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Review

The evolution of key functional floral traits in the early divergent angiosperm family Annonaceae

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Running title: functional floral traits in Annonaceae

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Abstract Potential key functional floral traits are assessed in the species-rich early divergent angiosperm family Annonaceae. Pollinators (generally beetles) are attracted by various cues (particularly visual, olfactory and thermogenic), with pollinators rewarded by nectar (generally as stigmatic exudate), heat and protection within the partially enclosed floral chamber. Petals sometimes function as pollinator brood sites, although this may be deceptive. Annonaceae species are self-compatible, with outcrossing promoted by a combination of protogyny, herkogamy, floral synchrony and dicliny. Pollination efficiency is enhanced by pollen aggregation, changes in anthesis duration, and pollinator trapping involving a close alignment between petal movements and the circadian rhythms of pollinators. Most Annonaceae flowers are apocarpous, with syncarpy restricted to very few lineages; fertilization is therefore optimized by

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intercarpellary growth of pollen tubes, either via stigmatic exudate (suprastylar extragynoecial compitum, EGC) or possibly the floral receptacle (infrastylar EGC). Although Annonaceae lack a distinct style, the stigmas in several lineages are elongated to form ‘pseudostyles’ that are hypothesized to function as sites for pollen competition. Flowers can be regarded as immature fruits in which the ovules are yet to be fertilized, with floral traits that may have little selective advantage during anthesis theoretically promoting fruit and seed dispersal. The plesiomorphic apocarpous trait may have been perpetuated in Annonaceae flowers since it promotes the independent dispersal of fruit monocarps (derived from separate carpels), thereby maximizing the spatial/temporal distance between seedlings. This might compensate for the lack of genetic diversity among seeds within fruits arising from the limited diversity of pollen donors.

Key words: circadian pollinator trapping, extragynoecial compitum, fertilization success, floral synchrony, pollen competition, pollination efficiency, pollinator attraction.

1 Introduction

Floral morphology is an outstanding model system for understanding evolutionary processes: the diversity of floral forms, with their often-flamboyant visual displays, attractive scents and energy-rich pollinator rewards, present excellent opportunities for investigating natural selection. Plant-pollinator interactions have undoubtedly driven many floral adaptations, with co-evolution occurring wherever there is a high degree of specificity. Evolution is also driven by sexual selection, which is manifested in angiosperms as pollen competition between microgametophytes as the pollen tubes penetrate the carpel and as female choice through selective pollination and zygote abortion (Moore & Pannell, 2011). Flowers can furthermore be regarded as immature fruits in which the ovules are yet to be fertilized: although floral structure inevitably imposes constraints on fruit structure (and vice versa), anatomical features of the flower that may have little selective advantage during anthesis can theoretically promote fruit and seed dispersal. Evolutionary considerations of floral form and function must therefore also accommodate corresponding assessments of the fruit.

Early divergent angiosperms conspicuously lack two widely recognized key evolutionary innovations associated with more derived angiosperm lineages: their carpels are apocarpous (not fused) and they lack a style. The evolution of syncarpy (the congenital fusion of carpels) endows significant advantages by enabling pollen grains deposited on any stigma to potentially fertilize any ovule in the flower, hence promoting pollination efficiency by minimizing ovule wastage and increasing seedset (Endress, 1982; Armbruster et al., 2002). The evolution of styles is likely to improve the accuracy of the spatial positioning of stigmas (mirroring the positioning of anthers conferred by filaments), hence enhancing the efficiency of pollen transfer to and from pollinators and providing greater evolutionary lability for enabling plant-pollinator specificity. Syncarpy and the evolution of styles have also been explained by reference to pollen competition (Lora et al., 2016), in which microgametophytes compete as they grow through the style and are selected by the sporophyte.

This review focuses on the species-rich early divergent angiosperm family Annonaceae, which is typical of other magnoliid lineages in possessing an apocarpous gynoecium composed of carpels that lack a distinct style (Saunders, 2010). The family is characterized by flowers that are typically pendent, trimerous and bisexual, with numerous free reproductive organs. The family lacks a biochemically mediated self-incompatibility mechanism, although there are various adaptations that enhance outcrossing (Pang & Saunders, 2014), including protogyny (the temporal separation of pistillate and staminate function within the flower), which is prevalent amongst early divergent angiosperms. Although the perianth in most early divergent lineages transition between sepal-like outer tepals and petal-like inner tepals, Annonaceae flowers possess whorls of distinct sepals and petals (Saunders, 2010). The two petal whorls are furthermore generally morphologically distinct, with the inner petals often convergent or connivent to form a partially enclosed floral chamber that is functionally important during pollination (Saunders, 2010).

Several characteristics of the family render it ideal for drawing inferences of broader relevance: it is a major component of tropical lowland rainforests both in terms of biomass and species richness (e.g., Gentry, 1993; Punyasena et al., 2008); it is well-known taxonomically, with many genera recently monographed (Erkens et al., 2012); robust, well-resolved phylogenies are available for most lineages (Guo et al., 2017b); and there are many detailed empirical assessments of the pollination ecology and breeding systems of representative taxa (Saunders, 2012). Early divergent angiosperm families such as Annonaceae provide invaluable insights into the early evolutionary diversification of floral morphology. Annonaceae are of phylogenetic importance as they possess several key apomorphic characteristics that are hypothesized to have evolved independently from those in eudicots, including differentiated perianth whorls, extragynoecial compita, syncarpy, and the evolution of ‘pseudostyles’ that are possibly functionally analogous with true styles in derived angiosperm lineages.

The morphology and function of Annonaceae floral traits are reviewed here to clarify our understanding of mechanisms that enhance pollinator attraction, maximize the efficiency of pollination and optimize fertilization success, whilst avoiding self-pollination and protecting floral reproductive organs against herbivory. Evolutionary innovations that overcome the limitations of apocarpy are likely to have been key to this success: these mechanisms are hypothesized here to include the evolution of extragynoecial compita that enable intercarpellary growth of pollen tubes, the evolutionary increase of ovule number per carpel, and the independent origin of syncarpy.

2 Floral adaptations to different pollinator guilds

Annonaceae flowers are predominantly pollinated by beetles (Coleoptera), but also by other insect orders, including thrips (Thysanoptera), flies (Diptera), bees (Hymenoptera) and rarely also cockroaches (Blattodea) (Saunders, 2012). There is little evidence for species-specific plant-pollinator co-evolution: the flowers are often visited by multiple species simultaneously and the dominant pollinating species are likely to vary geographically between populations and temporally between flowering seasons (Herrera, 2005), as observed in *Annona* (Kishore et al., 2012; Costa et al., 2017). Most Annonaceae species are consistently visited by representatives of a single pollinator guild, however, and distinct pollination syndromes are therefore recognizable (Saunders, 2012).

Two contrasting beetle-pollination syndromes have been identified based on the overall size of the beetle (Saunders, 2012). Most Annonaceae species are pollinated by small beetles in the families Curculionidae (weevils), Nitidulidae (sap beetles) and/or Staphylinidae (rove beetles); these beetles are invariably phytophagous and often consume nectar and pollen. Some Annonaceae lineages are pollinated by larger scarab beetles in Scarabaeidae subfamilies Melolonthinae and Dynastinae; scarab beetles are also phytophagous and since they often consume petals and other floral tissues the flowers are accordingly robust, with a thick, fleshy perianth.

Small-beetle pollination has been inferred as the ancestral pollination system in Annonaceae, with all other systems derived (Saunders, 2012). The most important families of small-beetle pollinators originated prior to Annonaceae, with Staphylinidae, Nitidulidae and Curculionidae having minimum stem ages estimated at 198.7, 184.2 and 118.7 Mya, respectively (McKenna & Farrell, 2009), whereas the Annonaceae stem lineage originated at least 108.6 Mya (Xue et al., 2020). Plant-pollinator interactions have undoubtedly served as significant evolutionary drivers of species diversity in Annonaceae, influencing floral form and function.

2.1 Petal color

Although many early studies implicitly assumed that phytophagous insects and insect pollinators rely on olfactory cues for locating host plants, subsequent research demonstrated the importance of vision, either in isolation or synergistically with olfaction (Reeves, 2011). Insects possess highly sensitive visual systems with up to six spectral classes of photoreceptors (Briscoe & Chittka, 2001). All the major guilds of Annonaceae pollinators are able to perceive a broad spectrum of light, ranging from 340 nm (ultraviolet, UV) through 650 nm (red), including beetles (Curculionidae: Hausmann et al., 2004; Nitidulidae: Döring et al., 2012) as well as thrips (Matteson et al., 1992), flies (Lunau, 2014) and bees (Avarguès-Weber et al., 2012). Most Annonaceae flowers have petals that are cream or yellow and are often flushed pink, although occasionally with a more intense red pigmentation. The pervasive hypothesis that bees are not attracted to red flowers has been refuted (e.g., Chittka & Waser, 1997), and there are examples of red-flowered Annonaceae species that are pollinated by bees (e.g., *Uvaria concava*: Silberbauer-Gottsberger et al., 2003). No published study has addressed the occurrence of UV reflectance in Annonaceae flowers, but it is predicted to occur given the ability of insect pollinators to perceive such short wavelengths of light.

The beetles that pollinate Annonaceae flowers typically exhibit crepuscular circadian rhythms (Lau et al., 2017b). They are therefore primarily active at dawn and dusk when ambient light intensities are low and generally blue-shifted (Endler, 1993). Crepuscular beetles have been demonstrated to possess considerable visual acuity, arising in part from their refracting superposition compound eyes that enable accurate color perception even at very low light intensities (Warrant & Dacke, 2011; Honkanen et al., 2017); crepuscular pollinators are therefore highly likely to employ visual cues to locate Annonaceae flowers despite low ambient light levels.

Flies are often particularly dependent on visual stimuli (Lunau, 2014), and fly-pollinated Annonaceae flowers often have a complex pattern of petal pigmentation with distinct stripes (*e.g.*, *Mitrephora vittata*: Fig. 1B; Weerasooriya & Saunders, 2010) or colored patches (sometimes with translucent ‘light windows,’ e.g., *Monodora myristica*: Fig. 1A; Couvreur, 2009) that are likely to act as pollinator guides. Flies rely on different color cues for diverse behavioral activities such as locating food and oviposition (Lunau, 2014), and a characteristic sapromyiophilous pollination syndrome is evident in which coprophagous, necrophagous or saprophagous flies are deceptively attracted to flowers that mimic faeces or dead/decaying organic matter. Although sapromyiophilous flowers rely heavily on olfactory attractants (discussed in Section 2.3), there are also distinctive visual syndromes, with dull red petals that are often enlarged and have a corrugated surface (Chen et al., 2015). Examples within Annonaceae include *Asimina parviflora* (Norman et al., 1992), *Meiogyne* species formerly classified as *Fitzalania* (Fig. 1C; Thomas et al., 2012), *Monodora tenuifolia* (Gottsberger et al., 2011), *Pseuduvaria megalopus* (Su et al., 2005) and *Stenanona flagelliflora* (Xicohténcatl-Lara et al., 2016). A similar saprocantharophilous syndrome has been reported for *Duguetia cadaverica* (Teichert et al., 2012), involving the attraction of nitidulid beetles rather than flies.

2.2 Floral chamber morphology

Annonaceae flowers typically possess a partially enclosed chamber that is variably formed by the convergence or connivence of petals around the reproductive organs. Seven different structural types of floral chamber were identified in a review of floral evolution in the family (see Saunders, 2010: Fig. 5 for illustrations), viz.: Type I, in which the chamber is formed from suberect petals that remain loosely contiguous; Type II, formed from petals that are basally constricted around the reproductive organs; Type III, formed from inner petals (or rarely outer petals: Guo et al., 2018) that are apically connivent, with small basal apertures between the inner petals that are either partially blocked by the outer petals or remain open throughout the functional floral phases; Type IV, formed from ‘boat-shaped’ inner petals that are convergent along their margins; Type V, formed from the bowl-shaped corolla, with an apical aperture; Type VI, formed from inner petals that are apically imbricate, with small apertures between the basal claws of the inner petals; and Type VII, formed from a corolla tube that results either from basal fusion of petals or free petals. The breadth of this structural diversity reflects the independent evolutionary origin of floral chambers in the family: mapping chamber types onto the molecular phylogeny unsurprisingly reveals considerable homoplasy, with multiple origins of each chamber type from an ancestral floral form that is inferred to have lacked any chamber (Saunders, 2010).

The independent origin of floral chambers in multiple lineages in Annonaceae suggests that the chamber is functionally important in pollinator attraction and/or reward. The chamber is hypothesized to create a protected environment for pollinators (often used as a tryst site for copulation, but also presumably for predator avoidance), as well as allowing maintenance of a micro-environment with elevated temperatures (discussed in Section 2.4), filtering out large and potentially destructive floral visitors that would not be effective pollinators, and in some cases enabling pollinator trapping (discussed in Section 4.4). The presence of a floral chamber is correlated with primary pollinator guild: it is widespread in beetle-, thrips- and fly-pollinated species (Saunders, 2012), but is unknown in species pollinated by bees (Carvalho & Webber, 2000; Silberbauer-Gottsberger et al., 2003; Teichert et al., 2009; Li et al., 2016) or cockroaches (Nagamitsu & Inoue, 1997).

2.3 Floral scent

Annonaceae flowers are highly aromatic, with *Cananga odorata* (ylang-ylang) flowers widely used in the perfume industry. Goodrich (2012) reviewed the diversity of floral scents in the family and used available subjective descriptions to classify odor types as perceived by human olfaction: 65% of species were determined as having a ‘pleasant’ smell (including fragrant, agreeable, fruity and sweet smells), 10% had a yeasty-fungal scent, and 8% were described as ‘unpleasant’ (including vomit, carrion or rubbery smells). The remaining species had miscellaneous scents (including lemongrass, spearmint, acetone, linseed oil or balsamic) or else were reported to lack any noticeable odor. Although this variability in floral scent is indicative of adaptations to different pollinators, interpretation is complicated by the highly dynamic nature of floral scents: as well as differing between species, they also vary between organs within a flower and between different phenological stages of the flower (Goodrich et al., 2006; Goodrich & Raguso, 2009; Goodrich, 2012).

In her review of Annonaceae floral scents, Goodrich (2012) classified the scent components into five major chemical classes, viz. aliphatics, aromatics (benzenoids), isoprenoids (terpenes), and nitrogen- and sulfur-containing compounds. The fruity floral scents emitted by many Annonaceae flowers often comprise chemically very disparate volatiles and are indicative of evolutionary convergence towards beetle pollination in different evolutionary lineages (Goodrich, 2012). Knowledge of floral scent chemistry in Annonaceae remains limited, however, with relatively few detailed studies available and with the taxa that have been studied often phylogenetically distant (Goodrich, 2012). Although fruit mimicry has often been highlighted in interpretations of floral scent, there are very few studies that directly compare floral scents against possible model species (Goodrich & Jürgens, 2018).

The floral scent in *Asimina* species (inclusive of *Deeringothamnus*) is particularly informative (Goodrich & Raguso, 2009). There are two distinct floral forms in the genus: the first group (comprising *A. parviflora*, *A. pygmaea*, *A. tetramera* and *A. triloba*) has small maroon flowers that emit a yeasty (sometimes fetid) smell and are pollinated by small flies and nitidulid beetles or rarely by large scarab beetles (Willson & Schemske, 1980; Norman & Clayton, 1986; Norman et al., 1992; Rogstad, 1993); whereas the second group (all other species) has large, white, pink or yellow flowers that emit a sweet, pleasant fragrance and are pollinated by large beetles or rarely by flies and thrips (Uphof, 1933; Norman & Clayton, 1986; Norman et al., 1992; Norman, 2003; Levitt et al., 2013; Barton & Menges, 2018). Although the pale-flowered species presumably employ a reward-based pollination system, the maroon-flowered species appear to have evolved deceptive pollination. The floral scents of *A. parviflora* and *A. triloba* resemble fermenting sugars and hence are likely to mimic rotting fruit, which is the food substrate or brood site for their pollinators (Goodrich & Raguso, 2009). These fermentation volatiles are also present in the floral scents of *A. pygmaea* and *A. tetramera*, although these latter species also contain dimethyl disulfide and indole, respectively, which are by-products arising from the microbial degradation of carrion and faeces; this suggests an evolutionary expansion of floral mimicry in the genus (Goodrich & Raguso, 2009).

There are several well-documented examples of Annonaceae floral scent compounds that serve to attract specific pollinators—including aliphatic esters and alcohols that attract nitidulid beetles (e.g., Peña et al., 1999; Jürgens et al., 2000), 4-methyl-5-vinylthiazole that attracts scarab beetles (Maia et al., 2012) and trans-carvone oxide that attracts male euglossine bees (Whitten et al., 1986; Teichert et al., 2009)—as well as numerous other studies that tentatively identify volatiles that have been implicated elsewhere as semiochemicals but which lack specific field bioassays to unequivocally demonstrate function. Floral scent can also function as a pollinator reward as well as an attractant: the male euglossine bees that pollinate *Unonopsis* flowers (Carvalho & Webber, 2000; Silberbauer-Gottsberger et al., 2003; Teichert et al., 2009) are reported to collect floral volatiles using specialized brushes on their forelegs, and to use the accumulated scent to attract female bees (Whitten et al., 1989). Floral volatiles undoubtedly play a key role in plant-pollinator co-evolution, and hence the identification of pollinator-specific attractants remains an integral component of studies demonstrating pollination specificity (e.g., Teichert et al., 2012).

2.4 Floral thermogenesis

Many angiosperm lineages are reported to have evolutionary adaptations that enable flowers to maximize the absorption and retention of exogenous heat, thereby enabling the optimization of metabolic processes, organ maturation, pollen germination and/or pollen tube growth, as well as the enhanced formation of nutritional rewards for pollinators (van der Kooi et al., 2019). Such adaptations are particularly important in cooler climates in which plants and their generally ectothermic pollinators are subject to thermal stresses. Although tropical species are unlikely to experience a significant night-time fall in ambient temperature, there is nevertheless widespread evidence for the independent evolution of endogenous floral heating (thermogenesis) across 11 angiosperm families (Thien et al., 2000; Luo et al., 2010). The biochemical basis for floral thermogenesis in Annonaceae is unknown, although studies of other thermogenic taxa (*Symplocarpus*, Araceae: Umekawa et al., 2016) have highlighted the endothermic production of NADPH, catalyzed by mitochondrial isocitrate dehydrogenase.

Floral thermogenesis is likely to promote pollination efficiency. Floral heat can act as a pollinator attractant, with some beetles, including Curculionidae (Hausmann et al., 2004), having infrared (IR) sensors—known as IR sensilla or IR pit organs—that can detect infrared radiation (Schmitz et al., 1997; Hammer et al., 2001). Floral heat can also directly serve as an energy reward for ectothermic pollinators, assisting with the maintenance of body temperature and stimulating reproduction, feeding and digestion (Thien et al., 2000; Seymour et al., 2003; Rands & Whitney, 2008). The initiation of flight consumes considerable energy, with beetles reported to require high thoracic temperatures, often exceeding 30 ºC (Seymour & Schultze-Motel, 1997). Elevated floral temperatures have also been postulated to mediate the synthesis and volatilization of floral scents (Sagae et al., 2008), with floral temperature fluctuations often correlated with changes in fragrance emission (e.g., Ratnayake et al., 2007). Floral thermogenesis does not necessarily function exclusively to promote pollination, however: as well as optimizing various metabolic and developmental processes, there are also examples from other early divergent angiosperm families of post-anthetic floral thermogenesis in which the heat assists larval development of gall midge pollinators (*Schisandra*, Schisandraceae: Luo et al., 2010).

Floral temperatures in Annonaceae are often raised up to 3–8 ºC above ambient conditions, with considerably larger increases reported in some species of *Annona* (c. 15 ºC: Gottsberger & Silberbauer-Gottsberger, 1988; Gottsberger, 1989) and *Xylopia* (12–13 ºC: Küchmeister et al., 1998). Thermogenesis is widespread in the family (Table 1), although field studies often fail to include measurements of floral temperature, and assessments have yet to be made for any species in subfamily Ambavioideae. Available records are phylogenetically disparate, with sister genera (e.g., *Artabotrys* and *Xylopia*) and congeneric species (e.g., within *Anaxagorea*, *Annona*, *Monoon* and *Xylopia*) often differing in their capacity to generate heat endogenously (Table 1); this suggests the independent evolution origin of (or loss of) thermogenesis. Floral thermogenesis is likely to be associated with the evolution of specific pollination systems in Annonaceae: all reports of floral thermogenesis are from flowers that are pollinated by small or large beetles, and there are no reports from fly- or bee-pollinated species. Significantly, all beetle-pollinated *Xylopia* species studied are thermogenic (Küchmeister et al., 1998; Jürgens et al., 2000; Silberbauer-Gottsberger et al., 2003; Ratnayake et al., 2007), whereas the predominantly thrips-pollinated congener *X. aromatica* lacks any endogenous heat (Jürgens et al., 2000; Silberbauer-Gottsberger et al., 2003). The apparent correlation with pollinator type may also be associated with floral adaptations to minimize heat loss, however: thermogenic flowers are typically larger, with thicker petals, since the low surface-to-volume ratio minimizes heat loss (Seymour & Schultze-Motel, 1997) and the partially enclosed floral chamber (discussed in Section 2.2) helps retain heat.

2.5 Floral nectar

Floral nectar functions as an important sugar-rich nutritive reward for pollinators, with specialized nectary tissues likely to have evolved independently in many different floral organs across disparate angiosperm lineages (Bernardello, 2007). Although nectaries have been reported from the base of the petals in Annonaceae flowers, most nectar in the family is stigmatic in origin (Fig. 1D, E; Lau et al., 2017a). Stigmatic exudate was previously hypothesized to have been the ancestral source of nectar in flowering plants (Lloyd & Wells, 1992; Endress, 1994), although this interpretation was based on the assumption that ‘wet’ stigmas (which form a fluid secretion when receptive) were ancestral to ‘dry’ stigmas (which have a dry proteinaceous extracellular pellicle layer). The latter assumption has recently been revised, and the wet stigmas characteristic of Annonaceae (Lora et al., 2011) are now interpreted as likely to be derived within the Magnoliales (Lau et al., 2017a, and references therein).

Nectar is rich in sugars, lipids and proteins, supplemented with amino acids, phenols, reactive oxygen/nitrogen species and calcium ions (Suárez et al., 2012; Rejón et al., 2014). The sugars provide an excellent energy source for pollinators (Galetto et al., 1998) and function as important phagostimulants for insects, including beetles (Mitchell & Gregory, 1979; Merivee et al., 2008). Floral nectar is dominated by a combination of sucrose and hexose sugars, with the latter (primarily consisting of glucose and fructose) particularly easily digested and rapidly metabolized (Simpson & Neff, 1983). The proportion of the different sugar types is often characteristic for the pollinator type, with higher sucrose-to-hexose ratios typical in insect-pollinated species (Gottsberger et al., 1984). The stigmatic nectar of *Uvaria grandiflora* (Annonaceae) was nevertheless shown to be dominated by fructose (72.2%), which is readily metabolized by the beetle pollinators, and with smaller proportions of glucose (19.3%) and sucrose (8.4%) (Lau et al., 2017a).

The amino acid composition of nectar not only contributes to its nutritive value (Lord & Webster, 1979) but also alters its taste as perceived by floral visitors (Mitchell & Gregory, 1979; Merivee et al., 2008). Ten of the 20 common amino acids cannot be synthesized by insects and hence must be obtained through their diet (Haydak, 1970): all these essential amino acids have significantly been recorded from floral nectar (Baker & Baker, 1975; Gottsberger et al., 1984), confirming the importance of nectar as a food source. Studies of the stigmatic exudate chemistry of Annonaceae species (*Uvaria grandiflora* and *U. macrophylla*: Lau et al., 2017a; and *Anaxagorea javanica*: Li & Xu, 2019) demonstrate the presence of most essential amino acids, although tryptophan is absent from all three species and lysine is furthermore absent from *U. macrophylla*. Many of the amino acids recorded from Annonaceae stigmatic nectar are reported to be sugar-sensitive cell stimulants for beetles and flies (Shiraishi & Kuwabara, 1970; Mitchell & Gregory, 1979), with phenylalanine particularly abundant. Phenylalanine has a significant phagostimulatory effect on honey bees (Inouye & Waller, 1984), which are known to be important secondary pollinators of *U. grandiflora* (C.-C. Pang & R.M.K. Saunders, unpublished data).

The Annonaceae genera *Anaxagorea* (Maas & Westra, 1984; Li & Xu, 2019) and *Xylopia* (van Heusden, 1992; Johnson & Murray, 2018) possess inner staminodes that are morphologically transitional between stamens and carpels. The inner staminodes in *Anaxagorea* possess an apical glandular area (Scharaschkin & Doyle, 2006) that has been interpreted as homologous with the stigma (Saunders, 2010). The staminode exudate is therefore comparable with stigmatic exudate and might also function as a pollinator food reward: the amino acid composition of the exudates of the two organs in *Anaxagorea javanica* are very similar (Li & Xu, 2019), although the staminode exudate appears to have significantly higher concentrations of most amino acids. Similar staminode glands have been reported from the closely related genera *Degeneria* (Degeneriaceae), *Eupomatia* (Eupomatiaceae) and *Galbulimima* (Himantandraceae) (Endress, 1984), although structural homology with the *Anaxagorea* glands is uncertain.

Nectaries are also common at the base of the adaxial surface of the inner petals in Annonaceae flowers (Fig. 1F), with reports from subfamilies Ambavioideae (*Tetrameranthus*), Annonoideae (*Asimina*, *Asteranthe*, *Diclinanona*, *Duguetia*, *Monodora*, *Porcelia*, *Uvaria* and *Xylopia*) and Malmeoideae (*Alphonsea*, *Meiogyne*, *Monoon*, *Orophea*, *Pseuduvaria* and *Sapranthus*) (Saunders, 2010). The disparate phylogenetic occurrence of petal glands implies extensive homoplasy (Saunders, 2010), although with the caveat that homology of these 'glands' has not been demonstrated and in many cases their function might not be nectar secretion. The petal nectaries of *Alphonsea glandulosa* (Xue et al., 2017) and *Pseuduvaria froggattii* (Silberbauer-Gottsberger et al., 2003; Su & Saunders, 2006) have received particular attention, and have been shown to consist of distinct secretory and ground parenchyma zones, with an epidermal layer in which modified stomata enable nectar secretion. The evolution of petal nectaries as an alternative to stigmatic exudate may have been favored as it would release the plant from the constraints imposed by protogyny, in which stigmatic exudate is unlikely to extend into the staminate floral phase.

2.6 Petals as pollinator brood sites

Dasymaschalon trichophorum (Annonaceae) flowers are pollinated by small *Endaenidius* beetles (Curculionidae) (Lau et al., 2017b). The beetles have been observed to copulate on the flowers, with the female beetles chewing small holes in the petal surface while mating and then ovipositing into these holes after the departure of the male (Fig. 1G, H; C.-C. Pang & R.M.K. Saunders, unpublished data). Although the hypothesis remains untested, it seems probable that the petals may function as a food source for the emerging beetle larvae, possibly in abscised petals on the forest floor (cf. Sakai, 2002), thereby contributing to the maintenance of functional populations of the pollinator.

The Annonaceae genus *Meiogyne* possesses elaborate inner petal corrugations (Fig. 1I) that have often been referred to as ‘glands’ (*e.g.*, van Heusden, 1992), although without confirmation of glandular function. The corrugations (‘strumae’) on *Meiogyne hainanensis* petals (Shao & Xu, 2015, as ‘*Oncodostigma*’) have been shown to be rich in polysaccharides and to be associated with thrips larvae. Although this might represent another example of pollinator brood-site adaptations of petals in Annonaceae, the study failed to demonstrate that thrips are the effective pollinator.

Another study (Collier & Armstrong, 2009) demonstrated that *Anaxagorea crassipetala* petals are co-opted as a larval substrate and pupation site by *Diathoneura* flies (Drosophilidae). The effective pollinators have previously been shown to be nitidulid and staphylinid beetles (Armstrong & Marsh, 1997), however, and drosophilid flies were never observed to enter the floral chamber (Collier & Armstrong, 2009).

Although there are very few studies of pollinator brood-site adaptations of petals in Annonaceae, it is likely that the phenomenon may be more widespread. Future studies need to be much more comprehensive, integrating assessment of effective pollination with empirical evidence to demonstrate completion of the insect life cycle, from copulation and ovipositing through larval development and pupation.

3 Floral adaptations that promote xenogamy

Numerous studies have demonstrated the capacity of Annonaceae species to set seed after autogamous and geitonogamous self-pollination (see Pang & Saunders, 2014: Table 1 for references). Although this is unequivocal evidence for the absence of a biochemically mediated self-incompatibility mechanism, Annonaceae species nevertheless appear to maintain predominantly xenogamous breeding systems, as evidenced by population genetic analyses (e.g., *Annona crassiflora*: de Almeida-Júnior et al., 2018; *Desmos chinensis*: Pang & Saunders, 2015; *Huberantha korinti*: Ratnayake et al., 2006b, as '*Polyalthia*'; and *Monoon coffeoides*: Ratnayake et al., 2006b, as '*Polyalthia*') and field-based controlled pollination experiments (e.g., *Asimina obovata* and *A. pygmaea*: Norman & Clayton, 1986; *Maasia glauca* and *M. hypoleuca*: Rogstad, 1994, as '*Polyalthia*'; *Popowia pisocarpa*: Momose et al., 1998; *Sapranthus palanga*: Bawa, 1974; *Uvaria elmeri*: Nagamitsu & Inoue, 1997; and *Xylopia championii*: Ratnayake et al., 2007). A population genetic study of *Annona crassiflora* based on microsatellite loci (de Almeida-Júnior et al., 2018) revealed spatially very restricted dispersal of pollen. The authors furthermore concluded that the behavior of the *Cyclocephala* scarab beetle pollinators, which rarely move between flowers, results in a considerable proportion of the ovules being fertilized by the same pollen donor (de Almeida-Júnior et al., 2018): although xenogamy dominates, paternal diversity in the progeny is likely to be very limited.

Annonaceae species promote xenogamy by adopting various strategies, including temporal separation of sexual function (protogyny), spatial separation of stamens and carpels (herkogamy), synchrony of floral reproductive function (synchronous dichogamy), and partial or complete separation of sexes (dicliny). These adaptations were reviewed by Pang & Saunders (2014), and the following account is largely based on this work, supplemented with recent additions to the literature.

3.1 Protogyny

Temporal separation of male and female function within hermaphroditic flowers (intrafloral dichogamy) is widespread among angiosperms and is an effective strategy for avoiding autogamous self-pollination. Protogyny, in which pistillate function precedes staminate function, is almost ubiquitous among early divergent lineages, with observations from all families except Gomortegaceae and Hernandiaceae, which remain unstudied (Endress, 2010). Protogyny is therefore undoubtedly the ancestral mechanism in flowering plants, including Annonaceae.

The pistillate and staminate phases in Annonaceae flowers are typically separated by a sexually non-functional interim phase that reinforces the effectiveness of protogyny. The duration of the interim phase varies according to overall anthesis duration: *Polyalthia suberosa*, which is typical of many species in the family, has anthesis over 48 hours and has a seven-hour interim phase (Fig. 2A; Lau et al., 2017b); whereas species with abbreviated anthesis (Fig. 2B, C) have a shorter interim phase (e.g., *Goniothalamus tapisoides*, which has anthesis over c. 23 hours has an interim phase of only three hours: Lau et al., 2016).

The evolutionary breakdown of protogyny is observed in several Annonaceae species, enabling increased reproductive assurance through autogamy (discussed in Section 5.4). Although the presence of stigmatic exudate is widely used as a proxy indicator of stigmatic receptivity, interpretation is complicated by the retention of exudate into the interim phase as a nectar reward for pollinators. The sugar content of the exudate in *Uvaria macrophylla* changes temporally (Lau et al., 2017a), however, rising from relatively low concentrations that are conducive for pollen germination during the peak pistillate phase to much higher concentrations that impede germination toward the end of the pistillate phase (Lau et al., 2017a).

3.2 Herkogamy

Herkogamy is the spatial separation of stamens and carpels within a flower, thereby reducing opportunities for autogamous self-pollination. The significance of this for Annonaceae is unclear given the prevalence of protogyny and perceptions regarding ‘mess-and-soil’ pollination (Fægri & van der Pijl, 1979), in which beetles randomly and destructively move around the flower. Herkogamy has nevertheless been hypothesized as a result of inner staminodes, asymmetric stigmas, conical receptacles and elongated pseudostyles.

The Annonaceae genera *Anaxagorea* (Maas & Westra, 1984; Li & Xu, 2019) and *Xylopia* (van Heusden, 1992; Johnson & Murray, 2018) possess inner staminodes that are effectively sterile stamens, transitional with carpels (Saunders, 2010). In *Anaxagorea* (and possibly also *Xylopia*) these staminodes may act as a physical barrier between the anthers and stigmas, elongating and curving inwards over the carpels as anthesis progresses (Maas-van de Kamer, 1993; Webber, 2002; Teichert et al., 2011). Lora et al. (2011) observed that the stigmas of the outermost carpels in *Annona cherimola* are asymmetrical, with a non-papillate, non-receptive surface facing the innermost stamens that presumably also minimizes intrafloral pollen transfer.

Some Annonaceae taxa (e.g., *Uvaria buchholzii*: Le Thomas, 1968, as ‘*Balonga*’; and *Toussaintia*: Deroin, 2000) possess an elongated conical floral receptacle that elevates the stigmas above the androecium; this spatial separation is also observed in genera with a convex receptacle (e.g., *Annona*: González & Cuevas, 2011). Several genera furthermore have stigmas that are elongated to form a ‘pseudostyle’ (e.g., *Goniothalamus*: Lau et al., 2016, 2017a); since the pollen tubes of *Goniothalamus parallelivenius* are only capable of penetrating the apex of the stigma (Lau et al., 2017a), the elongated pseudostyles may also promote herkogamy.

3.3 Floral synchrony

Although protogyny is effective for avoiding autogamy in Annonaceae, self-pollination between flowers of the same individual (geitonogamy) is likely to be common since the family is self-compatible. Geitonogamy can be minimized by reducing the number of co-occurring flowers, although this would be detrimental to seedset. Flowering in several phylogenetically disparate Annonaceae species is reported to be synchronized, with sexual function aligned within and between individuals. The most common manifestation of this is pistillate/staminate-phase floral synchrony (Pang & Saunders, 2014), in which all the flowers on an individual mature in concert, so that co-occurring flowers are either pistillate or staminate and hence avoid geitonogamy; synchrony in different individuals within the population is furthermore staggered between days, promoting cross-pollination. This form of synchronous dichogamy is reported from several phylogenetically disparate genera within Annonaceae, including *Annona* (Murray & Johnson, 1987, as '*Rollinia*'; González & Cuevas, 2011; Lora et al., 2011), *Dasymaschalon* (Pang & Saunders, 2014), *Desmos* (Pang & Saunders, 2014, 2015), *Guatteria* (Webber, 2002), *Maasia* (Rogstad, 1994, as '*Polyalthia*') and *Unonopsis* (Carvalho & Webber, 2000). At least one 'flower-free' day is required between each floral cohort in order to avoid geitonogamous pollen transfer; as a result, many synchronous species have abbreviated anthesis, thereby enabling more rapid floral turnover (discussed further in Section 4.3). Pistillate/staminate-phase synchrony is nevertheless imperfect, with some individuals producing flowers asynchronously within the population; this presumably enables greater genetic mixing within the population by avoiding the long-term perpetuation of distinct reproductive cohorts.

A more complex form of synchrony, known as heterodichogamy, is observed in *Anaxagorea* (Teichert et al., 2011) and *Annona* (Wester, 1910), involving the formation of distinct floral forms that are morphologically identical but with contrasting patterns of sexual function. In *Anaxagorea prinoides*, for example, two morphs co-exist in equal proportions: one with a relatively prolonged pistillate phase, and the other a shorter pistillate phase. The timing of the sexual phases in the two morphs are aligned so that pollen-laden beetles departing from late staminate-phase flowers are attracted to flowers of the opposite morph at the onset of the pistillate phase (Teichert et al., 2011; Pang & Saunders, 2014). Since each individual is consistently of a single morph with synchronized flowering within the plant, geitonogamy is minimized and almost uninterrupted flowering is feasible.

Although floral synchrony is relatively uncommon in angiosperms, it is noteworthy that empirical field studies that specifically aim to identify synchrony are rare, and the phenomenon may be more widespread. Temporal synchrony of floral sexual function is more common within Magnoliales and Laurales than in derived lineages (Endress, 2020).

3.4 Dicliny

Most Annonaceae species bear hermaphroditic flowers. This condition is ancestral for the family (Saunders, 2010), with structurally or functionally unisexual flowers (dicliny) achieved independently in several lineages as a strategy to promote xenogamy. Structurally unisexual flowers, arising following the loss of the androecium or gynoecium, have evolved in several disparate lineages in subfamilies Annonoideae (*Annona*, *Anonidium*, *Diclinanona* and *Uvariopsis*) and Malmeoideae (*Ephedranthus*, *Greenwayodendron*, *Klarobelia*, *Polyceratocarpus*, *Pseudephedranthus*, *Pseudomalmea*, *Pseuduvaria* and *Stelechocarpus*) (Pang & Saunders, 2014, and references therein). At the population level, floral unisexuality is variously manifested as monoecy (with separate pistillate and staminate flowers on the same plant) or andromonoecy (with separate staminate and bisexual flowers on the same plant), although there are some reports of dioecy or androdioecy (in which the different floral sexes are borne on different individuals). Many of the latter reports are based on incomplete sampling, however, often from herbarium collections.

Interpretations of floral sex are complicated by the occurrence of flowers that are structurally bisexual but which contain relatively few and apparently poorly developed stamens: these flowers have sometimes been interpreted as functionally pistillate with sterile staminodes (e.g., *Pseuduvaria mulgraveana*: Su & Saunders, 2006, 2009), although subsequent empirical fieldwork has demonstrated that staminate function is maintained, albeit limited (Pang et al., 2013). Phylogenetic reconstructions of *Pseuduvaria* have revealed evolutionary reversals from unisexual to bisexual flowers in some New Guinea lineages (Su et al., 2008); this may have been selectively advantageous for promoting self-pollination following the colonization of geographical regions that are topographically and ecologically complex.

Despite the contradictory interpretations of floral sex in *Pseuduvaria mulgraveana* alluded to above, other species in the genus bear structurally hermaphroditic flowers that are functionally unisexual. *Pseuduvaria macrocarpa*, for example, is reported to have unisexual flowers, with unambiguously staminate flowers together with structurally hermaphroditic flowers that bear functional carpels and a reduced number of staminodes that contain small, incompletely developed pollen grains that are presumably sterile (Su & Saunders, 2006).

Pseuduvaria mulgraveana has been shown to achieve functional unisexuality in structurally hermaphroditic flowers by delaying anther dehiscence until after petal abscission, after departure of the beetle pollinators (Pang et al., 2013). A parallel mechanism has been suggested for the congener *P. trimera* based on floral ontological investigation (Yang & Xu, 2016).

Androdioecy/andromonoecy has been demonstrated to be associated with rapid evolutionary diversification in Annonaceae, with the possession of exclusively hermaphroditic flowers conversely associated with the lowest diversification rate (Xue et al., 2020). Androdioecy/andromonoecy may be selectively advantageous in obligately outcrossing species in which gene flow is limited, with the reduced level of pistillate function countered by increased seedset arising from the greater availability of pollen (Lloyd, 1975).

4 Floral adaptations that enhance the efficiency of pollinator use

4.1 Pollen aggregation

Annonaceae pollen is generally dispersed as single grains (monads), with the formation of aggregate clusters of pollen grains inferred to have originated independently on multiple occasions across the family and to be synapomorphic for tribes Annoneae and Monodoreae within subfamily Annonoideae (Doyle & Le Thomas, 2012; Xue et al., 2020: Supplementary data). In most cases, the pollen aggregates are tetrads (Fig. 3A) that form due to the failure of microsporocytes to dissociate (e.g., *Annona*: Tsou & Fu, 2002; Lora et al., 2009; and

Pseuduvaria: Su & Saunders, 2003); in a small number of genera, however, larger octads (e.g., *Cymbopetalum*: Tsou & Fu, 2007; and *Disepalum*: Li et al., 2015) and polyads of up to 32 pollen grains (*Porcelia*: Le Thomas et al., 1986) arise due to two or more sporocytes developing in synchrony (Tsou & Fu, 2007). In addition to the direct cohesion between pollen grains within the pollen aggregate, neighboring tetrads in *Pseuduvaria* are also linked by non-sporopollenin pollen-connecting threads (Fig. 3A, B; Su & Saunders, 2003; Li & Xu, 2018). Similar threads have since been reported from *Asimina* (Zhang et al., 2014), *Disepalum* (Zhang et al., 2014) and *Monoon* (Ratnayake et al., 2006a, as '*Polyalthia*') and may be more widespread in the family as the standard acetolysis technique that is commonly applied in pollen preparation destroys threads that lack sporopollenin.

Aggregation of pollen grains—irrespective of whether it is due to direct cohesion between grains or pollen-connecting threads—is hypothesized to function as a mechanism to enhance siring success by enabling the transfer of multiple pollen grains following a single pollinator visit (Kress, 1981; Hesse et al., 2000; Harder & Johnson, 2008). This is likely to be particularly beneficial for species in which pollinator visits are infrequent and/or when pollen transfer between flowers is inefficient. This inevitably comes at a genetic cost, however, due to the increased proportion of sibling pollen grains received by stigmas; pollen aggregation will only be selectively favored if the consequences of aggregation increase overall reproductive performance (Harder & Johnson, 2008). In order to optimize pollination efficiency, pollen tubes growing from pollen aggregates must be able to access numerous ovules. Many Annonaceae genera with pollen aggregation are notably either syncarpous (*Monodora*, with up to 70 ovules per fused gynoecium) or else have multi-ovulate carpels, viz. *Cymbopetalum* (with up to 25 ovules per carpel), *Goniothalamus* (up to 10), *Meiocarpidium* (up to 20), *Porcelia* (up to 15), *Pseuduvaria* (up to 18), *Uvariastrum* (up to 25) and *Uvariopsis* (up to 15). Other Annonaceae genera exhibiting pollen aggregation have fewer ovules per carpel (e.g., *Annona*, *Anonidium*, *Disepalum*, *Duckeanthus* and *Fusaea*), but in these cases intercarpellary growth of pollen tubes is likely to be promoted by either partial syncarpy or the presence of an extragynoecial compitum (discussed further in Section 5).

In a recent study of the influence of specific traits on evolutionary diversification rates in Annonaceae, Xue et al. (2020) demonstrated that pollen aggregation is associated with reduced diversification. This may be associated with the potentially negative effects of pollen aggregation, such as the reduction in the number of pollen recipients reached by a pollen donor (reduced pollen ‘carryover,’ exacerbated when geitonogamy occurs) and consequently the reduced genetic variation in the pollen delivered (Harder & Johnson, 2008, and references therein). Attempts to assess correlations between evolutionary diversification rates and functional traits are complicated, however, by possible trait correlations: pollen aggregation, for example, is acknowledged to be closely aligned with anther septation (Tsou & Johnson, 2003).

4.2 Stamen abscission and secondary pollen presentation

The stamens in Annonaceae flowers partially abscise as the anthers begin to dehisce, although each stamen remains suspended within the pendent flower by the tracheary elements of its vascular tissue (Fig. 3C; Endress, 1985). Pollinator movements within the flower are likely to dislodge the stamens, further assisting pollen release.

Because of the pendent orientation of most Annonaceae flowers, the apically convergent or connivent pollination chamber often forms an inverted mitriform structure that captures fallen pollen grains (Fig. 1B). Dehisced pollen and abscised stamens have been observed to collect in the floral chamber in *Pseuduvaria mulgraveana* (Pang et al., 2013), where they mix with accumulated nectar; the pollinators inadvertently collect pollen grains as they consume the nectar. In some species (e.g., *Mitrephora*: Weerasooriya & Saunders, 2010) the adaxial surface of the floral chamber is adorned with hairs that may assist with the retention of dehisced pollen (Fig. 1B). These observations are therefore indicative of secondary pollen presentation, in which pollen is transferred from the thecae to an intermediary organ prior to collection by the pollinator (Howell et al., 1993; Yeo, 1993), and may serve to prolong the period during which pollen is available.

4.3 Anthesis duration

Anthesis is generally defined as the period during which a flower is sexually functional, with the onset of anthesis correlated with the opening of the perianth. This concept is problematic with respect to Annonaceae, however, since the sepals and petals often separate very early in development (although the inner petals sometimes remain apically convergent or connivent to form a partially enclosed floral chamber). Since Annonaceae flowers are protogynous, the beginning of anthesis is generally determined based on the formation of stigmatic exudate—used as a proxy for stigmatic receptivity and hence indicative of the pistillate phase—and with the end of anthesis (and the staminate phase) coinciding with petal abscission. The pistillate and staminate phases are often temporally separated by a non-sexual interim phase, although this is sometimes obscured by the continued retention of stigmatic exudate.

Anthesis duration in most hermaphroditic-flowered Annonaceae species is 36–54 hours, extending over two or three days depending on the timing of the onset of the pistillate phase (e.g., *Polyalthia suberosa*: Fig. 2A; Saunders, 2012). Considerably longer anthesis durations, however, are observed in several phylogenetically disparate genera (Table 2): most of these examples are pollinated by flies (or a combination of flies and small beetles), although other examples include pollination by meliponine bees, scarab beetles, tenebrionid beetles and thrips. These changes in flowering rhythm may represent adaptations to the activity patterns of pollinators to optimize pollination efficiency (Gottsberger, 2014): flies, for example, are irregular floral visitors, typically making very brief visits to each flower (Fægri & van der Pijl, 1979; Saunders, 2012) and hence pollination success is likely to be promoted by prolonged anthesis.

In striking contrast, however, several hermaphroditic-flowered Annonaceae species exhibit abbreviated anthesis over 23–30 hours (Table 2; e.g., *Desmos chinensis* and *Goniothalamus tapisoides*: Fig. 2B, C). Although short anthesis is sometimes correlated with unisexual flowers since there is only a single sexual functional phase (e.g., within one day in *Pseuduvaria froggattii*: Silberbauer-Gottsberger et al., 2003), most examples are of species with hermaphroditic flowers. *Dasymaschalon*, *Desmos* and *Friesodielsia* are phylogenetically closely related (Guo et al., 2017a) and their abbreviated anthesis is therefore likely to be synapomorphic for the entire clade (Lau et al., 2017b); the other four hermaphroditic genera with abbreviated anthesis (*Annona*, *Artabotrys*, *Goniothalamus* and *Unonopsis*) are phylogenetically disparate (Guo et al., 2017b), however, and hence there are at least five independent origins for abbreviated anthesis in the family.

Most Annonaceae species with standard anthesis duration (36–54 hours) have three coetaneous cohorts of flowers over three days: flowers entering their pistillate phase will co-occur with flowers that are a day older, which are entering their staminate phase, and flowers that are two days older, in which the staminate phase is ending (e.g., *Polyalthia suberosa*: Fig. 2A). Pollen-laden pollinators departing from post-staminate flowers are therefore likely to be attracted to two different cohorts of flowers: assuming that the different cohorts are equally common in the population, pollinators are equally likely to be attracted towards staminate-phase flowers as they are to pistillate-phase flowers (Fig. 2A). Species with abbreviated anthesis (e.g., *Desmos chinensis*, with anthesis over c. 27 hours: Fig. 2B) only have two coetaneous cohorts within the population, and hence pollinators leaving post-staminate flowers are much more likely to be attracted directly to flowers entering the pistillate phase, thereby increasing pollination efficiency.

Abbreviated anthesis is furthermore closely allied with pistillate/staminate-phase floral synchrony (discussed in Section 3.3), in which all flowers borne on an individual undergo the same sexual phase concurrently: although there are very few studies of floral synchrony in the family, many of the species shown to have abbreviated anthesis also display synchrony (Table 2). Synchronous species showing standard anthesis duration require a ‘flower-free’ day every third day to ensure that pollen from a staminate-phase flower cannot pollinate a pistillate-phase flower on the same plant the following day; synchronous species with abbreviated anthesis can therefore achieve much more rapid turnover of flowers (with a new flower forming on alternate days rather than every fourth day) and hence can increase seedset without undermining xenogamy. The species shown to have abbreviated anthesis in the absence of floral synchrony adopt a different strategy to avoid geitonogamy, with relatively few flowers borne concurrently (e.g., *Artabotrys blumei*: Chen et al., 2020; and *Goniothalamus suaveolens* and *G. tapisoides*: Lau et al., 2016), although this negatively impacts seedset.

4.4 Circadian pollinator trapping

Most Annonaceae species have hermaphroditic, protogynous flowers that are functional over 36–54 hours and are typically pollinated by crepuscular insects that exhibit a bimodal endogenous circadian rhythm. The *Carpophilus* beetles (Nitidulidae) that pollinate *Polyalthia suberosa* (Lau et al., 2017b), for example, have an evening activity peak that coincides with the onset of the pistillate floral phase (Fig. 2A); the beetles then remain relatively immobile within the flower until their next activity peak the following morning, which is aligned with the end of the pistillate phase. The staminate floral phase is similarly correlated with beetle activity levels, although pollen-laden beetles often remain in the flower until petal abscission, which is aligned with the onset of the pistillate phase in other flowers.

Goniothalamus species have an abbreviated anthesis of around 23–25 hours (Lau et al., 2016) and have firmly connivent inner petals that form a robust pollination chamber (Type III sensu Saunders, 2010), in which the narrow basal apertures between the inner petals are periodically blocked by movements of the alternately positioned outer petals. This floral arrangement enables ‘circadian trapping’ of pollinators within the flower: the curculionid and nitidulid beetles that pollinate *Goniothalamus tapisoides*, for example, are attracted during their morning activity peak to open flowers that are entering their pistillate phase (Fig. 2C); the beetles then remain largely immobile until their next activity peak, but at this point the beetles are unable to leave the flower due to closure of the floral apertures (Lau et al., 2017b). The beetles are finally released from the flower as the petals abscise after the end of the staminate phase, with their departure closely aligned with their activity peak the following morning, coincident with the onset of the pistillate phase in other flowers. This pollinator trapping mechanism is therefore heavily dependent on the close alignment of the timing of petal movements with the endogenous activity patterns of the pollinators (Lau et al., 2017b).

Similar patterns of pollinator trapping have been observed in *Artabotrys* (Fig. 3D, E; Chen et al., 2020) and *Friesodielsia* (Lau et al., 2017b), whereas the mechanism reported in *Dasymaschalon* differs slightly since the flowers of this genus have only a single whorl of three petals. The three petals in *Dasymaschalon* are inferred to be homologous with the outer petals of other Annonaceae (Guo et al., 2018), with the floral chamber opening and closing due to subtle lateral growth of the petals (Lau et al., 2017b). Although phylogenetic reconstructions demonstrate that *Dasymaschalon* and *Friesodielsia* are sister clades (Guo et al., 2017a), the different mechanisms underlying circadian trapping in the two genera preclude inferences regarding homology and it is therefore unclear whether evolutionary convergence has occurred (Lau et al., 2017b).

In addition to *Artabotrys*, *Dasymaschalon*, *Friesodielsia* and *Goniothalamus*, assessments of floral structure in other Annonaceae genera suggest that circadian trapping might also function in *Cyathocalyx*, *Drepananthus*, *Mitrella*, *Neostenanthera* and *Pseudartabotrys*, as well as in *Trivalvaria macrophylla* (Xue et al., 2020). Circadian trapping is therefore likely to have evolved multiple times in the family, suggesting that it endows a major selective advantage. In a recent study of the impact of floral traits on evolutionary diversification in Annonaceae, Xue et al. (2020) demonstrated that pollinator-trapping lineages are associated with significantly accelerated net diversification.

The genera that adopt circadian trapping invariably possess abbreviated anthesis, with the occurrence of the latter trait in *Desmos*—which is sister to the *Dasymaschalon*-*Friesodielsia* clade (Guo et al., 2017a) but which does not trap pollinators (Lau et al., 2017b)—suggesting that short anthesis evolved first and may be a prerequisite for circadian trapping. Species with abbreviated anthesis but lacking circadian trapping (e.g., *Desmos chinensis*: Fig. 2B) are liable to lose pollinators that exhibit an evening activity peak: pollination exclusively by morning-active unimodal pollinators is therefore likely to be more efficient. Species that trap pollinators (e.g., *Goniothalamus tapisoides*: Fig. 2C) benefit by utilizing an expanded range of pollinators, irrespective of whether they exhibit unimodal (morning or evening) or bimodal circadian rhythms (Lau et al., 2017b). Chen et al. (2020) furthermore noted that species with circadian trapping can stop scent emission earlier and hence can potentially avoid detection by floral antagonists (Schiestl, 2015).

5 Floral adaptations that optimize fertilization success

5.1 Extragynoecial compita

Unequal deposition of pollen loads onto the stigmas of apocarpous flowers can result in unbalanced ovule fertilization and hence the failure of some carpels to bear seed (e.g., *Liriodendron chinense*, Magnoliaceae: Huang & Guo, 2002). Previous research on the reproductive biology of early divergent angiosperms has identified several structural adaptations and mechanisms that have enabled this disadvantage of apocarpy to be overcome. Although pollen tube growth is typically channelled through specialized routes leading to the micropyle, the formation of extragynoecial compita (EGC) enable intercarpellary growth of pollen tubes, thereby liberating species from the constraints imposed by apocarpy (Endress, 1982; X.F. Wang et al., 2012). Three distinct forms of EGC have been identified (X.F. Wang et al., 2012): (a) suprastylar EGC, in which pollen tubes grow between stigmas that are either closely appressed or connected by stigmatic secretions; (b) extrastylar EGC, in which the pollen tubes do not penetrate the stigma but instead approach the ovule via an alternative route (such as the staminal filament); and (c) infrastylar EGC, in which the pollen tubes either extend down the pseudostyle before growing between carpels via an intercarpellary exudate, or else they grow to the base of one carpel before traversing the receptacle in order to penetrate another carpel. Of these three types, only suprastylar and infrastylar EGC are potentially applicable to Annonaceae.

A functional suprastylar EGC has previously been observed in three Annonaceae genera (*Annona*: Lora et al., 2011; *Asimina*: Losada et al., 2017; and *Goniothalamus*: Lau et al., 2017a), with intercarpellary growth of pollen tubes occurring through a stigmatic secretion (Fig. 3F). These three genera are phylogenetically close (all belong to a single clade within the tribe Annoneae: Chatrou et al., 2012; Guo et al., 2017b) and all develop copious exudate when the stigmas are receptive. Although Lau et al. (2017a) suggested that suprastylar EGC might be widespread in Annonaceae (and hence a key functional floral trait for the entire family), it is also possible that it is phylogenetically restricted within the tribe Annoneae and/or species with similarly extensive stigmatic exudate formation. Significantly, however, suprastylar EGC has also been reported from *Eupomatia* (in the sister family Eupomatiaceae) as well as the closely related genus *Galbulimima* (Himantandraceae) (Igersheim & Endress, 1997) and various Laurales (Endress & Igersheim, 1997), and hence its origin may have predated the origin of Annonaceae.

In the absence of copious stigmatic exudate, it is anticipated that a functional EGC could be achieved in Annonaceae if the stigmas of neighboring carpels are closely appressed to form a contiguous ‘stigmatic head’. The extensive variation in stigma size and shape observed in *Goniothalamus* (Saunders, 2002) is likely to represent distinct adaptations favoring suprastylar EGC, with very broad stigmas (e.g., *G. costulatus*: Saunders, 2002) enabling greater physical contact between neighboring carpels, whereas spatially divergent stigmas (e.g., *G. tapisoides*: Lau et al., 2017a) presumably rely on copious exudate to enable intercarpellary growth of pollen tubes.

Several *Sagittaria* (Alismataceae) species have been demonstrated to possess a functional infrastylar EGC in which pollen tubes traverse the floral receptacle before entering the ovule (X.F. Wang et al., 2002, 2006, 2012; Huang, 2003; Endress, 2011). In these cases, ovule placentation is invariably basal, presumably to enhance pollen tube access via the micropyle. Basal placentation necessarily limits the number of ovules per carpel, although this might be compensated for by an increase in the number of carpels per flower; it can be hypothesized that such an increase in carpel number would further reinforce the selective advantage of infrastylar EGC. The widespread occurrence of major Annonaceae lineages that exclusively or predominantly show basal placentation (including several species-rich genera such as *Annona*, *Artabotrys*, *Duguetia*, *Goniothalamus* and *Guatteria*: van Heusden, 1992) raises the possibility that a functional infrastylar EGC exists in the family. This has never been investigated, however.

5.2 Increased ovule number per carpel

Increased ovule number per carpel is potentially an alternative strategy for promoting seedset in apocarpous flowers. This might be correlated with a reduction in carpel number per flower and/or flower number per plant to avoid exceeding the optimal fruit-carrying capacity of the plant. Increased ovule numbers are observed in some species of *Fissistigma* and *Uvaria* (Annonaceae), with up to 20 and 30 ovules, respectively (van Heusden, 1992). The functional significance of this in relation to seedset has never been evaluated, however.

5.3 Syncarpy

Although syncarpy is widespread among angiosperms and often cited as a key evolutionary innovation, it is very rare within Annonaceae: complete syncarpy has previously only been reported from the sister genera *Isolona* and *Monodora* (Guédès & Le Thomas, 1981; Couvreur et al., 2008; Couvreur, 2009). Two contrasting hypotheses have been developed to explain the evolution of syncarpy (Endress, 1990): the ‘multiplication hypothesis,’ in which the gynoecium is initially reduced to a single carpel, but with a subsequent increase in carpel number due to branching of the carpel primordium; and the ‘fusion hypothesis,’ involving congenital fusion of separate carpels. Developmental studies of the gynoecium in *Monodora crispata* (Leins & Erbar, 1982) revealed similarities with that of a single carpel, supporting the former hypothesis. Anatomical interpretations subsequently led Deroin (1997) to favor the fusion hypothesis, however, as he observed gynoecial vascular patterns consistent with an origin from 6–14 fused carpels (see also Deroin, 1985). Molecular phylogenetic reconstructions of the tribe Monodoreae furthermore indicate that the *Isolona*-*Monodora* lineage is nested within a multicarpellate clade (Couvreur et al., 2008), adding further support to Deroin's interpretation.

The Annonaceae genus *Cyathocalyx* s.str. is weakly supported as sister to *Drepananthus* (formerly included in *Cyathocalyx*), and collectively sister to *Cananga* (Surveswaran et al., 2010; Guo et al., 2017*b*). *Cyathocalyx* is characterized by an inferred synapomorphy of a large peltate stigma, whereas *Drepananthus* and closely related genera such as *Cananga* possess smaller ellipsoid or obconical stigmas (Wang & Saunders, 2006; Surveswaran et al., 2010) that are more typical for Annonaceae. The large peltate stigma in *Cyathocalyx* resembles a cluster of fused stigmas, raising the possibility of an independent origin of syncarpy: significantly, the solitary pistil in *Cyathocalyx* flowers possesses up to 38 ovules, arranged in up to four rows (Wang & Saunders, 2006); *Drepananthus* species, in contrast, have up to 32 carpels per flower, with carpels possessing fewer ovules (generally up to six, but rarely 20) that are uniseriate or biseriate (Surveswaran et al., 2010; R.J. Wang & R.M.K. Saunders, unpublished data). Anatomical preparations of *Cyathocalyx* flowers of several species (Endress, 2008; Y. Chen & R.M.K. Saunders, unpublished data) invariably reveal multiple vascular traces in transverse sections through the pistil; although this is consistent with a compound structure derived from the fusion of several carpels, multiplication of vascular traces might have evolved to provide an adequate xylem and phloem supply to the developing fruit after fertilization (Endress, 2019).

Partial syncarpy has been reported in the Annonaceae genera *Annona*, *Anonidium*, *Cananga*, *Fusaea* and *Pseudartabotrys* (Deroin, 1988, 1997; van Heusden, 1992; Deroin & Bidault, 2017). Although the hypothesis remains untested, it is possible that this incomplete syncarpy endows the same benefits as full syncarpy—allowing pollen grains deposited on any stigma to fertilize any ovule in the flower—whilst enabling the development of separate fruit monocarps (fruit units derived from individual carpels) that can be dispersed individually, and hence avoiding the dispersal constraints imposed by large fruits (discussed further in Section 8).

5.4 Self-pollination

Annonaceae species lack any biochemically mediated self-incompatibility mechanism and hence are capable of autogamous and geitonogamous self-fertilization (Pang & Saunders, 2014). As discussed in Section 3, Annonaceae have various adaptations that promote xenogamy, and consequently most species predominantly out-cross. The most widespread of these adaptations is protogyny, in which pistillate floral function precedes stamen dehiscence. Several studies, however, have demonstrated temporal overlap between the pistillate and staminate phases (e.g., several *Asimina* species: Norman & Clayton, 1986; Norman et al., 1992; Norman, 2003, as '*Deeringothamnus*'; *Disepalum anomalum*: Li et al., 2016; and *Uvaria concava*: Silberbauer-Gottsberger et al., 2003). In some cases, the overlap between phases might represent an adaptation to specific pollination systems: the meliponine bees that pollinate *D. anomalum*, for example, are rewarded with pollen and hence would only be attracted to pistillate-phase flowers after anther dehiscence (Li et al., 2016). In other species, however, the overlap between the two phases might be an adaptation to ensure seedset when cross-pollination is limited, possibly because of a population bottleneck or because of the inadequate availability of effective pollinators. Population genetic studies of such species are lacking, however.

5.5 Apomixis

Controlled pollination experiments involving the Annonaceae species *Cymbopetalum brasiliense* (Braun et al., 2011) revealed significant fruitset in tests for spontaneous selfing (in which pre-anthetic flowers were bagged to exclude pollinators) and apomixis (in which pre-anthetic flowers were emasculated and then bagged). Although the results of the latter experiment convincingly indicate apomixis, fruitset arising from the former experiment was also probably due to apomixis since autogamy was precluded by the abscission of stigmas at the end of the pistillate phase prior to anther dehiscence. *Cymbopetalum brasiliense* is the only known example of apomixis in Annonaceae, although in the absence of comparable studies it is unclear how widespread this phenomenon may be. It is probably significant that

C. brasiliense is a triploid (Morawetz, 1986) and hence likely to be incapable of forming functioning gametes: gametophytic apomicts are almost invariably polyploids (Bicknell & Koltunow, 2004).

6 Floral adaptations that enhance pollen competition

Pollen competition often occurs in angiosperms as the pollen tubes penetrate the carpel, enabling favored genotypes to be selected by stigmatic and stylar tissues (Moore & Pannell, 2011). Although it could be argued that the minimal pollen loads typically carried by the beetles that pollinate most Annonaceae flowers are unlikely to generate conditions that would promote intense pollen competition, no attempt has previously been made to assess the significance of pollen competition in the family.

Many Annonaceae genera are characterized by enlarged stigmas. Although this might promote suprastylar EGC by enhancing physical contact between neighboring stigmas and/or be associated with increased exudate formation, it is also possible that enlarged stigmas directly increase opportunities for pollen deposition. Large stigmas would probably minimize pollen selection, however, since fertilization would be heavily influenced by the random location of pollen deposition on the stigma (Armbruster, 1996): pollen grains deposited close to the base of the stigma would be at a selective advantage since their pollen tubes would have a shorter distance to grow, and hence successful fertilization would not be as dependent on paternal vigor.

Stigma morphology is very diverse in Annonaceae, however, with many taxa—including *Fissistigma* and *Goniothalamus* (Fig. 1E)—often possessing highly elongated stigmas. Lau et al. (2017a) demonstrated that entry of pollen tubes is restricted to the apex of the stigma in *Goniothalamus parallelivenius*. In such cases, the elongated stigmatic stalk closely resembles the style in derived angiosperm lineages; this pseudostyle can therefore be hypothesized to function as a true style and possibly enhance pollen competition. The most extreme pseudostylar adaptation in Annonaceae is likely to be *Goniothalamus flagellistylus* (Tagane et al., 2015), which has a stigma/pseudostyle that is c. 8.5 mm long, greatly exceeding the length of the ovary (1.4–1.7 mm).

Pollen competition in the pseudostyle might be intensified in cases where the pistillate phase is prolonged (e.g., c. 44 h duration in *Fissistigma oldhamii*: J.Y.Y. Lau & R.M.K. Saunders, unpublished data). Pollen competition might also be promoted in Annonaceae if the pollen tubes are directed through an alternative route to the ovule, as in species with putative infrastylar EGC (discussed in Section 5.1).

As discussed in Section 3.1, most Annonaceae species have bisexual, protogynous flowers, in which the pistillate and staminate phenological phases are separated by a non-sexual interim phase that effectively precludes autogamy (Pang & Saunders, 2014). There are several recorded cases (discussed in Section 5.4), however, in which the pistillate phase appears to overlap temporally with the staminate phase. This overlap might be an adaptation to ensure seedset when cross-pollination is limited. Since xenogamous pollen would be deposited on the stigma earlier than autogamous pollen, however, xenogamous pollen would possibly be selected passively simply by virtue of its earlier germination.

7 Floral adaptations that protect against herbivory

Annonaceae species demonstrate several morphological and chemical adaptations that can most easily be explained by reference to protection against herbivory rather than as adaptations to promote pollination or fertilization. Although the partially enclosed floral chambers alluded to earlier (Section 2.2) are generally weakly formed from convergent or connivent petals that can easily be separated by phytophagous insects, several Annonaceae genera are characterized by much more robust chambers. In these genera (e.g., *Artabotrys*: Chen et al., 2020; *Dasymaschalon*: Guo et al., 2018; *Friesodielsia*: Guo et al., 2017a; and *Goniothalamus*: Lau et al., 2016) the floral chambers function as pollinator traps (discussed in

Section 4.4) and have petals that are very intimately connected, with narrow apertures. These apertures are sufficiently small to prevent access by larger and potentially destructive floral visitors, whilst allowing entry of smaller effective pollinators.

Annonaceae stamens show polycyclic phyllotaxis (Endress & Doyle, 2007), with the stamens closely appressed prior to anther dehiscence. The staminal connectives are often elongated and are typically either dilated laterally to cover the apex of the thecae or else lack such an extension (‘uvarioid’ and ‘miliusoid’ stamens, respectively, sensu Prantl, 1891). The uvarioid connective presumably protects the thecae from phytophagous insects prior to anther dehiscence, with the staminal connectives forming a closely appressed tessellated protective shield (Saunders, 2010).

Some *Xylopia* species (in sections *Stenoxylopia* p.p. and *Xylopia*: Johnson & Murray, 2018) are unusual in Annonaceae in possessing a deeply invaginated structure that surrounds the ovary. This structure has variously been interpreted as an extension of the floral receptacle (Kramer, 1969; Deroin, 1989) or as a ‘staminal cone,’ primarily formed from the fusion of staminal filaments, with a limited contribution from sepal and petal tissues (Verdcourt, 1971; Dias et al., 1998). Irrespective of the anatomical interpretation, the cone is likely to function by protecting the ovary from insects, mirroring the role of the hypanthium in derived angiosperm lineages.

Floral scents not only function as olfactory cues to attract pollinators, but often also incorporate volatiles that discourage potential herbivores (Pichersky & Gershenzon, 2002), with pollinator-attracting scents hypothesized to have evolved from ancestral defense volatiles (Pellmyr & Thien, 1986). Naphthalene has been widely reported as a component of floral scent in Annonaceae (e.g., *Annona*: Jürgens et al., 2000, as ‘*Rollinia*’; *Desmos*: Pang & Saunders, 2015; *Uvariopsis*: Gottsberger et al., 2011; and *Xylopia*: Jürgens et al., 2000; Ratnayake et al., 2007), although there is disagreement whether it protects flowers against herbivores (Azuma et al., 1996) or whether it is of anthropogenic origin (Jürgens et al., 2000). Limonene, which possibly functions as an insect repellent (El-Sayed, 2019, and references therein), has similarly been reported from the floral scents of *Desmos* (Pang & Saunders, 2015), *Duguetia* (Jürgens et al., 2000) and *Unonopsis* (Teichert et al., 2009; Oliviera et al., 2017; Gottsberger et al., 2018). Annonaceae floral volatiles that potentially function as herbivore deterrents require further study, however.

8 Floral constraints imposed by adaptations that promote seed dispersal

Although Annonaceae adopt various mechanisms to promote xenogamy, paternal diversity amongst seeds within a single fruit is nevertheless likely to be limited due to the restricted number of pollinator visits to staminate-phase flowers prior to the pollinator's arrival at a pistillate-phase flower (e.g., *Annona crassiflora*: de Almeida-Júnior et al., 2018) and pollen aggregation (discussed in Section 4.1). The retention of separate, unfused carpels in flowers may compensate for this by enhancing the geographical spread of seed paternal types by enabling the independent dispersal of fruit monocarps.

Flowers can be regarded as immature fruits in which the ovules are yet to be fertilized. Floral structure inevitably imposes constraints on fruit structure and vice versa: anatomical features of the flower that may have little selective advantage during anthesis can theoretically promote fruit and seed dispersal. Although there are clear disadvantages associated with floral apocarpy as detailed above, it can be hypothesized that the retention of separate, unfused carpels in flowers might subsequently serve to enhance patterns of seed dispersal. Four main functional fruit morphologies are identified in Annonaceae:

Whole fruits as dispersal units—Some Annonaceae species develop relatively large fruits in which the anatomically separate monocarps (fruit units derived from individual carpels) become closely appressed (functionally syncarpous) due to the limited development of monocarp stalks; in these cases, the dispersal unit is the entire fruit, with dispersal by relatively large frugivores such as primates (e.g., *Duguetia*, p.p.: Maas et al., 2003; *Goniothalamus*, p.p.: Tang et al., 2015). Some genera, including *Annona* and *Duguetia*, p.p.

(van Setten & Koek-Noorman, 1992), undergo differing degrees of post-fertilization fusion of carpels, resulting in 'pseudosyncarpy,' in which the entire fruit is again dispersed as a single unit.

Monocarps as dispersal units—Most Annonaceae species have fruits in which the base of each monocarp is elongated to form a stipe that ensures separation of monocarps at maturity; in these cases, individual monocarps sometimes mature at different rates and are dispersed separately, either by birds that swallow the monocarps whole and defecate the seed intact, or by primates that spit the seeds. A few genera (e.g., *Disepalum*: Li et al., 2015) possess 'carpophores' that closely resemble stipes, but which are extensions of the fruit receptacle and hence are not homologous; the convergent evolution of carpophores and stipes presumably reflects the functional importance of monocarp stalks.

Single-seeded monocarp segments as dispersal units—Monocarps of many species in the *Monanthotaxis-Dasymaschalon-Desmos* clade are elongated and moniliform, with constrictions between seeds (Guo et al., 2017a); each monocarp ripens progressively from apex to base, with single-seeded segments removed sequentially by avian frugivores as the fruit ripens (J. Wang et al., 2012). Increasing the temporal separation between seed dispersal events possibly minimizes potential density-dependent seedling mortality due to over-crowding, fungal infection, seed predation or unfavourable germination site. Although such dispersal units are unique to the *Monanthotaxis-Dasymaschalon-Desmos* clade within Annonaceae, it parallels the lomentum observed in some legumes (Spjut, 1994).

Seeds as dispersal units—The Annonaceae genera *Cardiopetalum*, *Cymbopetalum*, *Trigynaea* (Johnson & Murray, 1995) and *Xylopia* (Johnson & Murray, 2018) possess dehiscent monocarps that split along a dorsal suture to expose bird-dispersed seeds with a brightly colored aril or sarcotesta (e.g., Coates-Estrada & Estrada, 1988). Some *Anaxagorea* species furthermore have dehiscent monocarps with ballistic dispersal of non-arillate seeds over distances up to 5 m (Gottsberger, 2016).

Although it can be hypothesized that many of the floral adaptations highlighted in this review (such as EGC, increased ovule number per carpel, syncarpy, and the formation of pollen polyads) would promote pollination efficiency by enhancing seedset, it is also likely that this would be achieved at the expense of paternal genetic diversity. This lack of genetic diversity in seeds might be compensated for by ensuring maximum spatial distance between seedlings after dispersal. In species in which the individual monocarp is the dispersal unit, single-seeded monocarps would be most effective in maximising distance between seedlings. Although seeds in multi-seeded monocarps would likely be dispersed together, such monocarps are likely to develop from flowers that are pollinated by insects that undertake more extensive interfloral movements, resulting in seeds with greater paternal diversity: *Fissistigma oldhamii*, for example, has c. 10 seeds per monocarp but is predominantly pollinated by drosophilid flies (J.Y.Y. Lau & R.M.K. Saunders, unpublished data). Beetle-pollinated species with multi-seeded monocarps often disperse their seeds separately, either as single-seeded monocarp segments (in the *Monanthotaxis-Dasymaschalon-Desmos* clade: J. Wang et al., 2012), or as seeds in dehiscent monocarps (e.g., *Xylopia*: Johnson & Murray, 2018). Large fruits that are dispersed as a single unit (e.g., *Annona* and *Goniothalamus*, p.p.) are hypothesized to be less likely to evolve in lineages with multiple ovules per carpel.

In a recent analysis of evolutionary diversification in Annonaceae, Xue et al. (2020) used comparative phylogenetic methods to identify significant rate shifts and their correlations with specific traits. They revealed a strong correlation with seed dispersal unit: dispersal via single-seeded monocarp segments was associated with the highest diversification rate, followed by single monocarps and then entire fruits. Although these results conform to the predictions discussed above regarding adaptations that maximize the spatial distance between seedlings, Xue et al. (2020) also demonstrated that direct seed dispersal from dehiscent monocarps was surprisingly correlated with the lowest diversification rate. These analyses merely identify correlations without determining causality, however, and may also reflect correlations between traits that are subject to very different selective pressures.

9 Conclusions

Annonaceae possess visual, olfactory and thermogenic floral traits that attract pollinators, often either with a reward or by deceit. The petals provide a key visual cue, with crepuscular insect pollinators able to perceive a broad spectral range despite the low ambient light intensities at dawn and dusk. The flowers are typically highly fragrant, emitting scents that are either sweet (advertising a nectar reward) or deceptively mimicking the pollinator's food substrate or brood site. Many Annonaceae flowers are thermogenic, with beetle pollinators able to locate the flowers by sensing the heat using their infrared sensilla. Annonaceae flowers offer various pollinator rewards, including enclosed environments within the floral chamber (providing a reproductive tryst site and protection from predators) and stigmatic or petal-derived nectar. Other rewards include floral heat (providing the energy required by ectothermic pollinators), floral scent (with male euglossine bees reported to collect floral scent volatiles from *Unonopsis* flowers to attract female bees) and petals as brood sites (directly or indirectly providing a food source for emerging larvae). In some cases, flowers that appear to serve as potential brood sites are likely to be deceptive.

Annonaceae species lack a biochemically mediated self-incompatibility mechanism and hence are capable of self-fertilizing. Most reproduction in the family is nevertheless xenogamous, with outcrossing promoted by various means, viz.: (a) the temporal separation of sexual function (as protogyny); (b) the spatial separation of anthers and stigmas (herkogamy); (c) synchrony of floral reproductive function (synchronous dichogamy); and (d) partial or complete separation of sexes (dicliny). Despite the prevalence of xenogamy, most ovules in Annonaceae flowers are likely to be fertilized by the same pollen donor, significantly constraining paternal genetic diversity.

Various strategies have evolved to enhance the efficiency of pollinator use. The aggregation of pollen grains as tetrads or larger polyads occurs in several clades, with non-sporopollenin pollen-connecting threads further promoting the transfer of multiple pollen grains following a single pollinator visit. This is likely to be beneficial when pollinator visits are infrequent and/or when interfloral pollen transfer is inefficient; because of the increased proportion of sibling pollen grains received by stigmas, however, pollen aggregation will only be selectively favored if it increases overall reproductive performance. Pollen release is promoted by the partial abscission of stamens (which remain suspended in the pendent flower) and in some cases by secondary pollen presentation within the inverted floral chamber.

Anthesis usually extends over 36–54 hours, although it is sometimes extended up to 25 days (especially in fly- or bee-pollinated species) or abbreviated to only 23–30 hours (in those showing floral synchrony and/or pollinator trapping). Species with abbreviated anthesis have fewer coetaneous cohorts of flowers, enhancing pollination efficiency by promoting staminate-to-pistillate interfloral movement of pollinators. Many Annonaceae lineages with abbreviated anthesis have furthermore evolved circadian pollinator trapping, in which petal movements controlling the opening or closing of the floral chamber are closely aligned with the endogenous circadian rhythms of the pollinators. This mechanism, which appears to be unique to Annonaceae, serves to broaden the range of potential pollinators, including those with either unimodal or bimodal circadian rhythms.

Various strategies exist or are hypothesized to optimize fertilization success. Almost all Annonaceae species have unfused carpels (apocarpy); the reproductive limitations of this are circumvented by the formation of stigmatic exudate, which functions as a suprastylar extragynoecial compitum (EGC), enabling intercarpellary growth of pollen tubes. Suprastylar EGC has been confirmed for *Annona*, *Asimina* and *Goniothalamus* species, but is likely to be more widespread in the family and may represent a key evolutionary innovation. Observations of floral anatomy (especially the predominance of basal placentation in many species-rich genera) suggest that infrastylar EGC may also function in the family, with pollen tubes traversing the floral receptacle to access ovules. Other evolutionary strategies for optimizing fertilization success include: increased ovule number per carpel; carpel fusion (syncarpy), which is known from the *Isolona*-*Monodora* clade and hypothesized here for

Cyathocalyx; self-pollination, primarily due to breakdown of protogyny; and rarely also apomixis.

Other floral adaptations are likely to promote pollen competition. Many Annonaceae species possessing elongated stigmas that resemble styles; these ‘pseudostyles’ might enable sporophytic selection of microgametophytes based on fitness, with xenogamous pollen potentially selected over geitonogamous pollen.

Some floral adaptations provide protection against herbivory. These adaptations include the exclusion by the floral chamber of potentially destructive floral visitors, the protection of undehisced anthers by the closely appressed and tessellated stamen connectives, the staminal cone that surrounds and protects the carpels of some *Xylopia* species, and the emission of floral defense volatiles.

Flowers can be regarded as immature fruits in which the ovules are yet to be fertilized, with plesiomorphic floral structures perpetuated due to their benefits during fruit and/or seed dispersal rather than during anthesis. Apocarpy may have been maintained in flowers because it enables the independent dispersal of monocarps and hence promotes the geographical spread of seed genotypes. This would be particularly important given the limited genetic diversity among seeds within each fruit due to the limited interfloral movements of pollinators.

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Table 1 Evidence for thermogenesis in Annonaceae genera. Supraspecific classification follows Chatrou et al. (2012) and Guo et al. (2017b).

Taxon (no. species sampled/total)	Evidence for thermogenesis[1]	Reference(s)
Subfamily Anaxagoreoideae		
Anaxagorea (5/30)	–, +, ++	Küchmeister et al. (1998); Braun & Gottsberger (2011); Teichert et al. (2011)
Subfamily Annonoideae		
Tribe Bocageeae		
Cymbopetalum (3/27)	++	Murray (1993); Braun et al. (2011)
Tribe Duguetieae		
Duguetia (7/94)	–, +	Küchmeister et al. (1998); Jürgens et al. (2000); Silberbauer-Gottsberger et al. (2003)
Tribe Xylopieae		
Artabotrys (2/105)	–	Chen et al. (2020)
Xylopia (5/164)	–, +, +++	Küchmeister et al. (1998); Jürgens et al. (2000); Silberbauer-Gottsberger et al. (2003); Ratnayake et al. (2007)
Tribe Annoneae		
Annona (9/170)	–, ++, +++	Webber (1981); Gottsberger (1989, 1999, 2012); Jürgens et al. (2000), as ‘Rollinia’
Asimina (2/17)	–	Gottsberger (2012)
Disepalum (2/9)	–	Li et al. (2016)
Goniothalamus (3/134)	–	Silberbauer-Gottsberger et al. (2003); Lau et al. (2016)
Tribe Monodoreae		
Isolona (1/20)	–	Gottsberger et al. (2011)
Monodora (1/14)	–	Gottsberger et al. (2011)
Uvariodendron (2/15)	+	Gottsberger et al. (2011)
Uvariopsis (2/19)	–	Gottsberger et al. (2011)
Tribe Uvarieae		
Dasymaschalon (1/27)	–	C.-C. Pang & R.M.K. Saunders (unpublished data)
Desmos (1/22)	–	Pang & Saunders (2015)
Fissistigma (1/59)	–	J.Y.Y. Lau & R.M.K. Saunders (unpublished data)
Friesodielsia (1/38)	–	X. Guo & R.M.K. Saunders (unpublished data)
Melodorum (1/11)	–	Silberbauer-Gottsberger et al. (2003)
Uvaria (2/199)	–	A.M.A.S. Attanayake, C.-C. Pang & R.M.K. Saunders (unpublished data)

Subfamily Malmeoideae		
Tribe Piptostigmateae		
Piptostigma (1/13)	–	Gottsberger et al. (2011)
Tribe Malmeeae		
Bocageopsis (1/4)	–	Silberbauer-Gottsberger et al. (2003)
Mosannona (1/14)	–	Chatrou & Listabarth (1998)
Tribe Miliuseae		
Huberantha (1/27)	++	Ratnayake et al. (2006a), as ‘*Polyalthia*’
Meiogyne (1/26)	–	Silberbauer-Gottsberger et al. (2003)
Monoon (1/60)	–, ++	Silberbauer-Gottsberger et al. (2003), as ‘*Enicosanthum*’; Ratnayake et al. (2006a), as ‘*Polyalthia*’
Pseuduvaria (1/54)	–	Pang et al. (2013)

[1] –, no thermogenesis recorded (i.e., floral temperatures < 1 ºC above ambient conditions); +, weakly thermogenic (1–3 ºC above ambient conditions); ++, moderately thermogenic (3–8 ºC above ambient conditions); +++, strongly thermogenic (> 8 ºC above ambient conditions).

Table 2 Prolonged (> 3 days) and abbreviated (23–30 hours) anthesis in Annonaceae species, with correlated traits (primary pollinator type, floral sex expression, presence/absence of floral synchrony, and presence/absence of circadian pollinator trapping). Species with standard anthesis duration (36–54 hours) are not listed.

Anthesis type and species	Anthesis duration	Pollinators	Floral sex expression	Floral synchrony	Circadian trapping[1]	Reference(s)
Prolonged anthesis						
Asimina obovata	5–8 days	Scarab beetles	Bisexual	?	–	Norman & Clayton (1986)
Asimina parviflora	6–12 days	Flies	Bisexual	?	–	Norman et al. (1992)
Asimina pulchella	8–9 days	Flies, beetles, thrips	Bisexual	?	–	Norman (2003)
Asimina pygmaea	3–4 days	Scarab beetles	Bisexual	?	–	Norman & Clayton (1986)
Asimina rugelii	5–6 days	Flies, beetles, thrips	Bisexual	?	–	Norman (2003)
Asimina triloba	6–8 days	Flies, beetles	Bisexual	+	–	Willson & Schemske (1980);

						Rogstad (1993)
Disepalum anomalum	c. 25 days	Meliponine bees	Bisexual	–	–	Li et al. (2016)
Disepalum pulchrum	c. 20 days	Drosophilid flies, nitidulid beetles	Bisexual	–	–	Li et al. (2016)
Fissistigma oldhamii	c. 5 days	Drosophilid flies, nitidulid beetles	Bisexual	–	–	J.Y.Y. Lau & R.M.K. Saunders (unpublished data)
Monodora myristica	11–13 days	Flies?	Bisexual	?	–	Lamoureux (1975)
Popowia pisocarpa	c. 4 days	Thrips	Bisexual	?	–	Momose et al. (1998)
Sapranthus palanga	‘many’ days	Tenebrionid beetles	Bisexual	?	–	Schatz (1987)
Uvariopsis bakeriana	c. 4 days	Flies	Unisexual	–	–	Gottsberger et al. (2011)
Uvariopsis congolana	4–5 days	Flies	Unisexual	–	–	Gottsberger et al. (2011)
Abbreviated anthesis						
Annona mucosa	c. 24 hrs	Beetles	Bisexual	+	–	Murray & Johnson (1987), as ‘*Rollinia jimenezii*’
Artabotrys blumei	c. 27 hrs	Beetles?	Bisexual	–	+	Chen et al. (2020)
Dasymaschalon trichophorum	c. 26 hrs	Curculionid beetles	Bisexual	+	+	Pang & Saunders (2014); Lau et al. (2017b)
Desmos chinensis	c. 27 hrs	Nitidulid beetles	Bisexual	+	–	Pang & Saunders (2015); Lau et al. (2017b)
Friesodielsia borneensis	c. 26 hrs	Curculionid beetles, nitidulid beetles, staphylinid beetles	Bisexual	+	+	Lau et al. (2017b)
Goniothalamus suaveolens	c. 25 hrs	Curculionid beetles, nitidulid beetles	Bisexual	–	+	Lau et al. (2016)
Goniothalamus tapisoides	c. 23 hrs	Curculionid beetles,	Bisexual	–	+	Lau et al. (2016,

		nitidulid beetles				2017b)
Pseuduvaria froggattii	< 1 day	Flies	Unisexual	–	–	Silberbauer-Gottsberger et al. (2003)
Unonopsis guatterioides[2]	c. 30 hrs	Bees	Bisexual	?	–	Oliviera et al. (2017)

[1] Many negative assessments for circadian pollinator trapping are based on interpretation of floral morphology rather than empirical study.

[2] According to Oliviera et al. (2017) and Gottsberger et al. (2018) this is unlikely to be conspecific with the *Unonopsis guatterioides* populations studied by Carvalho & Webber (2000).

Figure captions

Fig. 1. Floral morphology and flower-pollinator interactions in selected Annonaceae species. **A**, *Monodora myristica* flower, showing patchy petal pigmentation. **B**, *Mitrephora vittata* flower, showing striped petal pigmentation. Hairs on the adaxial surface of the inner petals possibly assist with pollen retention during secondary pollen presentation. **C**, *Meiogyne bidwillii*, showing petal adaptations favoring sapromyiophily. **D**, Copious stigmatic exudate in *Disepalum anomalum*. **E**, Copious stigmatic exudate and elongated pseudostyles in *Goniothalamus palawanensis*. **F**, Inner petal nectaries (arrowed) in *Uvaria dulcis*. **G**, *Endaenidius* beetles copulating on a *Dasymaschalon trichophorum* petal; note that the female beetle is boring a hole into the petal with its mouthparts. **H**, Female *Endaenidius* beetle ovipositing into a petal *Dasymaschalon trichophorum* petal. **I**, Inner petal corrugations (arrowed) in *Meiogyne stenopetala*. (Photos: A, © R.M.K. Saunders, reproduced from Saunders, 2010; B, © J. Beaman, reproduced from Weerasooriya & Saunders, 2001; C, G–I, © C.-C. Pang; D, © P.-S. Li; E, © C.C. Tang, reproduced from Tang et al., 2013; F, © L. Averyanov).

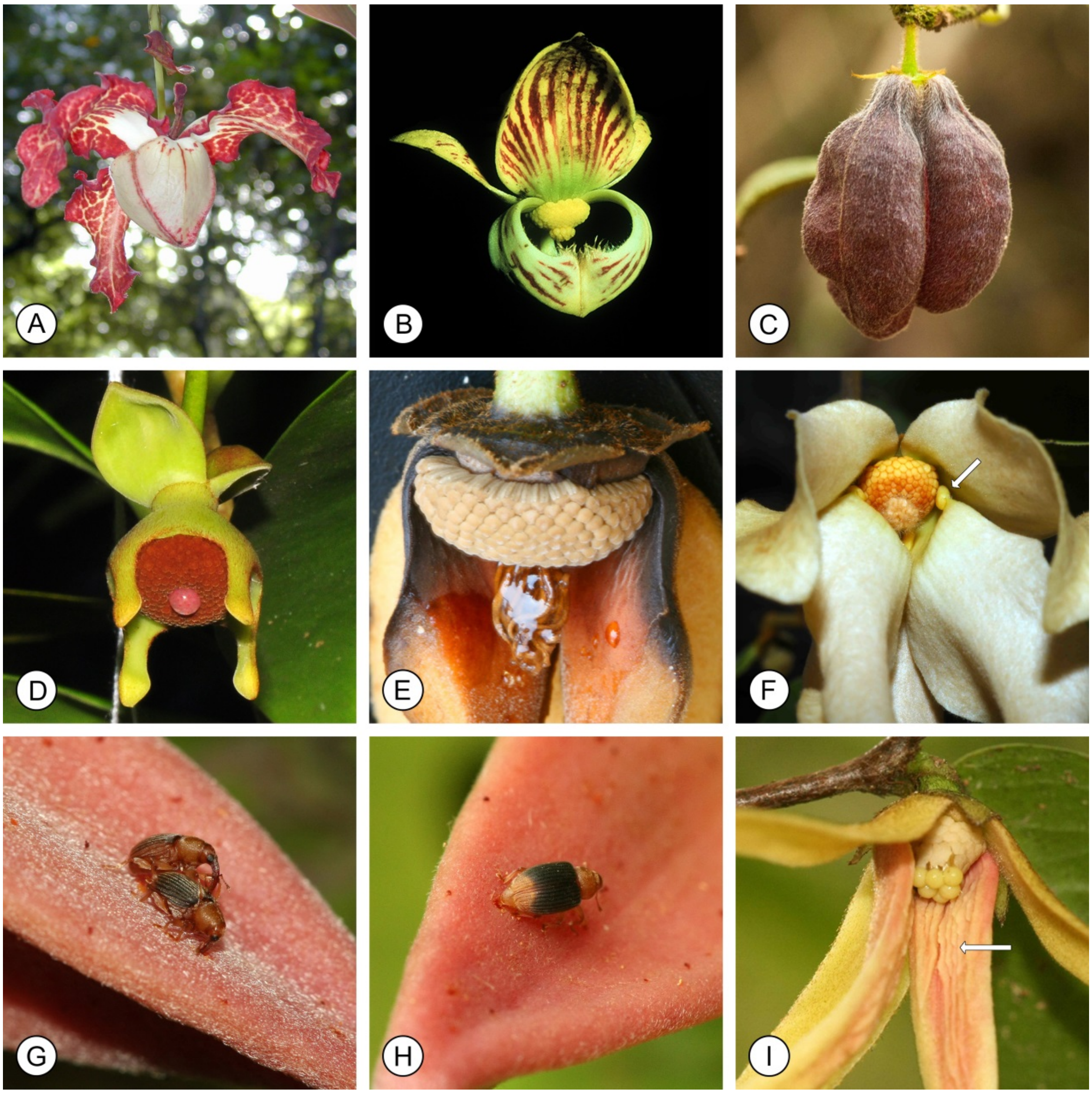
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Fig. 2. Floral phenology diagrams for selected Annonaceae species, showing schematic graphs of pollinator circadian rhythms (in gray) in relation to pistillate and staminate functions (pink and blue bars, respectively). Interfloral pollinator movements shown by large arrows: movement from pistillate to staminate flowers shown as arrows that transition from pink to blue; and reverse movement as arrows that transition from blue to pink. **A**, *Polyalthia suberosa*, which has anthesis over c. 48 hours and hence potentially has three coetaneous cohorts of flowers: only about half of the beetle pollinators departing from post-staminate flowers will move directly to pistillate-phase flowers. **B**, *Desmos chinensis*, which has abbreviated anthesis over c. 27 hours and hence only has two coetaneous cohorts of flowers: most beetle pollinators departing from post-staminate flowers move directly to pistillate-phase flowers, although those leaving post-pistillate flowers cannot directly access staminate-phase flowers. **C**, *Goniothalamus tapisoides*, which has abbreviated anthesis over c. 23 hours and circadian pollinator trapping, with two coetaneous cohorts of flowers: most of the beetle pollinators departing from post-staminate flowers are able to move directly to pistillate-phase flowers; beetles cannot leave the floral chamber at the end of the pistillate phase, however, to due to circadian trapping.

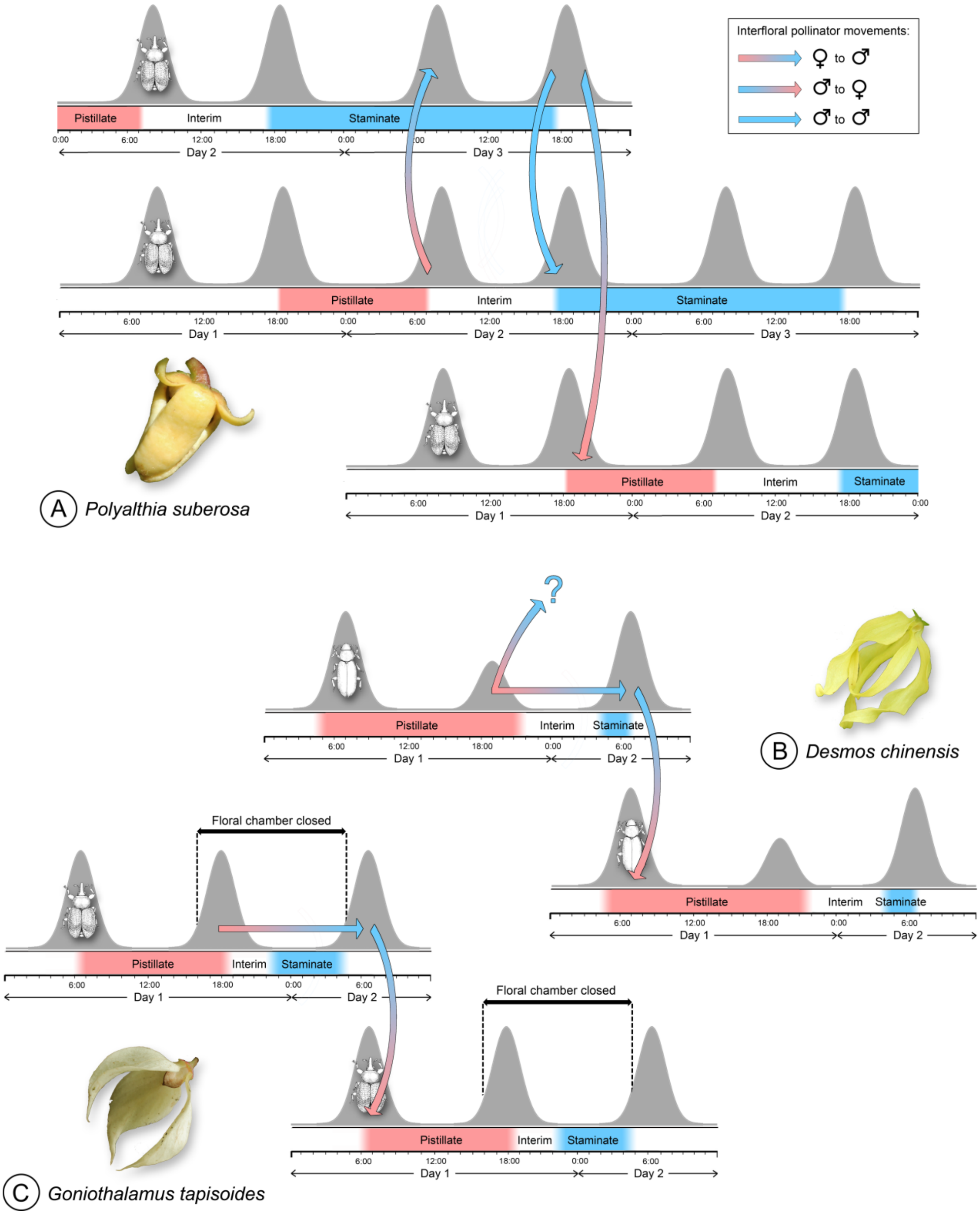
Interfloral pollinator movements:
♀ to ♂
♂ to ♀
♂ to ♂
Pistillate
Interim
Staminate
0:00
6:00
12:00
18:00
Day 1
Day 2
Day 3
A
Polyalthia suberosa
?
B
Desmos chinensis
Floral chamber closed
C
Goniothalamus tapisoides

Fig. 3. Pollen structure, floral morphology and pollen-stigma interactions in selected Annonaceae species. **A**, Pollen tetrads of *Pseuduvaria macrocarpa*, with pollen-connecting thread linking adjacent tetrads. Scale bar: 10 µm. **B**, Detail of a non-sporopollenin pollen-connecting thread in *Pseuduvaria macrocarpa*. Scale bar: 2 µm. **C**, Stamen abscission in a staminate-phase flower of *Disepalum anomalum*, showing stamens suspended by tracheary threads (arrowed in inset photo). **D**, *Artabotrys hexapetalus*, with outer petals raised to expose the apertures (arrowed) between the inner petals, opening the floral chamber. **E**, *Artabotrys hexapetalus*, with closed floral chamber. **F**, Intercarpellary growth of pollen tube through the extragynoecial compitum of *Goniothalamus tapisoides*. PT = pollen tube; SE = stigmatic exudate; St = stigma. Scale bar = 250 µm. (Photos: A, B, Y.C.F. Su; C, © P.-S. Li; D, E, © J. Chen; F, © J.Y.Y. Lau, reproduced from Lau et al., 2017a).