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

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3

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

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29 **Abstract**

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

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60 **Keywords**

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

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Introduction

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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 constrained to actively seeking out 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).

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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 pollen; Sakai 2002) of a plant as a reward for its pollination. It has independently evolved several times, mostly in tropical and subtropical biomes (Sakai 2002; Dufay & 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; Dufay & Anstett 2003; Kawakita & Kato 2009; Hembry & Althoff 2016). Textbook examples of brood-site pollination are traditionally exemplified by the highly specialized 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.

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Among the neglected insect lineages involved in BSPM, the weevils (Coleoptera: Curculionoidea) are probably the most overlooked. 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

145 pollination by weevils is generally considered anecdotal and is often overlooked in reviews
146 on brood-site pollination (Dufayé et al. 2003; Hembry & Althoff 2016; Toon et al. 2020).
147 Weevils are not even mentioned as one of the most relevant groups of beetle pollinators in
148 some studies (e.g., Kevan & Baker 1983; Wardhaugh 2015; IPBES 2016). However, in
149 recent decades, a number of plant-weevil interactions involving brood-site pollination have
150 been progressively documented and described in detail (Franz & Valente 2005, Caldara et
151 al. 2014; Nunes et al. 2018; de Medeiros et al. 2019; Saunders 2020; Toon et al. 2020).
152 Moreover, recent plant-focused studies on tropical pollinators have recovered weevils as one
153 of the most important pollinator groups (Krimse & Chaboo 2020; Paz et al. 2021). Taken
154 altogether, all these studies suggest that these associations may be more widespread than
155 previously thought (Caldara et al. 2014); it also contradicts the common view that weevils
156 are not pollinators, and suggests that much of the global insect pollinator diversity is
157 currently left unnoticed. For example, the combined species diversity of the three weevil
158 families containing brood-site pollinator lineages (ca. 350, 4400 and 51,000 species, for
159 Belidae, Brentidae and Curculionidae, respectively; Marvaldi & Ferrer 2014; Oberprieler
160 2014a, 2014b) is at least twice as large as the diversity of bees (ca. 20,000 species; Zattara
161 & Aizen 2021), which are usually considered to be the most important group of insect
162 pollinators (Potts et al. 2016). As we detail in this review, multiple and diverse weevil
163 lineages commonly visit flowers, and an ever-increasing number of them can be considered
164 true pollinators. This broad reassessment of the potential role of weevils as pollinators is
165 highly relevant for the understanding of ecosystem functioning (including for
166 agroecosystems), especially in tropical regions where bees are much less diverse than
167 weevils (Oberprieler et al. 2007; Orr et al. 2021; Freitas et al. 2022).

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

177 1. A wide spectrum of mutualistic interactions

178 Weevils are the most diverse group of insects that visit flowers and develop in reproductive
179 structures (Oberprieler et al. 2007; Kirmse & Chaboo 2020). This close interaction with the
180 reproductive structures of plants probably preceded the colonization and diversification of
181 weevils on angiosperms. The oldest weevil fossils (such as †*Belonotaris punctatissimus*)
182 were found in the Karabastau Formation (ranging from the Oxfordian to Callovian stages,
183 166.1 to 157.3 million years ago (Mya); Walker et al. 2018); at that time they were likely
184 associated with gymnosperm-dominated floras (e.g., see Oberprieler & Oberprieler 2012 for
185 slightly younger weevil fossils from the Tithonian stage, 150.8 to 145.5 Mya). Their origin
186 therefore clearly predates the rise to dominance of angiosperms during the Cretaceous
187 Terrestrial Revolution, from 125 to 80 Mya (Dilcher 2000; Magallón & Castillo 2009; Benton
188 2010). In addition, several early diverging weevil lineages, such as Caridae or

189 Nemonychidae, typically breed on gymnosperm male or female reproductive structures
190 (Oberprieler et al. 2007). Associations with angiosperm flowers and seeds evolved both
191 within these early-diverging lineages (Ferrer et al. 2011; Kuschel & Leschen 2011) but also
192 in more derived lineages belonging to the two most speciose weevil families (Brentidae and
193 Curculionidae). Weevils in these clades generally visit flowers when feeding on pollen and
194 ovipositing in buds, ovaries and fruits where larval development occurs (Oberprieler et al.
195 2007; Caldara et al. 2014). When adults fly between flowers to mate or oviposit on one or on
196 a fairly narrow range of hosts, they can carry pollen between conspecific plant species,
197 thereby pollinating them. Therefore, the flower-visiting and plant oviposition behaviors of
198 several weevil lineages create the context for the evolution of BSPM from antagonistic to
199 mutualistic interactions, or conversely (Figure 1). Interestingly, the ever-growing body of
200 accumulated knowledge on plant-weevil interactions suggests that increasingly diverse and
201 complex specialized plant-weevil BSPM interactions are to be expected (Franz & Valente
202 2005; Franz 2006; Saunders 2020; Toon et al. 2020).

203 The first report of weevil pollination activity refers to a palm-weevil interaction and
204 dates back to the 19th century (Von Martius 1823). Since then, most efforts to describe and
205 document weevil pollination have focused on palm-weevil and cycad-weevil mutualisms
206 (Franz & Valente 2005; Toon et al. 2020). This focus on cycads and palms can be explained
207 by their characteristic conspicuous inflorescences which attract massive gatherings of
208 weevils, so much so that they have triggered specific research. To date, weevil BSPM has
209 been reported for at least 87 palm species (Arecaceae) belonging to 26 genera (Table 1).
210 Weevils pollinating palms consist of about 200 species from 17 genera, mostly belonging to
211 the pantropical tribes Acalyptini and Derelomini (Curculionidae: Curculioninae) *sensu*
212 Caldara et al. (2014), hereafter called Derelomini or derelomine weevils; see also Franz
213 (2006) and Alonso-Zarazaga (2007) for nomenclatural uncertainties. Among the cycads,
214 weevil BSPM has been reported for 91 cycad species belonging to seven genera from all
215 three extant cycad families (Cycadaceae, Stangeriaceae and Zamiaceae). Weevils
216 pollinating cycads belong to a diverse range of lineages; they are predominantly found within
217 Curculioninae and Molytinae among the Curculionidae (ca. 50 species in six Paleotropical
218 genera), but also within Belidae (24 species in six Neotropical genera) and Brentidae (12
219 species in two Afrotropical genera).

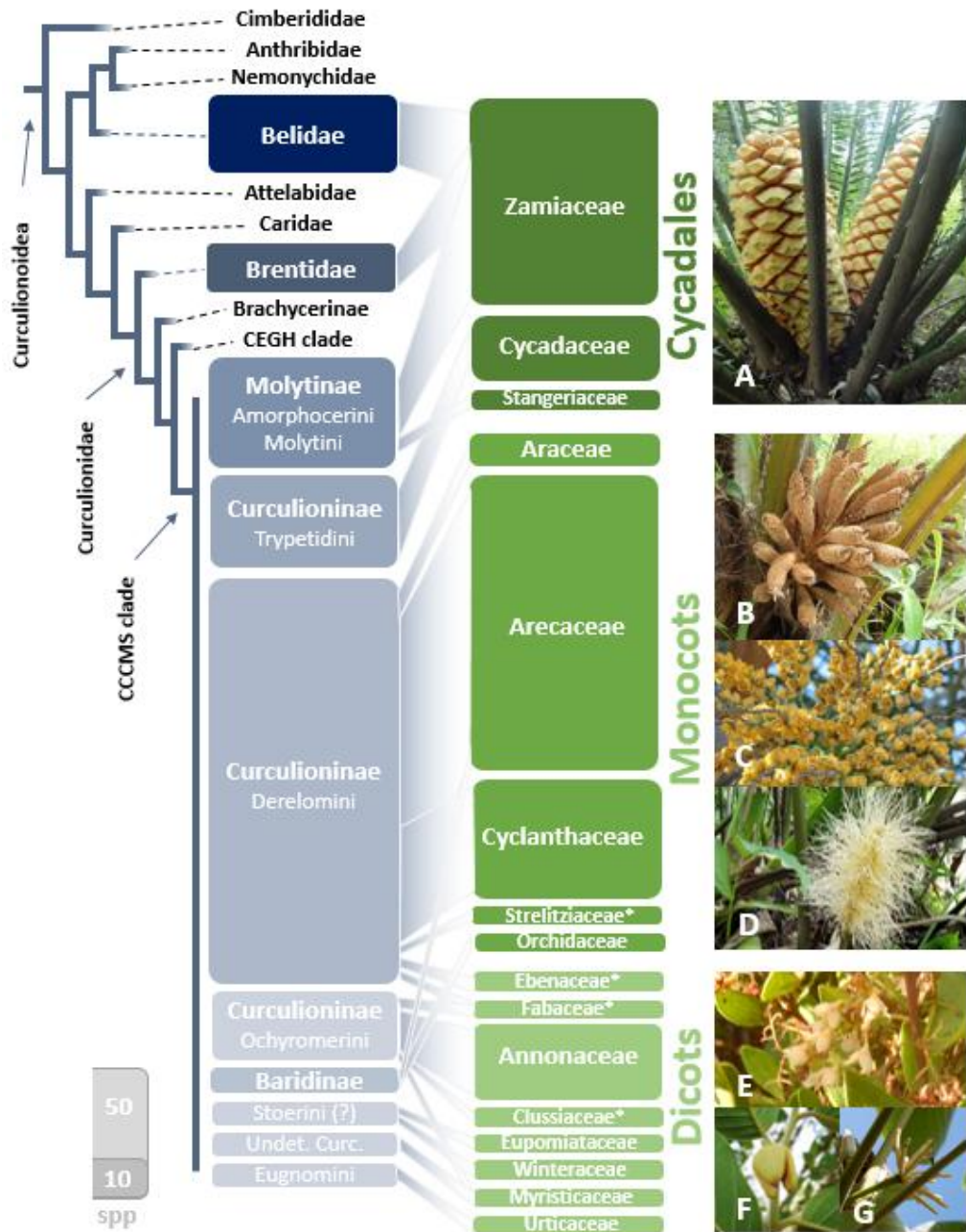
220 The study of these interactions, their mechanisms and their patterns of associations
221 with palms and cycads has stimulated the discovery of similar cases among several
222 monocot families of angiosperms. For instance, in Neotropical *Anthurium* (Araceae), 10
223 species are engaged in BSPM with *Cyclanthura* weevils (Derelomini, seven species; Franz
224 2003, 2006). In the same region, 34 species from eight genera of cyclanths (Cyclanthaceae)
225 are pollinated by 27 weevil species belonging to six genera of Derelomini (Franz 2007a,
226 2008). In Neotropical Orchidaceae, three weevil species belonging to two genera of
227 Baridinae (Curculionidae, alternatively classified as the supertribe Bariditae among
228 Conoderinae) ensure their pollination (Nunes et al. 2018). More anecdotally, *Strelitzia nicolai*
229 (Strelitziaceae) from southern Africa appears to be co-pollinated by two derelomine species
230 belonging to two distinct genera (Haran et al. 2022a; Haran unpublished). Importantly, the
231 majority of weevils engaged in BSPM show a marked pattern of phylogenetic niche
232 conservatism (PNC) at the genus level (Table 1, Table S1 & Appendix 1; Franz & Valente
233 2005; Toon et al. 2020; Haran et al. 2021, 2022b, see section 2.3.5 for details). Such a
234 pattern is far from unusual among groups of internal feeding insects, such as seed beetles

235 (Kergoat et al. 2007, 2015) or noctuid stem borers (Kergoat et al. 2018). Therefore, we
236 postulate that, in the absence of direct experimental evidence for a weevil species,
237 knowledge about other species in a genus may provide an indication of pollination activity.
238 This generalization can produce hypotheses to be tested and also provide a first assessment
239 of the extent of plant-weevil BSPM in overlooked tropical biomes (Toon et al. 2020).

240 Several dicot families have been also increasingly reported to be engaged in BSPM
241 with weevils. In the Australasian region, some species of *Eupomatia* (Eupomatiaceae),
242 *Myristica* (Myristicaceae) and *Exospermum* (Winteraceae) are pollinated by specific weevil
243 lineages (*Elleschodes* spp., indet. genus (see Caldara et al. 2014) and *Palontus* spp.
244 respectively; Armstrong & Irvine 1989a, 1989b, 1990; Pellmyr et al. 1990; Armstrong 1997).
245 In African Ebenaceae (*Euclea*), Lecythidaceae (*Napoleonaea*) and Malvaceae (*Thespesia*)
246 weevil pollination can be inferred on the basis of PNC since congeneric weevil species
247 associated with other plant groups are brood pollinators (Haran et al. 2022a, 2022b; Haran
248 pers. obs.). In the Neotropics, most species of *Cecropia* (Urticaceae) surveyed to date are
249 associated with weevils belonging to the genus *Udeus* (Curculioninae: Eugnomini), which
250 visit male inflorescences in all species (Lira et al. unpublished) and female inflorescences in
251 at least one case (Mendonça 2004). In the speciose pantropical family Annonaceae, at least
252 22 species in 13 genera are associated with 30 species of weevils pollinators belonging to
253 two Ochyromerini genera (Curculionidae: Curculioninae) and other unidentified weevil
254 groups (Momose et al. 1998; Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020; Dao et
255 al. 2023; B. de Medeiros unpublished).

256 All in all, the extensive literature search conducted in this review underlines that no
257 less than 600 instances of plant-weevils species-species BSPM interactions have been
258 recorded to date or suggested based on the marked trend of PNC for brood pollination
259 (Table 1; see Table S1 and Appendix 1 for details). Overall, BSPM with weevils has been
260 demonstrated experimentally in 12 of the 22 plant families involved in this mutualistic
261 system, with the remaining 10 families suggested based on both PNC of weevil genera and
262 traits of floral structures associated with cantharophily. Representatives of all major plant
263 lineages, gymnosperms, monocots and dicots, are engaged in BSPM with weevils;
264 collectively representing ca. 250 species belonging to 72 genera (Figure 1) associated with
265 about 300 species of weevils. In this regard, weevils are by far the most ecologically
266 successful group of insects engaged in BSPM interactions with the plant kingdom. Our
267 review shows that weevil-based BSPM has emerged several times independently with plants
268 involved in these interactions typically belonging to groups considered to be ancient lineages
269 (Pant 1987; Franz 2004; Saunders 2020; Baker & Couvreur 2013). We also show that this
270 type of interaction is currently predominantly found in tropical and subtropical regions of the
271 eastern and western hemisphere, with only a few cases under Mediterranean climates
272 (Figure 2).

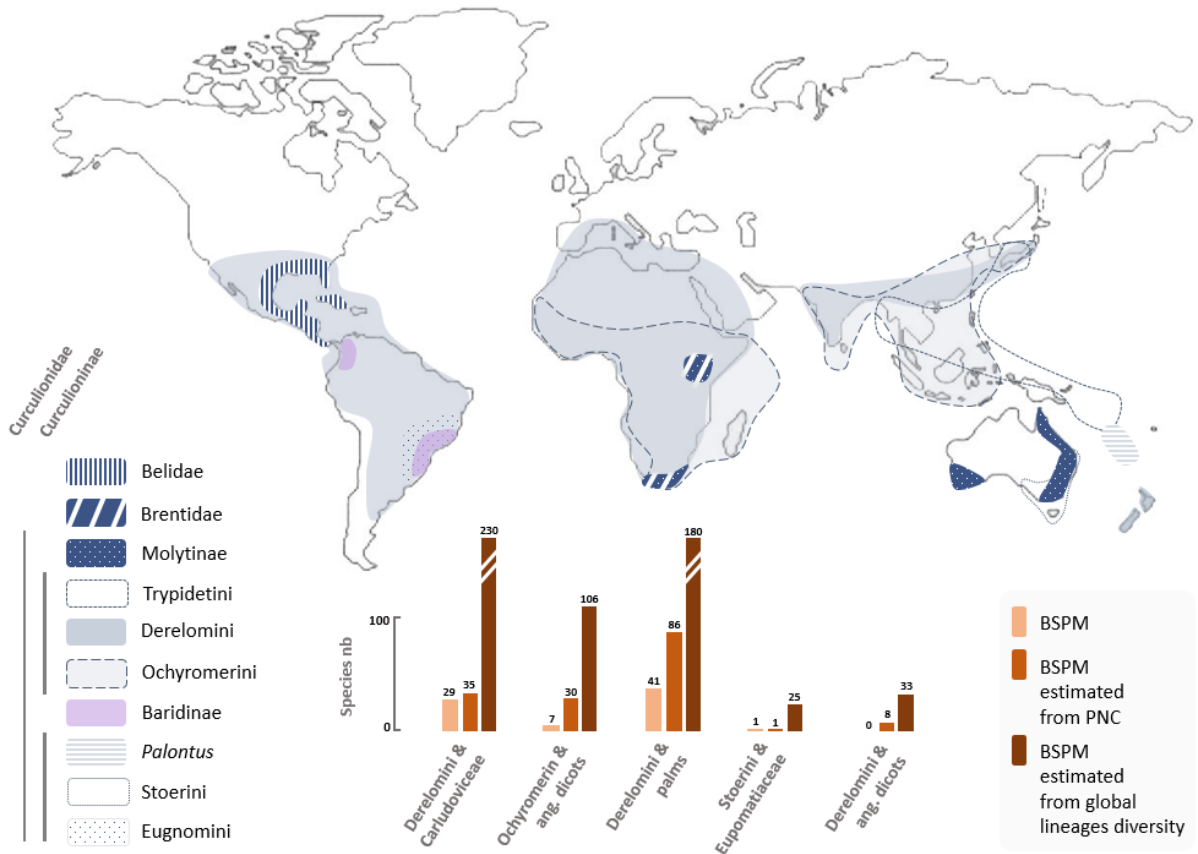
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275 **Figure 1.** Summary of known and expected brood-site pollination mutualisms (BSPM) between plants
 276 and weevils (Coleoptera: Curculionoidea). The boxes in blue and green refer respectively to the
 277 weevil and plant lineages involved (the size of boxes is correlated to the number of species involved;
 278 see also the approximate scale at the bottom left). The phylogenetic tree on the left presents a
 279 synthetic view of phylogenetic relationships among weevils based on the phylogenomic study of [Shin](#)
 280 [et al. \(2018\)](#). The relationships among the so-called CCCMS clade (for Baridinae, Cossoninae,
 281 Curculioninae, Molytinae and Scolytinae) are unresolved; several subfamilies belonging to this clade
 282 and not involved in BSPM (e.g., Scolytinae, Lixinae) are not shown. Most of the plant families reported
 283 here contain at least one experimentally verified case of BSPM; however, for the plant families
 284 highlighted with an “*”, BSPM interactions are postulated based on the phylogenetic niche
 285 conservatism of the weevil genera involved (see Methods in Appendix 1). Some minor interactions
 286 between several lineages of Curculioninae and dicots are not shown for clarity; see Table S1 for
 287 details. Pictures of selected examples of inflorescences of plant lineages involved: **A.** *Encephalartos*
 288 sp. (Zamiaceae) pollinated by weevils from the Brentidae family and Curculionidae Molytinae. **B.**

289 *Elaeis guineensis* (Arecaceae) pollinated by Derelomini. **C.** *Syagrus coronata* (Arecaceae) pollinated
 290 by Derelomini. **D.** *Carludovica palmata* (Cyclanthaceae) pollinated by Derelomini. **E.** *Euclea racemosa*
 291 (Ebenaceae) associated with Derelomini. **F.** *Annona senegalensis* (Annonaceae) pollinated by
 292 Ochyromerini. **G.** *Cecropia peltata* (Urticaceae), a genus including species pollinated by Eugnomini.
 293 (credits: A-B, E: J. Haran; C-D, G: B. de Medeiros, F: M. Gueye).



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295 **Figure 2.** Geographical distribution of brood-site pollination mutualism (BSPM) involving weevil
 296 lineages and estimates of knowledge gaps. Distribution data collated from [Alonso-Zarazaga & Lyal](#)
 297 [\(1999\)](#), articles listed in this review, and unpublished observations by the authors (note that the
 298 distribution of an unidentified weevil genus associated with Myristicaceae is not shown). Bars show
 299 the relative number of known and estimated BSPM interactions for a selection of plant-weevil
 300 interactions. Beige: number of plant species involved in verified interactions (involving brood-site
 301 and/or synchronization of weevil and flower phenology and/or pollen transfer observed). Light brown:
 302 number of plant species involved estimated based on floral visitors, including weevils and PNC of
 303 weevils involved. Dark brown: global diversity of interaction estimated from the diversity of plant
 304 lineages engaged in BSPM with weevils (Derelomini-Carludoviceae; [Franz & Valente 2005](#); [Franz](#)
 305 [2006](#); see details on Methods in Appendix 1) and the diversity of weevil genera engaged in these
 306 interactions (other interactions; Table S1, GBIF data and unpublished authors observations, see
 307 section 4.2). y-axis: species number.

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Weevil lineages	Genera (approximate number of species engaged or with inc
Curculionidae: Curculioninae:	<i>Mangrovea</i> (7), <i>Zygodontes</i> (1)
Curculionidae: Molytinae:	<i>Militarines</i> (3)
Belidae: <i>Meloe</i> :	<i>Meloe</i> (2), <i>Meloe</i> (4), <i>Cyaneus</i> (1), <i>Paralucicola</i>
Brentidae: <i>Brentus</i> :	<i>Brentus</i> (6), <i>Flavipes</i> (5)
Curculionidae: Molytinae:	<i>Amphipocerus</i> (5), <i>Forbesi</i> (16), <i>Tranes</i> (7)
Curculionidae: Curculioninae: Derelomini:	<i>Cyclanthura</i> (10)
Curculionidae: Curculioninae: Derelomini:	<i>Amphipocerus</i> (1), <i>Derelomus</i> (13), <i>Elythromicoides</i> (1), <i>Elaeobius</i> (8), <i>Py</i>
Curculionidae: Molytinae:	<i>Chelus</i> (3), <i>Homalobius</i> (2), <i>Gidontoides</i> (2)
Curculionidae: Baridinae:	<i>Angelicentus</i> (1), <i>Anthrenus</i> (1), gen. n. et sp. n
Curculionidae: Baridinae:	<i>Limnoscus</i> (1), <i>Alfarostrates</i> (3), <i>Nertesia</i> (4), <i>Favoscoloen</i>
Dryophthoridae: Dryophthorinae:	<i>Elaphopus</i> (4), <i>Foveolus</i> (2), <i>Melan</i>
Curculionidae: Curculioninae:	<i>Colthene</i> (1), <i>Cyclanthura</i> (1)
Curculionidae: Baridinae:	<i>Microtella</i> (2), gen. n. (1)
Curculionidae: Curculioninae: Derelomini:	<i>Derelomus</i> (1), gen. n. (1)
Curculionidae: Curculioninae: Derelomini:	<i>Derelomus</i> (1)
Curculionidae: Curculioninae: Ochyromerini:	<i>Endaeus</i> (?), <i>Endaeoides</i>
Curculionidae: Curculioninae: Derelomini:	<i>Ethenacobius</i> (2)
Curculionidae: Curculioninae: Ochyromerini:	<i>Endaeus</i> (1)
Curculionidae: Curculioninae: Derelomini:	<i>Derelomus</i> (1), <i>Ethenacobi</i>
Curculionidae: Curculioninae: Stoerini:	<i>Elythromicoides</i> (3)
Curculionidae: Curculioninae: Derelomini:	<i>Derelomus</i> (2), <i>Lamederus</i>
Curculionidae: Curculioninae: Ochyromerini:	<i>Endaeus</i> (2)
Curculionidae: Curculioninae: Ochyromerini:	<i>Endaeus</i> (1)
Curculionidae: Curculioninae: Ochyromerini:	<i>Endaeoides</i> (1), <i>undescri</i>
Curculionidae: Curculioninae: Derelomini:	<i>Ethenacobius</i> (1)
Curculionidae: Curculioninae: Eugnomini:	<i>Elythromicoides</i> (2)
Curculionidae: Curculioninae: Stoerini:	<i>Falconus</i> (1)

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Table 1. Synthetic list of known plant-weevils BSPM systems. See Table S1 for details on species-specific interactions, species authorship, tissues for larval development, presence of cryptic lineages and corresponding reference list. See Figure 2 for information on the geographic distribution of weevil lineages involved in BSPM.

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2. Traits related to BSPM by weevils

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2.1 Plant traits

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Flowers and inflorescences of plants engaged in BSPM with weevils generally display typical traits related to cantharophily (beetle pollination) and remarkable convergent morphologies, physiologies, phenology and reproductive strategies. Some of the traits in these flowers are associated with beetle pollination more generally and not specifically with brood pollination. Disentangling the role of each trait in the interaction is a task that remains to be done in most cases. Here we point out features that have been proposed to increase the attractiveness of flowers to weevils engaged in BSPM, provide them with food rewards and sometimes protect them from predators. They also may improve pollen transfer to weevil integuments and play a role in weevil pollinator selection and retention, thereby improving pollination efficiency.

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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

331 synchronized blooms (Ebenaceae – *Euclea*, Orchidaceae – *Dichaea*, *Grobya* etc). Field
332 observations and experiments on various Annonaceae flowers and Cyclanthaceae
333 inflorescences show that larger floral structures attract greater number of pollinators
334 (Gottsberger 1999; Franz 2007a), revealing that this floral trait has been independently
335 selected to increase weevil attraction and pollination.

336 The main characteristic of weevil-based cantharophily is the transformation of floral
337 structures to host the weevil larval stages. Two main types of floral morphology are typical of
338 weevil-pollinated plants: (i) **clustered inflorescences** (in cycads and all monocots involved
339 in BSPM except Orchidaceae and Strelitziaceae), and (ii) **individual floral chambers,**
340 **bowls or claws** (in most dicots involved in BSPM; Gottsberger 1999; Prance & Jongkind
341 2015; Saunders 2020). Clustered inflorescences provide fleshy and nutrient-rich tissues for
342 the development of weevil larvae, generally in male inflorescences (flower capsules,
343 microsporophylls and rachises; Anstett 1999; Downie et al. 2008; Teichert et al. 2018; Haran
344 et al. 2020). Within individual floral chambers, tissues for larval development include anthers,
345 or fleshy petals (Saunders 2020; Haran et al. 2022a; Dao et al. 2023). In clustered
346 inflorescences as in floral chambers, the modified structures effectively filter access to
347 specific pollinators and sometimes further retain and protect them. For instance, in
348 Cyclanthaceae, the inflorescences of *Asplundia*, *Evodianthus* and *Ludivia* exhibit narrow
349 interfloral entrances allowing only a specific weevil pollinator to reach the hidden floral
350 reproductive structures (Franz 2007a; Teichert et al. 2018), while larger, non-pollinating
351 species are prevented from reaching them. Narrow interfloral openings can also promote the
352 transfer of pollen from anthers to the integuments of pollinators as they exit the floral
353 chambers (Teichert et al. 2018). The Annonaceae provide the most striking examples of
354 enclosed floral chambers, which are used to retain and protect *Endaeus* weevil pollinators
355 and also ward reproductive tissues from predation (Gottsberger 1999; Ratnayake et al.
356 2006; Lau et al. 2017; Saunders 2020). Other structures associated with weevil pollination
357 include staminodes (in Cyclanthaceae and Eupomatiaceae), which are stamen-like
358 structures that do not produce pollen but rather sticky secretions or odoriferous oils
359 (elongated projections in Fig. 1D). They increase attraction, provide food, shelter or
360 protection for weevil pollinators (Armstrong & Irvine 1990; Franz 2007a; Teichert et al. 2018).
361 In Annonaceae sticky pollenkitt and short pollen-connecting threads create large aggregates
362 of pollen grains that are considered specific adaptations to improve the efficiency of pollen
363 transfer onto weevils integuments (Ratnayake et al. 2006). The fleshy petals and other floral
364 tissues of plants implicated in BSPM with weevils typically show extensive feeding damages
365 (Ratnayake et al. 2006; Saunder 2020; Haran et al. 2022a; Dao et al. 2023; Figure 3F),
366 indicating that these structures are also food sources for the adult pollinators.

367 The flowers of plant lineages engaged in BSPM with weevils are **predominantly**
368 **white or creamy white** (Figure 1), but pale red, pale yellow and pale green flowers are
369 occasionally encountered (Franz & Valente 2005; Ratnayake et al. 2006; Saunders 2020;
370 Toon et al. 2020). In Cyclanthaceae, weevils show a preference for natural white
371 inflorescences in contrast to those experimentally shaded by an opaque fabric (but letting
372 the fragrance to be emitted; Franz 2007a). It should be noted that many weevils lineages
373 involved in BSPM have nocturnal or crepuscular activity (Franz 2007a; Auffray et al. 2017;
374 Lau et al. 2017; Auffray et al. 2022; Haran et al. 2022a), where light intensity is low. Under
375 these conditions, the pale colors were hypothesized to provide better contrast with the
376 surrounding environment in a way that likely enhances their visual recognition by weevils

377 (Franz 2007a; Saunders 2020). This suggests that visual recognition of inflorescences is an
378 important dimension of weevil attraction, at least as important as olfaction (see below), and
379 that white or pale colors are more attractive to weevils.

380 All major plant lineages engaged in BSPM with weevils include representatives with
381 **thermogenic** activity, allowing inflorescence or flower temperatures to rise several degrees
382 above ambient temperature (Franz 2007a; Teichert et al. 2018; Saunders 2020; Toon et al.
383 2020). This phenomenon is postulated to act as an attractant for weevil and other beetle
384 pollinators, by increasing the emission of volatiles or infrared radiation itself. It has also been
385 hypothesized to provide an energy reward to individuals reaching floral tissues (Rands &
386 Whitney 2008), but this is likely not the case for weevils since thermogenic activity is usually
387 correlated with short phases of attraction and is not maintained during an 'interim' phase
388 when individuals stand on flowers or are enclosed in floral chambers (Teichert et al. 2018;
389 Toon et al. 2020). In Annonaceae, thermogenesis is identified as typical of flowers pollinated
390 by beetles, and weevils in particular (Gottsberger 1999). The temperature reached appears
391 to be positively correlated with inflorescence size (Franz 2007a), which may explain why
392 large flowers and inflorescences evolved convergently in weevil-pollinated plants. In several
393 systems (Carludovicoideae-Derelomini; Zamiaceae-Belidae), the first peak of thermogenesis
394 associated with the attraction phase of the weevils is followed, after an 'interim' phase of
395 several hours, by a second peak where weevils leave the inflorescences (Franz 2007a;
396 Teichert et al. 2018; Salzman et al. 2020). These second peaks of thermogenesis coincide
397 with the staminate phase and probably act as repellent or as an aid for improved take-off
398 that favors weevil departure once they are covered with pollen (Teichert et al. 2018). This
399 kind of push-pull mechanism where weevils are successively attracted and then repelled
400 during the circadian flowering cycle promotes pollinator movement between plant congeners
401 and thus cross-pollination (Salzman et al. 2020).

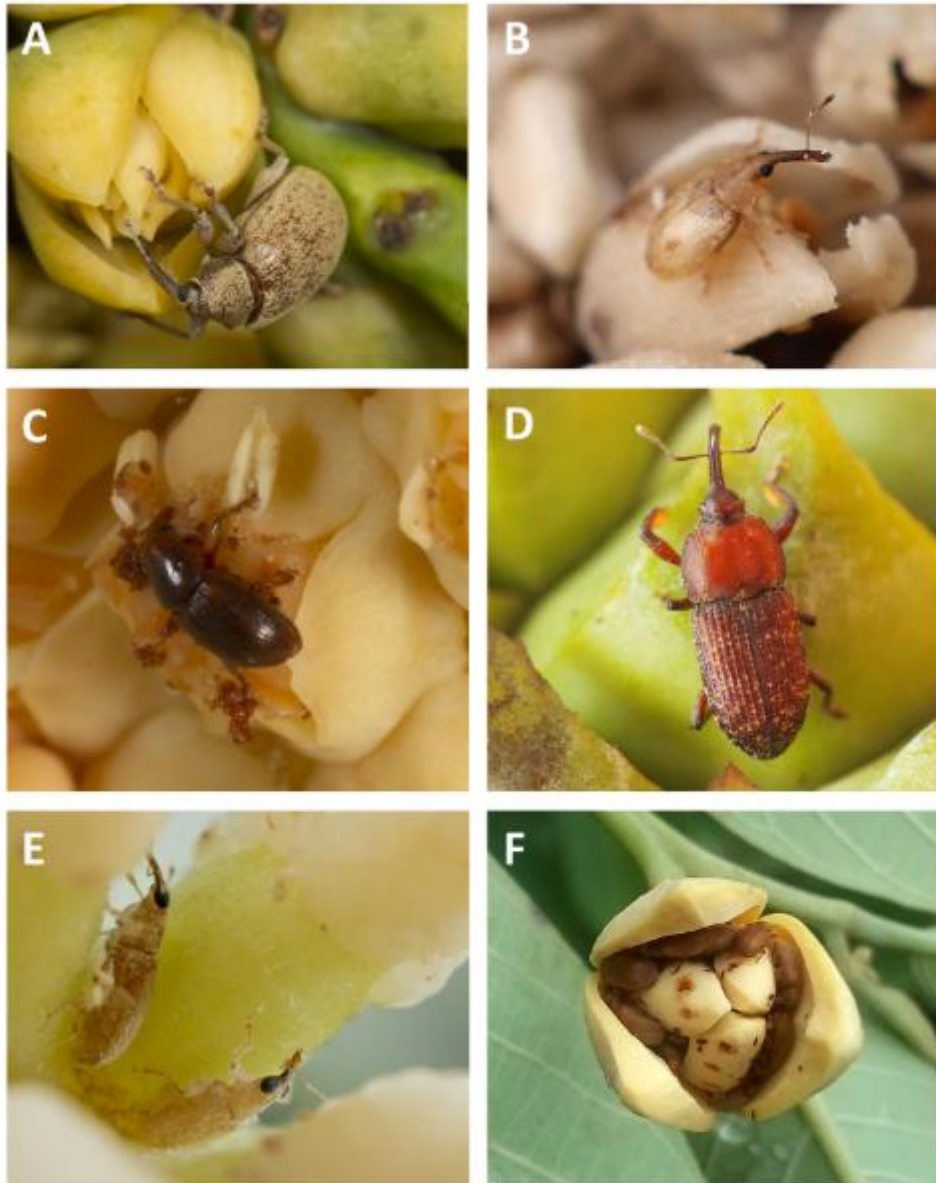
402 The **fragrances** produced by weevil-pollinated flowers during anthesis are strong
403 and detectable by human olfactory senses, and are commonly associated with fruity or floral
404 fragrances. In most genera of weevil-pollinated Cyclanthaceae (*Aspludia*, *Carludovica*,
405 *Chorigyne*, *Dicranopygium* and *Evodianthus*), production of aromas reminiscent of various
406 fruits and flowers has been reported (Franz 2007a). Similarly, in *Polyalthia* (Annonaceae), a
407 fruity odor is produced during anthesis (Ratnayake et al. 2006). In *Elaeis guineensis*
408 (Arecaceae), anthesis is correlated with the production of estragol (Lajis et al. 1985), while
409 in *Attalea phalerata* (Arecaceae), weevils and other beetle pollinators are attracted by a
410 strong emission of methyl acetate (Maia et al. 2021). In *Macrozamia* and *Zamia* (Zamiaceae)
411 the emission of linalool or methyl salicylate has been recorded (Toon et al. 2020; Salzman et
412 al. 2021). Overall, the emission in large amount of one or a few compounds that are specific
413 to the interaction seems to be a signature of chemical communication in BSPM involving
414 weevils (Ervik et al. 1999; Teichert et al. 2018; Salzman et al. 2021; T. Auffray pers. com.).
415 Notable exceptions of floral odor emission are found in *Chamaerops humilis* (Arecaceae),
416 which attracts *Derelomus* species via the volatiles emitted from the leaves (Dufay et al.
417 2003), and in *Syagrus coronata* (Arecaceae), where the volatiles are given off by a
418 persistent peduncular bract (Barbosa et al. 2020).

419 The morphological and physiological features described above are generally
420 organized into **timed phenological sequences** that coincide with **phases of flower and**
421 **inflorescence receptivity**. In most plant lineages producing large inflorescences (e.g.,

422 Araceae, Arecaceae, Zamiaceae), anthesis occurs over several days and is accompanied by
423 circadian thermogenic cycles and emission of volatiles (Franz 2007a; Auffray et al. 2017;
424 Toon et al. 2020). When flowers are isolated (in Annonaceae and Eupomatiaceae), but also
425 in Cyclanthaceae, each individual flower or inflorescence goes through one cycle of anthesis
426 with the following stages: (i) a phase of thermogenesis/attraction associated with the
427 receptivity of female reproductive structures (pistillate phase), (ii) an interim period when
428 weevils can be trapped in the floral chamber for a variable time, and (iii) a phase when
429 pollinators are released with exposure to male reproductive structures (stamen and pollen,
430 staminate phase), which can be achieved by abscission of the floral chamber petals and/or
431 by a second peak of thermogenesis (Armstrong & Irvine 1990; Franz 2007a; Lau et al. 2017;
432 Teichert et al. 2018; Saunders 2020). In the first case, the anthesis lasts between several
433 days and two weeks (Toon et al. 2020), while in the second case, the complete cycle of
434 anthesis is short and usually lasts at most 48h (Franz 2007a; Saunders 2020). Interestingly,
435 the pistillate and staminate phase cycles found in some Cyclanthaceae (*Asplundia*; Franz
436 2007a) are very similar to those found in some Annonaceae (Saunders 2020), indicating a
437 remarkable convergent evolution of plant-weevil pollination systems. With the notable
438 exception of cycads, orchids and some palms, in all plant-weevil BSPM systems, the
439 **pistillate and staminate phases coincide with peaks of crepuscular or nocturnal peaks**
440 **in pollinator activity** (Armstrong & Irvine 1990; K uchmeister et al. 1998; Franz 2007a;
441 Auffray et al. 2017; Saunders 2020; Auffray et al. 2022). These converging nocturnal
442 phenology suggest that nocturnal conditions improve pollination efficiency, possibly through
443 increased attraction of weevil pollinators. It has been also hypothesized that the movement
444 of pollinators and the dispersal of floral fragrances are facilitated at night because there is
445 less wind; lower temperatures also potentially improve the detection of thermogenic flowers
446 (Borges et al. 2016; Auffray et al. 2022).

447 A remarkable feature of plant lineages engaged in BSPM with weevils is the
448 **separation of sexes**. About 95% of the species recorded in this review show physical or
449 functional dioecy, a rare feature in the plant kingdom in general. In cycads, all species are
450 dioecious, with male plants producing pollen cones and female plants ovulate cones (Toon
451 et al. 2020). Weevil-pollinated palms may be dioecious or monoecious, but anthesis of male
452 and female flowers are always separated in time in the latter case (Barfod et al. 2011). One
453 example is the monoecious palm genus *Elaeis* (Arecaceae), in which individuals cyclically
454 produce functionally unisexual male and female inflorescences, resulting in an allogamous
455 mode of reproduction called temporal dioecy (Adam et al. 2011). In other genera, such as
456 *Acrocomia* and *Bactris* the pistillate and staminate phases of the **protogynous**
457 **inflorescences** are separated by a short interim phase resulting in circadian dioecy
458 (Henderson et al. 2000; Carre no-Barrera et al. 2021). Similar patterns are observed in other
459 monoecious plant lineages such as Annonaceae and Cyclanthaceae (Franz 2007a, 2007b;
460 Saunders 2020). In Annonaceae in particular, several other types of monoecy that may
461 result in functional dioecy have been reported (i.e. separate pistillate and staminate flowers
462 on the same plant, with a few flowers per individual at a time; Saunders 2020). Finally, a
463 number of palms exhibit **protandrous inflorescences** with very extended interim phases,
464 also resulting in functional dioecy (Silberbauer-Gottsberger et al, 2013; N u nez-Avellaneda et
465 al, 2008, 2015; de Medeiros et al. 2019). Another striking feature of systems involving
466 Arecaceae, Annonaceae and Cyclanthaceae is the small number of flowering inflorescences
467 per individual or the small number of flowering individuals at time, a strategy that also likely
468 promotes cross-pollination (Saunders 2020). The resulting low number of propagules

469 available at a certain time may be balanced by the long flowering periods of the plants
470 engaged in these BSPM interactions, for instance up to seven-months in *Asplundia*
471 (Cyclanthaceae; Franz 2007a) and many species of *Syagrus* (Arecaceae; Noblick 2017).
472 These long flowering periods have also been proposed as a strategy for constant breeding
473 of specialized brood pollinators (Carreño-Barrera et al. 2020).
474



475
476 **Figure 3.** Examples of weevils and plants engaged in brood-site pollination mutualisms. **A.** *Anchylorhynchus*
477 *trapezicollis* (Derelomini) on pistillate flowers of *Syagrus coronata* (Arecaceae) in South America. **B.** *Derelomus*
478 sp. (*costiger* group; Derelomini) pollinator of *Phoenix reclinata* (Arecaceae) in southern Africa. **C.** *Perelleschus*
479 *evelynae* (Derelomini) on pistillate flowers of *Carludovica palmata* (Cyclanthaceae) in Central America. **D.** *Tranes*
480 *lyterioides* (Molytinae) on sporophylls of *Macrozamia communis* (Zamiaceae) in Australia. **E.** *Udeus*
481 *eugnomoides* (Eugnomini) on pistillate flowers of *Cecropia peltata* (Urticaceae) in Central America. **F.** Flowers of
482 the African custard apple (*Annona senegalensis*; Annonaceae) with aggregation of *Endaeus* spp. pollinators
483 (Ochyromerini) in tropical Africa. (credits: A/C/E: B, E: B. de Medeiros, B: J. Haran, D: R. Oberprieler, F: Z. Dao).
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485 **2.2 Weevil morphology and behavior**

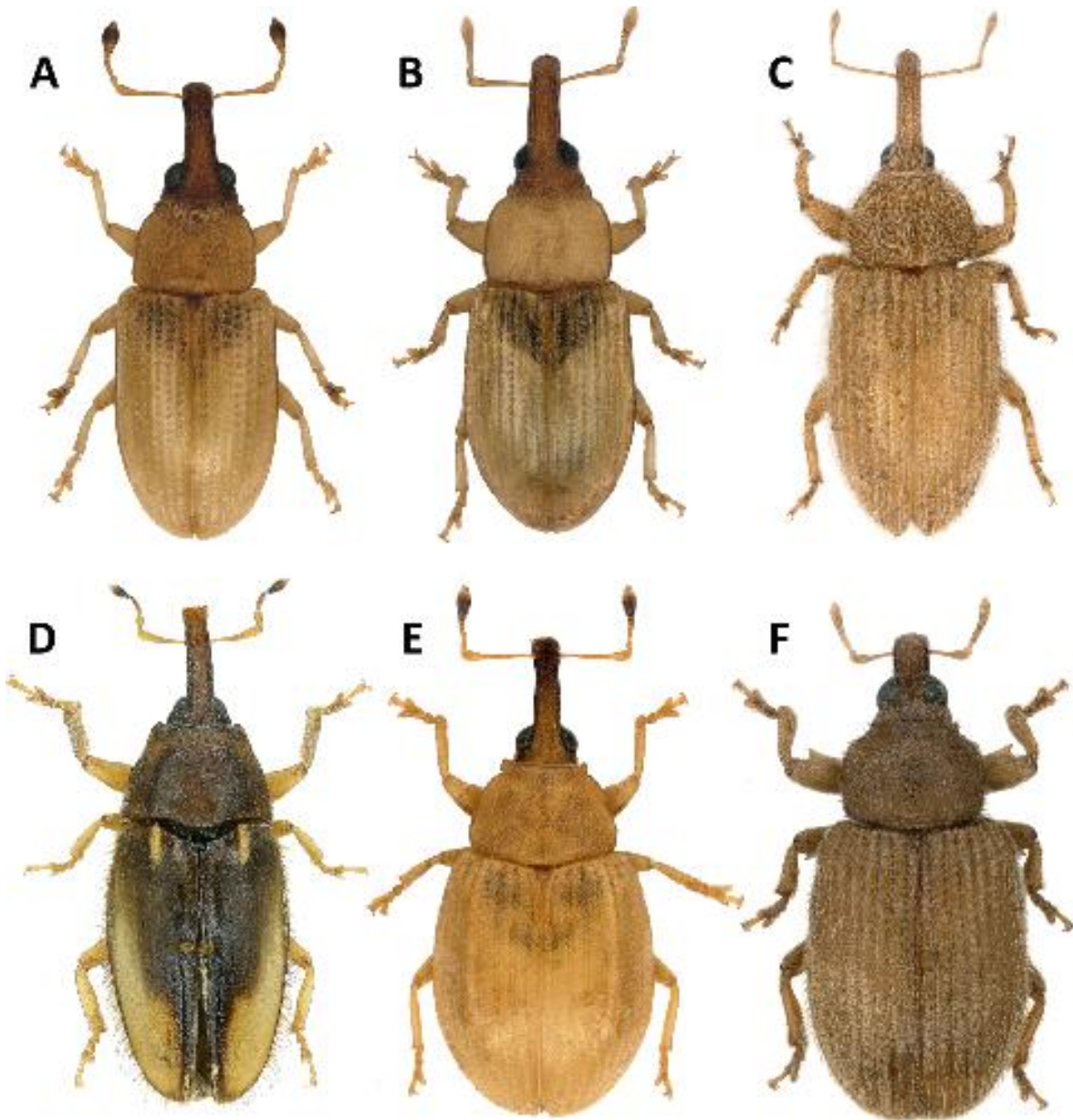
486 Like plants involved in BSPM, weevil pollinators display a series of morphological,
487 physiological and behavioral features that may constitute adaptations to pollination
488 mutualisms. Weevil pollinators have been less studied than the plants they pollinate, so not
489 only their shared morphological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

493
494 Known weevil species involved in BSPM are **small-sized beetles**, with body size
495 ranging from a few millimeters to about one centimeter (1.1 mm, *Staminodeus inermis*
496 (Franz 2001); 8.6 mm in *Anchylorhynchus burmeisteri* (de Medeiros & Vanin 2020), rostrum
497 excluded). Body shape is often consistent with floral morphology; for example, the body of
498 weevils associated with cycads in Belidae and Brentidae is very flat and allows individuals to
499 enter the cracks of megasporophylls. In most species, the body colors are **pale yellow,**
500 **reddish or brown**; they usually match the color or shape of their floral substrates, probably
501 to limit predation (Figures 3, 4). The matching colors are either obtained due to the color of
502 the integument itself (e.g., in *Andranthobius*, *Cotithene*, *Derelomus*, *Ebenacobius*,
503 *Elaeidobius*, *Prosoestus*) or due to the colors of the integument and scales covering it (e.g.,
504 in *Anchylorhynchus*; Valente & da Silva 2014; de Medeiros & Vanin 2020; Haran et al. 2020,
505 2022a). In some species, the shape of the elytra forms an angled surface mimicking the
506 shape of the petals of the host plant (e.g., *Derelomus subcostatus*, *D. costiger* and *D.*
507 *piriformis*; see Figure 4E). Overall, there seems to be a selective pressure to mimic floral
508 substrates as suggested by the various examples of strongly converging phenotypes among
509 unrelated species associated with the same host plant (e.g., *Derelomus pallidus* and
510 *Ebenacobius rectirostris* on *Euclea racemosa*; Haran et al. 2022b; Figure 4A, B), but
511 whether these phenotypes really provide an advantage in escaping predation has not been
512 formally explored. Interestingly, patterns of mimicry are generally found in species active
513 during the day on inflorescences, with little or no space to hide (i.e. most Derelomini
514 associated with Arecaceae or Ebenaceae). Conversely, in weevil lineages that remain
515 hidden in floral chambers or inflorescences during the day, the integuments are usually pale
516 brown or reddish in color, and they do not specifically match floral substrates (e.g., in
517 *Cyclanthura*; Ochyromerini; Figure 4C, F). Notable exceptions to this pattern include
518 *Montella* weevils (Baridinae), which exhibit a dark body integument contrasting with the color
519 of its host's flowers (Nunes et al. 2018) and some species of *Anchylorhynchus* weevils with
520 extreme polymorphism showing disruptive patterns such as black and yellow stripes (de
521 Medeiros & Vanin 2020).

522
523 A series of putative pollen-carrying morphologies are found in weevils engaged in
524 BSPM. Most of these lineages have species with **erect setae** on their body surface (Haran
525 et al. 2020, 2022a; Dao et al. 2023). Hair or scale cover on the integument are widespread in
526 weevils, so these may represent instances of exaptation. However, their peculiar size or
527 arrangement in some lineages acting as brood-site pollinators led to suggestions that they
528 may improve pollen transport (Syed et al. 1982). The erect setae can cover the entire body
529 surface (in Ochyromerini or in some *Ebenacobius* and *Celetes*; Valente 2005; Ratnayake et
530 al. 2006; Haran et al. 2022b; Figure 4C, F), or form combs on the edge of the elytra (in some
531 *Elaeidobius*; Figure 4D), or on the tibiae (in some *Derelomus*); setae may also be found on

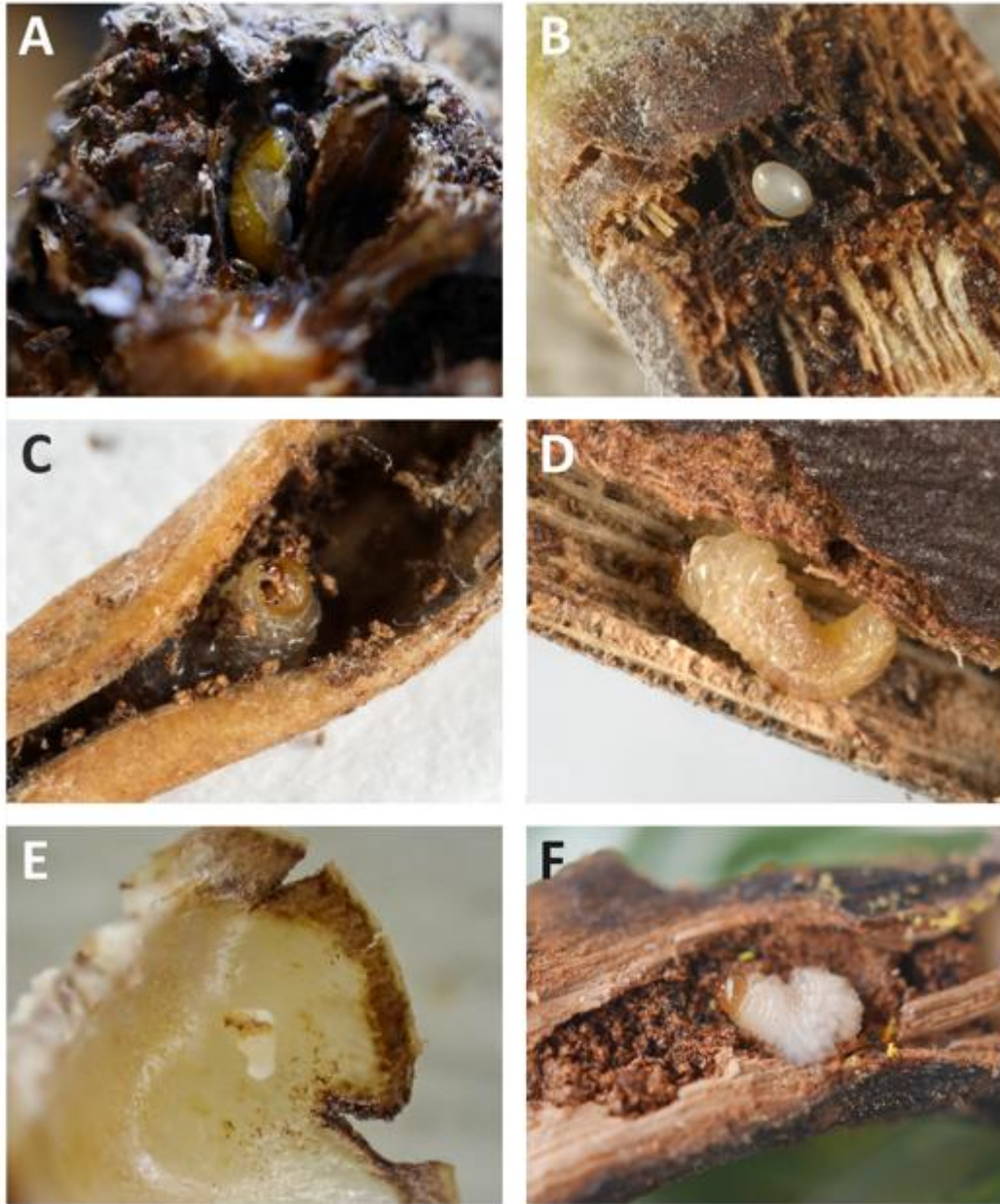
532 the ventral region (in some *Elaeidobius* and *Anchylorhynchus*). In *Anchylorhynchus*, a genus
533 that breeds on female flowers and thus may benefit directly from pollination, these ventral
534 setae may be highly branched in some species, reminiscent of setae found in bee corbiculae
535 (de Medeiros et al. 2019; de Medeiros & Vanin 2020). Interestingly, in some weevil species,
536 the presence of setae is a dimorphic feature, with only males exhibiting long setae,
537 suggesting that they may play a differential role in pollen transport (Haran et al. 2020; Hsiao
538 & Oberprieler 2022). That said, even weevil species without specific setae (e.g., *Derelomus*
539 *chamaeropsis*, *Andranthobius* spp., Baridinae and Belidae) are known to be effective
540 pollinators (Anstett 1999; Nunes et al. 2018; Salzman et al. 2020; Carreño-Barrera et al.
541 2021), suggesting that integuments alone can efficiently transport pollen. Several unrelated
542 lineages of weevils engaged in BSPM also exhibit prosternal processes or tubercles (in
543 *Andranthobius*, *Diplothemibius*, *Ebenacobius*, *Elaeidobius*, *Miltotranes*, *Porthetes*,
544 *Prosoestus*, *Tranes*; Bondar 1941; Valente & da Silva 2014; Haran et al. 2020, 2022a; Hsiao
545 & Oberprieler 2022; Haran pers. obs.) consisting of cuticular apophyses located near the
546 procoxae of males. In some Baridinae not involved in BSPM, such structures grow
547 allometrically and have been shown to be used in interspecific fights to dislodge competing
548 males (Eberhard & Garcia 2000; Eberhard et al. 2000; Davis & Engel 2010). Since fights
549 between males have been described in Derelomini (Franz 2003, 2006), it can be postulated
550 that these prosternal processes or tubercles probably have a similar function for the
551 aforementioned genera. Finally, in some weevil lineages, structural complexity and dense
552 cover of setae in these structures have been hypothesized to possibly improve pollen
553 transport (see Hsiao & Oberprieler 2022). It is not known why the weevils evolved these
554 pollen-carrying structures, except in the rare cases where the weevils directly benefit from
555 the pollination of their hosts. Indeed, there are only two known cases where weevils breed
556 on tissues that result from their direct pollination: in the genus *Montella* (Nunes et al. 2018)
557 and in the genus *Anchylorhynchus* (de Medeiros & Vanin 2020). *Montella* weevils display
558 active pollination behavior (carrying orchid pollinaries; Nunes et al. (2018), which is
559 consistent with other cases of specialized pollinating seed predators such as fig-wasps
560 (Jousselin et al. 2003) and yucca moths (Pellmyr 1997). For *Anchylorhynchus* the evidence
561 is more ambiguous; females rub their bodies against female flowers after oviposition, but it
562 remains to be shown whether this behavior serves to mark oviposition and avoid
563 competition, increases the likelihood of pollen deposition, or both (de Medeiros et al. 2014).

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Figure 4. Dorsal habitus 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 curvistetis* (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).

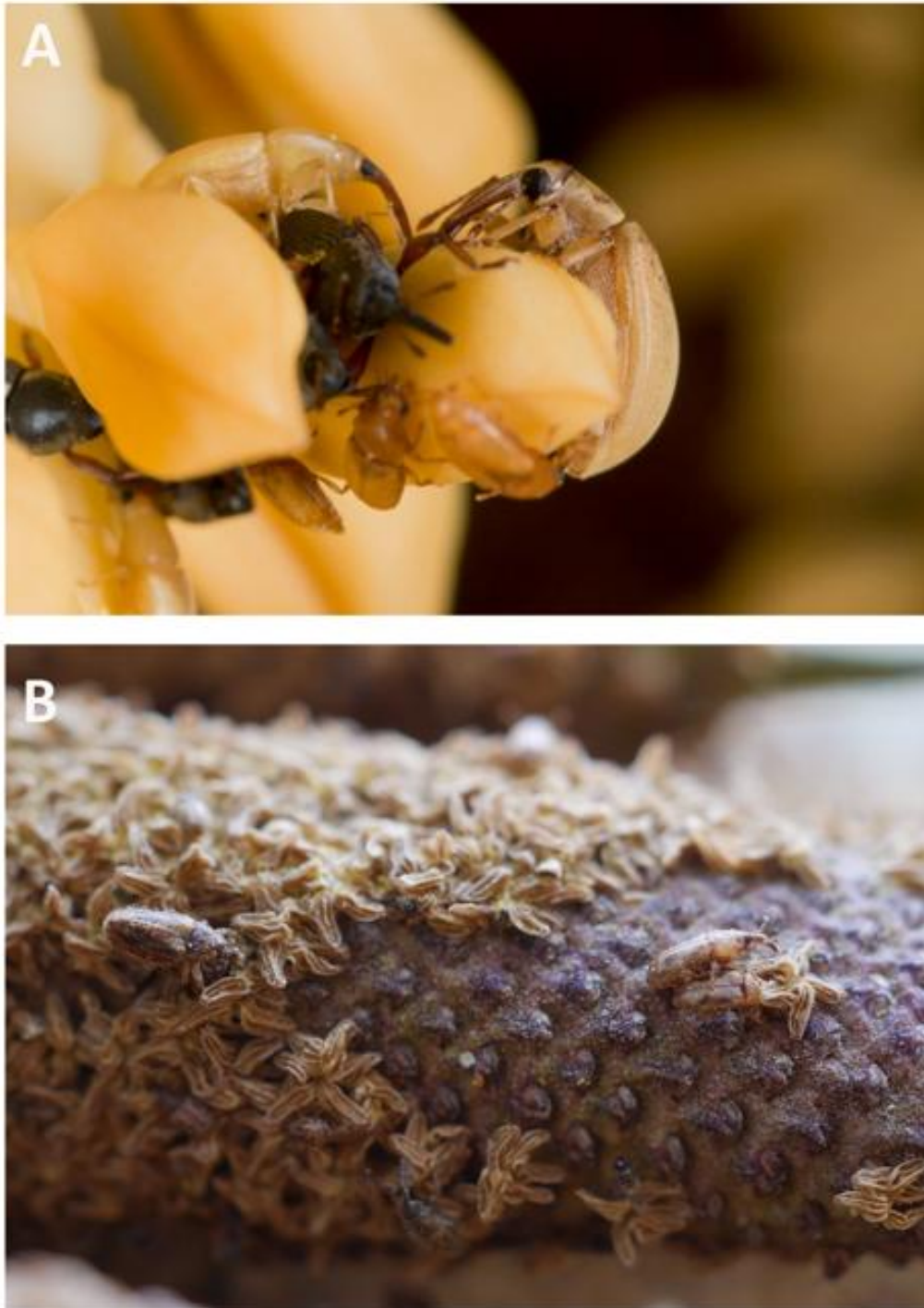


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577 **Figure 5.** Breeding sites of weevils engaged in BSPM. **A.** Pupa of *Elaeidobius plagiatus* (Derelomini) in flower
 578 capsules of male inflorescences of *Elaeis guineensis* (Arecaceae). **B.** Egg of *Phytotribus platyrhinus* (Derelomini)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

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586

587 **Figure 6.** Example of sympatric species assemblage of weevils of a host including species from other beetle
 588 lineages. **A.** Inflorescence of *Syagrus coronata* (Arecaceae) with *Anchylorhynchus trapezicollis* (Derelomini, top
 589 right), *Andranthobius bondari* (Derelomini, top left), *Microstrates ypsilon* (Baridinae, black weevils) and sap
 590 beetles (Nitidulidae, *Mystrops palmarum*). **B.** Inflorescences in anthesis of *Elaeis guineensis* (Areaceae) with
 591 multiple specific pollinators including weevils (*Elaeidobius plagiatus* (left), *E. piliventris* (right) and *E. subvittatus*
 592 (bottom left), Derelomini). (credits: A: B. de Medeiros, B: J. Haran).

593

594 Weevils engaged in BSPM likely have good **flight abilities**, which allow them to fly
 595 actively between inflorescences of distant hosts ([Auffray et al. 2017](#); [Lau et al. 2017](#);

596 [Saunders 2020](#); [Toon et al. 2020](#)). This is supported by experimental data in other small
597 weevils, which are capable to fly up to kilometers in flight mills ([McKibben et al. 1998](#);
598 [Evenden et al. 2014](#)) and by our own experience in collecting specimens on isolated hosts,
599 suggesting that they can move over long distances (J. Haran and B. de Medeiros pers.
600 obs.). Moreover, unlike social insects such as bees, the home range of pollinator weevils is
601 not constrained by the location of a nest. Adult weevils feed on pollen or nectar produced by
602 flowers ([de Medeiros et al. 2014](#); [Lau et al. 2017](#); [de Medeiros et al. 2019](#)) but also often on
603 floral structures themselves (*Elaeidobius*, *Ebenacobius*, *Endaeus*; [Haran et al. 2022a](#); [Dao](#)
604 [et al. 2023](#)). The active behavior of adults is not surprising, since weevils **respond well to**
605 **host specific floral volatiles**. This has, for example, been demonstrated in several cycad
606 specialists, with electroantennography experiments and pheromone traps ([Salzman et al.](#)
607 [2021](#)). Several weevil lineages have also developed specific olfactory globules in their
608 antennae which are considered to be adaptations for the detection of these volatiles
609 ([Crowson 1991](#); [Oberprieler 2004](#)). Following olfactory stimuli, weevils can reach or leave
610 the flowers and inflorescences of their hosts, according to circadian cycles remarkably
611 synchronized with flowering cycles ([Franz 2007a](#); [Auffray et al. 2017](#); [Mendeléz-Jácome et](#)
612 [al. 2019](#); [Saunders 2020](#); [Salzman et al. 2021](#)). The weevil's reaction to a volatile can be
613 concentration-dependent, with the same molecule acting as either an attractant or a
614 repellent depending on the amount emitted from the floral structures. This change in
615 behavior in turn creates a push-pull effect enhancing their movement between flowers and
616 therefore pollination ([Franz 2007a](#); [Salzmann et al. 2021](#)). When floral structures do not
617 produce peaks of volatiles (the so-called 'interim' phase'; [Saunders 2020](#)), weevils may
618 simply remain on the inflorescences (in cycads and palms; [Auffray et al. 2017](#); [de Medeiros](#)
619 [et al. 2019](#); [Toon et al. 2020](#)), be hidden or trapped there (in Araceae and Annonaceae;
620 [Franz 2007b](#); [Saunders 2020](#); [Dao et al. 2023](#)), or leave inflorescences ([Ratnayake et al.](#)
621 [2006](#); [de Medeiros et al. 2019](#)). In the genus *Ebenacobius*, many species have only been
622 collected from the leaf litter during the day, which suggests that they hide there between
623 their crepuscular and night phases of movements ([Haran et al. 2022a](#)). Weevils are fairly
624 long-lived insects, with an adult lifespan of up to 79 days (mean 31 days) in *Elaeidobius*
625 *subvittatus* ([Syed et al. 1982](#)). As the anthesis of the host inflorescence lasts only a few
626 hours or a few days (five days in the case of *Elaeis guineensis*), the same individual can visit
627 many flowers or inflorescences during its lifespan.

628
629 The **larval stages** of weevils **develop on the various types of substrates** provided
630 by their hosts. In all the weevil lineages engaged in BSPM, the larvae are generally
631 endophagous, developing either in live tissues or as detritivores on decaying plant material,
632 in more or less woody tissues (Figure 5; [Anstett 1999](#); [Franz 2007a,b](#); [Nunes et al. 2018](#);
633 [Toon et al. 2020](#); [Dao et al. 2023](#)). In Ebenaceae, which have small individual flowers, larvae
634 of pollinators are ectophagous and feed at the base of the anthers ([Haran et al. 2022a](#)). In
635 *Anchylorhynchus*, eggs are deposited externally between petals (Figure 5E) and first instars
636 drill into female flowers to continue their development internally ([de Medeiros et al. 2014](#)).
637 When larvae feed on limited spaces such as individual flowers or fruits, some species have
638 developed a cannibalistic behavior (Figure 5E) and morphology to cope with a potential
639 overpopulation in the brood site ([de Medeiros et al. 2014](#)). For most plant-weevil BSPM, the
640 interplay between the presence of secondary compounds in plant tissues and a potential
641 adaptation of associated weevil lineages has not been yet investigated, although they may
642 drive specialization patterns ([Wang et al. 2021](#)). For example in weevils associated with

643 cycads (Belidae), the larvae of some species have been found associated with specific
644 bacteria involved in the control of toxic compounds from their host (Salzman et al. 2018).
645

646 **2.3 Evolutionary trends**

647 **2.3.1 Larval host specificity**

648 The vast majority of weevils engaged in brood-site pollination appear to be strictly
649 monophagous as larvae (Franz & Valente 2005; de Medeiros & Núñez-Avellaneda 2013;
650 Valente & de Medeiros 2013; Toon et al. 2020; de Medeiros & Farrell 2020; de Medeiros &
651 Vanin 2020; Haran et al. 2021; Hsiao & Oberprieler 2022). Such a level of specialization is
652 rare for weevils and phytophagous insects in general, even when considering other groups
653 of endophagous feeders, which are known to be generally highly specialized (e.g., Gaston et
654 al. 1992; Anderson 1993; Bernays & Chapman 1994; Kergoat et al. 2008, 2018). One of the
655 most striking case reflecting this host specificity is the pollination ecology of sympatric palms
656 belonging to the genus *Oenocarpus* in the Amazon (Núñez-Avellaneda et al. 2015). The
657 three species studied have a very similar floral structure and phenology, but each has a
658 specific assemblage of weevil pollinators, only a few of which are able to visit several
659 *Oenocarpus* species. Also, in *Montella* weevils actively pollinating *Dichaea cogniauxiana*,
660 adults visit the flowers of another orchid species (*D. pendula*), but can only complete their
661 life cycle in the former due differences in self-compatibility of the reproductive system
662 (Nunes et al. 2016). Cases of oligophagy or polyphagy in weevil pollinators have been
663 suggested in several systems based on general observations of inflorescences visitors, but
664 these have never been formally tested (Franz & Valente 2005; Ratnayake et al. 2006;
665 Saunders 2020). In the Annonaceae – Ochyromerini system, a species of *Endaeus* has
666 been identified as the pollinator of two congeneric and sympatric *Polyalthia* species
667 (Ratnayake et al. 2006). In the Araceae – Derelomini and Cyclanthaceae – Derelomini
668 systems, a few intriguing cases of oligophagy or even polyphagy have been reported for
669 weevil species acting as effective pollinators (Franz & O'brien 2001a,b; Franz 2006, 2007);
670 however, most of these accounts should be viewed with caution as they are based on
671 observations of adult stages only. Weevils can be slightly eclectic in the selection of flowers
672 visited at the adult stages (Haran et al. 2022a) and over-interpretation of these visits can
673 lead to erroneous conclusions about larval host specificity. The complexity of the host plant
674 taxonomy can also make it difficult to interpret historical records and blur patterns of host-
675 associations (de Medeiros & Vanin 2020). All of this highlights that understanding the level of
676 species-specificity in these systems is primarily hampered by the lack of actual host plant
677 data for the larval stages (Franz 2004). More generally, integrative and detailed studies are
678 needed to accurately assess plant-weevil BSPM interactions. All detailed studies of host
679 plant associations using molecular data have found a higher than previously thought weevil
680 diversity and a very high degree of specialization on their hosts (Downie & Williams 2009;
681 Brookes et al. 2015; de Medeiros & Farrell 2020; Haran et al. 2021).

682 2.3.2 Sympatric species assemblages

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

689 With respect to weevil specialists, plants involved in BSPM are often pollinated by
690 diverse multi-species assemblages of weevil pollinators living in sympatry (Figures 3F, 6;
691 Hotchkiss 1958; Ervik et al. 1999; Franz & Valente 2005; Núñez-Avellaneda et al. 2015; de
692 Medeiros et al. 2019; Saunders 2020; Toon et al. 2020; Haran et al. 2021; 2022b; Auffray et
693 al. 2022; Dao et al. 2023). A remarkable aspect of these assemblages is their stability over
694 the range of their hosts (Núñez-Avellaneda et al. 2015; de Medeiros et al. 2019; Haran et al.
695 2020), in stark contrast to other brood-site pollination systems (Jousselin et al. 2008;
696 McLeish & van Noort 2012). Sympatric weevil assemblages may coexist on the same host
697 as they often develop on distinct ecological niches such as male or female inflorescences,
698 as observed in the genera *Elaeidobius* and *Prosoestus* on *Elaeis guineensis* (Syed 1979;
699 Alibert 1938) or in several cycad-associated weevils (Toon et al. 2020). Niche partitioning
700 can also be observed within monoecious inflorescences, either on different tissues (de
701 Medeiros et al. 2019; Figure 6) or in relation to distinct phenological anthesis stages (Haran
702 et al. in prep.). Unexpectedly, these sympatric multi-species assemblages have been
703 described in all plant-weevil mutualism systems, suggesting that they may be the rule rather
704 than the exception. The prevalence of these assemblages seems specific to weevil
705 pollinators; in other BSPM systems such as the fig/fig-wasp model, instances of multispecific
706 assemblages of pollinators are only reported in about 10% of associations (Cruaud et al.
707 2012), even though usage of molecular data for wasp species delimitation has been
708 increasing this number (Satler et al. 2022; Su et al. 2022). In comparison with other brood-
709 site pollinator systems, weevils also present the greatest diversity of congeneric species
710 associated with the same host: this is the case of the African oil Palm (*Elaeis guineensis*),
711 which hosts no less than eight species of *Elaeidobius* on its male inflorescences (Compton
712 et al. 2009; Haran et al. 2020a, 2021; Figure 6B). The exact role of these assemblages is not
713 yet elucidated and several potential evolutionary processes have been proposed to explain
714 their emergence. A first process is the lineage duplication induced by the fragmentation of
715 the host range in relation to past environmental changes (such as climate oscillations),
716 followed by the reconnection of host populations. This case has been highlighted in the
717 *Elaeis*-derelomine system where past cycles of fragmentation of *Elaeis guineensis*
718 populations into the upper and lower Guinean forest blocks would have led to the
719 diversification of *Elaeidobius* and *Prosoestus* species (Haran et al. 2021). When populations
720 reconnect after isolation, differences in generation times between the host plant and its
721 pollinators appear to allow palm populations to exchange genes again while weevil
722 populations are already too divergent and already correspond to distinct species. A second
723 process results from independent past colonizations (historical host shifts) of a host by
724 multiple lineages of weevils. This process is suggested by the structure of sympatric
725 assemblages themselves, where weevil species in an assemblage belong to distinct and
726 phylogenetically unrelated genera (Franz 2007a; de Medeiros et al. 2019; Toon et al. 2020;

727 [Haran et al. 2022b](#)). Interestingly these two processes are not mutually exclusive, as
728 underlined by the example of the weevil community associated with the inflorescences of
729 *Phoenix reclinata* (Arecaceae). Here, lineage duplication and independent colonizations led
730 to the emergence of a sympatric assemblage of six species of brood-site pollinators ([Haran
731 et al. 2022b](#)).

732 In plant-weevil BSPM, multi-species assemblages are not limited to weevils but also
733 include a range of insects of various orders that develop on host inflorescences ([Desmier de
734 Chenon 1981](#); [Búrquez et al. 1987](#); [Ervik et al. 1999](#); [Gottsberger 1999](#); [Núñez-Avellaneda
735 et al. 2015](#); [de Medeiros et al. 2019](#); [Toon et al. 2020](#); [Auffray et al. 2022](#)). It is very common,
736 for example, that weevil-pollinated plants are also visited by sap beetles (Nitidulidae, Figure
737 6A). In Annonaceae they belong to the genus *Carpophilus*, in Arecaceae the most common
738 genera are *Carpophilus*, *Microporum* and *Mystrops*, in cycads they belong to the genus
739 *Carpophilus*, and in Cyclanthaceae they belong to the genus *Mystrops* ([Desmier de Chenon
740 1981](#); [Knudsen et al. 2001](#); [Núñez-Avellaneda et al. 2005](#); [Ratnayake et al. 2006](#); [Franz
741 2007a](#); [Núñez-Avellaneda et al. 2015](#); [Toon et al. 2020](#)). Sap beetles range from the most
742 important pollinators in some plants to negligible in others ([Ratnayake et al. 2006](#); [Núñez-
743 Avellaneda et al. 2015](#); [Lau et al. 2017](#); [de Medeiros et al. 2019](#); [Toon et al. 2020](#); [Carreño-
744 Barrera et al. 2021](#)). Indeed, the patterns observed in cycad-associated brood-site
745 pollinators show that sap beetles, but also certain lineages belonging to other families of
746 beetles (Boganiidae, Erotylidae and Tenebrionidae) or even other orders of insects
747 (Lepidoptera and Thysanoptera) may have become brood-site pollinators of cycads ([Toon et
748 al. 2020](#)). It is therefore not surprising that species of various groups of insects have
749 independently colonized the same host and co-exist on it. In palms, multi-species
750 assemblages sometimes even include generalist insects that have also been identified as
751 pollinators. In some cases, bees are the most important pollinators with weevils being
752 accessory ([Núñez & Carreño, 2017](#); [Bezerra et al. 2020](#)), but more commonly generalist
753 pollinators play a minor role ([Desmier de Chenon 1981](#); [Núñez-Avellaneda et al. 2015](#); [de
754 Medeiros et al. 2019](#)). The latter echoes the fact that, whenever weevils are involved in
755 these diverse assemblages, they generally play a predominant role in host pollination
756 ([Desmier de Chenon 1981](#); [Ratnayake et al. 2006](#); [Núñez-Avellaneda et al. 2015](#); [Toon et al.
757 2020](#)). The precise role of these secondary pollinators (brood site or not) is not clear, but a
758 reduction of extinction risk by limiting dependence on a specialized mutualist has been
759 suggested ([Silberbauer-Gottsberger 1990](#); [Chomicki et al. 2020](#)).

760 **2.3.3 Cryptic and closely related weevil species**

761 The evolution of plant-weevil BSPM is a dynamic system with many instances of recent or
762 ongoing speciation processes. This trend was first suggested thanks to the results of several
763 morphological studies, which revealed that BSPM weevil genera often consist of diverse
764 closely related species ([Oberprieler 1996](#); [Oberprieler 2004](#); [Valente 2005](#); [Franz & Valente
765 2005](#); [de Medeiros & Vanin 2020](#); [Hsiao & Oberprieler 2022](#)). This trend has been confirmed
766 by molecular studies, which have revealed additional layers of hidden diversity in the form of
767 cryptic and closely related species often co-occurring on a single host ([Downie & Williams
768 2009](#); [Brookes et al. 2015](#); [Nunes et al. 2018](#); [de Medeiros & Farrell 2020](#); [Haran et al. 2021,
769 2022b,b](#)). All of these cryptic and closely related weevil species (Table S1) likely reflect
770 recent speciation events. For example, dating analyses from two recent molecular studies
771 have recovered numerous instances of recent speciation events (1.2 to 0.2 Mya old), which

772 may be associated with recent changes in paleoenvironments (Haran et al. 2021, 2022b).
773 Morphological features enabling to distinguish these closely related species include subtle
774 differences such as the location and size of certain setae on the male ventrites, the
775 arrangement of setae on the elytra or the ratios on the male genitalia. The repeated
776 occurrence of these cases of cryptic and closely related species highlight the need for
777 detailed taxonomic studies to properly estimate the levels of specificity of plant-weevil BSPM
778 systems.

779 **2.3.4 Trade offs in cost-benefit of interactions**

780 The balance between costs and benefits in plant-weevil BSPM interactions has been
781 investigated in several systems (e.g., Dufay & Anstett 2004; Franz 2004; Franz & Valente
782 2005; Nunes et al. 2018; Saunders 2020; Toon et al. 2020). Plants engaged in BSPM with
783 weevils require cross-pollination for a large fruit set. Therefore, a major pressure they have
784 experienced is pollen limitation, linked to inadequate pollen quality and/or quantity (Franz
785 2007a; Nunes et al. 2018), a widely observed condition for tropical flora (Tremblay et al.
786 2005; Wolowski et al. 2014). Under this pressure, the advantage of having specialized
787 pollinators is believed to be high (Silberbauer-Gottsberger 1990), especially in the
788 understory where small plants do not compete well for generalist pollinators because their
789 floral displays are less conspicuous (Turner 2001). The benefit to the plant is clear when
790 weevils develop only on male flowers or on non-reproductive tissues (e.g., live or decaying
791 stems, bracts and petals), and therefore do not affect propagule production (Dufay & Anstett
792 2003; Dao et al. 2023). This case is widely encountered in “pollination by deceit” systems
793 (Dufay & Anstett 2003) described in many palms (Arecaceae), where adult weevils search
794 for male inflorescences where development of larval stages take place but are misled by
795 female inflorescences producing similar attractants but no rewards. Such a benefit is,
796 however, less evident when the flower buds or seeds are destroyed during the larval
797 development of the weevils, and sometimes it even results in a sharp reduction in the fitness
798 of the host. For example, brentids in the genus *Antliarhinus* are ovule parasites that can
799 destroy up to 80% of the seeds of their cycad host *Encephalartos*. Despite this damage, it
800 has been shown that adults contribute up to 10% to the cross-pollination of their host
801 (Donaldson 1997). Similarly, the main pollinator of the palm *Syagrus coronata* is a specialist
802 weevil of the genus *Anchylorhynchus* (Derelomini), which are known to be seed predators
803 (de Medeiros et al. 2019). However, it has been recently shown that there is variation in the
804 genus, with some species only being able to develop on aborted female flowers and
805 therefore harmless to the plant (de Medeiros 2022 in press). Studies on these peculiar cases
806 can reveal why such costly pollination systems are maintained when less costly ones,
807 involving other specialist or generalist pollinators, are potentially available and how
808 interactions evolve along the mutualism-antagonism spectrum (Fenster et al. 2004; de
809 Medeiros et al. 2019).

810

811 In some cases, the detrimental effect of the larval development of weevil pollinators
812 is mitigated by specific plant adaptations. In the dwarf palm (*Chamaerops humilis*), the
813 process associated with fruit development leads to the termination of larval development on
814 female inflorescences of *Derelomus chamaeropis*. Thus, the maintenance of the populations
815 of this obligate pollinator relies solely on male inflorescence tissues, with no impact on seed
816 sets (Dufay & Anstett 2004). Control of the detrimental effects of larval development may
817 also include other organisms. For example, in the orchid *Dichaea cogniauxiana*, pollination

818 depends heavily on the activity of a baridine weevil developing as an ovule parasite.
819 Normally, about 20% of fruits are lost to weevil larvae, but the activity of a parasitic wasp
820 killing weevil larvae at an early stage can significantly reduce the fraction of seeds lost to the
821 weevil (Nunes et al. 2018). Such tripartite interactions involving a plant, a pollinator and a
822 parasitoid are probably overlooked, although they potentially play an important role in weevil-
823 based BSPM systems.

824

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

840 2.3.5 Evolutionary dynamics of host use

841 Since most of the plant groups actually associated with weevil brood pollinators are
842 categorized as ancient tropical lineages (Annonaceae, Araceae, Arecaceae, cycads,
843 Cyclanthaceae, Ebenaceae and Strelitziaceae; Franz & Valente 2005; Kress & Specht 2006;
844 Toon et al. 2020), extant plant-weevil associations have sometimes been assumed to be
845 ancient and possibly concurrent with the origin of plant lineages (Brenner et al. 2003;
846 Oberprieler 2004; Franz 2006). However, such a pattern has not been backed up by any
847 solid evidence, as all studies integrating knowledge of the fossil record and the results of
848 molecular dating analyses support the hypothesis that weevil brood pollinator lineages
849 began to diversify long after the origin of the plant lineages on which they specialize. For
850 example, the estimated origin of palm-specialists from the Derelomini tribe (ca. 40 Mya;
851 Haran et al. 2022b) significantly postdate the well-documented appearance of palms ca. 100
852 Mya (Baker & Couvreur 2013). Likewise, the phylogenetically diverse lineages of weevils
853 that shifted on cycads (Oberprieler 2004) colonized them relatively recently (Downie et al.
854 2008; Hsiao & Oberprieler 2022), well after their origin more than 250 Mya (Condamine et al.
855 2015).

856 Weevils show a marked pattern of phylogenetic niche conservatism for the specific
857 plant lineages they pollinate. Consistency of association with plant clades is observed at the
858 tribe, genus or species-group level (Franz & Valente 2005; de Medeiros & Vanin 2020;
859 Haran et al. 2021, 2022b; Figure 1). This consistency is particularly strong at the genus level
860 for BSPM interactions (Table S1). In other words, when a BSPM interaction is established
861 for a weevil species, it is very likely that congeneric species are also involved in such an
862 interaction. An exception to this pattern has been reported in the genus *Cotithene*

863 (Derelomini) associated with *Evodianthus* (Cyclanthaceae) in Amazonia: only one weevil
864 species in this genus is a brood site pollinator., Congeners visiting this cyclanth are not
865 engaged in such relationship due to a size mismatch with the host flower morphology
866 (Valente et al. 2019).

867 Unlike other brood-pollinators, weevils display a remarkable ability to shift to
868 unrelated plant lineages at various evolutionary scales. A striking example of this pattern is
869 seen in eastern hemisphere Derelomini with two parallel instances of secondary shifts from
870 palms (Arecaceae) to Ebenaceae (genus *Euclea*; Haran et al. 2022b). Interestingly, such
871 secondary shifts did not necessarily constitute evolutionary dead ends since they are
872 sometimes followed by lineage diversification and even additional secondary shifts (Haran et
873 al. 2022b). Other notable examples of host shifts include the parallel and independent
874 colonization of the closely related palms *Elaeis guineensis* and *Elaeis oleifera* by two distinct
875 lineages of derelomine weevils (Haran et al. 2021) and the independent colonization of the
876 legume tree *Baikiaea insignis* (Fabaceae) by both Ochyromerini (two species of *Endaeus*)
877 and Derelomini (*Lomederus ghesquierei*) (Marshall 1932, 1933). Overall, the evolutionary
878 pattern of host use in weevils engaged in BSPM is much more dynamic than what is
879 reported in other brood pollinators systems (Pellmyr 2003; Herre et al. 2008) and thus
880 reinforces the interest of using weevils as an additional model system to investigate
881 evolutionary dynamics of pollination mutualism in the tropics (Haran et al. 2022b).

882 3. Economic importance and conservation

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

891
892 Many weevil pollinated palms are an important source of food, goods and building
893 materials (e.g., *Acrocomia*, *Cocos*, *Euterpe*, *Oenocarpus*, *Phytelephas*, *Syagrus*; Núñez-
894 Avellaneda et al. 2015; de Medeiros et al. 2019; Bezerra et al 2020; Carreño-Barrera et al
895 2021; Auffray et al. 2022). In tropical and subtropical regions, wild fruits and leaves of
896 Annonaceae (e.g., *Annona senegalensis*), Clusiaceae (e.g., *Pentadesma butyracea*) and
897 Fabaceae (e.g., *Piliostigma reticulatum*) for which pollination by weevils is indicated based
898 on PNC are commonly consumed by local populations or have a cosmetic or medical use
899 (e.g., Babajide et al. 2008; Traoré et al. 2011; Dao et al. 2023). In cycad lineages primarily
900 pollinated by weevils (Toon et al. 2020), the high ornamental and subsequent economic
901 value of many cycad species has also led to over-collection (Mankga & Yessoufou 2017). In
902 these groups, reproductive failure, among habitat loss and medicinal use, has been
903 identified as one of the main drivers of population decline, highlighting the importance of
904 detailed investigations of their pollination ecology. More generally, while plant-weevil BSPM
905 probably emerged to balance some pollination constraints in tropical biomes, it is also a risky
906 evolutionary path if the specialized pollinators become rare or extinct. Yet too little is known

907 about the impact of pollinator population dynamics on the reproductive success and long-
908 term survival of the plants involved (Toon et al. 2020).

909 4. Oversights and estimates of global richness

910 4.1 The inconspicuousness of plant-weevils pollination 911 interaction

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

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

938 Second, the inconspicuous nature of many interactions hampered and slowed down
939 the discovery of several plant-weevil BSPM interactions. For example, in the case of the
940 Annonaceae – *Endaeus* mutualisms, the flowers are isolated and therefore the interactions
941 are thus far less conspicuous. In these systems, weevils typically reach flowers in very low
942 numbers, sometimes at a very specific time of the circadian flowering cycle (early in the
943 morning or late in the evening), and may be hidden or “enclosed” in floral chambers during
944 most of the day (Ratnayake et al. 2006; Lau et al. 2017; Saunders 2020) or present on the
945 flower only at night and notably absent during the day (Ratnayake et al. 2006). When not
946 enclosed in flowers, *Endaeus* weevils and related weevil genera are usually collected while
947 flying over the canopy (Kojima & Morimoto 1995; Sprick and Florent 2018), using light traps

948 (Kojima & Morimoto 1995; Haran et al. 2022a) or by beating plants only used as shelters,
949 generally in low numbers (Kojima & Morimoto 1995). Therefore, unraveling BSPM
950 interactions between weevils and their host plants is usually a difficult task. To illustrate this
951 point, a striking example of inconspicuous interactions is found in the *Anthurium* (Araceae) /
952 Derelomini mutualism. In this system, only a few individuals of the derelomine *Cyclanthura*
953 *carinata* reach *Anthurium* inflorescences at night during the 1-2 weeks of anthesis, and
954 further remain hidden in areas protected by the spathe, leaving the inflorescences
955 apparently empty. This inconspicuousness probably explains why this obligate pollination
956 mutualistic system has been overlooked for decades (Franz and Valente 2005; Franz
957 2007b).

958 **4.2 An underestimated diversity of species and** 959 **interactions**

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

965 For example, host plant identity information is available for most Neotropical
966 derelomine genera (Franz & Valente 2005). By comparison, host records are only available
967 for five of the 13 Paleotropical genera of Derelomini (Alonso-Zarazaga & Lyal 1999; Franz &
968 Valente 2005). The estimated number of derelomine species overall (ca. 300 species;
969 Caldara et al. 2014; de Medeiros & Vanin 2020; Haran et al. 2020, 2022a) pales in
970 comparison with the diversity estimates of their main hosts, because the species diversity in
971 the palm family (Arecaceae) is estimated at about 2500 species (Dransfield et al. 2008;
972 Baker & Couvreur 2013). Since pollination ecology and pollinators have only been identified
973 for a small fraction of extant palm species, we can hypothesize that dozens – if not hundreds
974 – of palm-weevil BSPM systems remain to be discovered. Additionally, even though
975 Derelomini are best known for their associations with palms, recent research has unraveled
976 that some of them are also associated with plants other than palms. For example, in the
977 Southern African derelomine fauna, the recently described genus *Ebenacobius* has been
978 found associated with Ebenaceae and other basal angiosperms. In this genus, no less than
979 14 new species have been recently described (Haran et al. 2022a) and at least four others
980 are awaiting description. Moreover, based on the inferred pattern of PNC in BSPM weevils,
981 Franz & Valente (2005) and Franz (2006) suggested that most of the ca. 230 species of
982 Carludovicoideae (Cyclanthaceae) and a significant part of the ca. 800 known *Anthurium*
983 (Araceae) species in the Neotropical region are pollinated by derelomine weevils. In cycad-
984 weevil BSPM systems, the range of interactions reported here only reflects our current state
985 of knowledge, and many cycads species have been insufficiently studied and many
986 interactions remain to be described (Toon et al. 2020).

987 The general lack of knowledge on plant-weevil BSPM systems can be exemplified by
988 our understanding of Ochyromerini. Pollination activity in this tribe has been only reported
989 between a few species of *Endaenidius* and *Endaeus* and their Annonaceae hosts and BSPM
990 has been only formerly identified in one system (*Annona senegalensis* - *Endaeus* spp.; Lau

991 [et al. 2017](#); [Saunders 2020](#); [Dao et al. 2023](#)). Importantly, Ochyromerini has been
992 determined to be the dominant weevil guild circulating above the canopy in a Southeast
993 Asian dipterocarp forest ([Sprick & Floren 2018](#)), with over 130 undescribed ochyromerine
994 species recorded on Borneo island alone. Similar species richness was also observed in
995 Cameroon using light traps (Haran unpublished). Finally, a multitude of undescribed
996 Ochyromerini species (mostly belonging to the genus *Endaeus*) have been reported by
997 several authors in Asia and Africa ([Hustache 1924](#); [Marshall 1926](#); [Oberprieler 1993](#);
998 [Momose et al. 1998](#)), and it can be suspected that this group could play an important role in
999 the pollination of Paleotropical rainforests.

1000 In the Annonaceae, a pantropical clade with more than 2400 species, cantharophily
1001 seems to be the most common pollination syndrome ([Momose et al. 1998](#); [Gottsberger
1002 1999](#); [Saunders 2020](#)). The Neotropical species in this plant family sum up to more than 950
1003 species ([Maas et al. 2011](#)), and it is in this region that cantharophilous flowers involving
1004 weevil pollination are the most widespread ([Gottsberger 1999](#); [Silberbauer-Gottsberger et al.
1005 2003](#); [Saravy et al. 2021](#)). This set of interactions requires further investigations in this
1006 region since the weevil lineages involved remain unidentified and possibly include
1007 undescribed lineages (the pollinators of Annonaceae reported (Ochyromerini) are
1008 exclusively paleotropical; [Alonso-Zarazaga & Lyal 1999](#)).

1009 Our general overview of weevil-based pollination shows that several additional
1010 pantropical families of angiosperms are – or at least can be considered as partially –
1011 pollinated by weevils (Table S1), with only a small fraction of these interactions having been
1012 uncovered so far. For example, in Clusiaceae, Ebenaceae, Lecythidaceae, Myristicaceae
1013 and Sapotaceae, BSPM by weevils have been only indicated for a small number of species;
1014 however there are likely many more of such interactions because cantharophilous flowers
1015 are known in several genera of these families and the associated weevil lineages also
1016 contain a significant number of undescribed species ([Oberprieler 1993](#); [Caldara et al. 2014](#);
1017 [Haran et al. 2022b](#)). In some cases, the weevil diversity also exceeds that of the known
1018 potential hosts; for example, 25 species of the Australian weevil genus *Elleschodes* are
1019 known ([Armstrong & Irvine 1990](#); [Caldara et al. 2014](#); [Pullen et al. 2014](#)), of which several
1020 species are known to pollinate the only three species of *Eupomatia* (Eupomoatiaceae) so it
1021 is likely that this genus also pollinates other plant families. Going further, the Orchidaceae-
1022 Baridinae system highlights the fact that even weevils lineages that are not known to be
1023 pollinators and that lack the associated typical morphological features can also be engaged
1024 in BSPM ([Nunes et al. 2018](#)), with a potential rich array of interactions ([van der Cingel 2001](#)).
1025 From the host plant perspective, the orchid species studied (*Dichaea cogniauxiana*) also
1026 lacks features associated with weevil pollination in other groups (i.e., it has a standard orchid
1027 floral morphology and phenology; [Nunes et al. 2018](#)). Such examples greatly expand the
1028 potential spectrum of brood-site mutualistic interactions between weevils and plants in
1029 tropical biomes and call for a complete shift in our perception of the role of these beetles in
1030 the functioning of tropical ecosystems.

1031 A preliminary estimate of the expected diversity of plant-weevil BSPM systems can
1032 be made based on the discrepancies between the number of systems described and inferred
1033 based on PNC (Figure 2; see Appendix 1). The calculation of the ratios for a selection of
1034 systems (see figure 2) shows that the expected total diversity of species involved is on
1035 average eight times richer than the number of species inferred from PNC and about 17 times

1036 richer than the number of species with experimentally-verified BSPM. Based on the species
1037 counts obtained in this review (see section 1), it is estimated that ca. 2000 plant species
1038 could be engaged in BSPM with weevils globally. Similarly, the species richness of weevils
1039 involved in these interactions could be around 2500 species. Thus, plant-weevil interactions
1040 probably represent the most speciose case of brood-site pollination mutualism, exceeding
1041 the diversity of other BSPM species-rich groups (e.g., [Lopez-Vaamonde et al. 2009](#); [Cruaud
1042 et al. 2010](#)).

1043 **5. Concluding remarks: a road map for future** 1044 **research**

1045 **5.1 Searching for new plant-weevil BSPM systems**

1046 Accumulating evidence for the role of weevils as specialized brood-pollinators of plants is
1047 changing our perspective on the role of this super-diverse group of beetles in tropical
1048 ecosystems and beyond. As such, it is time to expand our understanding of pollination
1049 ecology and to research and test this mutualism in a range of plant and weevil groups that
1050 have been overlooked. We show in this review that some common features associated with
1051 BSPM between plants and weevils can help identify novel systems. That said, we also show
1052 that these mutualistic interactions can exist between lineages that do not exhibit these
1053 characteristics at all. In this regard, we should also change our perception of the structure of
1054 these interactions themselves. In light of this reasoning, a wide range of plant-weevil
1055 interactions should be re-evaluated. A few selected “priority” examples include the potential
1056 role of several ancient weevil groups (Belidae, Caridae, Cimberididae and Nemonychidae)
1057 that visit and breed in gymnosperm cones. With the exception of cycads, they are not
1058 considered pollinators ([Oberprieler et al. 2007](#)), but these cases have never been verified in
1059 detail. In the Neotropics, *Oxycorynus* species (Belidae, Oxycoryninae) are known to visit the
1060 male and female flowers of parasitic plants of the genus *Lophophytum* (Balanophoraceae),
1061 the larvae developing in the inflorescences ([Ferrer et al. 2011](#)).

1062 Plant-weevil BSPM systems can also be expected in temperate regions, where the
1063 predominance of anemophily and entomophily based on generalist pollinators might have
1064 precluded investigations of more specialized systems. In some Western Palearctic willows
1065 (Salicaceae), flowering cycles show intriguing spikes of volatiles which are not correlated
1066 with the visits of pollinators considered as efficient ([Jürgens et al. 2014](#)). Interestingly, a part
1067 of these compounds (4-1 dimethoxybenzène) is also produced by several South American
1068 palms for the specific attraction of beetles, including weevils ([Knudsen et al. 2001](#); [Núñez-
1069 Avellaneda et al. 2005](#)). This case deserves special attention since the male and female
1070 inflorescences of these dioecious trees also harbor the larval stages of several typical
1071 genera of flower weevils (*Acalyptus*, *Dorytomus*, *Ellescus*; [Hoffmann 1958](#)).

1072 While this review focuses specifically on BSPM, it is also important to highlight that
1073 weevils may be involved in the pollination of generalist plants, and may not necessarily use
1074 breeding sites as rewards. One group within Curculionidae that deserves attention is the
1075 subfamily Baridinae. Here we found only one example of a demonstrated effective pollinator
1076 (*Montella*, a brood-site pollinator of orchids; [Nunes et al. 2018](#)), but this mainly Neotropical

1077 taxon harbors an extreme diversity with more than 4,000 described species, many of which
1078 are found in flowers as adults (Prena et al. 2014; B. de Medeiros pers. obs.). Due to their
1079 unresolved phylogeny, complex taxonomy and very high number of undescribed taxa (Davis
1080 2011), they are rarely identified beyond the subfamily or tribe level in pollination studies,
1081 preventing accumulation of knowledge. A great diversity of baridine pollinators, with or
1082 without brood sites as rewards, remains to be discovered. Interactions may also occur in
1083 even more unexpected groups of flower-associated weevils. In orchids, a species endemic
1084 to the Cayman Islands (*Myrmecophila thomsoniana*) is apparently pollinated by the weevil
1085 *Lachnopus vanessablockae* (Curculionidae: Entiminae; Girón et al. 2018) with pollinia
1086 transferred by contact of the elytra on the stigmatic surface of flowers. As typical for
1087 entimines, the larvae of this species reproduce in the soil on the root systems of plants
1088 (Girón et al. 2018), so it is unlikely to be a case of BSPM. These cases demonstrate the
1089 need for a better understanding of the evolution of pollinators in weevils more broadly, and
1090 the contexts leading to BSPM more specifically.

1091

1092 **5.2 Priority research axes**

1093 5.2.1 A plea for description of systems

1094 A better understanding of the diversity and functioning of plant-weevil BSPM systems
1095 requires detailed studies of the corresponding interactions ([Fenster et al. 2004](#)), but also of
1096 the identity and boundaries of the species involved. To date, too many plant-weevil BSPM
1097 studies have a focus on plants and poorly account for pollinator identity. This is partly due to
1098 the complexity of the taxonomy in these groups (species complexes, small sized species)
1099 but also to taxonomic shortfalls. As [Franz & Engel \(2010\)](#) pointed out, there are no shortcuts
1100 to understanding the evolution and diversification of plant-weevil interactions and only
1101 detailed case studies can provide relevant insights. Taxonomic descriptions are essential
1102 prerequisites for any study of pollination in the highly specialized plant-weevil BSPM
1103 systems, and this effort must be made with the relevant expertise of trained taxonomists
1104 using integrative approaches based on morphology and molecular tools ([Toon et al. 2020](#);
1105 [Engel et al. 2021](#)). When expertise is not available, we strongly recommend producing at
1106 least one DNA barcode sequence for each weevil morphospecies involved in a system and
1107 depositing it on international databases (e.g., [de Medeiros et al. 2019](#)), and using images in
1108 addition to names to document weevil flower visitors (e.g., [Núñez-Avellaneda & Rojas-
1109 Robles, 2008](#); [Núñez et al. 2015](#); [Guerrero-Olaya 2017](#); [de Medeiros et al. 2019](#)). The
1110 associated voucher specimens should also be deposited in permanent collections of
1111 museums or institutions. These two procedures will make it possible to considerably improve
1112 species description rates, but also the knowledge on their ecology and distribution.

1113 5.2.2 Evolutionary trajectories : when, why and how?

1114 Although preliminary insights on the emergence and maintenance of plant-weevil BSPM are
1115 readily available, a significant number of evolutionary aspects of these interactions remain to
1116 be investigated. A first aspect lies in the age of these interactions. Reliable fossils of weevil
1117 lineages engaged in BSPM are noticeably absent, precluding making precise inferences
1118 about the ages of these mutualisms. The reasons why so many ancient and more derived
1119 plant lineages have engaged in BSPM with weevils can be elucidated if their emergence
1120 coincides with specific past biogeographical or climatic events. More generally, plant-weevil
1121 BSPM systems offer a rich and diverse range of systems considered as potential models for
1122 understanding the conditions favoring: (i) the shift from detrimental to beneficial interactions,
1123 and the role of tripartite interactions in driving these interactions, (ii) transitions between
1124 pollination syndromes such as between BSPM, other kinds of entomophily, anemophily,
1125 intermediate or ambophilous systems, and (iii) whether there is a general trend towards
1126 higher frequency of specialized pollinators engaging in BSPM in tropical biomes.
1127 Interestingly, almost all plant lineages exhibiting cantharophilous and thermogenic flowers
1128 are widely associated with weevils. It remains to be determined to what extent the
1129 association with weevils specifically was a key factor in the emergence of cantharophily in
1130 general (Bernhardt 2000). Other poorly documented aspects of these interactions include
1131 the potential association with specific microorganisms for colonization of breeding sites and
1132 whether plants alter their physiology to favor the development of the hosted pollinators.
1133 Finally, an unexplored aspect of these specialized interactions lies in their evolution in the
1134 context of current human-induced ecosystem disruption. The present multifaceted changes
1135 affecting the biosphere and insects in particular (Potts et al. 2016; Vanderplanck et al. 2021;
1136 Wagner et al. 2021) provide a context for an assessment of the resilience or vulnerability of
1137 these systems.

1138

1139

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1150 **Conflict of interest disclosure**

1151 The authors of this article declare that they have no financial conflict of interest with the
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1997 **Supplementary information**

1998 **Table S1.** List of plant-weevil brood-site pollination mutualism obtained through literature
1999 review completed by unpublished observations. Weevil names and authorship follows the
2000 Weevil taxa database (accessed January 2023) otherwise stated. Plant names have been
2001 updated according to the World Flora Online (<http://www.worldfloraonline.org/>, accessed
2002 August 2022).

2003

2004 **Appendix 1**

2005

2006 **Material and Methods**

2007 The literature review was conducted directly through search of keywords on Web of Science
2008 and indirectly through reference cited in review papers on specific plant-weevil pollination
2009 systems. About 110 articles, including five review papers were screened to search for
2010 species-specific plant weevil interactions, but also the ecological, phenological and
2011 physiological traits associated with these interactions. These published data were completed
2012 by unpublished field observations provided by colleagues or the authors themselves. For
2013 each species-species interaction, we compiled an indication of classification (family rank),
2014 the location of the breeding site of larval stages and the known evidence of pollination
2015 mutualism. The experimental demonstration of an effective brood-site pollination mutualism
2016 requires the observation of breeding sites of larval stage of the putative pollinator and the
2017 investigation of pollination efficacy of the adults by a pollinator exclusion method. This time
2018 consuming process is rarely conducted, except for a few model systems. In order to
2019 integrate a consistent number of interactions without risk of overestimation, we followed the
2020 following rationale: BSPM interactions were reported only when, 1) the weevil species is
2021 identified at least at the tribal level, 2) BSPM interactions has been shown in a congeneric
2022 plant or weevil species (phylogenetic niche conservatism, see sections 1 and 2.3.5) and/or
2023 3) plants and/or weevils show typical traits associated with BSPM (see sections 1 and 2).
2024 We explicitly excluded cases of flower visitors reported in one publication that were
2025 demonstrated not to be relevant pollinators in another one. This strategy has limitations but
2026 reflects the current state of knowledge on these systems and should be seen as a first
2027 assessment of their extent in overlooked tropical biomes. When relevant, details or a
2028 discussion on knowledge gaps were added (see column "notes" in Table S1).

2029

2030 A subset of plant-weevil interactions was used to estimate the extent of undescribed
2031 interactions (Derelomini-angiosperms dicots/palms/Carludovicoideae, Ochyromerini-
2032 angiosperms dicots, Storerini-Eupomatiaceae). All these types of interactions have in
2033 common (except in the Derelomini-angiosperms dicots): effective BSPM has been reported
2034 at least in one system; highly similar interactions are known in closely related genera and
2035 species; and an estimate of the global diversity of the weevil of plant clade is available
2036 (published records or author unpublished observations, see section 4 and Table S1). For
2037 these five groups, we reported the number of effective BSPM interactions reported, the
2038 expected number of BSPM expected based on phylogenetic niche conservatism (see
2039 section 1 and above) and an estimate of the full diversity (of the weevil except for the
2040 Carludovicoideae) of the clade involved in the interactions (see statistics in figure 2). Based
2041 on these values obtained from the literature we computed the ratios between experimentally-
2042 verified BSPM and expected BSPM based on PNC, and also between experimentally-

2043 verified BSPM and the full diversity of the lineages included (ratio of 8 and 17 respectively).
2044 Considering the species counts obtained in this review (see section 1) and these ratios, we
2045 estimated that about 2000 plants (250 x 8) and around 2500 weevil species (300 x 8) could
2046 be engaged in BSPM globally. We chose the lower range estimates to avoid any
2047 overstatement.
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2049