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

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

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## 30 Abstract

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

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## 65 Keywords

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

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## 100 Introduction

101 Most of the extant biodiversity in tropical regions is concentrated in tropical rainforests, which  
102 were the first biomes to be coined as 'biodiversity hotspots' (Myers 1988). The outstanding  
103 diversity of pollinating systems in these ecosystems offers unique opportunities to study the  
104 evolution of reciprocally beneficial interactions among organisms. Pollination ecology in  
105 tropical rainforests indeed presents unique characteristics due to specific constraints. For  
106 instance, anemophily (wind pollination) is considered to be infrequent and potentially limited  
107 because of a combination of marked spatial constraints (evergreen canopy, structural  
108 heterogeneity and complexity) associated with frequent periods of high rainfall preventing  
109 pollen dispersal (Regal 1982; Williams & Adam 1994). Anemophilous plants are also  
110 presumably disadvantaged whenever they are over-dispersed (Regal 1982; see also below).  
111 Hence, pollination by animal vectors is predominant and can concern up to 100% of the plant  
112 species in some tropical rainforests (Bawa 1990; Ollerton et al. 2011; Rech et al. 2016). The  
113 high level of plant diversity that characterizes tropical rainforests is also associated with a  
114 spatial trend where the distribution of conspecific individuals is usually patchy (Bawa 1990;  
115 Williams & Adam 1994). The latter limits the efficiency of generalist pollinators, as they are not  
116 actively seeking specific plants (Whitehead 1968; Bawa 1990; but see Wolowski et al. 2014).  
117 To cope with these major constraints, the reliance on more intricate pollination mechanisms,  
118 involving specialist pollinators (especially insects), is a hallmark of tropical rainforests (Bawa  
119 1990; Renner & Feil 1993; Vizentin-Bugoni et al. 2018) and also widespread in all tropical or  
120 subtropical biomes (e.g., Gottsberger 1986; Ramirez 2004; Maruyama et al. 2013; Guy et al.  
121 2021).

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

139 Of the neglected lineages of insect pollinators, weevils (Coleoptera: Curculionoidea)  
140 are probably the biggest oversight. Weevils contain over 62,000 described species and a  
141 colossal amount of unknown diversity (Oberprieler et al. 2007). This clade of beetle is  
142 exclusively phytophagous and is the most speciose lineage of phytophagous insects, usually  
143 only depicted as antagonistic to plants (Anderson 1995). Indeed, brood-site pollination by

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

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

## 175 1. A wide spectrum of mutualistic interactions

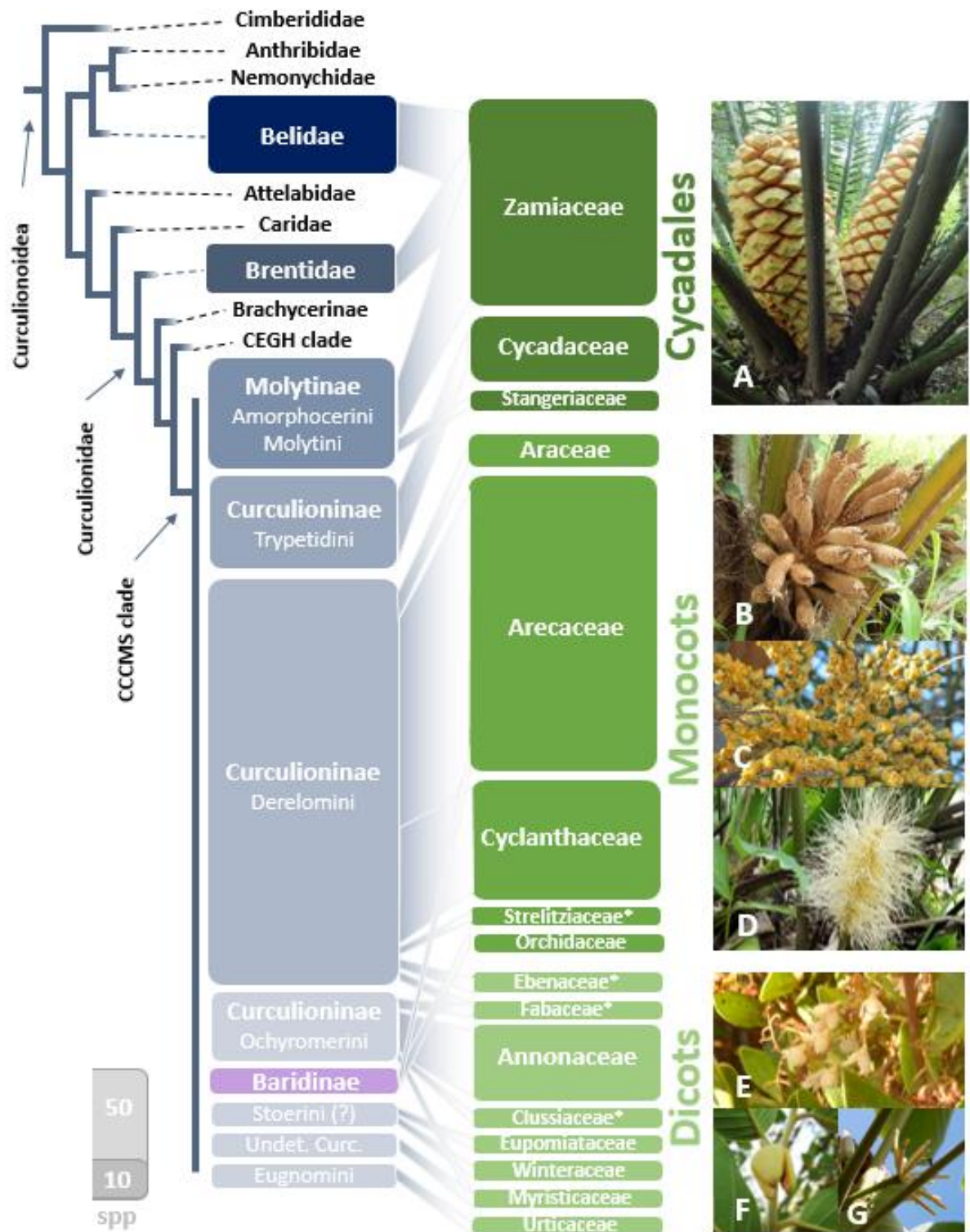
176 Weevils are the most diverse group of insects that visit flowers and develop in reproductive  
177 structures (Oberprieler *et al.* 2007; Kirmse & Chaboo 2020). This close interaction with the  
178 reproductive structures of plants probably preceded the association of weevils with  
179 angiosperm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

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

200 The first report of weevil pollination activity refers to a palm-weevil interaction and  
201 dates back to the 19<sup>th</sup> century (Von Martius 1823). Since then, most efforts to describe and  
202 document weevil pollination have focused on palm-weevil and cycad-weevil mutualisms  
203 (Franz & Valente 2005; Toon et al. 2020). This focus on cycads and palms can be explained  
204 by their characteristic conspicuous inflorescences which attract massive gatherings of weevils,  
205 so much so that they have triggered specific research. To date, weevil BSPM has been  
206 reported for about one hundred palm species (Arecaceae) belonging to 31 genera (Table 1;  
207 S1). Weevils pollinating palms consist of at least 146 species from 15 genera, mostly  
208 belonging to the pantropical tribes Acalyptini and Derelomini (Curculionidae: Curculioninae)  
209 sensu Caldara et al. (2014), hereafter called Derelomini or derelomine weevils (see also Franz  
210 (2006) and Alonso-Zarazaga (2007) for nomenclatural uncertainties). Among the cycads,  
211 weevil BSPM has been reported or suggested for 91 cycad species belonging to seven genera  
212 from all three extant cycad families (Cycadaceae, Stangeriaceae and Zamiaceae). Weevils  
213 pollinating cycads belong to a diverse range of lineages; they are predominantly found within  
214 Curculioninae and Molytinae among the Curculionidae (ca. 50 species in six genera), but also  
215 within Belidae (20 species in three genera) and Brentidae (12 species in two genera, Toon et  
216 al. 2020).

217 The study of these relationships, their mechanisms and their patterns of associations  
218 with palms and cycads has stimulated the discovery of similar cases among several monocot  
219 families of angiosperms. For instance, in Neotropical *Anthurium* (Araceae), 10 species are  
220 engaged in mutualism with *Cyclanthura* weevils (Derelomini, seven species; Franz 2003,  
221 2006). In the same region, 33 species from eight genera of cyclanths (Cyclanthaceae) are  
222 pollinated by 21 weevil species belonging to five genera of Derelomini (Franz 2007a, 2008).  
223 In Neotropical Orchidaceae, three weevil species belonging to two genera of Baridinae  
224 (Curculionidae, alternatively classified as the supertribe Bariditae among Conoderinae)  
225 ensure their pollination (Nunes et al. 2018). More anecdotally, *Strelitzia nicolai* (Strelitziaceae)  
226 from southern Africa appears to be pollinated by two derelomine species belonging to two  
227 distinct genera (Haran et al. 2022a; Haran unpublished). Importantly, the majority of weevils  
228 engaged in BSPM show a marked pattern of phylogenetic niche conservatism (PNC) at the  
229 genus level (Table 1 & Table S1; Franz & Valente 2005; Toon et al. 2020; Haran et al. 2021,  
230 2022b). Such a pattern is far from unusual among groups of internal feeding insects, such as  
231 seed beetles (Kergoat et al. 2007, 2015) or noctuid stem borers (Kergoat et al. 2018).  
232 Therefore, we postulate that, in the absence of direct experimental evidence for a weevil  
233 species, knowledge about other species in a genus may provide an indication of pollination

234 activity. This generalization can produce hypotheses to be tested and also provide a first  
 235 assessment of the extent of plant-weevil BSPM in overlooked tropical biomes (Toon et al.  
 236 2020).





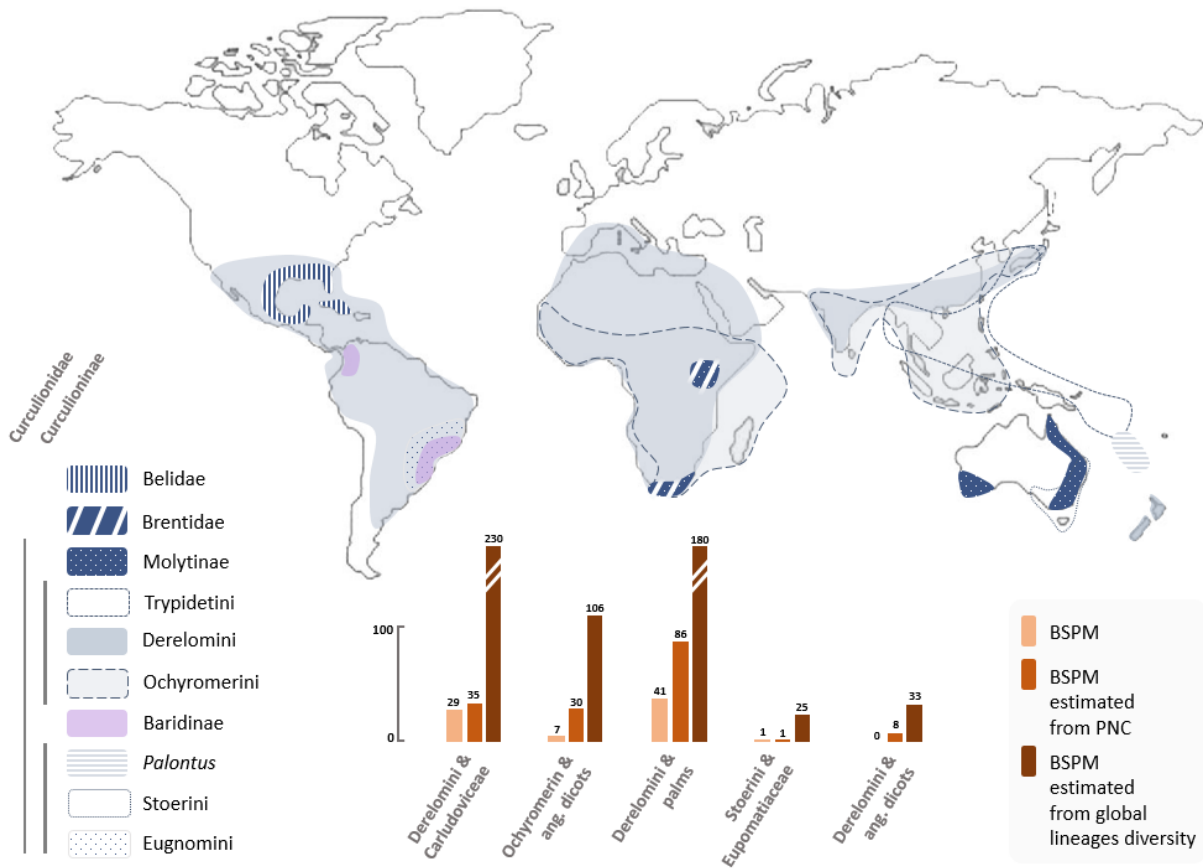
238 **Figure 1.** Summary of known and expected brood-site pollination mutualisms between plants and  
239 weevils (Coleoptera; Curculionoidea). The boxes in blue and green refer respectively to the weevil and  
240 plant lineages involved (the size of boxes is correlated to the number of species involved;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

256

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

273 All in all, the extensive literature search conducted in this review underlines that no  
274 less than 600 instances of plant-weevils species-species BSPM interactions have been  
275 recorded to date or suggested based on the marked trend of PNC for brood pollination (Table  
276 1; see Table S1 for details). Overall, BSPM with weevils has been demonstrated  
277 experimentally in 12 of the 22 plant families involved in this mutualistic system, with the  
278 remaining 10 families suggested based on PNC of weevil genera and/or adaptations of floral  
279 structures to cantharophily. Representatives of all major plant lineages, gymnosperms,  
280 monocots and dicots, are engaged in BSPM with weevils; collectively representing ca. 250  
281 species belonging to 72 genera (Figure 1) associated with about 300 species of weevils. In  
282 this regard, weevils are by far the most ecologically successful group of insects engaged in  
283 BSPM relationships with the plant kingdom. Our review shows that weevil-based BSPM has  
284 emerged several times independently and is currently present in all tropical regions (Figure 1,

285 2), with plants involved in these relationships typically belonging to groups considered to be  
 286 ancient lineages (Pant 1987; Franz 2004; Saunders 2012; Baker & Couvreur 2013).



287

288 **Figure 2.** Geographical distribution of weevil lineages engaged in BSPM with plants and estimates of  
 289 knowledge gaps. Distribution data collated from Alonso-Zarazaga & Lyal (1999), articles listed in this  
 290 review, and unpublished observations by the authors (note that the distribution of several minor  
 291 relationships is not shown for clarity). Bars show the relative number of known and estimated BSPM  
 292 relationships for a selection of plant-weevil interactions. Beige: number of plant species involved in  
 293 verified relationships (involving brood-site and/or synchronization of weevil and flower phenology and/or  
 294 pollen transfer observed). Light brown: number of plant species involved estimated based on floral  
 295 visitors, including weevils and PNC of weevils involved. Dark brown: global diversity of interaction  
 296 estimated from the diversity of plant lineages engaged in BSPM with weevils (Derelomini-  
 297 Carludoviceae; Franz & Valente 2005; Franz 2006) and the diversity of weevil genera engaged in these  
 298 interactions (other interactions; Table S1, GBIF data and unpublished authors observations, see section  
 299 4.2).

## 300 2. Reciprocal adaptations

### 301 2.1 Plant adaptations to BSPM by weevils

302 Flowers and inflorescences of plants engaged in BSPM with weevils generally display typical  
 303 adaptations to cantharophily (beetle pollination) and remarkable convergent morphologies,

304 physiologies, phenologies and reproductive strategies. All these characteristics enhance the  
305 attractiveness of flowers to weevils, provide them with food rewards, and sometimes protect  
306 them from predators; they also improve pollen transfer to weevil integuments and play a role  
307 in weevil pollinator selection and retention, thereby improving pollination efficiency.


308 A first major characteristic for weevil-pollinated plant lineages is that they tend to  
309 display **large flowers or inflorescences** (Figure 1). In cycads and most monocot lineages  
310 involved in BSPM (Araceae, Cyclanthaceae, some Arecaceae), flowers or female ovules are  
311 clustered in large compact cones or inflorescences (Franz & Valente 2005; Toon et al. 2020).  
312 Individual flowers can also reach substantial sizes in Annonaceae or Lecythidaceae (Prance  
313 & Jongkind 2015; Saunders 2020). In contrast, other plant lineages producing smaller  
314 individual flowers form either dense inflorescences (most Arecaceae) or synchronized blooms  
315 (Ebenaceae – *Euclea*, Orchidaceae – *Dichaea*, *Grobya* etc). Field observations and  
316 experiments on various Annonaceae flowers and Cyclanthaceae inflorescences show that  
317 larger floral structures attract greater number of weevil pollinators (Gottsberger 1999; Franz  
318 2007a), revealing that this floral trait has been independently selected to enhance weevil  
319 attraction and pollination.

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

349 [2006](#); [Saunders 2020](#); [Haran et al. 2022a](#); Dao et al. unpublished; Figure 3F), indicating that  
350 these structures are also food sources for the adult pollinators.

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

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

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

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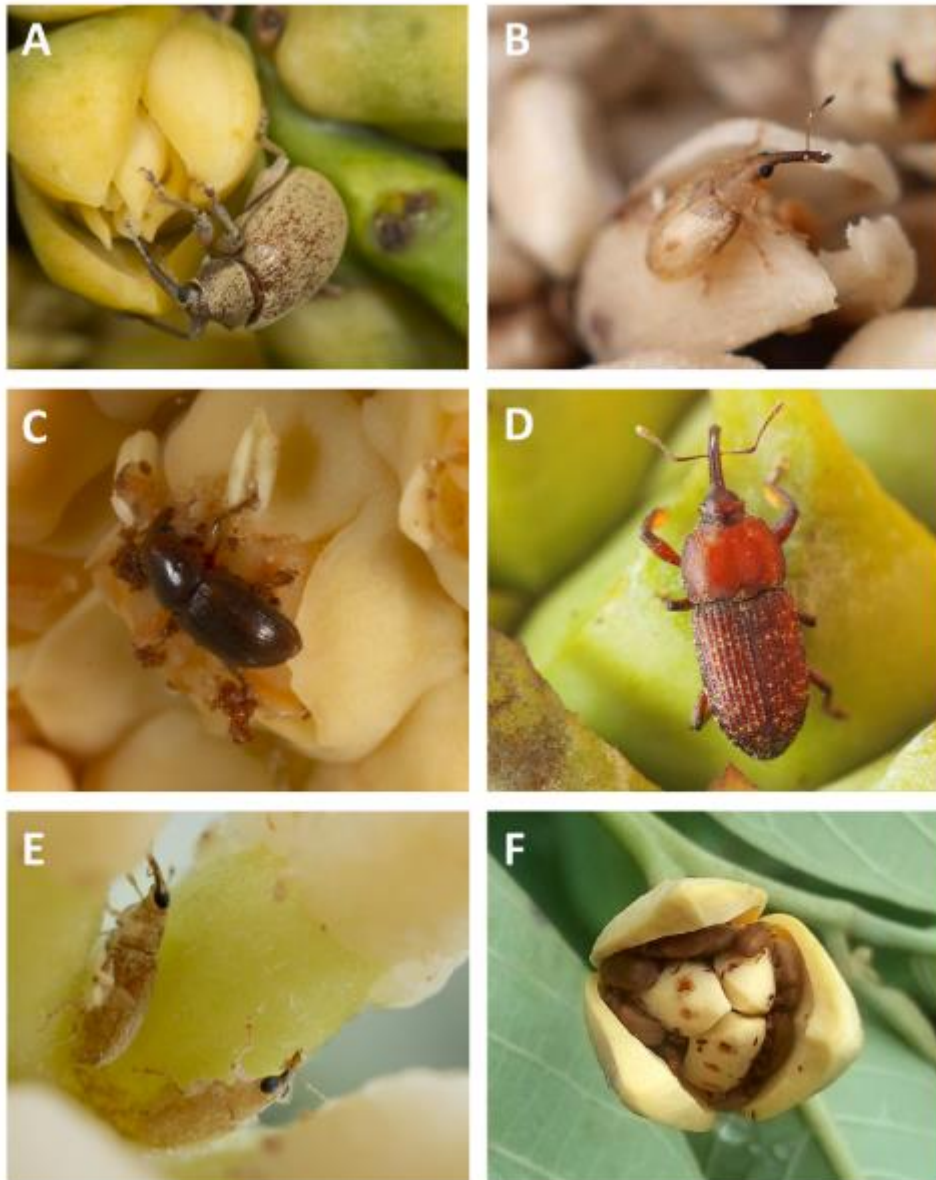
367 All major plant lineages engaged in BSPM with weevils include representatives with  
368 **thermogenic** activity, allowing inflorescence or flower temperatures to rise several degrees  
369 above ambient temperature (Franz 2007a; Teichert et al. 2018; Saunders 2020; Toon et al.  
370 2020). This phenomenon is postulated to act as an attractant for weevil pollinators, by  
371 increasing the emission of volatiles or IR radiations itself. It has also been hypothesized to  
372 provide an energy reward to individuals reaching floral tissues (Rands & Whitney 2008), but  
373 this is likely not the case for weevils since thermogenic activity is not maintained once  
374 individuals stand on flowers or are enclosed in floral chambers (Teichert et al. 2018; Toon et  
375 al. 2020). In Annonaceae, thermogenesis is identified as typical of flowers pollinated by  
376 beetles, and weevils in particular (Gottsberger 1999). The temperature reached appears to be  
377 positively correlated with inflorescence size (Franz 2007a), which may explain why large  
378 flowers and inflorescences evolved convergently in weevil-pollinated plants. Temperature  
379 peaks during the circadian cycle of the flowering cycle can also have a repellent effect and  
380 promote the departure of the weevils once they are covered in pollen (Franz 2007a; Teichert  
381 et al. 2018; Salzman et al. 2020).

382 The **fragrances** produced by weevil-pollinated flowers during anthesis are strong and  
383 detectable by human olfactory senses, and are commonly associated with fruity or floral  
384 fragrances. In most genera of weevil-pollinated Cyclanthaceae (*Aspludia*, *Carludovica*,  
385 *Chorigyne*, *Dicranopygium* and *Evodianthus*), production of aromas reminiscent of various  
386 fruits and flowers has been reported (Franz 2007a). Similarly, in *Polyalthia* (Annonaceae), a  
387 fruity odor is produced during anthesis (Ratnayake et al. 2006). In *Elaeis guineensis*  
388 (Arecaceae), anthesis is correlated with the production of a strong anise-like scent (Lajis et al.  
389 1985), while in *Attalea phalerata* (Arecaceae), weevils and other beetle pollinators are  
390 attracted by a strong emission of methyl acetate (Maia et al. 2021). In *Macrozamia* and *Zamia*  
391 (Zamiaceae) the emission of linalool or methyl salicylate has been recorded (Toon et al. 2020;  
392 Salzman et al. 2021). These scent blends appear to be species specific (Teichert et al. 2018),  
393 but their exact composition have not been thoroughly studied, and it is unclear whether similar  
394 compounds were independently acquired by phylogenetically distinct plant groups. Notable  
395 exceptions of floral odor emission are found in *Chamaerops humilis* (Arecaceae), which  
396 attracts *Derelomus* species via the volatiles emitted from the leaves (Dufaÿ et al. 2003), and  
397 in *Syagrus coronata* (Arecaceae), where the volatiles are given off by a persistent peduncular  
398 bract (Barbosa et al. 2020).

399 The morphological and physiological features described above are generally  
400 organized into **timed phenological sequences** that coincide with **phases of flower and**  
401 **inflorescence receptivity**. In most plant lineages producing large inflorescences (e.g.,  
402 Araceae, Arecaceae, Zamiaceae), anthesis occurs over several days and is accompanied by  
403 circadian thermogenic cycles and emission of volatiles (Franz 2007a; Auffray et al. 2017; Toon  
404 et al. 2020). When flowers are isolated (in Annonaceae and Eupomatiaceae), but also in  
405 Cyclanthaceae, each individual flower or inflorescence goes through one cycle of anthesis  
406 with the following stages: (i) a phase of thermogenesis/attraction associated with the  
407 receptivity of female reproductive structures (pistillate phase), (ii) an interim period when  
408 weevils can be trapped in the floral chamber for a variable time, and (iii) a phase when  
409 pollinators are released with exposure to male reproductive structures (stamen and pollen,  
410 staminate phase), which can be achieved by abscission of the floral chamber petals and/or by  
411 a second peak of thermogenesis (Armstrong & Irvine 1990; Franz 2007a; Lau et al. 2017;  
412 Teichert et al. 2018; Saunders 2020). In the first case, the anthesis lasts between several days

413 and two weeks (Toon et al. 2020), while in the second case, the complete cycle of anthesis is  
414 short and usually lasts at most 48h (Franz 2007a; Saunders 2020). Interestingly, the pistillate  
415 and staminate phase cycles found in some Cyclanthaceae (*Asplundia*; Franz 2007a) are very  
416 similar to those found in some Annonaceae (Saunders 2020), indicating a remarkable  
417 convergent evolution of plant-weevil pollination systems. With the notable exception of cycads  
418 and some palms, in all plant-weevil BSPM systems, the **pistillate and staminate phases**  
419 **coincide with peaks of crepuscular or nocturnal peaks in pollinator activity** (Armstrong  
420 & Irvine 1990; Franz 2007a; Auffray et al. 2017; Saunders 2020). These converging nocturnal  
421 phenologies suggest that nocturnal conditions improve pollination efficiency, possibly through  
422 enhanced attraction of weevil pollinators and avoidance of generalist pollinators active during  
423 the day. It has been also hypothesized (Borges et al. 2016; Auffray pers. com.) that the  
424 movement of pollinators and the dispersal of floral fragrances are facilitated at night because  
425 there is less wind; lower temperatures also potentially improve the detection of thermogenic  
426 flowers.

427 A remarkable feature of all plant lineages engaged in BSPM with weevils is the  
428 **separation of sexes**. In cycads, all species are dioecious, with male plants producing pollen  
429 cones and female plants ovulate cones (Toon et al. 2020). Weevil-pollinated palms may be  
430 dioecious or monoecious, but anthesis of male and female flowers are always separated in  
431 time in the latter case (Barfod et al. 2011). One example is the monoecious palm genus *Elaeis*  
432 (Arecaceae), in which individuals cyclically produce functionally unisexual male and female  
433 inflorescences, resulting in an allogamous mode of reproduction called temporal dioecy (Adam  
434 et al. 2011). In other genera, such as *Acrocomia* and *Bactris* the pistillate and staminate  
435 phases of the **protogynous inflorescences** are separated by a short interim phase resulting  
436 in circadian dioecy (Henderson et al. 2000; Carreño-Barrera et al. 2021). Similar patterns are  
437 observed in other monoecious plant lineages such as Annonaceae and Cyclanthaceae (Franz  
438 2007a, 2007b; Saunders 2020). Finally, a number of palms exhibit **protandrous**  
439 **inflorescences** with very extended interim phases, also resulting in functional dioecy  
440 (Silberbauer-Gottsberger et al, 2013; Núñez-Avellaneda et al, 2008, 2015; de Medeiros et al.  
441 2019). Another striking feature of systems involving Arecaceae, Annonaceae and  
442 Cyclanthaceae is the small number of flowering inflorescences per individual or the small  
443 number of flowering individuals at time, a strategy that also likely promotes cross-pollination  
444 (Saunders 2020). The resulting low number of propagules available at a certain time may be  
445 balanced by the long flowering periods of the plants engaged in these BSPM interactions, for  
446 instance up to seven-months in *Asplundia* (Cyclanthaceae; Franz 2007a) and many species  
447 of *Syagrus* (Arecaceae; Noblick 2017). These long flowering periods have also been proposed  
448 as a strategy for constant breeding of specialized brood pollinators (Carreño-Barrera et al.  
449 2020).  
450



451  
 452 **Figure 3.** Examples of weevils and plants engaged in brood-site pollination mutualisms. **A.** *Anchylorhynchus*  
 453 *trapezicollis* (Derelomini) on pistillate flowers of *Syagrus coronata* (Arecaceae) in South America. **B.** *Derelomus*  
 454 sp. (*costiger* group; Derelomini) pollinator of *Phoenix reclinata* (Arecaceae) in southern Africa. **C.** *Perellesschus*  
 455 *evelynae* (Derelomini) on pistillate flowers of *Carludovica palmata* (Cyclanthaceae) in Central America. **D.** *Tranes*  
 456 *lyterioides* (Molytinae) on sporophylls of *Macrozamia communis* (Zamiaceae) in Australia. **E.** *Udeus eugnomoides*  
 457 (Eugnomini) on pistillate flowers of *Cecropia peltata* (Urticaceae) in Central America. **F.** Flowers of the African  
 458 custard apple (*Annona senegalensis*; Annonaceae) with aggregation of *Endaeus* spp. pollinators (Ochrymerini)  
 459 in tropical Africa. (credits: A/C/E: B, E: B. de Medeiros, B: J. Haran, D: R. Oberprieler, F: Z. Dao).  
 460

## 461 **2.2 Weevil morphology and behavior**

462 Like plants involved in BSPM, weevil pollinators display a series of morphological,  
 463 physiological and behavioral features that may constitute adaptations to pollination  
 464 mutualisms. Weevil pollinators have been less studied than the plants they pollinate, so not  
 465 only their shared morphological features have been scarcely reported, but also the function  
 466 and adaptive significance of these features are generally unexplored. This section provides a



467 summary of what is known to date, with the aim of identifying general trends associated with  
468 BSPM pollination, as well as pointing out more peculiar cases.

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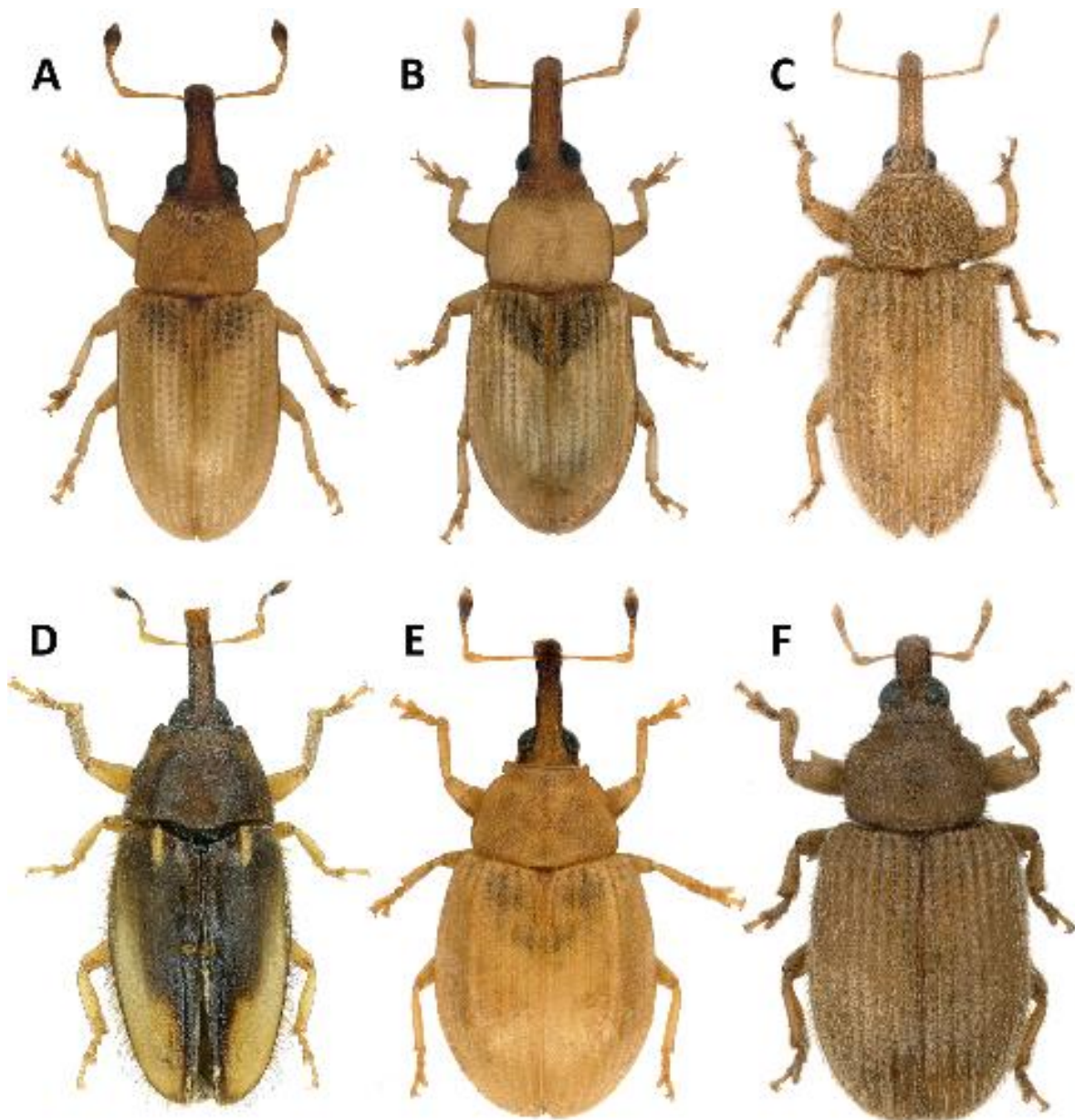
470 Known weevil species involved in BSPM are **small-sized beetles**, with body size  
471 ranging from a few millimeters to about one centimeter (1.1 mm, *Staminodeus inermis* (Franz  
472 2001); 8.6 mm in *Anchylorhynchus burmeisteri* (de Medeiros & Vanin 2020), rostrum  
473 excluded). Body shape is often consistent with floral morphology; for example, the body of  
474 weevils associated with cycads in Belidae and Brentidae is very flat and allows individuals to  
475 enter the cracks of megasporophylls. In most species, the body colors are **pale yellow,**  
476 **reddish or brown**; they usually match the color or shape of their floral substrates, probably  
477 to limit predation (Figures 3, 4). The matching colors are either obtained due to the color of  
478 the integument itself (e.g., in *Andranthobius*, *Cotithene*, *Derelomus*, *Ebenacobius*,  
479 *Elaeidobius*, *Prosoestus*) or due to the colors of the integument and scales covering it (e.g.,  
480 in *Anchylorhynchus*; Valente & da Silva 2014; Valente et al. 2019; de Medeiros & Vanin 2020;  
481 Haran et al. 2020, 2022a). In some species, the shape of the elytra forms an angled surface  
482 mimicking the shape of the petals of the host plant (e.g., *Derelomus subcostatus*, *D. costiger*  
483 and *D. piriformis*; see Figure 4E). Overall, there appears to be a strong selective pressure to  
484 mimic floral substrates as suggested by the various examples of strongly converging  
485 phenotypes among unrelated species associated with the same host plant (e.g., *Derelomus*  
486 *pallidus* and *Ebenacobius rectirostris* on *Euclea racemosa*; Haran et al. 2022b; Figure 4A, B).  
487 This pattern of mimicry is, however, found almost exclusively in species active during the day  
488 on inflorescences, with little or no space to hide (i.e. most Derelomini associated with  
489 Arecaceae or Ebenaceae). In weevil lineages that remain hidden in floral chambers or  
490 inflorescences during the day, the integuments are usually pale brown or reddish in color, and  
491 they do not specifically match floral substrates (e.g., in *Cyclanthura*; Ochyromerini; Figure 4C,  
492 F). Notable exceptions to this pattern include *Montella* weevils (Baridinae), which exhibit a  
493 dark body integument contrasting with the color of its host's flowers (Nunes et al. 2018) and  
494 some species of *Anchylorhynchus* weevils with extreme polymorphism showing disruptive  
495 patterns such as black and yellow stripes (de Medeiros & Vanin 2020).

496

497 A series of putative pollen-carrying morphologies are found in weevils engaged in  
498 BSPM. Most of these lineages have species with **erect setae** on their body surface (Haran et  
499 al. 2020, 2022a; Dao et al. unpublished), a feature thought to enhance pollen transport (Syed  
500 et al. 1981). The setae can cover the entire body surface (in Ochyromerini or in some  
501 *Ebenacobius* and *Celetes*; Valente 2005; Ratnayake et al. 2006; Haran et al. 2022b; Figure  
502 4C, F), or form combs on the edge of the elytra (in some *Elaeidobius*; Figure 4D), or on the  
503 tibiae (in some *Derelomus*); setae may also be found on the ventral region (in some  
504 *Elaeidobius* and *Anchylorhynchus*). In *Anchylorhynchus*, a genus that breeds on female  
505 flowers and thus may benefit directly from pollination, these ventral setae may be highly  
506 branched in some species, reminiscent of setae found in bee corbiculae (de Medeiros et al.  
507 2019; de Medeiros & Vanin 2020). Interestingly, in some weevil species, the presence of setae  
508 is a dimorphic feature, with only males exhibiting long setae, suggesting that they may play a  
509 differential role in pollen transport (Haran et al. 2020; Hsiao & Oberprieler 2022). That said,  
510 even weevil species without specific setae (e.g., *Derelomus chamaeropsis*, *Andranthobius*  
511 spp., Baridinae and Belidae) are known to be effective pollinators (Anstett 1999; Nunes et al.  
512 2018; Salzman et al. 2020; Carreño-Barrera et al. 2021), suggesting that integuments alone  
513 can efficiently transport pollen. Several unrelated lineages of weevils engaged in BSPM also  
514 exhibit prosternal processes or tubercles (in *Andranthobius*, *Diplothemiobius*, *Ebenacobius*,

515 *Elaeidobius*, *Miltotrane*s, *Porthetes*, *Prosoestus*, *Trane*s; Bondar 1941; Valente & da Silva  
516 2014; Haran et al. 2020, 2022; Hsiao & Oberprieler 2022; Haran pers. obs.) consisting of  
517 cuticular apophyses located near the procoxae of males. In some Baridinae not involved in  
518 BSPM, such structures grow allometrically and have been shown to be used in interspecific  
519 fights to dislodge competing males (Eberhard & Garcia 2000; Eberhard et al. 2000; Davis &  
520 Engel 2010). Since fights between males have been described in Derelomini (Franz 2003,  
521 2006), it can be postulated that these prosternal processes or tubercles probably have a  
522 similar function for the aforementioned genera. Finally, in some weevil lineages, structural  
523 complexity and dense cover of setae in these structures have been hypothesized to possibly  
524 enhance pollen transport (see Hsiao & Oberprieler 2022). It is not known why the weevils  
525 evolved these pollen-carrying structures, except in the rare cases where the weevils directly  
526 benefit from the pollination of their hosts. Indeed, there are only two known cases where  
527 weevils breed on tissues that result from their direct pollination: in the genus *Montella* (Nunes  
528 et al. 2018) and in the genus *Anchylorhynchus* (de Medeiros & Vanin 2020). *Montella* weevils  
529 display active pollination behavior (carrying orchid pollinaries; Nunes et al. (2018), which is  
530 consistent with other cases of specialized pollinating seed predators such as fig-wasps  
531 (Jousselin et al. 2003) and yucca moths (Pellmyr 1997). For *Anchylorhynchus* the evidence is  
532 more ambiguous; females rub their bodies against female flowers after oviposition, but it  
533 remains to be shown whether this behavior serves to mark oviposition and avoid competition,  
534 increases the likelihood of pollen deposition, or both (de Medeiros et al. 2014).

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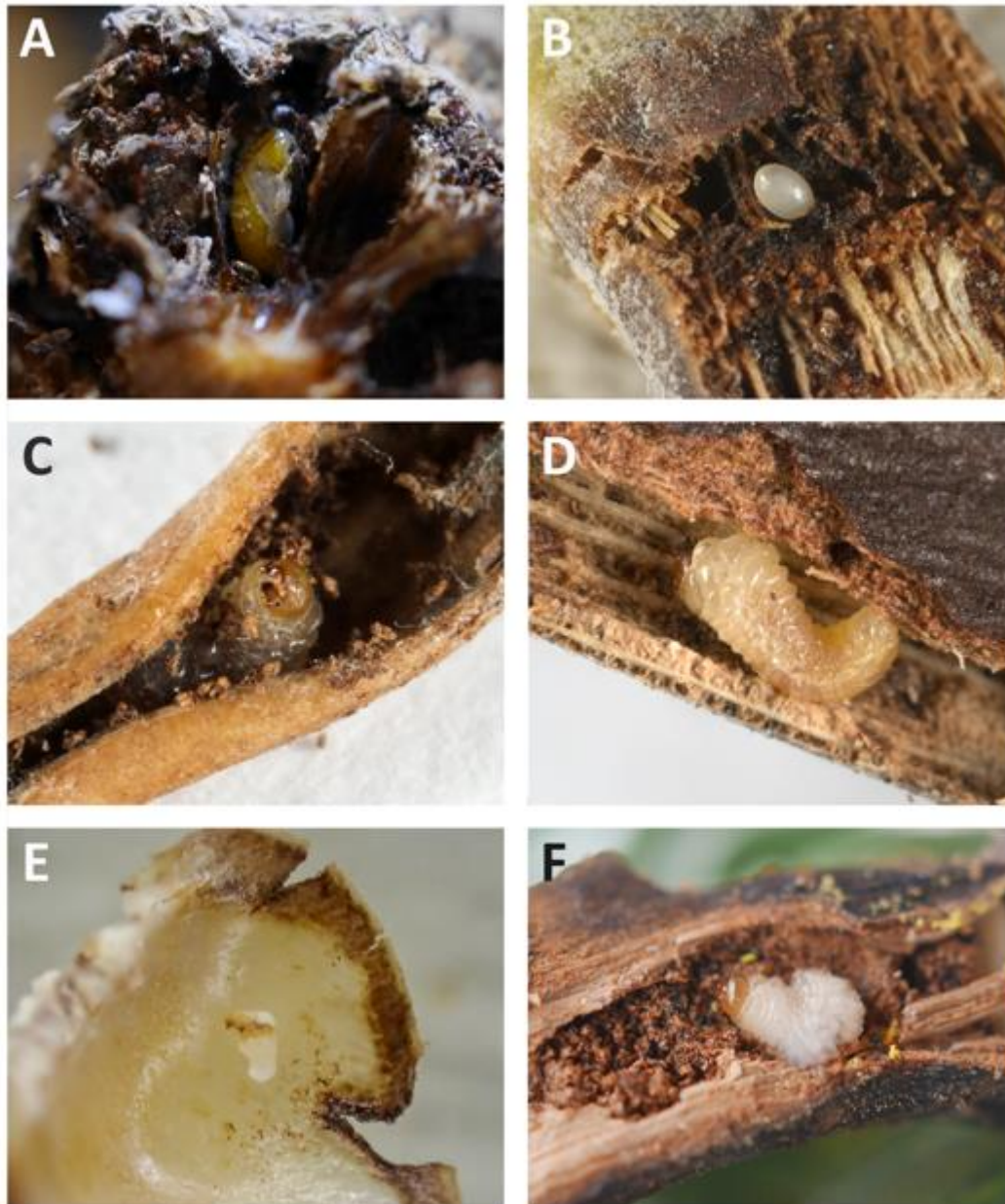
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**Figure 4.** Morphology of weevils involved in BSPM. **A-B.** *Derelomus pallidus* and *Ebenacobius rectirostris* (Derelomini), two species associated with inflorescences of *Euclea* bushes (Ebenaceae) showing a marked morphological convergence. **C.**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

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

554 2021). Several weevil lineages have also developed specific olfactory globules in their  
555 antennae which are considered to be adaptations for the detection of these volatiles (Crowson  
556 1991; Oberprieler 2004). Following olfactory stimuli, weevils can reach or leave the flowers  
557 and inflorescences of their hosts, according to circadian cycles remarkably adapted to  
558 flowering cycles (Franz 2007a; Auffray et al. 2017; Mendeléz-Jácome et al. 2019; Saunders  
559 2020; Salzman et al. 2021). The weevil's reaction to a volatile can be concentration-  
560 dependent, with the same molecule acting as either an attractant or a repellent depending on  
561 the amount emitted from the floral structures. This change in behavior in turn creates a push-  
562 pull effect enhancing their movement between flowers and therefore pollination (Franz 2007a;  
563 Salzmänn et al. 2021). When floral structures do not produce peaks of volatiles (the so-called  
564 'interim' phase'; Saunder 2020), weevils may simply remain on the inflorescences (in cycads  
565 and palms; Auffray et al. 2017; de Medeiros et al. 2019; Toon et al. 2020), be hidden or trapped  
566 there (in Araceae and Annonaceae; Franz 2007b; Saunders 2020; Dao et al. unpublished), or  
567 leave inflorescences (Ratnayake et al. 2006; de Medeiros et al. 2019). In the genus  
568 *Ebenacobius*, many species have only been collected from the leaf litter during the day, which  
569 suggests that they hide there between their crepuscular and night phases of movements  
570 (Haran et al. 2022a). Weevils are fairly long-lived insects, with an adult lifespan of up to 79  
571 days (mean 31 days) in *Elaeidobius subvittatus* (Syed et al. 1982). As the anthesis of the host  
572 inflorescence lasts only a few hours or a few days (five days in the case of *Elaeis guineensis*),  
573 the same individual can visit many flowers or inflorescences during its lifespan.



574

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

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584 The **larval stages** of weevils are **adapted to develop on the various types of**  
 585 **substrates** provided by their hosts. In all the weevil lineages engaged in BSPM, the larvae  
 586 are generally endophagous, developing either in live tissues or as detritivores on decaying  
 587 plant material, in more or less woody tissues (Figure 5; Anstett 1999; Franz 2007; Nunes et  
 588 al. 2018; Toon et al. 2020; Dao et al. unpublished). In Ebenaceae which have small individual

589 flowers, larvae of pollinators are ectophagous and feed at the base of the anthers (Haran et  
590 al. 2022a). In *Anchylorhynchus*, eggs are deposited externally between petals (Figure 5E) and  
591 first instars drill into female flowers to continue their development internally (de Medeiros et  
592 al. 2014). When larvae feed on limited spaces such as individual flowers or fruits, some  
593 species have developed a cannibalistic behavior (Figure 5E) and morphology to cope with a  
594 potential overpopulation in the brood site (de Medeiros et al. 2014). For most plant-weevil  
595 BSPM, the interplay between the presence of secondary compounds in plant tissues and a  
596 potential adaptation of associated weevil lineages has not been yet investigated, although  
597 they may drive specialization patterns (Wang et al. 2021). For example in some weevils  
598 associated with cycads (Belidae), the larvae of some species have been found associated  
599 with specific bacteria involved in the control of toxic compounds from their host (Salzman et  
600 al. 2018).  
601

## 602 **2.3 Evolutionary trends**

### 603 **2.3.1 Larval host specificity**

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

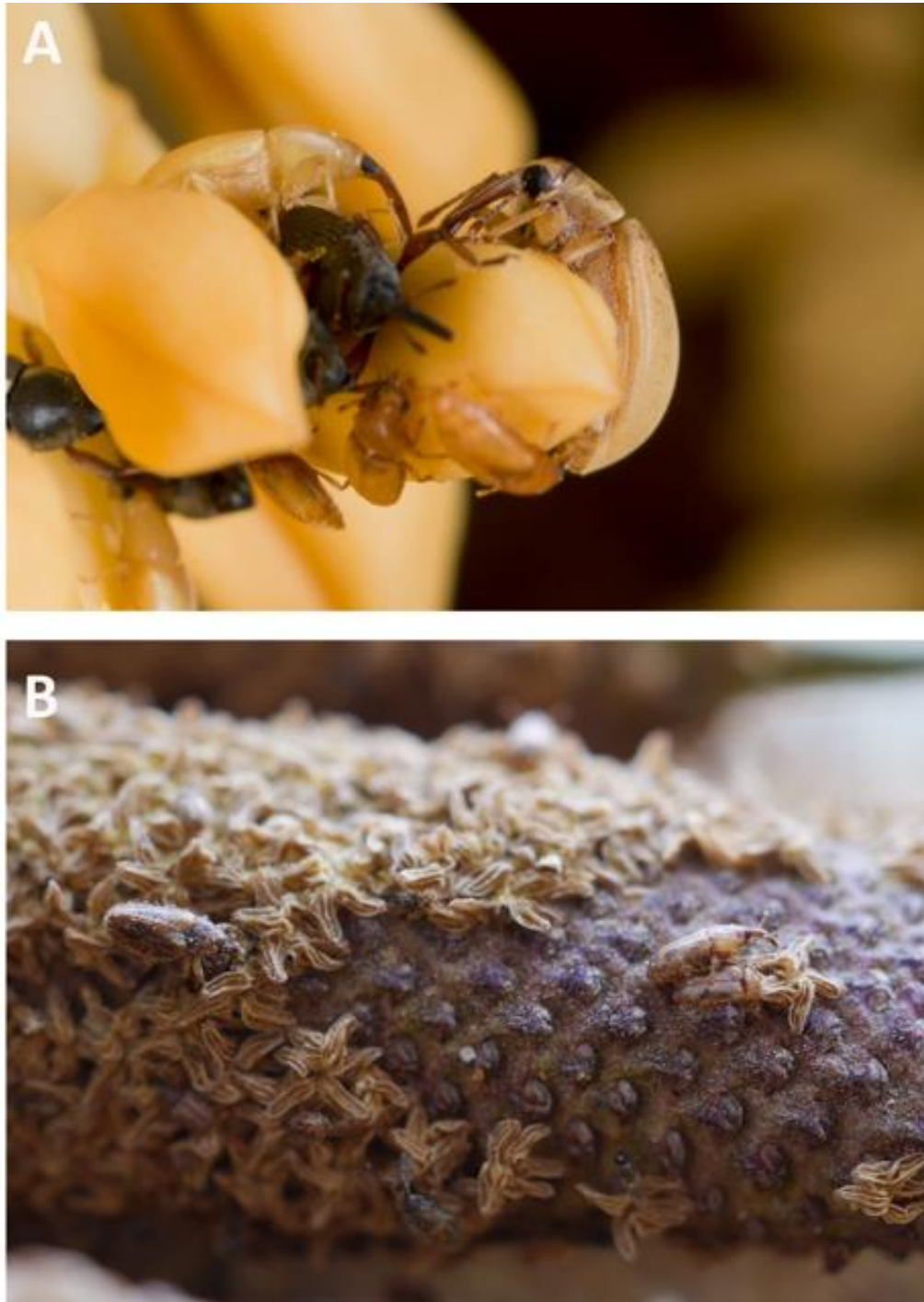
632 and a very high degree of specialization on their hosts (Downie & Williams 2009; Brookes et  
633 al. 2015; de Medeiros & Farrell 2020; Haran et al. 2021).

### 634 2.3.2 Sympatric species assemblages

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

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

676 themselves, where weevil species in an assemblage belong to distinct and phylogenetically  
677 unrelated genera (Franz 2007a; de Medeiros et al. 2019; Toon et al. 2020; Haran et al. 2022b).  
678 Interestingly these two processes are not mutually exclusive, as underlined by the example of  
679 the weevil community associated with the inflorescences of *Phoenix reclinata* (Arecaceae).  
680 Here, lineage duplication and independent colonizations led to the emergence of a sympatric  
681 assemblage of six species of brood-site pollinators (Haran et al. 2022b).



682

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



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

690 In plant-weevil BSPM, multi-species assemblages are not limited to weevils but also  
691 include a range of insects of various orders that develop on host inflorescences (Desmier de  
692 Chenon 1981; Búrquez et al. 1987; Ervik et al. 1999; Gottsberger 1999; Núñez-Avellaneda et  
693 al. 2015; de Medeiros et al. 2019; Toon et al. 2020). It is very common, for example, that  
694 weevil-pollinated plants are also visited by sap beetles (Nitidulidae, Figure 6A). In Annonaceae  
695 they belong to the genus *Carpophilus*, in Areaceae the most common genera are  
696 *Carpophilus*, *Microporum* and *Mystrops*, in cycads they belong to the genus *Carpophilus*, and  
697 in Cycanthaceae they belong to the genus *Mystrops* (Desmier de Chenon 1981; Knudsen et  
698 al. 2001; Núñez-Avellaneda et al. 2005; Ratnayake et al. 2006; Franz 2007a; Núñez-  
699 Avellaneda et al. 2015; Toon et al. 2020). Sap beetles range from the most important  
700 pollinators in some plants to negligible in others (Ratnayake et al. 2006; Núñez-Avellaneda et  
701 al. 2015; Lau et al. 2017; de Medeiros et al. 2019; Toon et al. 2020; Carreño-Barrera et al.  
702 2021). Indeed, the patterns observed in cycad-associated brood-site pollinators show that sap  
703 beetles, but also certain lineages belonging to other families of beetles (Boganiidae, Erotylidae  
704 and Tenebrionidae) or even other orders of insects (Lepidoptera and Thysanoptera) may have  
705 become brood-site pollinators of cycads (Toon et al. 2020). It is therefore not surprising that  
706 species of various groups of insects have independently colonized the same host and co-exist  
707 on it. In palms, multi-species assemblages sometimes even include generalist insects that  
708 have also been identified as pollinators. In some cases, bees are the most important  
709 pollinators with weevils being accessory (Núñez & Carreño, 2017; Bezerra et al. 2020), but  
710 more commonly generalist pollinators play a minor role (Desmier de Chenon 1981; Núñez-  
711 Avellaneda et al. 2015; de Medeiros et al. 2019). The latter echoes the fact that, whenever  
712 weevils are involved in these diverse assemblages, they generally play a predominant role in  
713 host pollination (Desmier de Chenon 1981; Ratnayake et al. 2006; Núñez-Avellaneda et al.  
714 2015; Toon et al. 2020). The precise role of these secondary pollinators (brood site or not) is  
715 not clear, but a reduction of extinction risk by limiting dependence on a specialized mutualist  
716 has been suggested (Silberbauer 1990; Chomiccki et al. 2020).

### 717 **2.3.3 Cryptic and closely related weevil species**

718 The evolution of plant-weevil BSPM is a dynamic system with many instances of recent or  
719 ongoing speciation processes. This trend was first suggested thanks to the results of several  
720 morphological studies, which revealed that BSPM weevil genera often consist of diverse  
721 closely related species (Oberprieler 1996; Oberprieler 2004; Valente 2005; Franz & Valente  
722 2005; de Medeiros & Vanin 2020; Hsiao & Oberprieler 2022). This trend has been confirmed  
723 by molecular studies, which have revealed additional layers of hidden diversity in the form of  
724 cryptic and closely related species often co-occurring on a single host (Downie & Williams  
725 2009; Brookes et al. 2015; Nunes et al. 2018; de Medeiros & Farrell 2020; Haran et al. 2021,  
726 2022a, 2022b). All of these cryptic and closely related weevil species (Table S1) likely reflect  
727 recent speciation events. For example, dating analyses from two recent molecular studies  
728 have recovered numerous instances of recent speciation events (1.2 to 0.2 Mya old), which  
729 may be associated with recent changes in paleoenvironments (Haran et al. 2021, 2022b).  
730 Morphological features enabling to distinguish these closely related species include subtle

731 differences such as the location and size of certain setae on the male ventrites, the  
732 arrangement of setae on the elytra or the ratios on the male genitalia. The repeated occurrence  
733 of these cases of cryptic and closely related species highlight the need for detailed taxonomic  
734 studies to properly estimate the levels of specificity of plant-weevil BSPM systems.

#### 735 **2.3.4 Trade offs in cost-benefit of interactions**

736 The balance between costs and benefits in plant-weevil BSPM interactions has been  
737 investigated in several systems (e.g., [Dufaj & Anstett 2004](#); [Franz 2004](#); [Franz & Valente](#)  
738 [2005](#); [Nunes et al. 2018](#); [Saunders 2020](#); [Toon et al. 2020](#)). Plants engaged in BSPM with  
739 weevils require cross-pollination for a large fruit set. Therefore, a major pressure they have  
740 experienced is pollen limitation, linked to inadequate pollen quality and/or quantity ([Franz](#)  
741 [2007a](#); [Nunes et al. 2018](#)), a widely observed condition for tropical flora ([Tremblay et al. 2005](#);  
742 [Wolowski et al. 2014](#)). Under this pressure, the advantage of having specialized pollinators is  
743 believed to be high ([Silberbauer 1990](#)), especially in the understorey where small plants do  
744 not compete well for generalist pollinators because their floral displays are less conspicuous  
745 ([Turner 2001](#)). The benefit to the plant is clear when weevils develop only on male flowers or  
746 on non-reproductive tissues (e.g., live or decaying stems, bracts and petals), and therefore do  
747 not affect propagule production ([Dufaj & Anstett 2003](#); Dao et al. unpublished). This case is  
748 widely encountered in “pollination by deceit” systems ([Dufaj & Anstett 2003](#)) described in  
749 many palms (Arecaceae), where adult weevils search for male inflorescences where  
750 development of larval stages take place but are misled by female inflorescences producing  
751 similar attractants but no rewards. Such a benefit is, however, less evident when the flower  
752 buds or seeds are destroyed during the larval development of the weevils, and sometimes it  
753 even results in a sharp reduction in the fitness of the host. For example, brentids in the genus  
754 *Antliarhinus* are ovule parasites that can destroy up to 80% of the seeds of their cycad host  
755 *Encephalartos*. However, as adults still play an important role in cross-pollinating their host,  
756 their association remains potentially stable over evolutionary times ([Donaldson 1997](#); [Toon et](#)  
757 [al. 2020](#)). Similarly, the main pollinator of the palm *Syagrus coronata* is a specialist weevil of  
758 the genus *Anchylorhynchus* (Derelomini), which are known to be seed predators ([de Medeiros](#)  
759 [et al. 2019](#)). However, it has been recently shown that there is variation in the genus, with  
760 some species only being able to develop on aborted female flowers and therefore harmless  
761 to the plant ([de Medeiros 2022 in press](#)). Studies of these two examples can reveal why such  
762 costly pollination systems are maintained when less costly ones, involving other specialist or  
763 generalist pollinators, are potentially available and how interactions evolve along the  
764 mutualism-antagonism spectrum ([Fenster et al. 2004](#); [de Medeiros et al. 2019](#)).

765  
766 In some cases, the detrimental effect of the larval development of weevil pollinators is  
767 mitigated by specific plant adaptations. In the dwarf palm (*Chamaerops humilis*), the process  
768 associated with fruit development leads to the termination of larval development on female  
769 inflorescences of *Derelomus chamaeropsis*. Thus, the maintenance of the populations of this  
770 obligate pollinator relies solely on male inflorescence tissues, with no impact on seed sets  
771 ([Dufaj & Anstett 2004](#)). Control of the detrimental effects of larval development may also  
772 include other organisms. For example, in the orchid genus *Dichaea*, pollination depends  
773 exclusively on the activity of a baridine weevil developing as an ovule parasite. Normally, about  
774 20% of fruits are lost to weevil larvae, but the activity of a parasitic wasp killing weevil larvae  
775 at an early stage can significantly reduce the fraction of seeds lost to the weevil ([Nunes et al.](#)

776 2018). Such tripartite interactions are probably overlooked although they potentially play a  
777 significant role for weevil-based BSPM systems.

778

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

### 793 2.3.5 Evolutionary dynamics of host use

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

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

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

### 826 3. Economic importance and conservation

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

835  
836 Many weevil pollinated palms are an important source of food, goods and building  
837 materials (e.g., *Acrocomia*, *Cocos*, *Euterpe*, *Oenocarpus*, *Phytelephas*, *Syagrus*; Núñez-  
838 Avellaneda et al. 2015; de Medeiros et al. 2019; Bezerra et al 2020; Carreño-Barrera et al  
839 2021; Auffray et al. unpublished). In tropical and subtropical regions, wild fruits and leaves of  
840 Annonaceae (e.g., *Annona senegalensis*), Clusiaceae (e.g., *Pentadesma butyracea*) and  
841 Fabaceae (e.g., *Piliostigma reticulatum*) for which pollination by weevils is indicated based on  
842 PNC are commonly consumed by local populations or have a cosmetic or medical use (e.g.,  
843 Babajide et al. 2008; Traoré et al. 2011; Dao et al. unpublished). In cycad lineages primarily  
844 pollinated by weevils (Toon et al. 2020), the high ornamental and subsequent economic value  
845 of many cycad species has also led to over-collection (Mankga & Yessoufou 2017). In these  
846 groups, reproductive failure, among habitat loss and medicinal use, has been identified as one  
847 of the main drivers of population decline, highlighting the importance of detailed investigations  
848 of their pollination ecology. More generally, while plant-weevil BSPM probably emerged to  
849 balance pollination constraints in tropical biomes, it is also a risky evolutionary path if the  
850 specialized pollinators become rare or extinct. Yet too little is known about the impact of  
851 pollinator population dynamics on the reproductive success and long-term survival of the  
852 plants involved (Toon et al. 2020).

### 853 4. Oversights and estimates of global richness

#### 854 4.1 The inconspicuousness of plant-weevils pollination 855 relationships

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

861 First, it can be explained by common misconceptions about plant and weevil biology.  
862 For example, in the cycad/molytine and palm/derelomine systems, massive aggregations of  
863 weevils on inflorescences are highly suggestive of pollination activity. Although these  
864 associations have been known for a long time (e.g., von Martius 1823), the common  
865 misconception that palms and cycads are primarily anemophilous groups has hampered  
866 research on brood-site mutualism in these systems for decades (Von Martius 1823; Lepesme  
867 1947; Bondar 1943; Henderson 1986; Anstett & Dufaÿ 2003; Barfod et al 2011; Toon et al.  
868 2020). These flower visitors have long been considered parasites, providing no pollination  
869 service (Bondar 1943; Lepesme 1947), consistent with antagonistic relationships generally  
870 reported in weevils (Oberprieler et al. 2007). In a striking example of how prior misconceptions  
871 can prevent discovery, a study characterizing floral visitors of *Butia catarinensis* by collecting  
872 only during the day and using sweep nets failed to find a relevant number of beetles in female  
873 flowers (Rosa 2000). However, B. de Medeiros visited the same locality less than 10 years  
874 later and found hundreds of individuals of *Anchylorhynchus eriospathae* hiding at the base of  
875 inflorescences during the day (de Medeiros & Vanin 2020). These weevils breed on female  
876 flowers (de Medeiros et al. 2014) and adequate collection and observation methods could  
877 have recorded them visiting active female flowers for oviposition. To date, the cycad and palm-  
878 weevil associations remain by far the best studied plant-weevil BSPM systems, in particular  
879 because the abundance of these insects on the inflorescences and their specialized nature  
880 greatly facilitates the identification of the relationships (Franz & Valente 2005).

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

## 900 **4.2 An underestimated diversity of species and interactions**

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

906 For example, for most derelomine Neotropical genera information on host plant use is  
907 available (Franz & Valente 2005). By comparison, host records are only available for five of  
908 the 13 Paleotropical genera of Derelomini (Alonso-Zarazaga & Lyal 1999; Franz & Valente  
909 2005). The estimated number of derelomine species overall (ca. 300 species; Caldara et al.  
910 2014; de Medeiros & Vanin 2020; Haran et al. 2020, 2022a) pales in comparison with the  
911 diversity estimates of their main hosts, because the species diversity in the palm family  
912 (Arecaceae) is estimated at about 2500 species (Dransfield et al. 2008; Couvreur and Baker  
913 2013). Since pollination ecology and pollinators have only been identified for a small fraction  
914 of extant palm species, we can hypothesize that dozens – if not hundreds – of palm-weevil  
915 BSPM systems remain to be discovered. Additionally, even though Derelomini are best known  
916 for their associations with palms, recent research has unraveled that some of them are also  
917 associated with plants other than palms. For example, in the Southern African derelomine  
918 fauna, the recently described genus *Ebenacobius* has been found associated with Ebenaceae  
919 and other basal angiosperms. In this genus, no less than 14 new species have been recently  
920 described (Haran et al. 2022a) and at least four others are awaiting description. Moreover,  
921 based on the inferred pattern of PNC in BSPM weevils, Franz & Valente (2005) and Franz  
922 (2006) suggested that most of the ca. 230 species of Carludovicoideae (Cyclanthaceae) and  
923 a significant part of the ca. 800 known *Anthurium* (Araceae) species in the Neotropical region  
924 are pollinated by derelomine weevils. In cycad-weevil BSPM systems, the range of interactions  
925 reported here only reflects our current state of knowledge, and many cycads species have  
926 been insufficiently studied and many relationships remain to be described (Toon et al. 2020).

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

940 In the pantropical Annonaceae (more than 2400 species), cantharopilous flowers are  
941 the most common and have been identified as being typical of weevil pollination (Momose et  
942 al. 1998; Gottsberger 1999; Saunders 2020). It is notably the case of the Neotropical  
943 Annonaceae (ca. 950 species; Maas et al. 2011), where cantharophilous flowers involving  
944 weevil pollination are the most widespread (Gottsberger 1999; Silberbauer-Gottsberger et al.  
945 2003; Saravy et al. 2021). This set of relationships requires further investigations in this region  
946 since the only known specialized pollinators of Annonaceae (Ochyromerini) are exclusively  
947 paleotropical (Alonso-Zarazaga & Lyal 1999).

948 Our general overview of weevil-based pollination shows that several additional  
949 pantropical families of angiosperms are – or at least can be considered as partially – pollinated  
950 by weevils (Table S1), with only a small fraction of these relationships having been uncovered

951 so far. For example, in Clusiaceae, Ebenaceae, Lecythidaceae, Myristicaceae and  
952 Sapotaceae, BSPM by weevils have been only reported for a small number of species;  
953 however there are likely many more BSPM weevil relationships because cantharophilous  
954 flowers are known in several genera of these families and the associated weevil lineages also  
955 contain a significant number of undescribed species (Oberprieler 1993; Caldara et al. 2014;  
956 Haran et al. 2022b). In some cases, the weevil diversity also exceeds that of the known  
957 potential hosts; for example, 25 species of the Australian weevil genus *Elleschodes* are known  
958 (Armstrong & Irvine 1990; Caldara et al. 2014; Pullen et al. 2014), of which several species  
959 are known to pollinate the only three species of *Eupomatia* (Eupomatiaceae) so it is likely  
960 that this genus also pollinates other plant families. Going further, the Orchidaceae-Baridinae  
961 system highlights the fact that even weevils lineages that are not known to be pollinators and  
962 that lack the associated typical morphological features can also be engaged in BSPM (Nunes  
963 et al. 2018), with a potential rich array of interactions (van der Cingel 2001). From the host  
964 plant perspective, the orchid species studied (*Dichaea cogniauxiana*) also lacks features  
965 associated with weevil pollination in other groups (standard orchid floral morphology and  
966 phenology; Nunes et al. 2018). Such examples greatly expand the potential spectrum of  
967 brood-site mutualistic interactions between weevils and plants in tropical biomes and call for  
968 a complete shift in our perception of the role of these beetles in the functioning of tropical  
969 ecosystems.

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

## 981 **5. Concluding remarks: a road map for future** 982 **research**

### 983 **5.1 Searching for new plant-weevil BSPM systems**

984 Accumulating evidence for the role of weevils as specialized brood-pollinators of plants is  
985 changing our perspective on the role of this super-diverse group of beetles in tropical  
986 ecosystems and beyond. As such, it is time to expand our understanding of pollination ecology  
987 and to research and test this mutualism in a range of plant and weevil groups that have been  
988 overlooked. We show in this review that some common features associated with BSPM  
989 between plants and weevils can help identify novel systems. That said, we also show that  
990 these mutualistic relationships can exist between lineages that do not exhibit these  
991 characteristics at all. In this regard, we should also change our perception of the structure of  
992 these relationships themselves. In light of this reasoning, a wide range of plant-weevil

993 interactions should be re-evaluated. A few selected “priority” examples include the potential  
994 role of several ancient weevil groups (Belidae, Caridae, Cimberididae and Nemonychidae)  
995 that visit and breed in gymnosperm cones. With the exception of cycads, they are not  
996 considered pollinators (Oberprieler et al. 2007), but these cases have never been verified in  
997 detail. In the Neotropics, *Oxycorynus* species (Belidae, Oxycoryninae) are known to visit the  
998 male and female flowers of parasitic plants of the genus *Lophophytum* (Balanophoraceae),  
999 the larvae developing in the inflorescences (Ferrer et al. 2011). One group within  
1000 Curculionidae that needs attention is the subfamily Baridinae. Here we found a single example  
1001 of demonstrated effective pollinator (*Montella* in orchids), but this mostly Neotropical taxon  
1002 harbors an extreme diversity with more than 4,000 described species, many of them found in  
1003 flowers as adults (Prena et al. 2014; B. de Medeiros pers. obs.). Because of their difficult  
1004 phylogeny, taxonomy and very high number of undescribed taxa (Davis 2011), they are rarely  
1005 identified beyond subfamily or tribe level in pollination studies, preventing accumulation of  
1006 knowledge. Relationships can also occur in even more unexpected groups of weevils  
1007 associated with flowers. In orchids, a species endemic to the Cayman Islands (*Myrmecophila*  
1008 *thomsoniana*) is apparently pollinated by the weevil *Lachnopus vanessabloekae*  
1009 (Curculionidae, Entiminae; Girón et al. 2018) with pollinia transferred on elytra on the stigmatic  
1010 surface of flowers. Although this case deserves more detailed investigation, it should be noted  
1011 that, as typical for entimines, the larvae of this species reproduce in the soil on the root  
1012 systems of plants (Girón et al. 2018).

1013 Plant-weevil BSPM systems can also be expected in temperate regions, where the  
1014 predominance of anemophily and entomophily based on generalist pollinators might have  
1015 precluded investigations of more specialized systems. In some Western Palearctic willows  
1016 (Salicaceae), flowering cycles show intriguing spikes of volatiles which are not correlated with  
1017 the visits of efficient pollinators expected for this plant (bees and moths; Jürgens et al. 2014).  
1018 Interestingly, a part of these compounds (4-1 dimetoxybenzène) is also produced by several  
1019 South American palms for the specific attraction of beetles, including weevils (Knudsen et al.  
1020 2001; Núñez-Avellaneda et al. 2005). This case deserves special attention since the male and  
1021 female inflorescences of these dioecious trees also harbor the larval stages of several typical  
1022 genera of flower weevils (*Acalyptus*, *Dorytomus*, *Ellescus*; Hoffmann 1958).



## 1023 **5.2 Priority research axes**

### 1024 5.2.1 A plea for description of systems

1025 A better understanding of the diversity and functioning of plant-weevil BSPM systems requires  
1026 detailed studies of the corresponding interactions (Fenster et al. 2004), but also of the identity  
1027 and boundaries of the species involved. To date, too many plant-weevil BSPM studies follow  
1028 a phytocentric approach and poorly account for pollinator identity, in part due to taxonomic  
1029 shortfalls. As Franz & Engel (2010) pointed out, there are no shortcuts to understanding the  
1030 evolution and diversification of plant-weevil interactions and only detailed case studies can  
1031 provide relevant insights. Taxonomic descriptions are essential prerequisites for any study of  
1032 pollination in the highly specialized plant-weevil BSPM systems, and this effort must be made  
1033 with the relevant expertise of trained taxonomists (Toon et al. 2020; Engel et al. 2021). When  
1034 expertise is not available, we strongly recommend producing at least one DNA barcode  
1035 sequence for each weevil morphospecies involved in a system and depositing it on  
1036 international databases (e.g., de Medeiros et al. 2019), and using images in addition to names  
1037 to document weevil flower visitors (e.g., Núñez-Avellaneda & Rojas-Robles, 2008; Núñez et  
1038 al. 2015; Guerrero-Olaya 2017; de Medeiros et al. 2019). The associated voucher specimens  
1039 should also be deposited in permanent collections of museums or institutions. These two  
1040 procedures will make it possible to considerably improve species description rates, but also  
1041 the knowledge on their ecology and distribution.

### 1042 5.2.2 Evolutionary trajectories : when, why and how?

1043 Although preliminary insights on the emergence and maintenance of plant-weevil BSPM are  
1044 readily available, a significant number of evolutionary aspects of these relationships remain to  
1045 be investigated. A first aspect lies in the age of these relationships. Reliable fossils of weevil  
1046 lineages engaged in BSPM are noticeably absent, precluding making precise inferences about  
1047 the ages of these mutualisms. The reasons why so many ancient and more derived plant  
1048 lineages have engaged in BSPM with weevils can be elucidated if their emergence coincides  
1049 with specific past biogeographical or climatic events. More generally, plant-weevil BSPM  
1050 systems offer a rich and diverse range of systems considered as potential models for  
1051 understanding the conditions favoring: (i) the shift from detrimental to beneficial relationships,  
1052 and the role of tripartite interactions in driving these interactions, (ii) transitions between  
1053 pollination syndromes such as anemophily to BSPM and conversely, including intermediate  
1054 or ambophilous systems, and (iii) whether there is a general trend towards specialization of  
1055 pollination systems in tropical biomes. Interestingly, almost all plant lineages exhibiting  
1056 cantharophilous and thermogenic flowers are widely associated with weevils. It remains to be  
1057 determined to what extent the association with weevils specifically was a key factor in the  
1058 emergence of cantharophily in general (Bernhardt 2000). Other poorly documented aspects  
1059 of these relationships include the potential association with specific microorganisms for  
1060 colonization of breeding sites and whether plants alter their physiology to favor the  
1061 development of the hosted pollinators. Finally, in the age of genomics, tools are also available  
1062 to investigate the genomic consequences of selective pressures associated with transitions  
1063 between antagonism and mutualism in weevils.

### 1064 5.2.3 The challenges of the anthropocene

1065 How do specialized BSPM systems involving weevils cope with the anthropocene? At a time  
1066 of unprecedented human-induced ecosystem disruption, many aspects of these complex  
1067 relationships may be affected. Fragmentation of forests resulting in greater distances between  
1068 plant conspecifics, general collapse of insect diversity and biomass, or interference with host  
1069 plant locations due to light pollution or deterioration of chemical communication associated  
1070 with ozone concentration and global warming are all likely to decrease the effectiveness of  
1071 these specialized pollination systems (Potts et al. 2016; Vanderplanck et al. 2021; Wagner et  
1072 al. 2021). On the resilience or vulnerability of this type of mutualism will depend the  
1073 maintenance of reproduction of a significant part of the tropical flora.

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### 1083 Conflict of interest disclosure

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## 1893 **Supplementary material**

1894 **Table S1.** List of plant-weevil brood-site pollination mutualism. Relationships reported when  
1895 at least one species of the weevil genus was identified as actual brood-site pollinator.  
1896 Relationship from congeneric species inferred based on phylogenetic niche conservatism at  
1897 genus level. Relationships are also reported when plants and/or weevils show typical  
1898 adaptations associated with BSPM (see sections 1 and 2).