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Most diverse, most neglected: weevils (Coleoptera: Curculionoidea) are ubiquitous specialized brood-site pollinators of tropical flora

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Abstract

In tropical environments, and especially tropical rainforests, a major part of pollination services is provided by diverse insect lineages. Unbeknownst to most, beetles, and more specifically hyperdiverse weevils (Coleoptera: Curculionoidea), play a substantial role there as specialist mutualist brood pollinators. The latter contrasts with a common view where they are only regarded as plant antagonists. This study aims at giving a comprehensive understanding of what is known on plant-weevil mutualist interactions, through a review of the known reciprocal behavioral, morphological and physiological adaptations found in plant-weevil systems, and the identification of potential knowledge gaps to fill. To date, plant-weevil associations have been described or indicated in no less than 600 instances. Representatives of all major plant lineages (gymnosperms, angiosperms monocots and dicots) are involved in these interactions, which have emerged independently at least a dozen times. Strikingly, these mutualistic interactions have led to a range of multiple convergent adaptations in plants and weevils. Plants engaged in weevil-mediated pollination are generally of typical cantharophilous type and they also show specific structures to host the larval stages of their specialist pollinators. Another characteristic feature is that flowers often perform thermogenesis and exhibit a range of strategies to separate sexual phases, either physically or chronologically. Conversely, lineages of brood-site weevil pollinators present numerous behavioral and physiological adaptations, and often form multispecific assemblages of closely related species on a single host; recent studies also revealed that they generally display a high degree of phylogenetic niche conservatism. This pollination mutualism occurs in all tropical regions, and the contrasts between the known and expected diversity of these systems suggests that a wide range of interactions remain to be described globally. Our early estimates of the species richness of the corresponding weevil clades and the marked pattern of phylogenetic niche conservatism of host use further suggest that weevil-based pollination far exceeds the diversity of other brood-site mutualistic systems, which are generally restricted to one or a few groups of plants. As such, weevil pollinators constitute a relevant model to explore the emergence and evolution of specialized brood-site pollination systems in the tropics.

Keywords

Cantharophily, entomophily, mutualism, nursery pollination, plant-insect interactions, tropical rainforests

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Introduction

Most of the extant biodiversity in tropical regions is concentrated in tropical rainforests, which were the first biomes to be coined as ‘biodiversity hotspots’ (Myers 1988). The outstanding diversity of pollinating systems in these ecosystems offers unique opportunities to study the evolution of reciprocally beneficial interactions among organisms. Pollination ecology in tropical rainforests indeed presents unique characteristics due to specific constraints. For instance, anemophily (wind pollination) is considered to be infrequent and potentially limited because of a combination of marked spatial constraints (evergreen canopy, structural heterogeneity and complexity) associated with frequent periods of high rainfall preventing pollen dispersal (Regal 1982; Williams & Adam 1994). Anemophilous plants are also presumably disadvantaged whenever they are over-dispersed (Regal 1982; see also below). Hence, pollination by animal vectors is predominant and can concern up to 100% of the plant species in some tropical rainforests (Bawa 1990; Ollerton et al. 2011; Rech et al. 2016). The high level of plant diversity that characterizes tropical rainforests is also associated with a spatial trend where the distribution of conspecific individuals is usually patchy (Bawa 1990; Williams & Adam 1994). The latter limits the efficiency of generalist pollinators, as they are not actively seeking specific plants (Whitehead 1968; Bawa 1990; but see Wolowski et al. 2014). To cope with these major constraints, the reliance on more intricate pollination mechanisms, involving specialist pollinators (especially insects), is a hallmark of tropical rainforests (Bawa 1990; Renner & Feil 1993; Vizentin-Bugoni et al. 2018) and also widespread in all tropical or subtropical biomes (e.g., Gottsberger 1986; Ramirez 2004; Maruyama et al. 2013; Guy et al. 2021).

A mode of specialized pollination that particularly stands out is brood-site pollination (or nursery pollination; hereafter called BSPM for brood-site pollination mutualism), a system where immature stages of a pollinator develop within tissues (either flowers, ovules or pollens; Sakai 2002) of a specific plant as a reward for its pollination. It has independently evolved several times, mostly in tropical and subtropical biomes (Sakai 2002; Dufaÿ & Anstett 2003). These specialized mutualistic systems have been unequivocally documented in at least a dozen plant families and five insect orders (Coleoptera, Diptera, Hymenoptera, Lepidoptera and Thysanoptera) (Sakai 2002; Dufaÿ & Anstett 2003; Kawakita & Kato 2009; Hembry & Althoff 2016). Textbook examples of brood-site pollination are traditionally exemplified by the fig/fig-wasp and yucca/yucca-moth models (Janzen 1979; Wiebes 1979; Pellmyr 2003; Herre et al. 2008); studies on these models have yielded important discoveries on the origin and maintenance of mutualisms and on the degree of co-evolution, with obligatory interactions possibly leading to evolutionary co-diversifications (e.g., Hembry & Althoff 2016). However, the number of insect and plant lineages engaging in brood-site pollination likely goes well beyond the few iconic interactions typically studied. Here we advocate the need to consider other systems to obtain a broader and more complete view of the ecology and evolution of biological interactions in general, and pollination in particular.

Of the neglected lineages of insect pollinators, weevils (Coleoptera: Curculionoidea) are probably the biggest oversight. Weevils contain over 62,000 described species and a colossal amount of unknown diversity (Oberprieler et al. 2007). This clade of beetle is exclusively phytophagous and is the most speciose lineage of phytophagous insects, usually only depicted as antagonistic to plants (Anderson 1995). Indeed, brood-site pollination by weevils is generally considered anecdotal and is often overlooked in reviews on brood-site pollination (Dufaÿ et al. 2003; Hembry & Althoff 2016; Toon et al. 2020). Weevils are not even mentioned as one of the most relevant groups of beetle pollinators in some studies (e.g., Kevan & Baker 1983; Wardhaugh 2015; IPBES 2016). However, in recent decades, a number of plant-weevil relationships involving brood-site pollination have been progressively documented and described in detail (Franz & Valente 2005, Caldara et al. 2014; Nunes et al. 2018; de Medeiros et al. 2019; Saunders 2020; Toon et al. 2020). Moreover, recent phytocentric studies on tropical pollinators have recovered weevils as one of the most important pollinator groups (Krimse & Chaboo 2020; Paz et al. 2021). Taken altogether, all these studies suggest that these associations may be more widespread than previously thought (Caldara et al. 2014); it also contradicts the common view that weevils are not pollinators, and suggests that much of the global insect pollinator diversity is currently left unnoticed. For example, the combined species diversity of the three weevil families containing pollinator lineages (ca. 350, 4400 and 51,000 species, for Belidae, Brentidae and Curculionidae, respectively; Marvaldi & Ferrer 2014; Oberprieler 2014a, 2014b) is at least twice as large as the diversity of bees (ca. 20,000 species; Zattara & Aizen 2021), which are usually considered to be the most important group of insect pollinators (Potts et al. 2016). As we detail in this review, multiple and diverse weevil lineages commonly visit flowers, and an ever-increasing number of them can be considered true pollinators. This broad reassessment of the potential role of weevils as pollinators is highly relevant for the understanding of ecosystem functioning (including for agroecosystems), especially in tropical regions where bees are much less diverse than weevils (Oberprieler et al. 2007; Orr et al. 2021; Freitas et al. 2022).

The aim of this review is to provide a synthetic overview of all plant-weevil pollination mutualisms described to date. We begin by aggregating available data about weevil flower visitors and detail the extent of plant and weevil lineages known to be engaged in such interactions. We further summarize known reciprocal adaptations and evolutionary trends to highlight both common patterns and specificities within these relationships. Finally, we investigate possible reasons why weevils have been previously overlooked in the pollination literature, estimate the extent of potential undescribed relationships, and conclude with a road map for future research on plant-weevil pollination mutualisms.

1. A wide spectrum of mutualistic interactions

Weevils are the most diverse group of insects that visit flowers and develop in reproductive structures (Oberprieler et al. 2007; Kirmse & Chaboo 2020). This close interaction with the reproductive structures of plants probably preceded the association of weevils with angiosperm flowers. The oldest weevil fossils (such as †*Belonotaris punctatissimus*) were found in the Karabastau Formation (ranging from the Oxfordian to Callovian stages, 166.1 to 157.3 million years ago (Mya); Walker et al. 2018); at that time they were likely associated with gymnosperm-dominated floras (e.g., see Oberprieler & Oberprieler 2012 for slightly younger weevil fossils from the Tithonian stage, 150.8 to 145.5 Mya). Their origin therefore clearly predates the rise to dominance of angiosperms during the Cretaceous Terrestrial Revolution, from 125 to 80 Mya (Dilcher 2000; Magallón & Castillo 2009; Benton 2010). In addition, several early diverging weevil lineages, such as Caridae or Nemonychidae, typically breed on gymnosperm male or female reproductive structures (Oberprieler et al. 2007).

Associations with angiosperm flowers and seeds evolved both within these early-diverging lineages (Ferrer et al. 2011; Kuschel & Leschen 2011) but also in more derived lineages belonging to the two most speciose weevil families (Brentidae and Curculionidae). Weevils generally visit flowers when feeding on pollen and ovipositing in buds, ovaries and fruits where larval development occurs (Oberprieler et al. 2007). When adults fly between flowers to mate or oviposit on one or on a fairly narrow range of hosts, they can carry pollen between conspecific plant species, thereby passively pollinating them. Therefore, the flower-visiting and plant oviposition behaviors of several weevil lineages create the context for the evolution of BSPM from antagonistic to mutualistic interactions, or conversely (Figure 1). Interestingly, the ever-growing body of accumulated knowledge on plant-weevil interactions suggests that increasingly diverse and complex specialized plant-weevil BSPM interactions are to be expected (Franz & Valente 2005; Franz 2006; Saunders 2020; Toon et al. 2020).

The first report of weevil pollination activity refers to a palm-weevil interaction and dates back to the 19th century (Von Martius 1823). Since then, most efforts to describe and document weevil pollination have focused on palm-weevil and cycad-weevil mutualisms (Franz & Valente 2005; Toon et al. 2020). This focus on cycads and palms can be explained by their characteristic conspicuous inflorescences which attract massive gatherings of weevils, so much so that they have triggered specific research. To date, weevil BSPM has been reported for about one hundred palm species (Arecaceae) belonging to 31 genera (Table 1; S1). Weevils pollinating palms consist of at least 146 species from 15 genera, mostly belonging to the pantropical tribes Acalyptini and Derelomini (Curculionidae: Curculioninae) *sensu* Caldara et al. (2014), hereafter called Derelomini or derelomine weevils (see also Franz (2006) and Alonso-Zarazaga (2007) for nomenclatural uncertainties). Among the cycads, weevil BSPM has been reported or suggested for 91 cycad species belonging to seven genera from all three extant cycad families (Cycadaceae, Stangeriaceae and Zamiaceae). Weevils pollinating cycads belong to a diverse range of lineages; they are predominantly found within Curculioninae and Molytinae among the Curculionidae (ca. 50 species in six genera), but also within Belidae (20 species in three genera) and Brentidae (12 species in two genera, Toon et al. 2020).

The study of these relationships, their mechanisms and their patterns of associations with palms and cycads has stimulated the discovery of similar cases among several monocot families of angiosperms. For instance, in Neotropical *Anthurium* (Araceae), 10 species are engaged in mutualism with *Cyclanthura* weevils (Derelomini, seven species; Franz 2003, 2006). In the same region, 33 species from eight genera of cyclanths (Cyclanthaceae) are pollinated by 21 weevil species belonging to five genera of Derelomini (Franz 2007a, 2008). In Neotropical Orchidaceae, three weevil species belonging to two genera of Baridinae (Curculionidae, alternatively classified as the supertribe Bariditae among Conoderinae) ensure their pollination (Nunes et al. 2018). More anecdotally, *Strelitzia nicolai* (Strelitziaceae) from southern Africa appears to be pollinated by two derelomine species belonging to two distinct genera (Haran et al. 2022a; Haran unpublished). Importantly, the majority of weevils engaged in BSPM show a marked pattern of phylogenetic niche conservatism (PNC) at the genus level (Table 1 & Table S1; Franz & Valente 2005; Toon et al. 2020; Haran et al. 2021, 2022b). Such a pattern is far from unusual among groups of internal feeding insects, such as seed beetles (Kergoat et al. 2007, 2015) or noctuid stem borers (Kergoat et al. 2018). Therefore, we postulate that, in the absence of direct experimental evidence for a weevil species, knowledge about other species in a genus may provide an indication of pollination activity. This generalization can produce hypotheses to be tested and also provide a first assessment of the extent of plant-weevil BSPM in overlooked tropical biomes (Toon et al. 2020).

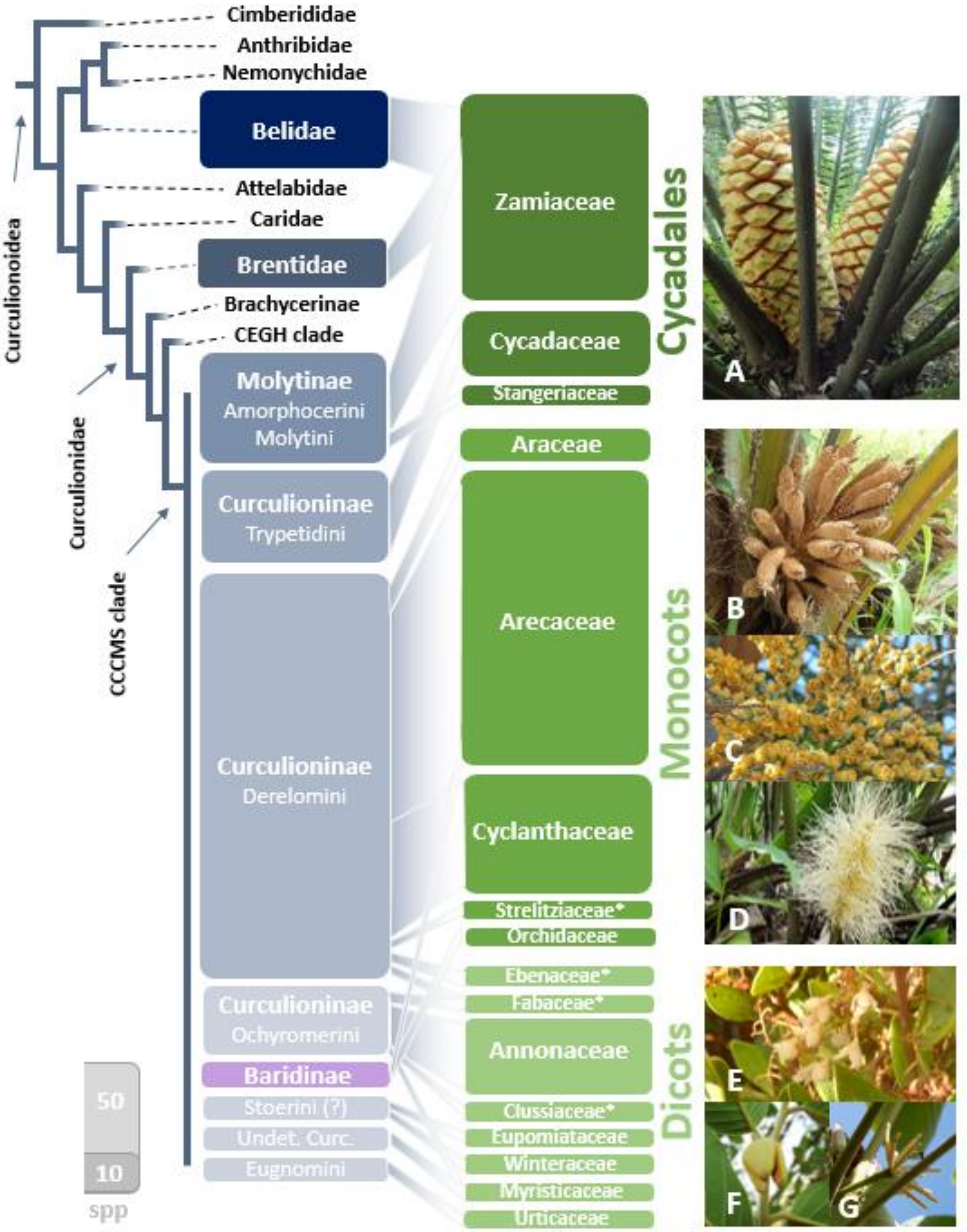

Figure 1. Summary of known and expected brood-site pollination mutualisms between plants and weevils (Coleoptera; Curculionoidea). The boxes in blue and green refer respectively to the weevil and plant lineages involved (the size of boxes is correlated to the number of species involved; see also the approximate scale at the bottom left). The phylogenetic tree on the left presents a synthetic view of phylogenetic relationships among weevils based on the phylogenomic study of Shin et al. (2017). The relationships among the so-called CCCMS clade (for Baridinae, Cossoninae, Curculioninae, Molytinae and Scolytinae) are unresolved; several subfamilies belonging to this clade and not involved in BSPM (e.g., Scolytinae, Lixinae) are not shown. Most of the plant families reported here contain at least one experimentally verified case of BSPM; however, for the plant families highlighted with an "*", BSPM relationships are postulated based on the niche conservatism of the weevil genera involved. Some minor relationships are not shown for clarity; see Table S1 for details. Pictures of selected examples of inflorescences of plant lineages involved: **A**. *Encephalartos* sp. (Zamiaceae) pollinated by weevils from the Brentidae family and Curculionidae Molytinae. **B**. *Elaeis guineensis* (Arecaceae) pollinated by Derelomini. **C**. *Syargus coronata* (Arecaceae) pollinated by Derelomini. **D**. *Carludovica palmata* (Cyclanthaceae) pollinated by Derelomini. **E**. *Euclea racemosa* (Ebenaceae) associated with Derelomini. **F**. *Annona senegalensis* (Annonaceae) pollinated by Ochyromerini. **G**. *Cecropia peltata* (Urticaceae), a genus including species pollinated by Eugnomini. (credits: A-B, E: J. Haran; C-D, G: B. de Medeiros, F: M. Gueye).

Several dicot families have been also increasingly reported to be engaged in BSPM with weevils. In the genera *Eupomatia* (Eupomatiaceae), *Myristica* (Myristicaceae) and *Exospermum* (Winteraceae), species pollinated by specific weevil lineages have been identified (*Elleschodes* spp., indet. genus (see Caldara et al. 2014) and *Palontus* spp. respectively; Armstrong & Irvine 1989a, 1989b, 1990; Pellmyr et al. 1990; Armstrong 1997). In African Ebenaceae (*Euclea*), Lecythidaceae (*Napoleonaea*) and Malvaceae (*Thespesia*) weevil pollination can be inferred on the basis of PNC since congeneric weevil species associated with other plant groups are brood pollinators (Haran et al. 2022a, 2022b; Haran pers. obs.). In the Neotropics, most species of *Cecropia* (Urticaceae) surveyed to date are associated with weevils belonging to the genus *Udeus* (Curculioninae: Eugnomini), which visit male inflorescences in all species (Lira et al. unpublished) and female inflorescences in at least one case (Mendonça 2004). In the speciose pantropical family Annonaceae, at least 25 species in 14 genera are associated with species of weevils pollinators belonging to two Ochyromerini genera (Curculionidae: Curculioninae) and other unidentified weevil groups (Momose et al. 1998; Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020; B. de Medeiros unpublished; Dao et al. unpublished).

All in all, the extensive literature search conducted in this review underlines that no less than 600 instances of plant-weevils species-species BSPM interactions have been recorded to date or suggested based on the marked trend of PNC for brood pollination (Table 1; see Table S1 for details). Overall, BSPM with weevils has been demonstrated experimentally in 12 of the 22 plant families involved in this mutualistic system, with the remaining 10 families suggested based on PNC of weevil genera and/or adaptations of floral structures to cantharophily. Representatives of all major plant lineages, gymnosperms, monocots and dicots, are engaged in BSPM with weevils; collectively representing ca. 250 species belonging to 72 genera (Figure 1) associated with about 300 species of weevils. In this regard, weevils are by far the most ecologically successful group of insects engaged in BSPM relationships with the plant kingdom. Our review shows that weevil-based BSPM has emerged several times independently and is currently present in all tropical regions (Figure 1, 2), with plants involved in these relationships typically belonging to groups considered to be ancient lineages (Pant 1987; Franz 2004; Saunders 2012; Baker & Couvreur 2013).

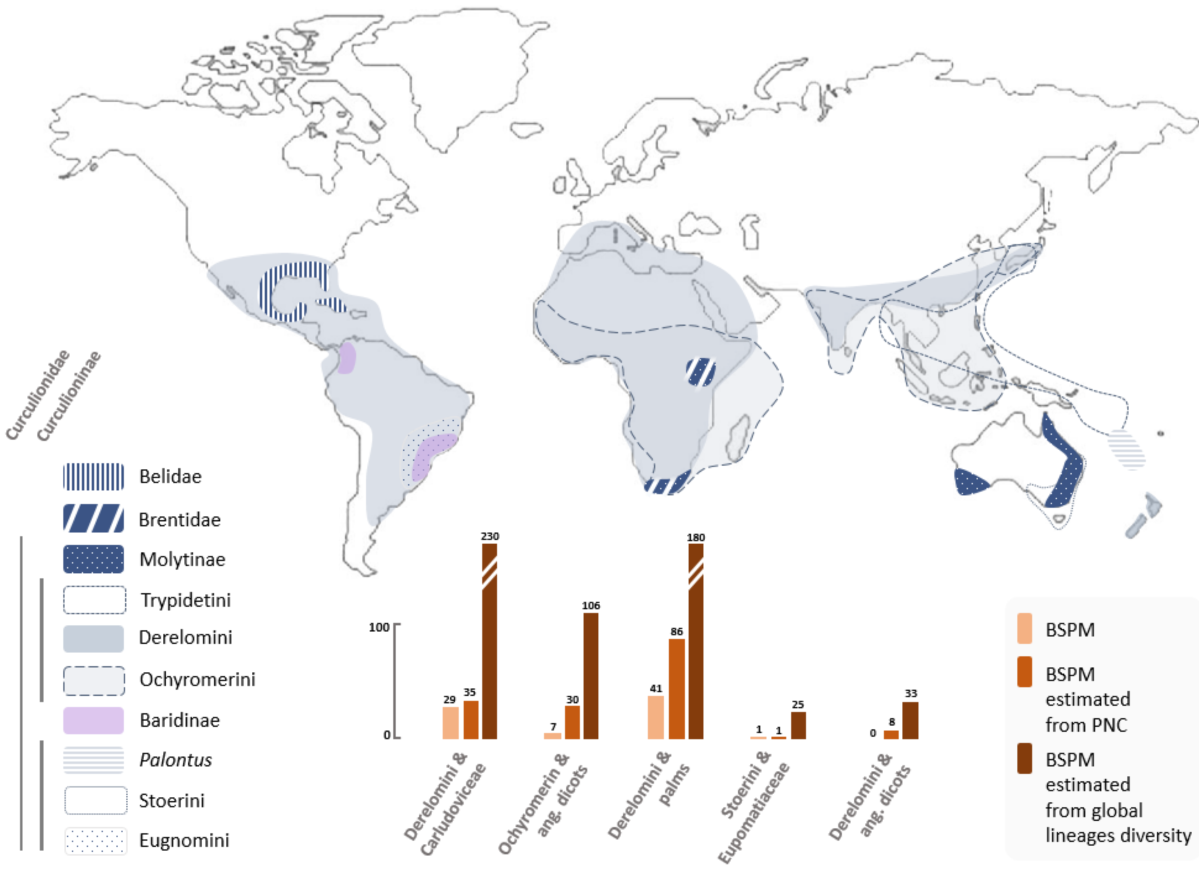

Figure 2. Geographical distribution of weevil lineages engaged in BSPM with plants and estimates of knowledge gaps. Distribution data collated from Alonso-Zarazaga & Lyal (1999), articles listed in this review, and unpublished observations by the authors (note that the distribution of several minor relationships is not shown for clarity). Bars show the relative number of known and estimated BSPM relationships for a selection of plant-weevil interactions. Beige: number of plant species involved in verified relationships (involving brood-site and/or synchronization of weevil and flower phenology and/or pollen transfer observed). Light brown: number of plant species involved estimated based on floral visitors, including weevils and PNC of weevils involved. Dark brown: global diversity of interaction estimated from the diversity of plant lineages engaged in BSPM with weevils (Derelomini-Carludoviceae; Franz & Valente 2005; Franz 2006) and the diversity of weevil genera engaged in these interactions (other interactions; Table S1, GBIF data and unpublished authors observations, see section 4.2).

2. Reciprocal adaptations

2.1 Plant adaptations to BSPM by weevils

Flowers and inflorescences of plants engaged in BSPM with weevils generally display typical adaptations to cantharophily (beetle pollination) and remarkable convergent morphologies, physiologies, phenologies and reproductive strategies. All these characteristics enhance the attractiveness of flowers to weevils, provide them with food rewards, and sometimes protect them from predators; they also improve pollen transfer to weevil integuments and play a role in weevil pollinator selection and retention, thereby improving pollination efficiency.

A first major characteristic for weevil-pollinated plant lineages is that they tend to display **large flowers or inflorescences** (Figure 1). In cycads and most monocot lineages involved in BSPM (Araceae, Cyclanthaceae, some Arecaceae), flowers or female ovules are clustered in large compact cones or inflorescences (Franz & Valente 2005; Toon et al. 2020). Individual flowers can also reach substantial sizes in Annonaceae or Lecythidaceae (Prance & Jongkind 2015; Saunders 2020). In contrast, other plant lineages producing smaller individual flowers form either dense inflorescences (most Arecaceae) or synchronized blooms (Ebenaceae – *Euclea*, Orchidaceae – *Dichaea*, *Grobya* etc). Field observations and experiments on various Annonaceae flowers and Cyclanthaceae inflorescences show that larger floral structures attract greater number of weevil pollinators (Gottsberger 1999; Franz 2007a), revealing that this floral trait has been independently selected to enhance weevil attraction and pollination.

The main characteristic of weevil-based cantharophily is the transformation of floral structures to host the weevil larval stages. Two main types of floral morphology are typical of weevil-pollinated plants: *(i)* **clustered inflorescences** (in cycads and all monocots involved in BSPM except Orchidaceae and Strelitziaceae), and *(ii)* **individual floral chambers, bowls or claws** (in most dicots involved in BSPM; Gottsberger 1999; Prance & Jongkind 2015; Saunders 2020). Clustered inflorescences provide fleshy and nutrient-rich tissues for the development of weevil larvae, generally in male inflorescences (flower capsules, microsporophylls and rachises; Anstett 1999; Downie et al. 2008; Teichert et al. 2018; Haran et al. 2020). Within individual floral chambers, tissues for larval development include anthers, fleshy petals, flower buds or fruits (Nunes et al. 2018; Saunders et al. 2020; Haran et al. 2022a; Dao et al. unpublished). In clustered inflorescences as in floral chambers, the modified structures effectively filter access to specific pollinators and sometimes further retain and protect them. For instance, in Cyclanthaceae, the inflorescences of *Asplundia*, *Evodianthus* and *Ludivia* exhibit narrow interfloral entrances allowing only a specific weevil pollinator to reach the hidden floral reproductive structures (Franz 2007a; Teichert et al. 2018), while larger, non-pollinating species are prevented from reaching them. Narrow interfloral openings can also promote the transfer of pollen from anthers to the integuments of pollinators as they exit the floral chambers (Teichert et al. 2018). The Annonaceae provide the most striking examples of enclosed floral chambers, which are used to retain and protect *Endaeus* weevil pollinators and also ward reproductive tissues from predation (Gottsberger 1999; Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020). Other structures associated with weevil pollination include staminodes (in Cyclanthaceae and Eupomatiaceae), which are stamen-like structures that do not produce pollen but rather sticky secretions or odoriferous oils (elongated projections in Fig. 1D). They increase attraction, provide food, shelter or protection for weevil pollinators (Armstrong & Irvine 1990; Franz 2007a; Teichert et al. 2018). In Annonaceae sticky pollenkitt and short pollen-connecting threads create large aggregates of pollen grains that are considered specific adaptations to improve the efficiency of pollen transfer onto weevil integuments (Ratnayake et al. 2006). The fleshy petals and other floral tissues of plants implicated in BSPM with weevils typically show extensive feeding damages (Ratnayake et al.

2006; Saunder 2020; Haran et al. 2022a; Dao et al. unpublished; Figure 3F), indicating that these structures are also food sources for the adult pollinators.

The flowers of plant lineages engaged in BSPM with weevils are **predominantly white or creamy white** (Figure 1), but pale red, pale yellow and pale green flowers are occasionally encountered (Franz & Valente 2005; Ratnayake et al. 2006; Saunders 2020; Toon et al. 2020). In Cyclanthaceae, weevils show a preference for natural white inflorescences rather than those shaded by an opaque cloth (but letting the fragrance to be emitted; Franz 2007a). It should be noted that many weevils lineages involved in BSPM have nocturnal or crepuscular activity (Franz 2007a; Auffray et al. 2017; Lau et al. 2017; Haran et al. 2022a), where light intensity is low. Under these conditions, the pale colors were hypothesized to provide better contrast with the surrounding environment in a way that likely enhances their visual recognition by weevils (Franz 2007a; Saunders 2020). This suggests that visual recognition of inflorescences is an important dimension of weevil attraction, at least as important as olfaction (see below), and that white or pale colors are more attractive to weevils.

Plant lineages	Plant Genera (number of species engaged)	**Weevil lineages :** Genera (approximate number of species engaged or with indications of it)	Selected references
Gymnosperms			
Cycadaceae	*Cycas* (18)	**Curculionidae: Curculioninae:** *Nanoplaxes* (7), *Tychiodes* (11)	Toon et al. 2020
Stangeriaceae	*Bowenia* (2)	**Curculionidae: Molytinae:** *Miltotranes* (3)	Hsiao & Oberprieler 2020, 2022
Zamiaceae	*Dioon* (13), *Encephalartos* (23), *Lepidozamia* (2), *Macrozamia* (12), *Zamia* (20)	**Belidae:** *Notorhopalotria* (4), *Parallocorynus* (12), *Rhopalotria* (6). **Brentidae:** *Antliarhinus* (6), *Platymerus* (5); **Curculionidae: Molytinae:** *Amorphocerus* (5), *Porthetes* (16), *Tranes* (7)	Toon et al. 2020
Angiosperms Monocots			
Araceae	*Anthurium* (10)	**Curculionidae: Curculioninae: Derelomini:** *Cyclanthura* (10)	Franz 2003, 2007, 2008
Arecaceae	*Acrocomia* (1), *Allagoptera* (2), *Aphandra* (1), *Arenga* (1), *Astrocaryum* (5), *Attalea* (12), *Bactris* (14), *Butia* (6), *Ceroxylon* (3), *Chamaerops* (1), *Cocos* (1), *Desmoncus* (2), *Elaeis* (2), *Euterpe* (3), *Geonoma* (3), *Mauritia* (1), *Mauritiella* (1), *Nypa* (1), *Oenocarpus* (6), *Phoenix* (2), *Phytelephas* (3), *Prestoea* (1), *Raphidophyllum* (1), *Rhapis* (1), *Sabal* (2), *Salacca (1),* *Socratea* (1), *Syargus* (22), *Trithrinax* (1), *Thrynax* (1), *Wettinia* (1)	**Curculionidae: Curculioninae: Derelomini:** *Anchylorhynchus* (23), *Andranthobius* (9), *Celetes* (44), *Derelomorphus* (1), *Derelomus* (13), *Diplothemiobius* (1), *Elaeidobius* (8), *Prosoestus* (2), *Grasidius (1),* *Notolomus* (2), *Parimera* (1), *Perelleschus* (2), *Phyllotrox* (21), *Phytotribus* (14), *Terires* (3) **Curculionidae: Molytinae:** *Cholus* (3), *Homalinotus* (1), *Odontoderes* (2) **Curculionidae: Baridinae:** *Angelocentris* (1), *Anthenius* (1), gen. n. et sp. n. (4), *Groatus* (1), *Hustachea* (2), *Limnonotus* (1), *Microstrates* (3), *Notesia* (1), *Parisoschoenus* (3), *Tonesia* (1), *Zyzzyva* (1) **Dryophthoridae: Dryophthorinae:** *Belopoeus* (2), *Metamasius* (1)	Franz & Valente 2005; De Medeiros & Vanin 2020; De Medeiros et al. 2019; Nunes et al. 2015 Ervik & Feil 1997 Nunes et al. 2018 Küchmeister et al. 1998; Vaurie 1968
Cyclanthaceae	*Asplundia* (18), *Carludovica* (4), *Chorigyne* (1), *Cyclanthus* (1), *Dicranopygium* (4), *Evodianthus* (1), *Sphaeradina* (3), *Thoracocarpus* (1)	**Curculionidae: Curculioninae: Derelomini:** *Coithene* (1), *Cyclanthura* (4), gen. 2 (3) *Ganglionus* (5), *Perelleschus* (8)	Franz & O'Brien 2001 Franz & Valente 2005
Orchidaceae	*Dichaea* (2), *Grobya* (1)	**Curculionidae: Baridinae:** *Montella* (2); gen. n. (1)	Nunes et al. 2018
Strelitziaceae	*Strelitzia* (1)	**Curculionidae: Curculioninae: Derelomini:** *Derelomus* (1), gen. n. (1)	J. Haran unpublished
Angiosperms Dicots			
Anacardiaceae	*Searsia* (1)	**Curculionidae: Curculioninae: Derelomini:** *Derelomus* (1)	Haran et al. 2022b
Annonaceae	*Annona* (1), *Cathostemma* (1), *Dasymashalon* (1), *Enicosanthum* (2), *Fissisignata* (1), *Friesodielsia* (3), *Goniothalamus* (1), *Huberantha* (2) *Meiogyne* (1), *Monocarpia* (1), *Monoon* (4), *Polyalthia* (5), *Uvaria* (1), *Xylopia* (1)	**Curculionidae: Curculioninae: Ochyromerini:** *Endaeus* (?), *Endaenidius* (?)	Momose et al. 1998; Raknayak et al. 2006; Lau et al. 2017
Apocynaceae	*Acokanthera* (1)	**Curculionidae: Curculioninae: Derelomini:** *Ebenacobius* (2)	Haran et al. 2022a, 2022b
Burseraceae	*Canarium* (1)	**Curculionidae: Curculioninae: Ochyromerini:** *Endaeus* (1)	J. Haran unpublished
Clusiaceae	*Allanblackia* (1), *Pentadesma* (1)	**Curculionidae: Curculioninae: Ochyromerini:** *Endaeus* (1)	J. Haran unpublished
Ebenaceae	*Euclea* (3-4)	**Curculionidae: Curculioninae: Derelomini :** *Derelomus* (1), *Ebenacobius* (7)	Haran et al. 2022a, 2022b
Eupomatiaceae	*Eupomatia* (1)	**Curculionidae: Curculioninae: Stoerini:** *Elleschodes* (3)	Amstrong & Irvine 1990
Fabaceae	*Baikiaea* (1), *Piliostigma* (1), *Vachellia* (2)	**Curculionidae: Curculioninae: Derelomini:** *Derelomus* (2), *Lomederus* (1) **Ochyromerini:** *Endaeus* (2)	Haran et al. 2022b J. Haran unpublished
Lecythidaceae	*Napoleonaea* (1)	**Curculionidae: Curculioninae: Ochyromerini:** *Endaeus* (2)	J. Haran unpublished
Malvaceae	*Thespesia* (1)	**Curculionidae: Curculioninae: Ochyromerini :** *Endaeus* (1)	J. Haran unpublished
Myristicaceae	*Knema* (1), *Myristica* (1)	**Curculionidae: Curculioninae: Ochyromerini** : *Endaenidius* (1); undescribed genus (?)	Amstrong & Irvine 1989a, 1989b
Sapotaceae	*Mimusops* (1)	**Curculionidae: Curculioninae: Derelomini :** *Ebenacobius* (1)	Haran et al. 2022a, 2022b
Urticaceae	*Cecropia* (1)	**Curculionidae: Curculioninae: Eugnomini:** *Udeus* (2)	Mendonça 2004
Winteraceae	*Exospermum* (?)	**Curculionidae: Curculioninae: Stoerini :** *Palontus* (1)	Pellmyr et al. 1990

Table 1. Synthetic list of known plant-weevils BSPM systems. See Table S1 for details on species-specific interactions, tissues for larval development, presence of cryptic lineages and corresponding reference list.

All major plant lineages engaged in BSPM with weevils include representatives with **thermogenic** activity, allowing inflorescence or flower temperatures to rise several degrees above ambient temperature (Franz 2007a; Teichert et al. 2018; Saunders 2020; Toon et al. 2020). This phenomenon is postulated to act as an attractant for weevil pollinators, by increasing the emission of volatiles or IR radiations itself. It has also been hypothesized to provide an energy reward to individuals reaching floral tissues (Rands & Whitney 2008), but this is likely not the case for weevils since thermogenic activity is not maintained once individuals stand on flowers or are enclosed in floral chambers (Teichert et al. 2018; Toon et al. 2020). In Annonaceae, thermogenesis is identified as typical of flowers pollinated by beetles, and weevils in particular (Gottsberger 1999). The temperature reached appears to be positively correlated with inflorescence size (Franz 2007a), which may explain why large flowers and inflorescences evolved convergently in weevil-pollinated plants. Temperature peaks during the circadian cycle of the flowering cycle can also have a repellent effect and promote the departure of the weevils once they are covered in pollen (Franz 2007a; Teichert et al. 2018; Salzman et al. 2020).

The **fragrances** produced by weevil-pollinated flowers during anthesis are strong and detectable by human olfactory senses, and are commonly associated with fruity or floral fragrances. In most genera of weevil-pollinated Cyclanthaceae (*Aspludia, Carludovica, Chorigyne*, *Dicranopygium* and *Evodianthus*), production of aromas reminiscent of various fruits and flowers has been reported (Franz 2007a). Similarly, in *Polyalthia* (Annonaceae), a fruity odor is produced during anthesis (Ratnayake et al. 2006). In *Elaeis guineensis* (Arecaceae), anthesis is correlated with the production of a strong anise-like scent (Lajis et al. 1985), while in *Attalea phalerata* (Arecaceae), weevils and other beetle pollinators are attracted by a strong emission of methyl acetate (Maia et al. 2021). In *Macrozamia and Zamia* (Zamiaceae) the emission of linalool or methyl salicylate has been recorded (Toon et al. 2020; Salzman et al. 2021). These scent blends appear to be species specific (Teichert et al. 2018), but their exact composition have not been thoroughly studied, and it is unclear whether similar compounds were independently acquired by phylogenetically distinct plant groups. Notable exceptions of floral odor emission are found in *Chamaerops humilis* (Arecaceae), which attracts *Derelomus* species via the volatiles emitted from the leaves (Dufaÿ et al. 2003), and in *Syagrus coronata* (Arecaceae), where the volatiles are given off by a persistent peduncular bract (Barbosa et al. 2020).

The morphological and physiological features described above are generally organized into **timed phenological sequences** that coincide with **phases of flower and inflorescence receptivity.** In most plant lineages producing large inflorescences (e.g., Araceae, Arecaceae, Zamiaceae), anthesis occurs over several days and is accompanied by circadian thermogenic cycles and emission of volatiles (Franz 2007a; Auffray et al. 2017; Toon et al. 2020). When flowers are isolated (in Annonaceae and Eupomatiaceae), but also in Cyclanthaceae, each individual flower or inflorescence goes through one cycle of anthesis with the following stages: *(i)* a phase of thermogenesis/attraction associated with the receptivity of female reproductive structures (pistillate phase), *(ii)* an interim period when weevils can be trapped in the floral chamber for a variable time, and *(iii)* a phase when pollinators are released with exposure to male reproductive structures (stamen and pollen, staminate phase), which can be achieved by abscission of the floral chamber petals and/or by a second peak of thermogenesis (Armstrong & Irvine 1990; Franz 2007a; Lau et al. 2017; Teichert et al. 2018; Saunders 2020). In the first case, the anthesis lasts between several days and two weeks (Toon et al. 2020), while in the second case, the complete cycle of anthesis is short and usually lasts at most 48h (Franz 2007a; Saunders 2020). Interestingly, the pistillate and staminate phase cycles found in some Cyclanthaceae (*Asplundia*; Franz 2007a) are very similar to those found in some Annonaceae (Saunders 2020), indicating a remarkable convergent evolution of plant-weevil pollination systems. With the notable exception of cycads and some palms, in all plant-weevil BSPM systems, the **pistillate and staminate phases coincide with peaks of crepuscular or nocturnal peaks in pollinator activity** (Armstrong & Irvine 1990; Franz 2007a; Auffray et al. 2017; Saunders 2020). These converging nocturnal phenologies suggest that nocturnal conditions improve pollination efficiency, possibly through enhanced attraction of weevil pollinators and avoidance of generalist pollinators active during the day. It has been also hypothesized (Borges et al. 2016; Auffray pers. com.) that the movement of pollinators and the dispersal of floral fragrances are facilitated at night because there is less wind; lower temperatures also potentially improve the detection of thermogenic flowers.

A remarkable feature of all plant lineages engaged in BSPM with weevils is the **separation of sexes**. In cycads, all species are dioecious, with male plants producing pollen cones and female plants ovulate cones (Toon et al. 2020). Weevil-pollinated palms may be dioecious or monoecious, but anthesis of male and female flowers are always separated in time in the latter case (Barfod et al. 2011). One example is the monoecious palm genus *Elaeis* (Arecaceae), in which individuals cyclically produce functionally unisexual male and female inflorescences, resulting in an allogamous mode of reproduction called temporal dioecy (Adam et al. 2011). In other genera, such as *Acrocomia* and *Bactris* the pistillate and staminate phases of the **protogynous inflorescences** are separated by a short interim phase resulting in circadian dioecy (Henderson et al. 2000; Carreño-Barrera et al. 2021). Similar patterns are observed in other monoecious plant lineages such as Annonaceae and Cyclanthaceae (Franz 2007a, 2007b; Saunders 2020). Finally, a number of palms exhibit **protandrous inflorescences** with very extended interim phases, also resulting in functional dioecy (Silberbauer-Gottsberger et al, 2013; Núñez-Avellaneda et al, 2008, 2015; de Medeiros et al. 2019). Another striking feature of systems involving Arecaceae, Annonaceae and Cyclanthaceae is the small number of flowering inflorescences per individual or the small number of flowering individuals at time, a strategy that also likely promotes cross-pollination (Saunders 2020). The resulting low number of propagules available at a certain time may be balanced by the long flowering periods of the plants engaged in these BSPM interactions, for instance up to seven-months in *Asplundia* (Cyclanthaceae; Franz 2007a) and many species of *Syagrus* (Arecaceae; Noblick 2017). These long flowering periods have also been proposed as a strategy for constant breeding of specialized brood pollinators (Carreño-Barrera et al. 2020).

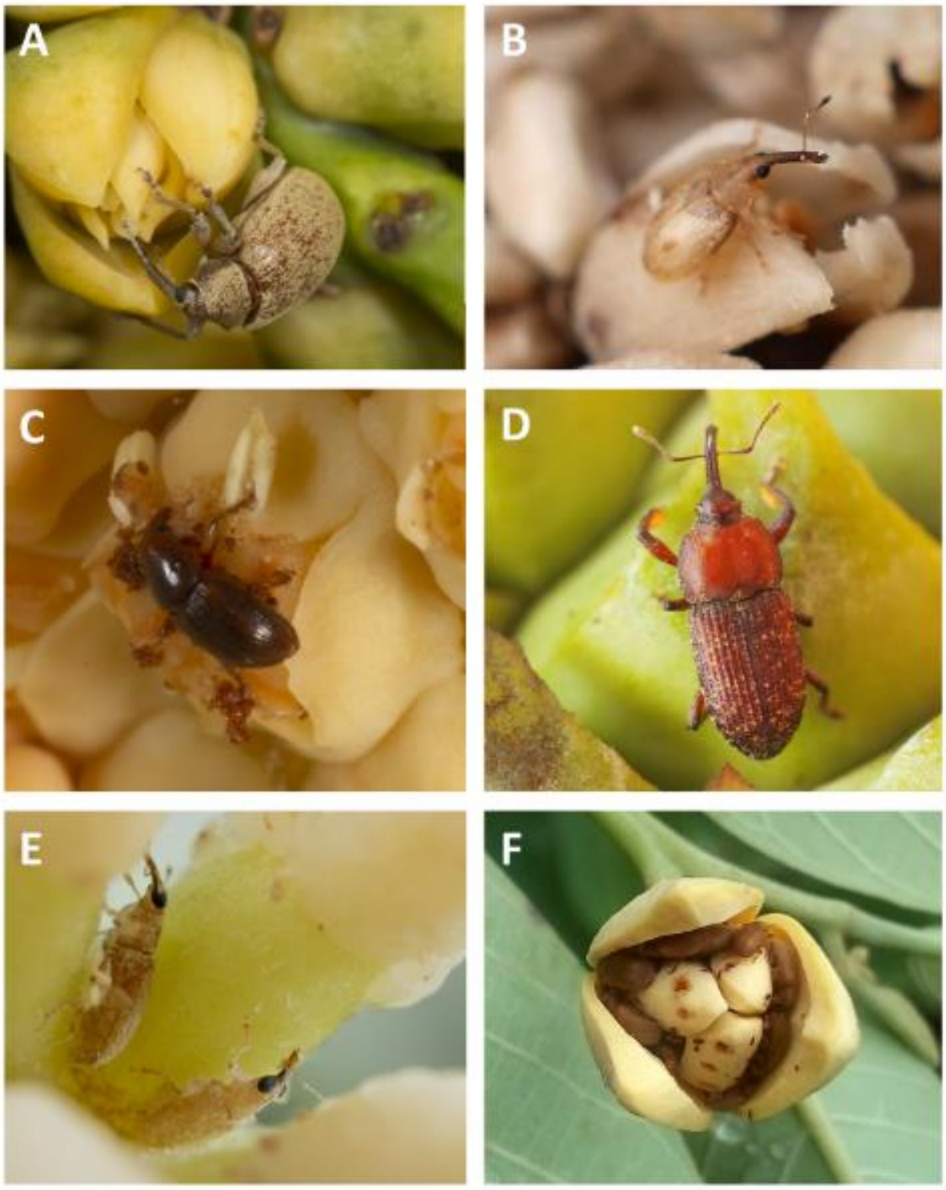

Figure 3. Examples of weevils and plants engaged in brood-site pollination mutualisms. **A**. *Anchylorhynchus trapezicollis* (Derelomini) on pistillate flowers of *Syagrus coronata* (Arecaceae) in South America. **B**. *Derelomus* sp. (*costiger* group; Derelomini) pollinator of *Phoenix reclinata* (Arecaceae) in southern Africa. **C**. *Perelleschus evelynae* (Derelomini) on pistillate flowers of *Carludovica palmata* (Cyclanthaceae) in Central America. **D**. *Tranes lyterioides* (Molytinae) on sporophylls of *Macrozamia communis* (Zamiaceae) in Australia. **E**. *Udeus eugnomoides* (Eugnomini) on pistillate flowers of *Cecropia peltata* (Urticaceae) in Central America. **F**. Flowers of the African custard apple (*Annona senegalensis*; Annonaceae) with aggregation of *Endaeus* spp. pollinators (Ochyromerini) in tropical Africa. (credits: A/C/E: B, E: B. de Medeiros, B: J. Haran, D: R. Oberprieler, F: Z. Dao).

2.2 Weevil morphology and behavior

Like plants involved in BSPM, weevil pollinators display a series of morphological, physiological and behavioral features that may constitute adaptations to pollination mutualisms. Weevil pollinators have been less studied than the plants they pollinate, so not only their shared morphological features have been scarcely reported, but also the function and adaptive significance of these features are generally unexplored. This section provides a summary of what is known to date, with the aim of identifying general trends associated with BSPM pollination, as well as pointing out more peculiar cases.

Known weevil species involved in BSPM are **small-sized beetles**, with body size ranging from a few millimeters to about one centimeter (1.1 mm, *Staminodeus inermis* (Franz 2001); 8.6 mm in *Anchylorhynchus burmeisteri* (de Medeiros & Vanin 2020), rostrum excluded). Body shape is often consistent with floral morphology; for example, the body of weevils associated with cycads in Belidae and Brentidae is very flat and allows individuals to enter the cracks of megasporophylls. In most species, the body colors are **pale yellow, reddish or brown**; they usually match the color or shape of their floral substrates, probably to limit predation (Figures 3, 4). The matching colors are either obtained due to the color of the integument itself (e.g., in *Andranthobius, Cotithene, Derelomus, Ebenacobius, Elaeidobius, Prosoestus*) or due to the colors of the integument and scales covering it (e.g., in *Anchylorhynchus*; Valente & da Silva 2014; Valente et al. 2019; de Medeiros & Vanin 2020; Haran et al. 2020, 2022a). In some species, the shape of the elytra forms an angled surface mimicking the shape of the petals of the host plant (e.g., *Derelomus subcostatus, D. costiger* and *D. piriformis*; see Figure 4E). Overall, there appears to be a strong selective pressure to mimic floral substrates as suggested by the various examples of strongly converging phenotypes among unrelated species associated with the same host plant (e.g., *Derelomus pallidus* and *Ebenacobius rectirostris* on *Euclea racemosa*; Haran et al. 2022b; Figure 4A, B). This pattern of mimicry is, however, found almost exclusively in species active during the day on inflorescences, with little or no space to hide (i.e. most Derelomini associated with Arecaceae or Ebenaceae). In weevil lineages that remain hidden in floral chambers or inflorescences during the day, the integuments are usually pale brown or reddish in color, and they do not specifically match floral substrates (e.g., in *Cyclanthura*; Ochyromerini; Figure 4C, F). Notable exceptions to this pattern include *Montella* weevils (Baridinae), which exhibit a dark body integument contrasting with the color of its host's flowers (Nunes et al. 2018) and some species of *Anchylorhynchus* weevils with extreme polymorphism showing disruptive patterns such as black and yellow stripes (de Medeiros & Vanin 2020).

A series of putative pollen-carrying morphologies are found in weevils engaged in BSPM. Most of these lineages have species with **erect setae** on their body surface (Haran et al. 2020, 2022a; Dao et al. unpublished), a feature thought to enhance pollen transport (Syed et al. 1981). The setae can cover the entire body surface (in Ochyromerini or in some *Ebenacobius* and *Celetes*; Valente 2005; Ratnayake et al. 2006; Haran et al. 2022b; Figure 4C, F), or form combs on the edge of the elytra (in some *Elaeidobius*; Figure 4D), or on the tibiae (in some *Derelomus*); setae may also be found on the ventral region (in some *Elaeidobius* and *Anchylorhynchus*). In *Anchylorhynchus*, a genus that breeds on female flowers and thus may benefit directly from pollination, these ventral setae may be highly branched in some species, reminiscent of setae found in bee corbiculae (de Medeiros et al. 2019; de Medeiros & Vanin 2020). Interestingly, in some weevil species, the presence of setae is a dimorphic feature, with only males exhibiting long setae, suggesting that they may play a differential role in pollen transport (Haran et al. 2020; Hsiao & Oberprieler 2022). That said, even weevil species without specific setae (e.g., *Derelomus chamaeropsis*, *Andranthobius* spp., Baridinae and Belidae) are known to be effective pollinators (Anstett 1999; Nunes et al. 2018: Salzman et al. 2020; Carreño-Barrera et al. 2021), suggesting that integuments alone can efficiently transport pollen. Several unrelated lineages of weevils engaged in BSPM also exhibit prosternal processes or tubercules (in *Andranthobius*, *Diplothemiobius*, *Ebenacobius*, *Elaeidobius, Miltotranes, Porthetes, Prosoestus*, *Tranes*; Bondar 1941; Valente & da Silva 2014; Haran et al. 2020, 2022; Hsiao & Oberprieler 2022; Haran pers. obs.) consisting of cuticular apophyses located near the procoxae of males. In some Baridinae not involved in BSPM, such structures grow allometrically and have been shown to be used in interspecific fights to dislodge competing males (Eberhard & Garcia 2000; Eberhard et al. 2000; Davis & Engel 2010). Since fights between males have been described in Derelomini (Franz 2003, 2006), it can be postulated that these prosternal processes or tubercules probably have a similar function for the aforementioned genera. Finally, in some weevil lineages, structural complexity and dense cover of setae in these structures have been hypothesized to possibly enhance pollen transport (see Hsiao & Oberprieler 2022). It is not known why the weevils evolved these pollen-carrying structures, except in the rare cases where the weevils directly benefit from the pollination of their hosts. Indeed, there are only two known cases where weevils breed on tissues that result from their direct pollination: in the genus *Montella* (Nunes et al. 2018) and in the genus *Anchylorhynchus* (de Medeiros & Vanin 2020). *Montella* weevils display active pollination behavior (carrying orchid pollinaries; Nunes et al. (2018), which is consistent with other cases of specialized pollinating seed predators such as fig-wasps (Jousselin et al. 2003) and yucca moths (Pellmyr 1997). For *Anchylorhynchus* the evidence is more ambiguous; females rub their bodies against female flowers after oviposition, but it remains to be shown whether this behavior serves to mark oviposition and avoid competition, increases the likelihood of pollen deposition, or both (de Medeiros et al. 2014).

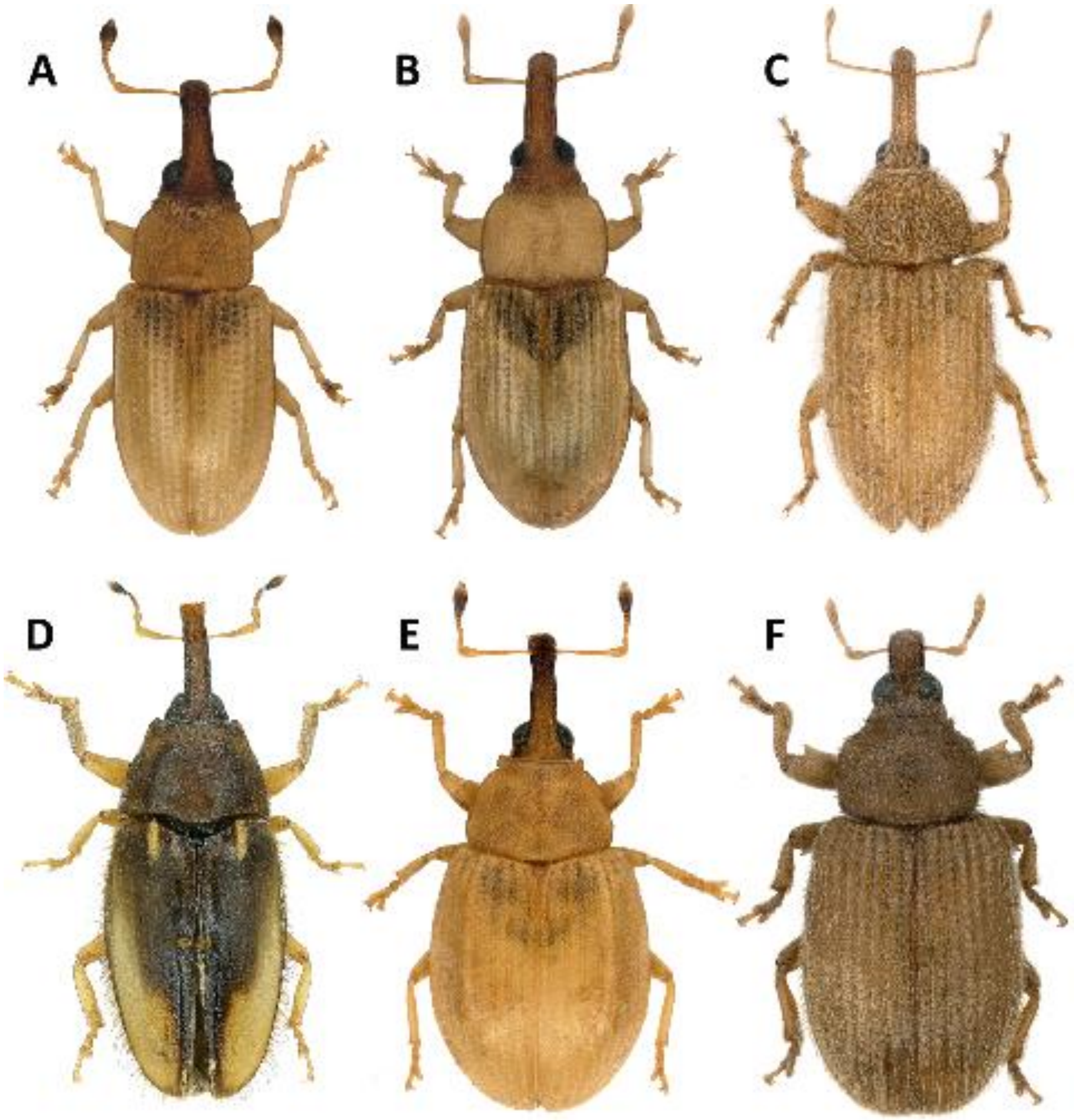

Figure 4. Morphology of weevils involved in BSPM. **A-B**. *Derelomus pallidus* and *Ebenacobius rectirostris* (Derelomini), two species associated with inflorescences of *Euclea* bushes (Ebenaceae) showing a marked morphological convergence. **C**. *Ebenacobius curvisetis* (Derelomini), a species with body surface covered with erect setae, thought to be an adaptation to pollen transportation. **D.** *Elaeidobius kamerunicus* (Derelomini) pollinator of *Elaeis guineensis* (Arecaceae) with combs of setae on edge of elytra in males. **E**. *Derelomus costiger* (Derelomini) with shape of elytra mimicking the structure of petals of its host *Phoenix reclinata* (Arecaceae). **F**. *Endaeus floralis* (Ochyromerini) pollinator of *Annona senegalensis* (Annonaceae) with body surface covered by setae. (credits: A-F: J. Haran).

Weevils engaged in BSPM are known for their good **flight abilities**, which allow them to fly actively between inflorescences of distant hosts (Auffray et al. 2017; Lau et al. 2017; Saunders 2020; Toon et al. 2020). Adult weevils feed on pollen or nectar produced by flowers (de Medeiros et al. 2014; Lau et al. 2017; de Medeiros et al. 2019) but also often on floral structures themselves (*Elaeidobius*, *Ebenacobius, Endaeus*; Haran et al. 2022a; Dao et al. unpublished). The active behavior of adults is not surprising, since weevils **respond well to host specific floral volatiles**. This has for example been demonstrated in several cycad specialists, with electroantennography experiments and pheromone traps (Salzman et al.

2021). Several weevil lineages have also developed specific olfactory globules in their antennae which are considered to be adaptations for the detection of these volatiles (Crowson 1991; Oberprieler 2004). Following olfactory stimuli, weevils can reach or leave the flowers and inflorescences of their hosts, according to circadian cycles remarkably adapted to flowering cycles (Franz 2007a; Auffray et al. 2017; Mendeléz-Jácome et al. 2019; Saunders 2020; Salzman et al. 2021). The weevil's reaction to a volatile can be concentration-dependent, with the same molecule acting as either an attractant or a repellent depending on the amount emitted from the floral structures. This change in behavior in turn creates a push-pull effect enhancing their movement between flowers and therefore pollination (Franz 2007a; Salzmann et al. 2021). When floral structures do not produce peaks of volatiles (the so-called 'interim' phase'; Saunder 2020), weevils may simply remain on the inflorescences (in cycads and palms; Auffray et al. 2017; de Medeiros et al. 2019; Toon et al. 2020), be hidden or trapped there (in Araceae and Annonaceae; Franz 2007b; Saunders 2020; Dao et al. unpublished), or leave inflorescences (Ratnayake et al. 2006; de Medeiros et al. 2019). In the genus *Ebenacobius*, many species have only been collected from the leaf litter during the day, which suggests that they hide there between their crepuscular and night phases of movements (Haran et al. 2022a). Weevils are fairly long-lived insects, with an adult lifespan of up to 79 days (mean 31 days) in *Elaeidobius subvittatus* (Syed et al. 1982). As the anthesis of the host inflorescence lasts only a few hours or a few days (five days in the case of *Elaeis guineensis*), the same individual can visit many flowers or inflorescences during its lifespan.

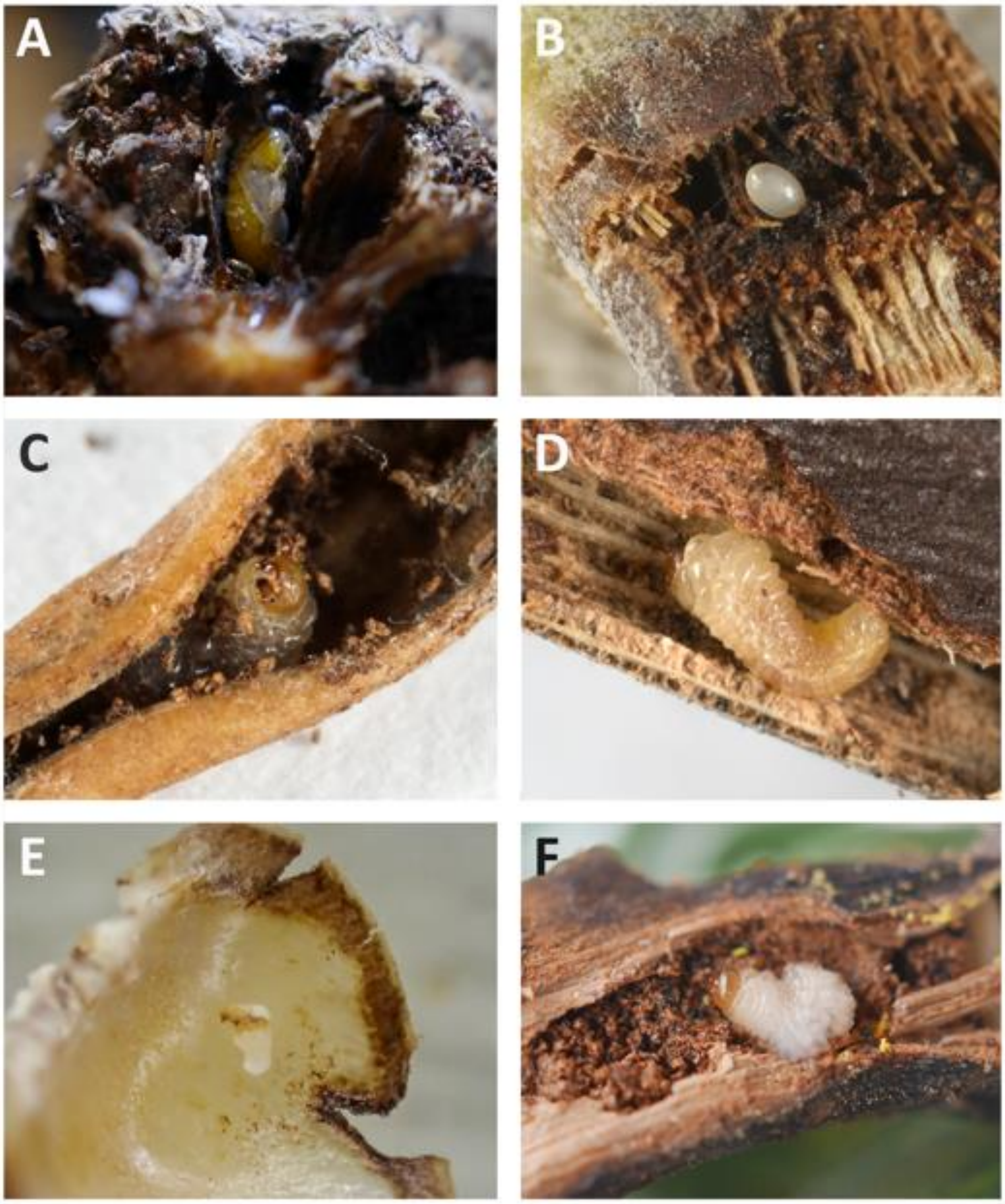

Figure 5. Breeding sites of weevils engaged in BSPM. **A**. Pupa of *Elaeidobius plagiatus* (Derelomini) in flower capsules of male inflorescences of *Elaeis guineensis* (Arecaceae). **B**. Egg of *Phytotribus platyrhinus* (Derelomini) inside rachis of inflorescence of *Syagrus coronata* (Arecaceae). **C**. Larva of *Andranthobius bondari* (Derelomini) in aborted staminate flower of *Syagrus coronata* (Arecaceae). **D**. Larva of *Celetes impar* (Derelomini) in a spathe of *Syagrus coronata* (Arecaceae). **E**. Larvae of *Anchylorhynchus bicarinatus* (Derelomini) inside a pistillate flower petal of *Oenocarpus mapora* (Arecaceae). **F**. Larva of *Derelomus chamaeropsis* (Derelomini) inside a rachis of male inflorescence of *Chamaerops humilis* (Arecaceae). (credits: A, F: J. Haran, B-E: B. de Medeiros).

The **larval stages** of weevils are **adapted to develop on the various types of substrates** provided by their hosts. In all the weevil lineages engaged in BSPM, the larvae are generally endophagous, developing either in live tissues or as detritivores on decaying plant material, in more or less woody tissues (Figure 5; Anstett 1999; Franz 2007; Nunes et al. 2018; Toon et al. 2020; Dao et al. unpublished). In Ebenaceae which have small individual flowers, larvae of pollinators are ectophagous and feed at the base of the anthers (Haran et al. 2022a). In *Anchylorhynchus*, eggs are deposited externally between petals (Figure 5E) and first instars drill into female flowers to continue their development internally (de Medeiros et al. 2014). When larvae feed on limited spaces such as individual flowers or fruits, some species have developed a cannibalistic behavior (Figure 5E) and morphology to cope with a potential overpopulation in the brood site (de Medeiros et al. 2014). For most plant-weevil BSPM, the interplay between the presence of secondary compounds in plant tissues and a potential adaptation of associated weevil lineages has not been yet investigated, although they may drive specialization patterns (Wang et al. 2021). For example in some weevils associated with cycads (Belidae), the larvae of some species have been found associated with specific bacteria involved in the control of toxic compounds from their host (Salzman et al. 2018).

2.3 Evolutionary trends

2.3.1 Larval host specificity

The vast majority of weevils engaged in brood-site pollination appear to be strictly monophagous as larvae (Franz & Valente 2005; de Medeiros & Núñez-Avellaneda 2013; Valente & de Medeiros 2013; Toon et al. 2020; de Medeiros & Farrell 2020; de Medeiros & Vanin 2020; Haran et al. 2021; Hsiao & Oberprieler 2022). Such a level of specialization is rare for phytophagous insects, even when considering other groups of endophagous feeders, which are known to be generally highly specialized (e.g., Gaston et al. 1992; Bernays & Chapman 1994; Kergoat et al. 2008, 2018). One of the most striking case reflecting this host specificity is the pollination ecology of sympatric palms belonging to the genus *Oenocarpus* in the Amazon (Núñez-Avellaneda et al. 2015). The three species studied have a very similar floral structure and phenology, but each has a specific assemblage of weevil pollinators, only a few of which are able to visit several *Oenocarpus* species. Cases of oligophagy or polyphagy in weevil pollinators have been suggested in several systems based on general observations of inflorescences visitors, but these have never been formally tested (Franz & Valente 2005; Ratnayake et al. 2006; Saunders 2020). In the Annonaceae – Ochyromerini system, a species of *Endaeus* has been identified as the pollinator of two congeneric and sympatric *Polyalthia* species (Ratnayake et al. 2006). In the Araceae – Derelomini and Cyclanthaceae – Derelomini systems, a few intriguing cases of oligophagy or even polyphagy have been reported for weevil species acting as effective pollinators (Franz & O'brien 2001a, 2001b; Franz 2006, 2007); however, most of these accounts should be viewed with caution as they are based on observations of adult stages only. Weevils can be slightly eclectic in the selection of flowers visited at the adult stages (Haran et al. 2022a) and over-interpretation of these visits can lead to erroneous conclusions about larval host specificity. The complexity of the host plant taxonomy can also make it difficult to interpret historical records and blur patterns of host-associations (de Medeiros & Vanin 2020). All of this highlights that understanding the level of species-specificity in these systems is primarily hampered by the lack of actual host plant data for the larval stages (Franz 2004). More generally, integrative and detailed studies are needed to accurately assess plant-weevil BSPM relationships. All detailed studies of host plant associations using molecular data have found a higher than previously thought weevil diversity and a very high degree of specialization on their hosts (Downie & Williams 2009; Brookes et al. 2015; de Medeiros & Farrell 2020; Haran et al. 2021).

2.3.2 Sympatric species assemblages

While most weevils engaged in pollination mutualism are specialized and dependent on a single host, the reciprocal condition does not apply to plants, which are usually pollinated by various insect guilds. This imbalanced pattern, also referred to as mutualism asymmetry, is a well-known trend in mutualistic associations as a whole, and it has been hypothesized that it could potentially determine the stability of associations over time and their level of specificity (Chomicki et al. 2020).

With respect to weevil specialists, plants involved in BSPM are often pollinated by diverse multi-species assemblages of weevil pollinators living in sympatry (Figures 3F, 6; Hotchkiss 1958; Ervik et al. 1999; Franz & Valente 2005; Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Saunders 2020; Toon et al. 2020; Haran et al. 2021; 2022b; Dao et al. unpublished). A remarkable aspect of these assemblages is their stability over the range of their hosts (Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Haran et al. 2020a), in stark contrast to other brood-site pollination systems (Jousselin et al. 2008; McLeish & van Noort 2012). Sympatric weevil assemblages may coexist on the same host as they often develop on distinct ecological niches such as male or female inflorescences, as observed in the genera *Elaeidobius* and *Prosoestus* on *Elaeis guineensis* (Syed 1979: Alibert 1938) or in several cycad-associated weevils (Toon et al. 2020). Niche partitioning can also be observed within monoecious inflorescences, either on different tissues (de Medeiros et al. 2019; Figure 6) or in relation to distinct phenological anthesis stages (Haran et al. in prep.). Unexpectedly, these sympatric multi-species assemblages have been described in all plant-weevil mutualism systems, suggesting that they may be the rule rather than the exception. The prevalence of these assemblages seems specific to weevil pollinators; in other BSPM systems such as the fig/fig-wasp model, instances of multispecific assemblages of pollinators are only reported in about 10% of associations (Cruaud et al. 2012), even though usage of molecular data for wasp species delimitation has been increasing this number (Satler et al. 2022; Su et al. 2022). In comparison with other brood-site pollinator systems, weevils also present the greatest diversity of congeneric species associated with the same host: this is the case of the African oil Palm (*Elaeis guineensis*), which hosts no less than eight species of *Elaeidobius* on its male inflorescences (Compton et al. 2009; Haran et al. 2020a, 2021; Figure 6B). The exact role of these assemblages is not yet elucidated and several potential evolutionary processes have been proposed to explain their emergence. A first process is the lineage duplication induced by the fragmentation of the host range in relation to past environmental changes (such as climate oscillations), followed by the reconnection of host populations. This case has been highlighted in the *Elaeis*-derelomine system where past cycles of fragmentation of *Elaeis guineensis* populations into the upper and lower Guinean forest blocks would have led to the diversification of *Elaeidobius* and *Prosoestus* species (Haran et al. 2021). When populations reconnect after isolation, differences in generation times between the host plant and its pollinators appear to allow palm populations to exchange genes again while weevil populations are already too divergent and already correspond to distinct species. A second process results from independent past colonizations (historical host shifts) of a host by multiple lineages of weevils. This process is suggested by the structure of sympatric assemblages themselves, where weevil species in an assemblage belong to distinct and phylogenetically unrelated genera (Franz 2007a; de Medeiros et al. 2019; Toon et al. 2020; Haran et al. 2022b). Interestingly these two processes are not mutually exclusive, as underlined by the example of the weevil community associated with the inflorescences of *Phoenix reclinata* (Arecaceae). Here, lineage duplication and independent colonizations led to the emergence of a sympatric assemblage of six species of brood-site pollinators (Haran et al. 2022b).

Figure 6. Example of sympatric species assemblage of weevils of a host including species from other beetle lineages. **A.** Inflorescence of *Syagrus coronata* (Arecaceae) with *Anchylorhynchus trapezicollis* (Derelomini, top right), *Andranthobius bondari* (Derelomini, top left), *Microstrates ypsilon* (Baridinae,

black weevils) and sap beetles (Nitidulidae, *Mystrops palmarum*). **B**. Inflorescences in anthesis of *Elaeis guineensis* (Areacaceae) with multiple specific pollinators including the weevils *Elaeidobius plagiatus* (Derelomini, left), *E. piliventris* (Derelomini, right) and *E. subvittatus* (Derelomini, bottom left). (credits: A: B. de Medeiros, B: J. Haran).

In plant-weevil BSPM, multi-species assemblages are not limited to weevils but also include a range of insects of various orders that develop on host inflorescences (Desmier de Chenon 1981; Búrquez et al. 1987; Ervik et al. 1999; Gottsberger 1999; Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Toon et al. 2020). It is very common, for example, that weevil-pollinated plants are also visited by sap beetles (Nitidulidae, Figure 6A). In Annonaceae they belong to the genus *Carpophilus*, in Arecaceae the most common genera are *Carpophilus*, *Microporum* and *Mystrops*, in cycads they belong to the genus *Carpophilus*, and in Cyclanthaceae they belong to the genus *Mystrops* (Desmier de Chenon 1981; Knudsen et al. 2001; Núñez-Avellaneda et al. 2005; Ratnayake et al. 2006; Franz 2007a; Núñez-Avellaneda et al. 2015; Toon et al. 2020). Sap beetles range from the most important pollinators in some plants to negligible in others (Ratnayake et al. 2006; Núñez-Avellaneda et al. 2015; Lau et al. 2017; de Medeiros et al. 2019; Toon et al. 2020; Carreño-Barrera et al. 2021). Indeed, the patterns observed in cycad-associated brood-site pollinators show that sap beetles, but also certain lineages belonging to other families of beetles (Boganiidae, Erotylidae and Tenebrionidae) or even other orders of insects (Lepidoptera and Thysanoptera) may have become brood-site pollinators of cycads (Toon et al. 2020). It is therefore not surprising that species of various groups of insects have independently colonized the same host and co-exist on it. In palms, multi-species assemblages sometimes even include generalist insects that have also been identified as pollinators. In some cases, bees are the most important pollinators with weevils being accessory (Núñez & Carreño, 2017; Bezerra et al. 2020), but more commonly generalist pollinators play a minor role (Desmier de Chenon 1981; Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019). The latter echoes the fact that, whenever weevils are involved in these diverse assemblages, they generally play a predominant role in host pollination (Desmier de Chenon 1981; Ratnayake et al. 2006; Núñez-Avellaneda et al. 2015; Toon et al. 2020). The precise role of these secondary pollinators (brood site or not) is not clear, but a reduction of extinction risk by limiting dependence on a specialized mutualist has been suggested (Silberbauer 1990; Chomicki et al. 2020).

2.3.3 Cryptic and closely related weevil species

The evolution of plant-weevil BSPM is a dynamic system with many instances of recent or ongoing speciation processes. This trend was first suggested thanks to the results of several morphological studies, which revealed that BSPM weevil genera often consist of diverse closely related species (Oberprieler 1996; Oberprieler 2004; Valente 2005; Franz & Valente 2005; de Medeiros & Vanin 2020; Hsiao & Oberprieler 2022). This trend has been confirmed by molecular studies, which have revealed additional layers of hidden diversity in the form of cryptic and closely related species often co-occurring on a single host (Downie & Williams 2009; Brookes et al. 2015; Nunes et al. 2018; de Medeiros & Farrell 2020; Haran et al. 2021, 2022a, 2022b). All of these cryptic and closely related weevil species (Table S1) likely reflect recent speciation events. For example, dating analyses from two recent molecular studies have recovered numerous instances of recent speciation events (1.2 to 0.2 Mya old), which may be associated with recent changes in paleoenvironments (Haran et al. 2021, 2022b). Morphological features enabling to distinguish these closely related species include subtle differences such as the location and size of certain setae on the male ventrites, the arrangement of setae on the elytra or the ratios on the male genitalia. The repeated occurrence of these cases of cryptic and closely related species highlight the need for detailed taxonomic studies to properly estimate the levels of specificity of plant-weevil BSPM systems.

2.3.4 Trade offs in cost-benefit of interactions

The balance between costs and benefits in plant-weevil BSPM interactions has been investigated in several systems (e.g., Dufaÿ & Anstett 2004; Franz 2004; Franz & Valente 2005; Nunes et al. 2018; Saunders 2020; Toon et al. 2020). Plants engaged in BSPM with weevils require cross-pollination for a large fruit set. Therefore, a major pressure they have experienced is pollen limitation, linked to inadequate pollen quality and/or quantity (Franz 2007a; Nunes et al. 2018), a widely observed condition for tropical flora (Tremblay et al. 2005; Wolowski et al. 2014). Under this pressure, the advantage of having specialized pollinators is believed to be high (Silberbauer 1990), especially in the understorey where small plants do not compete well for generalist pollinators because their floral displays are less conspicuous (Turner 2001). The benefit to the plant is clear when weevils develop only on male flowers or on non-reproductive tissues (e.g., live or decaying stems, bracts and petals), and therefore do not affect propagule production (Dufaÿ & Anstett 2003; Dao et al. unpublished). This case is widely encountered in “pollination by deceit” systems (Dufaÿ & Anstett 2003) described in many palms (Arecaceae), where adult weevils search for male inflorescences where development of larval stages take place but are mislead by female inflorescences producing similar attractants but no rewards. Such a benefit is, however, less evident when the flower buds or seeds are destroyed during the larval development of the weevils, and sometimes it even results in a sharp reduction in the fitness of the host. For example, brentids in the genus *Antliarhinus* are ovule parasites that can destroy up to 80% of the seeds of their cycad host *Encephalartos*. However, as adults still play an important role in cross-pollinating their host, their association remains potentially stable over evolutionary times (Donaldson 1997; Toon et al. 2020). Similarly, the main pollinator of the palm *Syagrus coronata* is a specialist weevil of the genus *Anchylorhynchus* (Derelomini), which are known to be seed predators (de Medeiros et al. 2019). However, it has been recently shown that there is variation in the genus, with some species only being able to develop on aborted female flowers and therefore harmless to the plant (de Medeiros 2022 in press). Studies of these two examples can reveal why such costly pollination systems are maintained when less costly ones, involving other specialist or generalist pollinators, are potentially available and how interactions evolve along the mutualism-antagonism spectrum (Fenster et al. 2004; de Medeiros et al. 2019).

In some cases, the detrimental effect of the larval development of weevil pollinators is mitigated by specific plant adaptations. In the dwarf palm (*Chamaerops humilis*), the process associated with fruit development leads to the termination of larval development on female inflorescences of *Derelomus chamaeropsis*. Thus, the maintenance of the populations of this obligate pollinator relies solely on male inflorescence tissues, with no impact on seed sets (Dufaÿ & Anstett 2004). Control of the detrimental effects of larval development may also include other organisms. For example, in the orchid genus *Dichaea*, pollination depends exclusively on the activity of a baridine weevil developing as an ovule parasite. Normally, about 20% of fruits are lost to weevil larvae, but the activity of a parasitic wasp killing weevil larvae at an early stage can significantly reduce the fraction of seeds lost to the weevil (Nunes et al.

2018). Such tripartite interactions are probably overlooked although they potentially play a significant role for weevil-based BSPM systems.

Entirely detrimental relationships for the plants have also emerged within weevil lineages generally recognized as pollinators. The species involved have been labeled as 'cheaters' because they develop in the tissues of their hosts without providing pollination service (Franz, 2003, 2004; Franz & Valente, 2005; de Medeiros et al., 2019; de Medeiros & Farrell, 2020). In several plant-weevil BSPM, beneficial and detrimental weevil lineages coexist on the host inflorescence. For example, in the cyclanths (genus *Carludovica*) – weevil BSPM system, pollination is ensured by *Ganglionus* weevils (Derelomini) developing in the male flowers of the monoecious inflorescences. However, they coexist with another genus of derelomine weevils (genus *Systenotelus*), which predates *Carludovica* seeds while providing no pollination service. Since most derelomine weevils are brood pollinators, this cheater habit has therefore been inferred as a transformation from a beneficial to a detrimental one (Franz & Valente 2005). Such transitions of beneficial to detrimental life habits are a common feature of brood-pollinators system, and have been extensively documented in fig/fig-wasp and yucca/yucca-moth systems (e.g., Pellmyr et al. 1996; West et al. 1996; Segraves et al. 2005).

2.3.5 Evolutionary dynamics of host use

Since most of the plant groups actually associated with weevil brood pollinators are categorized as ancient tropical lineages (Annonaceae, Araceae, Arecaceae, cycads, Cyclanthaceae, Ebenaceae and Strelitziaceae; Franz & Valente 2005; Kress & Specht 2006; Toon et al. 2020), extant plant-weevil associations have sometimes been assumed to be ancient and possibly concurrent with the origin of plant lineages (Brenner et al. 2003; Oberprieler 2004; Franz 2006). However, such a pattern has not been backed up by any solid evidence, as all studies integrating knowledge of the fossil record and the results of molecular dating analyses support the hypothesis that weevil brood pollinator lineages began to diversify long after the origin of the plant lineages on which they specialize. For example, the estimated origin of palm-specialists from the Derelomini tribe (ca. 40 Mya; Haran et al. 2022b) significantly postdate the well-documented appearance of palms ca. 100 Mya (Baker & Couvreur 2013). Likewise, the phylogenetically diverse lineages of weevils that shifted on cycads (Oberprieler 2004) colonized them relatively recently (Downie et al. 2008; Hsiao & Oberprieler 2022), well after their origin more than 250 Mya (Condamine et al. 2015).

Weevils show a marked pattern of phylogenetic niche conservatism for the specific plant lineages they pollinate. Consistency of association with plant clades is observed at the subfamily, genus or species-group level (Franz & Valente 2005; de Medeiros & Vanin 2020; Haran et al. 2021, 2022b; Figure 1). However, unlike other brood-pollinators, weevils also display a remarkable ability to shift to unrelated plant lineages. A striking example of this pattern is seen in eastern hemisphere Derelomini with two parallel instances of secondary shifts from palms (Arecaceae) to Ebenaceae (genus *Euclea*; Haran et al. 2022b). Interestingly, such secondary shifts did not necessarily constitute evolutionary dead ends since they are sometimes followed by lineage diversification and even additional secondary shifts (Haran et al. 2022b). Other notable examples of host shifts include the parallel and independent colonization of the closely related palms *Elaeis guineensis* and *Elaeis oleifera* by two distinct lineages of derelomine weevils (Haran et al. 2021) and the independant colonization of the legume tree *Baikiaea insignis* (Fabaceae) by both Ochyromerini (two species of *Endaeus*) and

Derelomini (*Lomederus ghesquierei*) (Marshall 1932, 1933a). Overall, the evolutionary pattern of host use in weevils engaged in BSPM is much more dynamic than what is reported in other brood pollinators systems (Pellmyr 2003; Herre et al. 2008) and thus reinforces the interest of using this model system as a relevant alternative model to investigate evolutionary dynamics of pollination mutualism in the tropics (Haran et al. 2022b).

3. Economic importance and conservation

Many plants engaged in BSPM with weevils have economic, cultural or ornamental values, features that have sometimes triggered the discovery and study of these mutualistic systems. Thanks to a better understanding of the plant-weevil BSPM systems, it was possible to achieve practical objectives. For example, a classic application in agriculture is the introduction of the derelomine weevil *Elaeidobius kamerunicus* from Africa to Asia, to improve pollination of cultivated African oil palm (*Elaeis guineensis*; Syed et al. 1982). The successful establishment of this weevil, also known as the 'million dollar weevil', has resulted in a dramatic increase in pollination rates and yields (Krantz & Poinar 2004; Li et al. 2019).

Many weevil pollinated palms are an important source of food, goods and building materials (e.g., *Acrocomia*, *Cocos*, *Euterpe*, *Oenocarpus, Phytelephas*, *Syagrus*; Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Bezerra et al 2020; Carreño-Barrera et al 2021; Auffray et al. unpublished). In tropical and subtropical regions, wild fruits and leaves of Annonaceae (e.g., *Annona senegalensis*), Clusiaceae (e.g., *Pentadesma butyracea*) and Fabaceae (e.g., *Piliostigma reticulatum*) for which pollination by weevils is indicated based on PNC are commonly consumed by local populations or have a cosmetic or medical use (e.g., Babajide et al. 2008; Traoré et al. 2011; Dao et al. unpublished). In cycad lineages primarily pollinated by weevils (Toon et al. 2020), the high ornamental and subsequent economic value of many cycad species has also led to over-collection (Mankga & Yessoufou 2017). In these groups, reproductive failure, among habitat loss and medicinal use, has been identified as one of the main drivers of population decline, highlighting the importance of detailed investigations of their pollination ecology. More generally, while plant-weevil BSPM probably emerged to balance pollination constraints in tropical biomes, it is also a risky evolutionary path if the specialized pollinators become rare or extinct. Yet too little is known about the impact of pollinator population dynamics on the reproductive success and long-term survival of the plants involved (Toon et al. 2020).

4. Oversights and estimates of global richness

4.1 The inconspicuousness of plant-weevils pollination relationships

One may wonder why such widespread mutualistic relationships have taken so long to be described and recognized. Pollination ecology is a dynamic discipline and pollination syndromes have been explored for a significant range of tropical flora (Momose et al. 1998; Schleuning et al. 2012; Vizentin-Bugoni et al. 2018), several causes may be invoked for the delays in description of plant-weevil BSPM systems.

First, it can be explained by common misconceptions about plant and weevil biology. For example, in the cycad/molytine and palm/derelomine systems, massive aggregations of weevils on inflorescences are highly suggestive of pollination activity. Although these associations have been known for a long time (e.g., von Martius 1823), the common misconception that palms and cycads are primarily anemophilous groups has hampered research on brood-site mutualism in these systems for decades (Von Martius 1823; Lepesme 1947; Bondar 1943; Henderson 1986; Anstett & Dufaÿ 2003; Barfod et al 2011; Toon et al. 2020). These flower visitors have long been considered parasites, providing no pollination service (Bondar 1943; Lepesme 1947), consistent with antagonistic relationships generally reported in weevils (Oberprieler et al. 2007). In a striking example of how prior misconceptions can prevent discovery, a study characterizing floral visitors of *Butia catarinensis* by collecting only during the day and using sweep nets failed to find a relevant number of beetles in female flowers (Rosa 2000). However, B. de Medeiros visited the same locality less than 10 years later and found hundreds of individuals of *Anchylorhynchus eriospathae* hiding at the base of inflorescences during the day (de Medeiros & Vanin 2020). These weevils breed on female flowers (de Medeiros et al. 2014) and adequate collection and observation methods could have recorded them visiting active female flowers for oviposition. To date, the cycad and palm-weevil associations remain by far the best studied plant-weevil BSPM systems, in particular because the abundance of these insects on the inflorescences and their specialized nature greatly facilitates the identification of the relationships (Franz & Valente 2005).

Second, the inconspicuous nature of many relationships hampered and slowed down the discovery of several plant-weevil BSPM relationships. For example, in the case of the Annonaceae – *Endaeus* mutualisms, the flowers are isolated and therefore the relationships are thus far less conspicuous. In these systems, weevils typically reach flowers in very low numbers, sometimes at a very specific time of the circadian flowering cycle (early in the morning or late in the evening), and may be hidden or “enclosed” in floral chambers during most of the day (Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020) or present on the flower only at night and notably absent during the day (Ratnayake et al. 2006). When not enclosed in flowers, *Endaeus* weevils and related weevil genera are usually collected while flying over the canopy (Kojima & Morimoto 1995; Sprick and Florent 2018), using light traps (Kojima & Morimoto 1995; Haran et al. 2022a) or by beating plants only used as shelters, generally in low numbers (Kojima & Morimoto 1995). Therefore, unraveling BSPM relationships between weevils and their host plants is usually a difficult task. To illustrate this point, a striking example of inconspicuous relationships is found in the *Anthurium* (Araceae) / Derelomini mutualism. In this system, only a few individuals of the derelomine *Cyclanthura carinata* reach *Anthurium* inflorescences at night during the 1-2 weeks of anthesis, and further remain hidden in areas protected by the spathe, leaving the inflorescences apparently empty. This inconspicuousness probably explains why this obligate pollination mutualistic system has been overlooked for decades (Franz and Valente 2005; Franz 2007b).

4.2 An underestimated diversity of species and interactions

How much of the diversity of weevil-based pollination is still unknown? A basic calculation of the discrepancies between the number of species whose biology is reported and the total richness of their clade suggests that only a small portion of the interactions are at least superficially known (Figure 2). There is also a strong geographic and taxonomic bias in the description of plant-weevil BSPM systems.

For example, for most derelomine Neotropical genera information on host plant use is available (Franz & Valente 2005). By comparison, host records are only available for five of the 13 Paleotropical genera of Derelomini (Alonso-Zarazaga & Lyal 1999; Franz & Valente 2005). The estimated number of derelomine species overall (ca. 300 species; Caldara et al. 2014; de Medeiros & Vanin 2020; Haran et al. 2020, 2022a) pales in comparison with the diversity estimates of their main hosts, because the species diversity in the palm family (Arecaceae) is estimated at about 2500 species (Dransfield et al. 2008; Couvreur and Baker 2013). Since pollination ecology and pollinators have only been identified for a small fraction of extant palm species, we can hypothesize that dozens – if not hundreds – of palm-weevil BSPM systems remain to be discovered. Additionally, even though Derelomini are best known for their associations with palms, recent research has unraveled that some of them are also associated with plants other than palms. For example, in the Southern African derelomine fauna, the recently described genus *Ebenacobius* has been found associated with Ebenaceae and other basal angiosperms. In this genus, no less than 14 new species have been recently described (Haran et al. 2022a) and at least four others are awaiting description. Moreover, based on the inferred pattern of PNC in BSPM weevils, Franz & Valente (2005) and Franz (2006) suggested that most of the ca. 230 species of Carludovicoideae (Cyclanthaceae) and a significant part of the ca. 800 known *Anthurium* (Araceae) species in the Neotropical region are pollinated by derelomine weevils. In cycad-weevil BSPM systems, the range of interactions reported here only reflects our current state of knowledge, and many cycads species have been insufficiently studied and many relationships remain to be described (Toon et al. 2020).

The general lack of knowledge on plant-weevil BSPM systems can be exemplified by our understanding of Ochyromerini. Pollination activity in this tribe has been only reported between a few species of *Endaenidius* and *Endaeus* and their Annonaceae hosts and BSPM has been only formerly identified in one system (*Annona senegalensis* - *Endaeus* spp.; Lau et al. 2017; Saunders 2020; Dao et al. unpublished). Importantly, Ochyromerini has been determined to be the dominant weevil guild circulating above the canopy in a Southeast Asian dipterocarp forest (Sprick & Floren 2018), with over 50 undescribed ochyromerine species recorded in a single site. Similar species richness was also observed in Cameroon using light traps (Haran unpublished). Finally, a multitude of undescribed Ochyromerini species (mostly belonging to the genus *Endaeus*) have been reported by several authors in Asia and Africa (Hustache 1924; Marshall 1926; Oberprieler 1993; Momose et al. 1998), and it can be suspected that this group could play an important role in the pollination of Paleotropical rainforests.

In the pantropical Annonaceae (more than 2400 species), cantharopilous flowers are the most common and have been identified as being typical of weevil pollination (Momose et al. 1998; Gottsberger 1999; Saunders 2020). It is notably the case of the Neotropical Annonaceae (ca. 950 species; Maas et al. 2011), where cantharophilous flowers involving weevil pollination are the most widespread (Gottsberger 1999; Silberbauer-Gottsberger et al. 2003; Saravy et al. 2021). This set of relationships requires further investigations in this region since the only known specialized pollinators of Annonaceae (Ochyromerini) are exclusively paleotropical (Alonso-Zarazaga & Lyal 1999).

Our general overview of weevil-based pollination shows that several additional pantropical families of angiosperms are – or at least can be considered as partially – pollinated by weevils (Table S1), with only a small fraction of these relationships having been uncovered so far. For example, in Clusiaceae, Ebenaceae, Lecythidaceae, Myristicaceae and Sapotaceae, BSPM by weevils have been only reported for a small number of species; however there are likely many more BSPM weevil relationships because cantharophilous flowers are known in several genera of these families and the associated weevil lineages also contain a significant number of undescribed species (Oberprieler 1993; Caldara et al. 2014; Haran et al. 2022b). In some cases, the weevil diversity also exceeds that of the known potential hosts; for example, 25 species of the Australian weevil genus *Elleschodes* are known (Armstrong & Irvine 1990; Caldara et al. 2014; Pullen et al. 2014), of which several species are known to pollinate the only three species of *Eupomatia* (Eupomoatiaceae) so it is likely that this genus also pollinates other plant families. Going further, the Orchidaceae-Baridinae system highlights the fact that even weevils lineages that are not known to be pollinators and that lack the associated typical morphological features can also be engaged in BSPM (Nunes et al. 2018), with a potential rich array of interactions (van der Cingel 2001). From the host plant perspective, the orchid species studied (*Dichaea cogniauxiana*) also lacks features associated with weevil pollination in other groups (standard orchid floral morphology and phenology; Nunes et al. 2018). Such examples greatly expand the potential spectrum of brood-site mutualistic interactions between weevils and plants in tropical biomes and call for a complete shift in our perception of the role of these beetles in the functioning of tropical ecosystems.

A preliminary estimate of the expected diversity of plant-weevil BSPM systems can be made based on the discrepancies between the number of systems described and inferred based on PNC (Figure 2). The calculation of the ratios for a selection of systems (see figure 2) shows that the expected total diversity of species involved is on average eight times richer than the number of species inferred from PNC and about 17 times richer than the number of species with experimentally-verified BSPM. Based on the species counts obtained in this review (see section 1), it is estimated that ca. 2000 plant species could be engaged in BSPM with weevils globally. Similarly, the species richness of weevils involved in these relationships could be around 2500 species. Thus, plant-weevil relationships probably represent the most speciose case of brood-site pollination mutualism, exceeding the diversity of other BSPM species-rich groups (e.g., Lopez-Vaamonde et al. 2009; Cruaud et al. 2010).

5. Concluding remarks: a road map for future research

5.1 Searching for new plant-weevil BSPM systems

Accumulating evidence for the role of weevils as specialized brood-pollinators of plants is changing our perspective on the role of this super-diverse group of beetles in tropical ecosystems and beyond. As such, it is time to expand our understanding of pollination ecology and to research and test this mutualism in a range of plant and weevil groups that have been overlooked. We show in this review that some common features associated with BSPM between plants and weevils can help identify novel systems. That said, we also show that these mutualistic relationships can exist between lineages that do not exhibit these characteristics at all. In this regard, we should also change our perception of the structure of these relationships themselves. In light of this reasoning, a wide range of plant-weevil interactions should be re-evaluated. A few selected “priority” examples include the potential role of several ancient weevil groups (Belidae, Caridae, Cimberididae and Nemonychidae) that visit and breed in gymnosperm cones. With the exception of cycads, they are not considered pollinators (Oberprieler et al. 2007), but these cases have never been verified in detail. In the Neotropics, *Oxycorynus* species (Belidae, Oxycoryninae) are known to visit the male and female flowers of parasitic plants of the genus *Lophophytum* (Balanophoraceae), the larvae developing in the inflorescences (Ferrer et al. 2011). One group within Curculionidae that needs attention is the subfamily Baridinae. Here we found a single example of demonstrated effective pollinator (*Montella* in orchids), but this mostly Neotropical taxon harbors an extreme diversity with more than 4,000 described species, many of them found in flowers as adults (Prena et al. 2014; B. de Medeiros pers. obs.). Because of their difficult phylogeny, taxonomy and very high number of undescribed taxa (Davis 2011), they are rarely identified beyond subfamily or tribe level in pollination studies, preventing accumulation of knowledge. Relationships can also occur in even more unexpected groups of weevils associated with flowers. In orchids, a species endemic to the Cayman Islands (*Myrmecophila thomsoniana*) is apparently pollinated by the weevil *Lachnopus vanessablockae* (Curculionidae, Entiminae; Girón et al. 2018) with pollinia transferred on elytra on the stigmatic surface of flowers. Although this case deserves more detailed investigation, it should be noted that, as typical for entimines, the larvae of this species reproduce in the soil on the root systems of plants (Girón et al. 2018).

Plant-weevil BSPM systems can also be expected in temperate regions, where the predominance of anemophily and entomophily based on generalist pollinators might have precluded investigations of more specialized systems. In some Western Palearctic willows (Salicaceae), flowering cycles show intriguing spikes of volatiles which are not correlated with the visits of efficient pollinators expected for this plant (bees and moths; Jürgens et al. 2014). Interestingly, a part of these compounds (4-1 dimetoxybenzène) is also produced by several South American palms for the specific attraction of beetles, including weevils (Knudsen et al. 2001; Núñez-Avellaneda et al. 2005). This case deserves special attention since the male and female inflorescences of these dioecious trees also harbor the larval stages of several typical genera of flower weevils (*Acalyptus*, *Dorytomus*, *Ellescus*; Hoffmann 1958).

5.2 Priority research axes

5.2.1 A plea for description of systems

A better understanding of the diversity and functioning of plant-weevil BSPM systems requires detailed studies of the corresponding interactions (Fenster et al. 2004), but also of the identity and boundaries of the species involved. To date, too many plant-weevil BSPM studies follow a phytocentric approach and poorly account for pollinator identity, in part due to taxonomic shortfalls. As Franz & Engel (2010) pointed out, there are no shortcuts to understanding the evolution and diversification of plant-weevil interactions and only detailed case studies can provide relevant insights. Taxonomic descriptions are essential prerequisites for any study of pollination in the highly specialized plant-weevil BSPM systems, and this effort must be made with the relevant expertise of trained taxonomists (Toon et al. 2020; Engel et al. 2021). When expertise is not available, we strongly recommend producing at least one DNA barcode sequence for each weevil morphospecies involved in a system and depositing it on international databases (e.g., de Medeiros et al. 2019), and using images in addition to names to document weevil flower visitors (e.g., Núñez-Avellaneda & Rojas-Robles, 2008; Núñez et al. 2015; Guerrero-Olaya 2017; de Medeiros et al. 2019). The associated voucher specimens should also be deposited in permanent collections of museums or institutions. These two procedures will make it possible to considerably improve species description rates, but also the knowledge on their ecology and distribution.

5.2.2 Evolutionary trajectories : when, why and how?

Although preliminary insights on the emergence and maintenance of plant-weevil BSPM are readily available, a significant number of evolutionary aspects of these relationships remain to be investigated. A first aspect lies in the age of these relationships. Reliable fossils of weevil lineages engaged in BSPM are noticeably absent, precluding making precise inferences about the ages of these mutualisms. The reasons why so many ancient and more derived plant lineages have engaged in BSPM with weevils can be elucidated if their emergence coincides with specific past biogeographical or climatic events. More generally, plant-weevil BSPM systems offer a rich and diverse range of systems considered as potential models for understanding the conditions favoring: (*i*) the shift from detrimental to beneficial relationships, and the role of tripartite interactions in driving these interactions, (*ii*) transitions between pollination syndromes such as anemophily to BSPM and conversely, including intermediate or ambophilous systems, and (*iii*) whether there is a general trend towards specialization of pollination systems in tropical biomes. Interestingly, almost all plant lineages exhibiting cantharophilous and thermogenic flowers are widely associated with weevils. It remains to be determined to what extent the association with weevils specifically was a key factor in the emergence of cantharophily in general (Bernhardt 2000). Other poorly documented aspects of these relationships include the potential association with specific microorganisms for colonization of breeding sites and whether plants alter their physiology to favor the development of the hosted pollinators. Finally, in the age of genomics, tools are also available to investigate the genomic consequences of selective pressures associated with transitions between antagonism and mutualism in weevils.

5.2.3 The challenges of the anthropocene

How do specialized BSPM systems involving weevils cope with the anthropocene? At a time of unprecedented human-induced ecosystem disruption, many aspects of these complex relationships may be affected. Fragmentation of forests resulting in greater distances between plant conspecifics, general collapse of insect diversity and biomass, or interference with host plant locations due to light pollution or deterioration of chemical communication associated with ozone concentration and global warming are all likely to decrease the effectiveness of these specialized pollination systems (Potts et al. 2016; Vanderplanck et al. 2021; Wagner et al. 2021). On the resilience or vulnerability of this type of mutualism will depend the maintenance of reproduction of a significant part of the tropical flora.

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Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article. Gael J. Kergoat is one of the *PCI Ecology* recommenders.

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Supplementary material

Table S1. List of plant-weevil brood-site pollination mutualism. Relationships reported when at least one species of the weevil genus was identified as actual brood-site pollinator. Relationship from congeneric species inferred based on phylogenetic niche conservatism at genus level. Relationships are also reported when plants and/or weevils show typical adaptations associated with BSPM (see sections 1 and 2).