopsis* species. Dark green whorl represents calyx, light green whorl are the outer and inner petals, aqua whorl is the androecium and orange whorl is the gynoecium. Photography: María F. Martínez-Velarde.

Table 1. Taxonomic diversity of Annonaceae in Mexico and variability of some floral morphological traits in each genus.

Genus	Species in Mexico	Inflorescence position	Merism	Flower color diversity
<i>Anaxagorea</i>	1	Axillary	Trimerous	Yellow, cream
<i>Annona</i>	18	Axillary, trunciflory, ramiflory	Trimerous	Yellow, green pink, white, cream
<i>Cymbopetalum</i>	8	Axillary	Trimerous	Yellow, green, cream
<i>Desmopsis</i>	24	Axillary, ramiflory, trunciflory, flagelliflory	Trimerous, tetramerous	Yellow, green, pink, red
<i>Guatteria</i>	3	Axillary	Trimerous	Yellow, green
<i>Mosannonna</i>	1	Axillary	Trimerous	Yellow
<i>Oxandra</i>	2	Axillary	Trimerous	White, yellow, cream
<i>Sapranthus</i>	6	Axillary, ramiflory, trunciflory	Trimerous	Yellow, red
<i>Tridimeris</i>	10	Axillary, trunciflory	Dimerous	Green, white
<i>Unonopsis</i>	1	Ramiflory	Trimerous	Yellow
<i>Xylopia</i>	1	Axillary	Trimerous	White

Adaptive significance of cauliflory. The phenomenon of flowers arising on the trunk or stems that do not produce leaves is called cauliflory (Fries 1948, Richards 1952, Schatz & Wendt 2004). Cauliflory is present in Mexican Annonaceae and exhibits several variations (Table 1) and is likely representing an adaptive response within tropical environments (Richards 1952, Endress 2010). This trait may enhance visibility for pollinators and seed dispersers by positioning reproductive structures away from foliage (Fries 1948, Endress 2010, Hayden 2013). Extreme examples include *Desmopsis flagelliflora* and *D. terriflora* which produce inflorescences on specialized flagella that spread over the forest floor, meters from the trunk (Xicohténcatl-Lara *et al.* 2016, Martínez-Velarde *et al.* 2023).

Perianth diversity and functional specialization. The typical Annonaceae flower presents a perianth with three consecutive whorls, each composed of three pieces (van Heusden 1992, Xu & Ronse De Craene 2010). The most striking variations in the corolla and calyx in Mexican species, include a meristic reduction in the endemic genus *Tridimeris*, which shows sepals and petals in three whorls of two parts each, and the two sepals basally fused (Baillon 1869, Ortiz-Rodriguez *et al.* 2024), instead of the typical trimerous pattern in the family (Figures 1C, 2A, 2D). There are also reports of species with tetramerous flowers such as *Desmopsis cauliflora* (Schatz *et al.* 2018a) that present eight petals and four sepals. The changes in merisms are reported in other genera such as *Tetrameranthus*, some species of *Disepalum*, *Anaxagorea*, *Malmea* and *Ephedranthus* (Chatrou 1997, Maas *et al.* 2003, Westra & Maas 2012, Lopes *et al.* 2014, 2018, Li *et al.* 2016). The different observations in species of several clades suggest that changes in merism have arisen many times in the evolutionary history of Annonaceae. Analyses of the development and reduction of perianth elements are scarce, nevertheless some hypothesis suggests that is a phenomenon widely distributed throughout Annonaceae (Saunders 2010). The repeated occurrence of dimery within trimerous lineages suggests its origin lies in the loss of a single sector from every whorl of the flower but it has not been proved (Ronse Decraene & Smets 1994). The tetramery observed in the Mexican *Desmopsis cauliflora* as well as in many genera (*Desmos*, *Cananga*, *Uvaria*, and *Artabotrys*), has also not been fully clarified and it is considered a derivation of the trimery that arises either from a change in the developmental plan (tetramerous merism) or through a mechanism of duplication of the primordia in the inner whorl (Ronse Decraene & Smets 1994).

Mexican species exhibit striking variation in coloration, size, texture and shape of corolla. Colors span a broad spectrum, from green in *Cymbopetalum* to beige, pink, yellow, orange and deep red-violet as in *Sapranthus* and *Desmopsis*. Flowers are minute, 1 cm in *Desmopsis chimalapensis*, to large, 10 cm petals in *Sapranthus foetidus*. Petal texture and shape vary, including the delicate membranaceous petals of *Tridimeris hahniana*; the elongated and delicate in *D. humilis*, the fleshy, elongated in *D. migueliana*, oblanceolate and membranous in *S. foetidus* and ovate and rigid in *Cymbopetalum* species (Figure 2).

At maturity, petals of some species form pollination chambers that enclose and protect reproductive whorls, while also serving as shelter and feeding sites for pollinating insects (Gottsberger 1999, Silberbauer-Gottsberger *et al.* 2003). In other species, such as *Annona*, *Tridimeris* and *Sapranthus*, the inner petals develop basal thickenings, referred to as “food bodies” which exhibit a coloration distinct from the rest of the petal, rich in lipids and starch with a function as food for pollinators (Gottsberger & Webber 2018). A similar structure has been described on the margins of inner petals of *Cymbopetalum* species, and coleopteran pollinators were observed feeding on this specialized tissue (Murray 1993).

While the corolla function is pollinator attraction and food reward, it is hypothesized that the calyx protects the inner whorls during the early stages of development and protect the carpels after pollination (Silberbauer-Gottsberger *et al.* 2003). In *Desmopsis uxpanapensis*, the sepals persist after anthesis and fold over the carpels, suggesting a protective function (pers. obs.).

Within the different lineages of Mexican Annonaceae, Sapranthinae present a remarkable morphological diversity of the corolla, reflecting adaptations to distinct pollinator guilds across habitats ranging from dry forests to evergreen rainforests. Martínez-Velarde *et al.* (2025) analyzed the morphological evolution of flowers in Neotropical Sapranthinae and found that traits such as corolla color and shape could impacted in the attraction of different floral visitors and thus present a phylogenetic sign that supports the hypotheses of flower influencing the evolutionary history of each

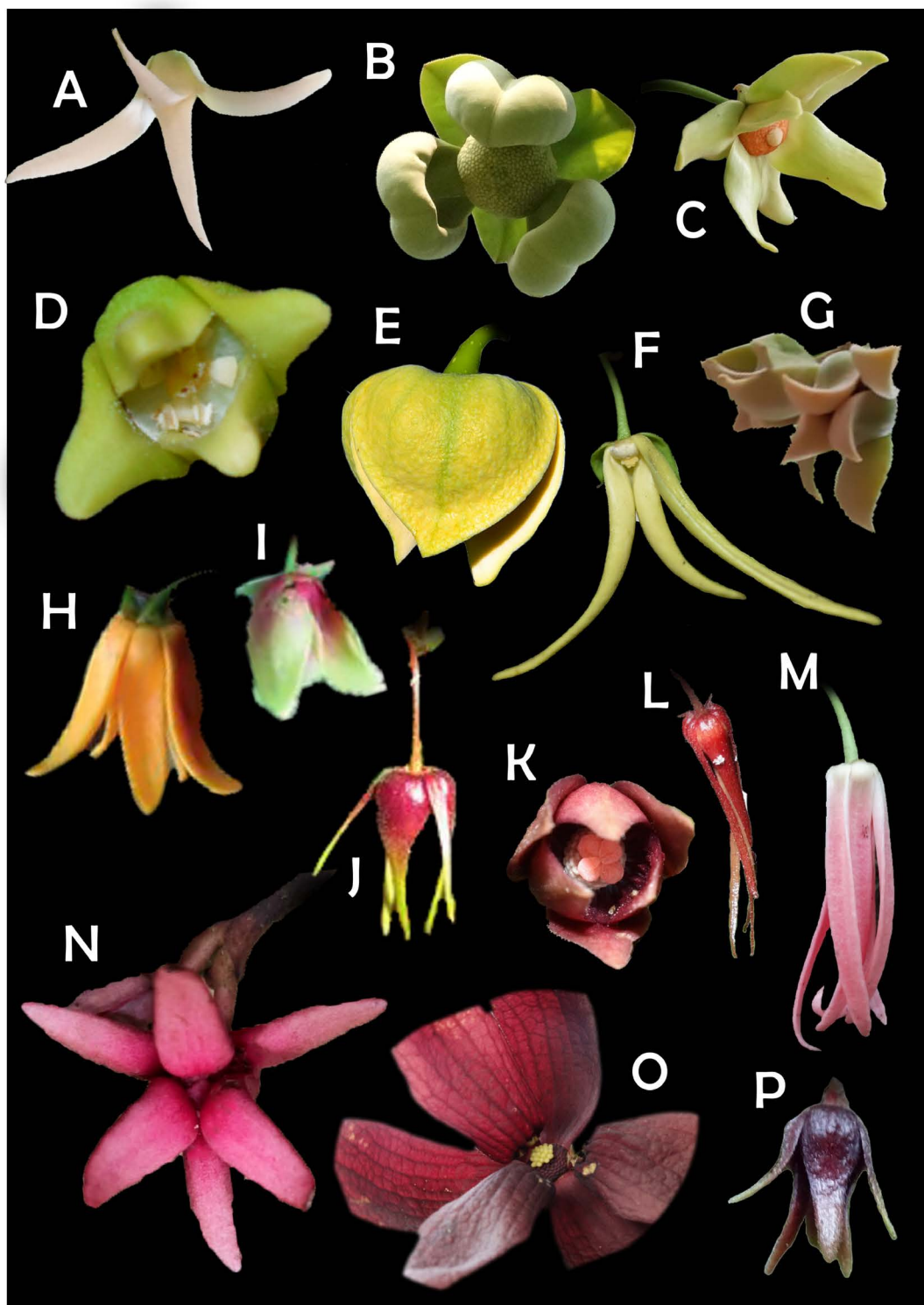


Figure 2. Morphological floral diversity in Mexican species of Annonaceae. A. *Tridimeris huatuscoana*, B. *Cymbopetalum baillonii*, C. *Guatteria galeotiana*, D. *Tridimeris nebulosa*, E. *Annona glabra*, F. *Desmopsis uxpanapensis*, G. *Desmopsis dubia*, H. *Desmopsis lanceolata*, I. *Sapranthus microcarpus*, J. *Desmopsis monticola*, K. *Desmopsis flagelliflora*, L. *Desmopsis humilis*, M. *Desmopsis migueliana*, N. *Desmopsis terriflora*, O. *Sapranthus violaceus*, P. *Desmopsis chimalapensis*. Photography authors: Guadalupe Amancio (F), María F. Martínez-Velarde (A-C, G, L-P), Leopoldo Hurtado Reveles (D) and Andrés Ortiz-Rodríguez (H-K).

lineage. Examples in Mexican species are *Desmopsis terriflora* that have red flowers and is visited by flies (Martínez-Velarde *et al.* 2023). During field observations on reproductive stages of *Desmopsis* flowers made by the authors in 2024 and 2025, we have observed that flowers of *Desmopsis dubia* and *D. uxpanapensis* are visited by small beetles. These two species exhibit yellow to orange corollas, coinciding with the findings of Martínez-Velarde *et al.* (2025).

The androecium and gynoecium. The androecium in Annonaceae varies from rarely few stamens (3-6) to generally more than 12. In Mexican species stamens are generally numerous, laminar with a bisporangiate thecae that dehisce longitudinally and a shield-shaped connective prolongations that protect developing anthers and may prevent self-pollination during the male phase (Webber & Gottsberger 1996, Pang & Saunders 2014).

The gynoecium in Annonaceae is apocarpous, with free and separate carpels ranging from only 1-5 in *Tridimeris* to more than one hundred in *Annona* species. Each carpel is topped by the sessile stigma that captures pollen and facilitates its germination. Stigma morphology varies widely among species but is generally rounded; the style is generally absent or is difficult to separate from the stigma. During anthesis, stigmas may or may not produce exudates. In *Annona*, stigmas form a *compitum*, a shared-receptive surface that allows pollen germination and facilitates the pollen tube to reach any ovule within the carpels, enhancing fertilization probability (Endress 1982).

Studies in Mexican species. What do we know about the Annonaceae reproduction?

Studies in Mexican species relate to varied topics, mainly taxonomic where some data on reproduction is included. In this respect, revisions of major genera have been made (*e.g.*, Murray 1993, Schatz *et al.* 2018a, 2018b), as well as in descriptions of new species. Works on phenology, pollination and seed dispersion and germination are especially scanty. Below we present the most relevant findings for Mexican species.

Floral phenology in Mexican Annonaceae. Phenology examines the timing of recurrent biological events (leafing, flowering, fruiting) and their biotic/abiotic drivers (Lieth 1974). This field is crucial for understanding ecological and evolutionary processes, from organismal physiology to global nutrient cycles (Forrest & Miller-Rushing 2010). In Annonaceae, reproductive phenology directly influences pollinator and disperser interactions, flowering responds to environmental signals (photoperiod, temperature, precipitation) interacting with genetic controls (Primack 1985, 1987, Mouradov *et al.* 2002). Biotic factors like pollinators and herbivores further shape these cycles (Brody 1997). Reproductive phenology correlates strongly with rainfall and solar irradiation (Wright & van Schaik 1994), particularly in seasonal forests where flowering often coincides with rainy season onset (Bullock & Solís-Magallanes 1990). While tropical rainforest phenology was historically considered non-seasonal, recent work demonstrates solar irradiation and global events (*e.g.*, El Niño) drive marked seasonality even in equatorial zones (Mendoza *et al.* 2017).

The sole field study in Mexico, regarding phenology in Annonaceae, examined the phenological strategies of three *Annona* species commercially relevant in Chiapas dry forest, finding divergent reproductive timing: *A. reticulata* flowered in the dry season (November-December), while *A. macroprophyllata* and *A. purpurea* peaked during rains (May-June) (González-Esquinca *et al.* 2016).

Herbarium records of Mexican Annonaceae found in literature suggest most species bloom from winter to summer, with autumn declines. Genera show distinct patterns: *Cymbopetalum* flowers from March to June, *Unonopsis mexicana* flowers in April (Maas *et al.* 2007), *Guatteria* (January-May; Jun-November) (Maas *et al.* 2015), and *Annona* (primarily March-May), as well as *Desmopsis*, which flowers year-round, peaking in March. In contrast, *Tridimeris* has blooming periods from October-December and March-May (Ortiz-Rodríguez & Marinero-Sobal 2022, Ortiz-Rodríguez *et al.* 2024) or August (Ortiz-Rodríguez *et al.* 2016).

An analysis of 464 Sapranthinae specimens (Table S1), revealed flowering peaks during spring: *Desmopsis* flowers predominantly in March, while *Sapranthus* and *Tridimeris* mainly bloom in May (Figure 3). These synchronous patterns may be shaped by evolutionary history since these ecological traits in plants are phylogenetically conserved, despite competitive exclusion prediction (Hardin 1960), which would predict community assemblages composed of highly divergent species as an adaptive response to a history of competition among similar species (Webb *et al.* 2002).

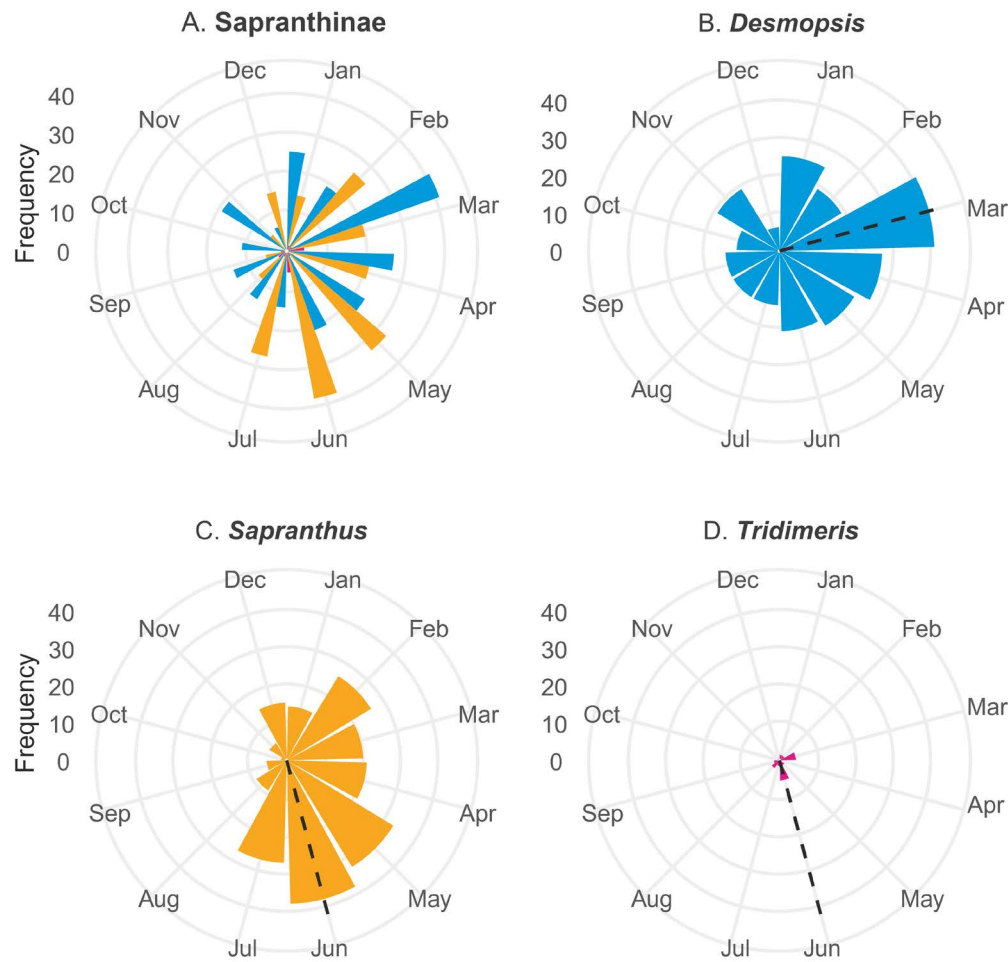


Figure 3. Flowering peaks of the three genera of Sapranthinae subtribe (N = 464 herbarium specimens with flowers). The black dashed line shows the month corresponding to the flowering peak of each genus.

However, the opposite pattern is frequently observed in natural communities (Bengtsson *et al.* 1994). Among other conditions, ecologically similar or closely related species may coexist if there is local selection for diverse phenotypes or if individual variation allows species to coexist (Cadotte *et al.* 2017). In the case of flowering among sympatric Annonaceae species, pronounced peaks occur in which most species within the group bloom during the same season (e.g., *Desmopsis* spp. Figure 3). The exact causes of this pattern remain unknown, but the family provides an excellent model for studying these ecological paradoxes.

Reproductive systems. Plant reproductive systems encompass the processes by which species generate offspring, operating through either asexual or sexual mechanisms. In asexual reproduction, plants produce genetically identical offspring without fertilization in varied forms (de Kroons & Hutchings 1995). Often plants reproduce both sexually and asexually, avoiding dependence on a single reproduction method (Evert & Eichhorn 2013, Simpson 2019, Taiz *et al.* 2023). In Annonaceae, some species can reproduce both sexually and asexually, for example, through stolons. Four Mexican species belonging to the genus *Desmopsis* are clonal and phylogenetically related: *D. chimalapensis*, *D. humilis*, *D. monticola*, and *D. flagelliflora* (Ortiz-Rodriguez *et al.* 2018, Martínez-Velarde *et al.* 2023). These species develop a horizontal stem known as a stolon, which grows underground and, through its apical meristem, gives rise to a new individual that eventually becomes independent once the stolon breaks.

Although this phenomenon has not been thoroughly studied, clonal species also produce flowers and fruits, indicating mixed reproductive strategies ensuring genetic variation at the population level. It also has been inferred that these species employ different reproductive strategies depending on environmental conditions where cloning ensures survival under unfavorable conditions (Kemball & Marshall 1995), while sexual reproduction is the predominant mechanism during stable periods (Niva *et al.* 2006).

Sexual reproduction systems involve genetic recombination between two gametes, which may originate from the same flower (autogamy), from different flowers of the same individual (geitonogamy), or from flowers of different individuals (xenogamy). The genetic compatibility of these three reproductive modes is related to their ability to recombine DNA with genetically similar plants. These reproductive systems are particularly interesting because much of the genetic diversity within a population depends on the mode of crossing, which in turn is closely influenced by the efficiency of pollinators in transporting pollen.

In autogamy, flowers typically do not require a vector to transfer pollen from the theca to the stigma. Autogamous plants are usually characterized by self-compatibility, and this trait enables fecundation by auto pollination. Some Annonaceae species reported to exhibit autogamy include *Guatteria* (Gottsberger 1970), *Polyalthia littoralis* (Okada 1990), and *Cymbopetalum brasiliense* (Braun *et al.* 2011). They develop strategies involving changes in the position of floral structures during anthesis, ensuring that pollen reaches the stigma of the same flower.

Autogamy occurs when a population faces environmental stress that may compromise reproductive success; it is more frequent in pioneer or colonizing plants establishing in new sites where the effective population size remains small and opportunities for cross-pollination are limited (Svensson *et al.* 2006). However, in Annonaceae self-pollination occurs multiple times throughout phylogeny and is considered a conserved state (Saunders 2020). Some studies in Asian species such as *Disepalum anomalum* (Li *et al.* 2016), *Uvaria concava* (Silberbauer-Gottsberger *et al.* 2003), and Neotropical species such as *Asimina rugelii* (Norman 2003), *Anaxagorea dolichocarpa* (Braun & Gottsberger 2012) and *A. crassipetala* (Armstrong & Marsh 1997) observed the presence of seed production after self-pollination as a consequence of sexual phases overlapping. Under these conditions, autogamy emerges as a successful strategy that ensures seed production despite limited cross-pollination (Saunders 2020). Although autogamy is analyzed in Annonaceae, in the case of Mexican species and their relatives, there are no data about the autogamy effects in the reproductive ecology.

Self-compatible plants present strategies to prevent self-pollination during specific reproductive phases, known as incompatibility systems. These strategies share a common trait: they help maintain heterozygosity within the population (Frankel & Galun 1977).

Certain incompatibility systems are regulated by a series of genes that activate in both male and female structures, particularly in the stigma and style. Likewise, floral phenology can influence the degree and frequency of reproductive systems within the family (Armstrong & Marsh 1997).

In Annonaceae, some species have developed a temporal separation system for sexual whorls' maturation, in which the gynoecium matures and becomes receptive first, followed by pollen release (Saunders 2020, Martínez-Velarde *et al.* 2023). This mechanism, where sexual whorls develop at different times, is known as dichogamy (Endress 2010). Dichogamy generally manifests in two strategies: protogyny, where the female phase activates first, and protandry, where pollen is released first. Most Annonaceae species are protogynous (Saunders 2012) making this strategy the most well-documented in relation to anthesis within the family.

In Mexico, anthesis has been studied in the endemic *Desmopsis terriflora* (Martínez-Velarde *et al.* 2023). These protogynous flowers initiate the female phase by forming a pollination chamber, which consists of petals converging at the apex while leaving cavities at the base of the flower. These openings restrict entry to insects of specific sizes, which are potential pollinators. Such insects are attracted by floral fragrances released at the onset of the female phase. Fragrances vary by species and, from a human perspective, range from fermented fruit-like scents, as observed in *D. terriflora*, *Annona cherimola*, and *D. dubia* (Tsukada *et al.* 2017, Espinosa-Jiménez and Ortiz-Rodríguez 2020), to bad smelling odors resembling decaying flesh, such as in some *Sapranthus* species (Schatz *et al.* 2018b). A recent study showed that in *Annona macrophyllata* emitted different odors during anthesis: an attractive sweet

and fruity scent when the flower was in female phase, and a repellent fermented odor during male phase (Llaven-Albores *et al.* 2025). During female phase, stigmas become turgid, increasing in size, and in some cases, secrete exudates that serve both as germination mediums for pollen grains and as attractants for pollinators. Subsequently, the flower enters an interphase, during which stigmas lose receptivity, detach from carpels, fragrance release ceases, petals close, but anthers remain sealed. This interphase is highly variable but is generally shorter than the female phase. This moment in anthesis is critical, as it distinctly separates female and male phases within a single flower, increasing the likelihood of cross-pollination.

Finally, petals open, exposing anthers to pollinators. Floral fragrance release resumes, and anthers progressively dehisce, allowing pollen liberation. The male phase is the shortest in anthesis, as both stamens and petals detach at its onset. Ultimately, the only remaining structures attached to the pedicel are the carpels, which, if fertilized, will develop into fruit. Figure 4 outlines the general phenological behavior of the flowers in a dichogamous species, similar to the studied Mexican species.

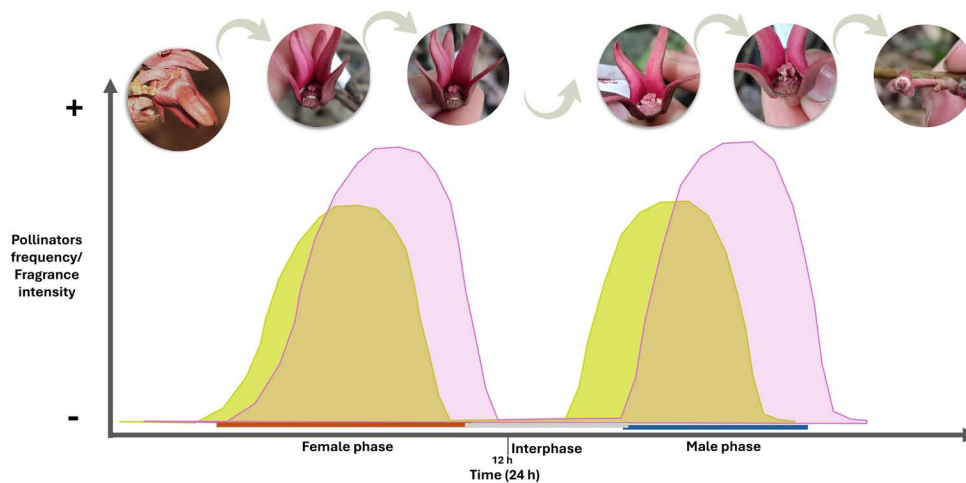


Figure 4. Illustrative scheme of the anthesis in a flower of Sapranthinae subtribe. The yellow curve shows the release of fragrance, and the purple curve shows the floral visitors frequency. Circles with photographs show morphological changes in *Desmopsis terriflora* flowers during anthesis.

The duration of anthesis varies among species groups, ranging from 3.5 hours in *Annona crassiflora* (Saravy *et al.* 2022) to 4-5 days in *Uvariopsis congolana* (Gottsberger *et al.* 2011). In *D. uxpanapensis*, an endemic species to southern Mexico, anthesis lasts around 25 hours.

The degree of incompatibility has been demonstrated in various Annonaceae species, particularly those of economic value, such as *Annona cherimola*. Lora *et al.* (2011) analyzed stigma receptivity to pollen from the same individual as well as from other trees in different environments. Their results indicated that a portion of the seeds were produced through self-fertilization and that self-pollination is possible even in dichogamous species.

Pollinators and floral visitors. Annonaceae flowers are predominantly entomophilous, relying on insects for pollination through specialized adaptations including distinctive colors, scents, and pollination chambers that function as attractants and rewards. Small beetles (Curculionidae, Nitidulidae) are recognized as the family's ancestral pollinators globally (Saunders 2012, Gottsberger 2014).

Pioneering studies on Annonaceae floral biology were conducted at the UNAM Los Tuxtlas Tropical Biological Station in Veracruz uncovered three different pollination mechanisms within the same ecosystem. At this site Schatz (1987), studied the flower of *Mosannonna depressa* (then identified as *Malmea* aff. *depressa*) and found that the margins of the inner petals showed a distinctive bright, white and glossy appearance, suggesting a high lipid content. Schatz identified these as “food bodies” as he had observed in other genera, like *Sapranthus*, though differing in

morphology. Further field observations confirmed that *Cyclocephala sparsa* (Scarabaeidae: Dynastinae) actively fed upon the food bodies. The ingestion of the food bodies forced the insect to a position where its body touched simultaneously the stigmas and stamens, facilitating pollen transfer.

Also at Los Tuxtlas, Murray & Johnson (1987) documented the anthesis in *Annona mucosa* (then reported as *Rollinia jimenezii*). The flowers in this species are fleshy, pale yellow, with petals fused at the base forming a pollination chamber. The anthesis begins with the release of a “sweet, yeasty scent” during the female phase that lowers in intensity from 23 h to 5:00 h and increases again until the shedding of stigmas at 14:00 h the next day. The pollen release (male phase) is preceded by an hour of no activity, between 14:00 and 15:00 h. The 12 monitored trees showed a synchronized flowering pattern initiating every 48 h period, where flowers are mostly female one day and mostly male the following day. However, there are also periods of asynchronous flowering which changes the pool of potential individuals for outcrossing. This flexibility in the strategy reduces geitonogamy, while allowing for a variety of outcrossing partners. The presence of unquantified small Nitidulidae inside the flowers throughout the anthesis led to considering them effective pollinators.

The third early work on Annonaceae reproductive ecology carried out at Los Tuxtlas was on *Cymbopetalum baillonii* (Murray 1993). She observed the floral biology and anthesis events of 85 marked flowers from 5 individuals, over six days. This species showed cantharophilous, big, fleshy, cymbiform inner petals with a distinct strip at their base rich in protein and carbohydrates. The anthesis were protogynous but occurred over two consecutive nights, where the flowers were thermogenic and emitted a “light pleasant fruity” during the female phase, that changed to a “sweet-spicy” scent during the male phase. *Cyclocephala sparsa* (Scarabaeidae) was the only species visiting the flowers although with an extremely low visitation rate, with only four insects recorded. Nevertheless, *C. sparsa* was appointed as the potential pollinator from a combination of evidence: the discovery of *C. baillonii* pollen on one beetle, the recorded of another individual up to 20 h within a single flower across both sexual phases, and the presence of gnawing marks on the food tissue.

Not all floral visitors function as effective pollinators. In *Desmopsis flagelliflora*, 18 visitor species were recorded - including flies, ants, and non-insect arthropods (spiders, springtails) - yet only the abundant fly *Puliciphora* sp. (Phoridae) showed frequent reproductive structure contact suggesting pollinator status (Xicohtencatl-Lara *et al.* 2016). Similarly, *D. terriflora* appears pollinated by an ant-dipteran combination (Martínez-Velarde *et al.* 2023). The most recent study on the reproductive ecology of the Mexican species *Annona macropophyllata* examined 10 trees and 3,035 flowers within an agroforestry ecosystem in Chiapas. The researchers found that this species exhibits a nocturnal anthesis lasting eight hours, characterized by a synchronous pattern of female and male phases. They also documented 15 pollinator species belonging to the beetle genera *Colopterus* and *Carpophilus* (Coleoptera: Nitidulidae). Finally, they analyzed the chemical composition of floral fragrances released during anthesis and observed that the scents produced in the female and male phases differ in their molecular composition, being attractive to insects during the female phase and repellent during male phase (Llaven-Albores *et al.* 2025). These few documented cases underscore the critical need for comprehensive studies of anthesis events, visitor effectiveness and pollination across Mexico's Annonaceae, particularly in understudied regions.

Fruit and seed production. Successful pollination leads to fruit and seed development, a process governed by multiple factors including resource availability, pollen quality and quantity, and pollinator effectiveness (Armstrong & Marsh 1997). Following fertilization, the combined selective pressures of pollinators and seed predators shape reproductive outcomes (Augspurger 1981). In Annonaceae, it has been inferred that the ancestral fruit was small and apocarpous with a short stipe, a low number of fruitlets (monocarps), as well as few, small seeds. It was most likely indehiscent and potentially moniliform (Onstein *et al.* 2019). Fruits in extant species are mostly apocarpic, although some genera present syncarpic or pseudosyncarpic fruits. The genus *Annona*, including commercially important species, is characterized by pseudosyncarpic fruits. In Mexico, research on Annonaceae fruit production has been largely limited to commercially important species, with few studies examining wild populations. One of the rare exceptions focused on a population of *Desmopsis flagelliflora*, where researchers monitored reproductive stages from buds

through fruit development across 51 individuals during a single season. The study found that while 57 % of flowers produced fruits, only 47.5 % of these fruit initials reached maturity, and merely 10.8 % ultimately contained viable seeds (Xicohténcatl-Lara *et al.* 2016).

These metrics collectively demonstrate remarkably low reproductive efficiency in this species, highlighting both the need for broader investigations of wild Annonaceae populations and the potential constraints affecting their reproductive success.

Seed dispersal. Successful reproduction requires seeds to be dispersed by frugivores before falling victim to insects, fungi, or bacteria. This mutualistic process involves seed consumption, transportation from the parent plant, and deposition in suitable germination sites (Jordano 2000). Regarding seed dispersal in Annonaceae, Onstein *et al.* (2019) correlated fruit morphology (15 traits from a pool of 228 species) to different dispersers. They found correlations between large fruits and seeds with large bodied frugivores; dull green or brown colors with mammal, mainly primate dispersal and smooth, bright colored exocarps and dehiscent fruits with bird dispersal. In all these cases there were implications for Long Distance Dispersion events (LDD). However, despite the association of bats to cauliflory, they failed to find a correlation between cauliflory and LDD. More recently, Lopes *et al.* (2024) concluded that the success of LDD in Annonaceae depends on the availability of frugivore lineages that can interact with existing fruit syndromes. They described two key biogeographical events that exemplify this. First, the ancestor of the tribe Bocageae dispersion from Africa via the Boreotropical corridor during the Eocene and posterior colonization of the Neotropics, probably was facilitated by a megafauna syndrome (large, syncarpous fruits). Later, during the Miocene, the genus *Cymbopetalum* probably expanded northwards from South America by a bird dispersal syndrome (dehiscent and brightly colored fruits); this process coincided with the radiation of passerine frugivorous birds in the region. In Mexican Annonaceae are represented all the above-mentioned fruit characteristics but only the ecology of *Cymbopetalum baillonii* has been studied at Los Tuxtlas.

The first study conducted at Los Tuxtlas, on ten *C. baillonii* trees revealed critical dispersal dynamics: when fruits remained beneath parent trees, two rodent species consumed 80 % of seeds, and > 90 % of germinated seedlings died within a year. The research identified 24 bird species and the squirrel *Sciurus deppei* as key dispersers. Crucially, seeds deposited > 30 m from parent trees or beneath heterospecific plants showed significantly higher germination and survival than those near parent trees or under conspecifics (Coates-Estrada & Estrada 1988).

During her work at Los Tuxtlas, Murray (1993) made observations on fruit maturation and seed dispersal on the same species. She found that the fruits, aggregates of monocarps that dehisce longitudinally early in the morning, exposed numerous, conspicuous black seeds with an orange-red aril. She reported a total of 31 bird species feeding on the seeds of *C. baillonii*; most of these were effective dispersers, while only one bird species, *Amazona autumnalis* was a destructive seed predator, along with squirrels (*Sciurus deppei*). Fruit maturation was highly asynchronous, resulting in a prolonged availability of seeds throughout the fruiting season, peaking from March to May. The seeds on open fruits were quickly removed, often in less than 24 h after opening. Seeds that fall into the ground, however, were consumed by rodents (*e.g.*, *Heteromys* and *Peromyscus*) leading to low seedling recruitment under the parent tree. Since all *Cymbopetalum* species have a similar fruit morphology and seed presentation, she inferred that the dispersal in the genus was by birds. Further studies conducted at Los Tuxtlas revealed that the rodent population consumes seeds from various species, including *Cymbopetalum baillonii*, after their dispersal, probably influencing the forest's floristic composition (Sánchez-Cordero & Martínez-Gallardo 1998). As shown by these studies, research on only one species has provided insights into classic ecological questions such as escape the parent tree, mutualistic and antagonistic networks with dispersers and predators, community assembly and biodiversity. Evolutionary implications of these interactions are the adaptations to bird dispersal, life history strategies as well as coevolution with dispersers.

Seed germination. Regarding germination, existing studies are limited to commercially important *Annona* species, with only one case documenting successful seed germination in wild *Tridimeris huatuscoana* (Ortiz-Rodriguez & Marinero-Sobal 2022). Annonaceae seed are mainly orthodox (they survive periods of desiccation and freezing dur-

ing ex situ conservation), some species are recalcitrant (they do not survive drying and freezing during ex situ conservation) (Ferreira *et al.* 2019) with implications in their dispersion that remain to be studied. Research has found that lirinodine appears in early developmental stages of *Annona diversifolia*, suggesting a protective role and involvement in cellular regulation (de la Cruz-Chacón *et al.* 2011). In *Annona macrophyllata*, acetogenins and alkaloids have been detected in idioblasts of the endosperm and embryonic axis, indicating potential functions in embryonic development and seed metabolism (Brechú-Franco *et al.* 2016). Additionally in *A. macrophyllata* and *A. purpurea*, soaking seeds in GA has shown to accelerate germination (Ferreira *et al.* 2016). Further research is needed to explore the adaptive and evolutionary significance of seeds in Mexican species, since biomechanical adaptations have been identified that ensure germination while maintaining protection against predators (Lopes *et al.* 2024).

Reflections

The striking floral morphological diversity observed in Mexican Annonaceae species strongly suggests corresponding complexity in their ecological relationships and reproductive strategies. Given their taxonomic richness and evolutionary significance in Mexican tropical forests, existing research provides valuable yet incipient insights into processes such as floral phenology, anthesis, pollination, fruiting and seed production and dispersal mechanisms.

The exceptional endemism of Mexican Annonaceae offers unique insights into the family's ecological adaptations and evolutionary patterns. Addressing current knowledge gaps requires expanded research on reproductive ecology across habitats and lineages, which would simultaneously advance our understanding of diversification processes and inform tropical ecosystem conservation.

Supplementary material

Supplemental data for this article can be accessed here: <https://doi.org/10.17129/botsci.3742>

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