



Centre de Biologie pour la Gestion des Populations - CBGP  
Campus International de Baillarguet  
755 avenue du Campus Agropolis - CS 30016  
34988 Montferrier-sur-Lez - France  
<http://www6.montpellier.inrae.fr/cbgp>

February, 16<sup>th</sup> 2023

Julien Haran

*Centre de Biologie pour la Gestion des Populations*

Dear Dr. Arroyo,

Thank you very much for you very the very thorough assessment of our manuscript

Following your instruction we have responded and addressed all the comments made by you and the four reviewers, and modified the manuscript accordingly. A Material & Methods section has been made and is presented as an Appendix. Overall we feel that this review has greatly benefited from all comments and we are very grateful to you and all four reviewers for that! We are thus pleased to submit the corresponding revised version, along with point-by-point answers to all comments and suggestions (your comments and the comments of the reviewers are in black, and our responses in [blue](#)).

We hope you find our revision acceptable and we look forward to receiving your response.

Best wishes,

Julien Haran, on behalf of all co-authors,

A handwritten signature in black ink, appearing to be 'J. Haran', enclosed in a thin black rectangular border.

Dear Julien M. Haran,

Your article, entitled *Most diverse, most neglected: weevils (Coleoptera: Curculionoidea) are ubiquitous specialized brood-site pollinators of tropical flora*, has now been reviewed.

The referees' comments and the recommender's decision are shown below. As you can see, the recommender found your article very interesting but suggests certain revisions.

We shall, in principle, be happy to recommend your article as soon as it has been revised in response to the points raised by the referees.

When revising your article, we remind you that your article must contain the following sections (see our Guide for Authors in the Help section of the PCIEcology website):

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Data, statistical scripts, command lines and simulation code must be made available to readers. They should either be included in the article or deposited in an open repository such as Zenodo with a DOI. A perennial URL can be provided if no DOI is available; please note that GitHub URL are not perennial.

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The "Data, script and code availability" section must clearly indicate where and how data can be accessed.

Wherever possible, data, scripts and code should be provided in machine-readable formats. Avoid PDFs other than for textual supplementary information.

Metadata should accompany the data, to make the data understandable and reusable by the reader.

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Supplementary information (text, tables, figures, videos, etc.) can be referred to in the article. It must be available in an open repository (such as Zenodo, Dryad, OSF, Figshare, Morphobank, Morphosource, Github, MorphoMuseum, Phenome10k, etc. or any institutional repository, etc...) with a DOI. A perennial URL can be provided if no DOI is available.

A reference to the supplementary information, with a DOI or a perennial URL, must be provided in the reference list and in the "Supplementary information" section.

List all documents attached to the manuscript as Supplementary Information in the "Supplementary Information" section.

### **3) Funding (mandatory)**

All sources of funding must be listed in a separate "Funding section". The absence of funding must be clearly indicated in this section.

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Authors should declare any potential non-financial conflict of interest (financial conflicts of interest are forbidden, see the PCI code of conduct).

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Details of experimental procedures and quantitative analyses must be made fully available to readers, in the text, as appendices, or as Supplementary Information deposited in an open repository, such as Zenodo, Dryad or institutional repositories with a DOI.

For specimen-based studies, complete repository information should be provided and institutional abbreviations should be listed in a dedicated subsection (if applicable). Specimens on which conclusions are based must be deposited in an accessible and permanent repository.

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We thank you in advance for submitting your revised version.

Yours sincerely,

The Managing Board of PCIEcology

Thanks for all the detailed information. To account for your instructions, the revised version of the MS now includes a Material & Methods section attached as an Appendix (see Appendix 1 at the end of the manuscript).

## Editor comments

by Juan Arroyo, 24 Dec 2022 01:05

Manuscript: <https://hal.inrae.fr/hal-03780127>

Haran's et al 2022 preprint merits a revision

Decision about the manuscript by

Julien Haran, Gael J. Kergoat, Bruno and A.S. de Medeiros. Most diverse, most neglected: weevils (Coleoptera: Curculionioidea) are ubiquitous specialized brood-site pollinators of tropical flora. 2022. hal-03780127

Submitted to PCI Ecology

We have already received four reports by reviewers of this manuscript and all of them are quite enthusiastic about the potential value of this review paper, which is considered both timely and containing relevant information as to be of interest of the PCI Ecology community and similar scholar readership. However, all of them expressed in their reports or in the annotated files some concerns in diverse extent which I consider are worth to be addressed, in order to produce a more comprehensive and useful document for the future use of the research community.

Thank you so much for your work on our study and for the very qualitative, comprehensive and constructive comments and suggestions made by the four reviewers!

As highlighted beforehand, we revised our study accordingly and provided point-by-point answers to all comments, remarks and suggestions.

Apart from the concerns raised by the reviewers, which I agree, I would add some other issues to be considered:

There is a thoroughly consideration of BSMP as a specialized pollination mutualism. However, I do not find the kind of specialization endorsed here. There is a plethora of literature on the topic of generalization/specialization, in particular applied to pollination; for instance, Fenster et al. (2004), cited by the authors, and many others as Gómez, J. M., & Zamora, R. (2006). Ecological factors that promote the evolution of generalization in pollination systems. Plant–pollinator interactions: from specialization to generalization, 145-166, which may consider specialization when there is a little number, only one in the extreme case, of pollinator species of a single plant species or, alternatively, it might be considered when there is a single

functional group of pollinators in a single flower structure, independently of the number of species involved in the functional group. Probably, authors consider that the BMSP is specialized because the system seems to be very particular on functional grounds, but this seems to be an anthropocentric view, due to its comparatively low presence in the literature (which deserves this review paper). Moreover, given that it involves antagonist and mutualist roles of weevils, the balance between these roles will probably determine the specialization degree, for which data are very scarce to ascertain it. My view is that the issue is so important along the text as to be dealt with in a single paragraph at the start of the manuscript, explaining your endorsement. Consider that in the similar BSPM of yucca-moths and fig-wasps, specialization occurs also at taxonomic level (number of spp involved in both partners, plants and insects).

Thanks for highlighting this point. In fact, BSPM in weevils is characterized by a high level of specialization, generally at the species level, so we are far from having a system with generalist species. We would like to clarify that we mean specialized in the sense that the number of plant species a pollinator interacts with is comparatively small, a fact not subject to an anthropocentric view, and not that the features of insects and plants involved are unusual or peculiar.

In order to keep the message of the introduction compact and to avoid breaking the flow, we decided not to discuss this point at this early stage of the manuscript. The question of the level of specificity in these relationships is discussed in detail later in the text:

2.3.1 -> levels of host specificity for larval stages and adults

2.3.2 -> asymmetry in specificity: multispecific weevil assemblages on a single host. Relationships with other groups of pollinators

2.3.4 -> reviews information available on the trade offs in cost-benefit of pollination when it includes specialized weevils and generalist pollinators.

Another general comment concerns the use the term adaptation across the manuscript. It is not clear that in many cases the term is correctly applied, and even less is reciprocal adaptations. In particular, I would rename the section 2. "Reciprocal adaptations", as suggested by one reviewer. Some of the traits are probably adaptations (e.g. scents), other might be exaptations. If you have in hands some specific studies demonstrating adaptations, please focus only on them; otherwise, tone down to "traits related with BSPM".

Thanks for pointing this out. Indeed, in this context the use of the term adaptation is not always appropriate as formal adaptations in plants and weevils have been rarely demonstrated. The term "adaptations" was replaced by "traits" as suggested. In the revised version of the manuscript, we only retain this term when it is used to formulate hypotheses on the meaning of a feature.

L. 176-179 seem to be contradictory.

The first sentence refers to the diversity of plant-weevils interactions and the second tells about the age of these relationships. The second sentence has been reworded to avoid misunderstanding:

L. 187: *“This close interaction with the reproductive structures of plants probably preceded the colonization and diversification of weevils on angiosperms.”*

I profoundly agree with some of the reviewers that claimed for more clarity about the use of phylogenetic niche conservatism (PNC) method here, and in particular that “we postulate that, in the absence of direct experimental evidence for a weevil species, knowledge about other species in a genus may provide an indication of pollination activity” (L. 232-234) needs clarification.

This is a complex point that we tried to clarify in the first version of the manuscript, but we probably did not succeed. In the revised version of the study, we have clarified our approach in a dedicated section of the Material and Methods (see Appendix 1), and have made it clear that this only reflects what can be done with the current state of knowledge:

L. 2000 *“The experimental demonstration of an effective brood-site pollination mutualism requires the observation of breeding sites of larval stage of the putative pollinator and the investigation of pollination efficacy of the adults by a pollinator exclusion method. This time consuming process is rarely conducted, except for a few model systems. In order to integrate a consistent number of relationships without risk of overestimation, we followed the following rationale: BSPM relationships were reported only when, 1) the weevil species is identified at least at tribe level, 2) BSPM relationships has been shown in a congeneric plant or weevil species (phylogenetic niche conservatism, see sections 1 a 2.3.5) and/or 3) plants and/or weevils show typical traits associated with BSPM (see sections 1 and 2). This strategy has clear limitations but reflects the current state of knowledge on these systems and should be seen as a first assessment of their extent in overlooked tropical biomes. When possible, precisions to refine the details or knowledge gap of the relationships reported were indicated (see column “notes” in Table S1).”*

Also, we clarified in the section 2.3.5 the phylogenetic niche conservatism we observed in this system and its implication for the relationships we retained:

L. 844: *“Weevils show a marked pattern of phylogenetic niche conservatism for the specific plant lineages they pollinate. Consistency of association with plant clades is observed at the subfamily, genus or species-group level (Franz & Valente 2005; de Medeiros & Vanin 2020; Haran et al. 2021, 2022b; Figure 1). This consistency is particularly strong at genus level for BSPM relationships (Table S1). In other words, when a BSPM relationship is established for a weevil species, it is highly likely that congeneric species will be also involved in such a relationship.”*

This review is a bit lengthy and deals with many interlocking aspects that sometimes make it difficult to organize it in a consistent way. To avoid breaking the flow of the introduction, we now refer the reader to other sections and supplementary material for more details about the use of the term PNC in this paper:

L. 228: “*Importantly, the majority of weevils engaged in BSPM show a marked pattern of phylogenetic niche conservatism (PNC) at the genus level (Table 1 & Table S1; Franz & Valente 2005; Toon et al. 2020; Haran et al. 2021, 2022b, see section 2.3.5 and appendix 1).*”

I would add plant phylogenetic relationships (widely available) to Figure 1, just for comparison with weevil phylogenetic relationships, even if it means to delete photos, which could be moved to supplementary material, if you consider they are worth (with enhanced quality).

This is a good suggestion and we considered it at first. However, we ultimately decided that adding such a tree overloaded the figure without providing additional relevant information. We agree that plant-insect interactions are often presented this way, but in the case of weevils there are so many independent colonisations of disparate plant lineages that the phylogeny of the plants itself has little meaning (see section 2.3.5 for details). Therefore, we decided to report the main plant lineages involved (Gymnosperms, Angiosperms monocots and dicots) which largely inform the phylogenetic positions of the families included. Lastly, we think it is important to display examples of flowers and inflorescences involved in BSPM, as their structure is discussed in the review. The quality was *de facto* reduced during the generation of the PDF, high quality versions of all figures are available for the final publication and on request for the reviewers if needed.

Even that I understand, and admit, that this review manuscript is mostly narrative, with little quantitative analysis, it could be convenient to provide information of how many reviewed manuscripts contain quantitative vs qualitative, or experimental vs observational information of BSPM. Perhaps it is included in Supplementary Material, but this was not available to the recommender and the reviewers.

Thanks for this suggestion. We added a Material & Methods section (as Appendix 1) detailing the approach followed for the literature review and some features of the articles/data included. We have also taken the opportunity to provide more details on the calculation of the estimates displayed in Figure 2 and section 4.2.

I also agree that Figure 2 is very useful, but it deserves an appropriate treatment in a dedicated section to biogeographical setting of BSPM. By the way, Figure 2 is mentioned in text for the first time in L. 904, much after figures 3, 4...If you include a Biogeographical section much before, you can cite Figure 2 there.

We agree, this information was lacking. We added details on the biogeography in section 1:

L. 267: “*We also show that this type of interaction is currently predominantly found in tropical and subtropical regions of the eastern and western hemisphere, with only a few cases under Mediterranean climates (Figure 2).*”

We also kept this information compact, as there is not much to say without going into too many details.

Figure 2 is mentioned in text for the first time in the Introduction (section 1) L. 269, just after Figure 1.

The section 2.3 “Evolutionary trends” should be renamed, or deleted, and going directly to the subheadings there. There is not information in the manuscript, in the form of phylogenetic reconstructions, as to determine evolutionary trends, transitions or so on. Perhaps only subheading 2.3.5 deserves the title “Evolutionary...”

We thought carefully about how to change this, but after repeated readings of the content of this section, we could not find a better title or arrangement for the plan.

In our view, sections 2.1 and 2.2 are descriptive sections, while (almost) all subsections in section 2.3 have an evolutionary aspect and include reviews of studies with morphological or molecular phylogenies. Therefore they are all labeled with an evolutionary aspect.

2.3.1: host specificity inferred from phylogenetic analyses (see Downie & Williams 2009; Brookes et al. 2015; de Medeiros & Farrell 2020; Haran et al. 2021)

2.3.2: evolutionary process that led to the emergence of sympatric weevil assemblages (see Haran et al. 2021, 2022b)

2.3.3: the emergence of cryptic or closely related species (see Downie & Williams 2009; Brookes et al. 2015; Nunes et al. 2018; de Medeiros & Farrell 2020; Haran et al. 2021, 2022b)

2.3.4: this section discusses the evolution of the system from an ecological perspective with a highlight on the cost-benefit of the interaction.

2.3.5: Dynamic of host use on longer temporal scales (see Franz 2006; Haran et al. 2022).

We are open to further discussion on this point, but in our opinion, the evolutionary aspects developed in this review are probably one of the most interesting aspects. We therefore do not wish to take away this evolutionary dimension from the readers by using inappropriate titles.

#### **Other minor issues:**

or the meaning of “recent phytocentric studies on tropical pollinators” (L. 151), why phytocentric? perhaps it is better “tropical pollination”?

We used the term “phytocentric” in its basic meaning: based/focused on plants. It is used in the review as an adjective to depict pollination studies that provide a lot of detail on plant-related traits but do not focus on pollinator species identity (see details in section 5.2.1). In L. 153, we give examples of two studies that report weevils as important pollinators but not give details on their identity. That said, to avoid ambiguity, we replaced the two occurrences of the term with “plant-focused”

Why do you consider that weevils “passively pollinating...” (L. 194)



Here we meant that even without active deposition of pollen in stigmas (well documented only in the case of *Montella* sp. reported in the review) weevils that visit flower may be pollinators. We removed the adverb for clarity.

What do you mean specifically here for tripartite interactions? (L. 1052).

The sentence has been clarified to make it clearer what we mean by 'tripartite interaction':

L. 811: "*Such tripartite interactions involving a plant, a pollinator and a parasitoid are probably overlooked although they potentially play a significant role for weevil-based BSPM systems.*"

The assumption that "(iii) whether there is a general trend towards specialization of pollination systems in tropical biomes" depends on how specialization is measured (see former comments).

We agree; please see our answer above on the relevance of specialization-generalization in the context of BSPM. Moreover, in this section we do not present an assumption, but a suggestion of the kinds of general questions that weevils and their host plants can help to answer. We clarified the concept of specialization in the previous answer and reworded this sentence to make it clear that it pertains to frequency of BSPM including specialized pollinators, not that the plants are necessarily specialized as well.

Although the manuscript reads well, I am not a native English speaker, thus I would recommend a thoroughly English revision, just to avoid e.g. the use of "pollens" instead "pollen grains" (L. 124). What is the exact meaning of "the flower-visiting and plant oviposition behaviors of several weevil lineages create the context for the evolution of BSPM from antagonistic to mutualistic interactions, or conversely"? (L. 194-196). "Independant" instead, "independent" (L. 819). Is the term "alternative model" correct? (L. 824).

Thank you for pointing out some occurrences of typos and unusual constructions. We thoroughly reviewed the whole text to improve its readability.

Please, go directly to the comments/suggestions/corrections by the reviewers and me and explain in a letter attached to the revised version details of how and where you responded to these issues in the new manuscript. This new version will be reviewed again by at least some of the reviewers and myself.

## **Reviewer 1 Susan Kirmse**

Reviewed by Susan Kirmse, 15 Oct 2022 09:32

Beetles are the most species-rich order of insects. Weevils (Curculionoidea) represent with more than 62,000 described species one of the major radiations among the Coleoptera. All weevils are phytophagous and associated with plants in very different ways. One of the most neglected interactions with plants is their role in pollination. In recent decades, there is

increasing awareness that beetles including weevils provide important pollination services particularly in tropical ecosystems.

Haran, Kergoat and de Medeiros address this important question reviewing all available information about weevil pollination focusing on brood-site pollination mutualism. This mode of specialized pollination is well investigated in the known fig/fig-wasp and yucca/yucca-moth systems. However, brood-site pollination mutualism by weevils exceeds these known systems regarding the number of involved species and their economic importance by far. Still, the research on weevil brood-site pollination is in the beginning.

The authors evaluated possible reasons for the delay in this research including the traditional expectation of antagonistic weevil-plant interactions. Their contribution to the highly specialized brood-site pollination system in weevils sheds light on the intimate and ambivalent relationship between weevils and their host plants. This can invoke a shift in our perception of the role of weevils in the functioning of tropical ecosystems. Moreover, the review gives an impulse to reevaluate evolutionary trends in pollinations systems, specialization in mutualistic interactions, patterns of sympatric coexistence, and diversification in speciose taxa. All in all, the review should be of interest for a wider audience.

Thank you for the very positive review and constructive comments on this study, all points raised have been addressed and are responded to point-by-point below.

There are some general issues which I want to address first: It is necessary to state clearly and differentiate it precisely throughout the entire review, if weevil pollination in general or BSPM are described.

Exactly, we have not made it sufficiently clear that all the weevils discussed in this review are engaged or expected to be engaged in BSPM. This point was clarified in the introduction, when the weevils are first introduced:

L. 141: "*Among the neglected insect lineages involved in BSPM, the weevils (Coleoptera: Curculionoidea) are probably the most overlooked*"

There may be many more instances of weevil pollination other than BSPM. The authors advice on the typical cantharophilous syndrome. According to Bernhardt (2000) there are different flower types pollinated by beetles including brush flowers (e.g. Acacia) which are also visited by weevils. Many of the plant traits mentioned as possible adaptation to BSPM including, for instance, nocturnal and protogynous anthesis and large flowers are widely distributed in many different plant taxa independent of beetle pollination; chambers and thermophily are widely distributed among basal angiosperms associated with different pollination systems (Gottsberger & Silberbauer-Gottsberger 2014). Flowers specialized in pollination, for instance by scarabs (Cyclocephala), share most of the characteristics with BSPM flowers.

We agree on this point, many of the floral traits discussed are found in systems involving other beetle lineages. In the section 2.1 (plant traits), we refer specifically to cantharophily in general, and then we present specific systems involving weevils:

L. 312: *"Flowers and inflorescences of plants engaged in BSPM with weevils generally display typical traits related to cantharophily (beetle pollination) and remarkable convergent morphologies, physiologies, phenology and reproductive strategies."*

Now we added a sentence following that one to clarify that plant traits may not be specific to BSPM and that deserves further research:

L. 314 : *"Some of the traits in these flowers are associated with beetle pollination more generally and not specifically with brood pollination. Disentangling the role of each trait in the interaction is a task that remains to be done in most cases."*

Furthermore, in the second section of 2.3.2 we present a few other groups of beetles that co-pollinate with or replace weevils. This highlights the idea that the plant traits described are not strictly limited to interactions with weevils.

Regarding brush flowers, we have not found any example of weevil-based BSPM involving this flower type (except for the two *Vachellia* species, for which BSPM is only inferred based on the known phylogenetic niche conservatism among the genus *Derelomus*), so it has not been developed in detail in the review. More generally, many weevil lineages are common flower visitors (as they oviposit in fruit or seeds), but this potential contribution to general pollination is not the focus of the review and we decided not to discuss this point.

I doubt that all these plant traits associated with BSMP can be considered really as reciprocal adaptations as Derelomini are much younger than palms and may have just adapted to preexisting conditions.

Indeed, the term 'adaptation' is not appropriate here, we are discussing traits that could be adaptations or maybe even exaptations from prior interactions as suggested by the reviewer, but none of them have been formally identified as an adaptation. The term 'adaptation' has been replaced or nuanced where needed in the revised version of the manuscript.

Specialization in pollination systems may be a point of view and is controversially debated. Regarding the functional group, specialization may prevail (e.g. Fenster et al. 2004). However, there is increasing evidence that pollination networks are highly dynamic with many of them generalized also in the tropics (e.g. Williams & Adam 1994, Petanidou et al. 2008, Simanonok & Burkle 2014, CaraDonna et al. 2017, Drager et al. 2021). Such generalized systems also include palms of the genus *Oenocarpus* (Núñez-Avellaneda et al. 2015) which are jointly visited by a bulk of Curculionidae, Nitidulidae, and Staphylinidae with many species contributing with different efficiency to the pollination.

This is a very valid point, in the case of BSPM involving weevils, interactions are highly species specific from the weevil perspective, see details and arguments in section 2.3.1 'Larval host specificity'. However, this is sometimes less clear from the plant perspective (some palms in particular) where multiple pollinators, with various degrees of specificity, may be involved in pollination (see section 2.3.2 'Sympatric species assemblages'). We reviewed the text to clarify that in most cases we refer to insect specialization, since there is already a section in the text about the asymmetry with plants.

In general, the insects in the BSPM systems reported in this review are specialized (Franz & Valente 2005; Toone et al. 2020; Saunders et al. 2020) and we think that this term is appropriate. We are open to further discussion on this point if needed.

Furthermore, I recommend considering to name the authors of species and genera in the first instance and ask to check the numeration of the pages.

We have carefully considered this suggestion and here are our thoughts: this review has a lot of names but it should be relatively easy to read. One reviewer commented that this review was too long and contained too many scientific names. In order to keep this review as concise and readable as possible, the authors' names have not been included in the main text and have only been reported in Table S1. We believe that readers specifically looking for this information can refer to this table. The caption of Table 1 has been modified to indicate this to readers:

L. 307: “*Table 1. Synthetic list of known plant-weevils BSPM systems. See Table S1 for details on species-specific interactions, **species authorship**, tissues for larval development, presence of cryptic lineages and corresponding reference list.*”

The second part of the manuscript starting from “2.2 Weevil morphology and behavior” seems much better constructed and quite more reasonable discussed.

Thank you, we have reworked the first part of the manuscript in several sections to provide more detail, but also to nuance some terms and statements (following the request of other reviewers). We hope that the whole text is now better constructed and discussed.

In the following, I give a list of detailed comments:

Title: Should be adjusted as it can be misunderstood, e.g. most weevils are brood-site pollinators.

We tried many versions of the title for this review. This is the most compact, informative and eye-catching we could find. In order to make sure to avoid any misunderstanding, we asked colleagues their opinion about the meaning of this title. It does not seem to be a problem, in fact, it is commonly known that many weevils are pests in agriculture and forestry or simply wingless garden beetles, and as such that the majority of this group has no link with pollination.

Abstract:

It is necessary to mention exactly what was reviewed: BSPM studies, basal angiosperms, weevil pollination, cantharophily, ... L 36: plant-weevil mutualistic interactions: there may be many different instances of pollination services provided by weevils (e.g. Baridinae) that exceeds most likely that of BSPM by far. If not all plant-weevil mutualistic interactions are reviewed, I recommend to remain precisely. L 38: plant-weevil associations: Does it concern BSPM or all associations including antagonistic leaf feeders?

We have made the specific objectives of the review clearer:

L. 36: “*This study aims at giving a comprehensive understanding of what is known on **plant-weevil brood-site mutualistic interactions**, through a review of the known (...)*”

L 42: Are these convergent adaptations due to BSPM or beetle pollination in general?

The term ‘adaptations’ has been replaced by ‘features’, and we also reworded this statement to include a reference to beetle pollination in general:

L. 42: “*Strikingly, these mutualistic interactions are **associated with a range of convergent adaptations or traits** in plants and weevils. Plants engaged in weevil-mediated pollination are generally **of typical cantharophilous type** and they also **show specific structures to host the larval stages** of their specialist pollinators.*”

In the second sentence, we also report the specificity found in weevil-based cantharophily (presence of brood site).

L 43-45: Typical cantharophily includes different flower syndromes: I suggest defining the traits of BSPM flowers.

In the revised version, we have clarified the main traits of the flowers examined:

L. 43: “*Plants engaged in weevil-mediated pollination are generally of typical cantharophilous type **exhibiting large, white and fragrant flowers or inflorescences** and they also show specific structures to host the larval stages of their specialist pollinators.*”

Introduction:

I recommend focusing on animal/insect/beetle/weevil pollination as this is the topic. L 105-110: I recommend omitting anemophily in the introduction even if both anemophilous and insectophilous species occur among palms. There are comprehensive studies about anemophily (in what ecosystems and in what taxa it occurs) and the transitions between these modes of pollination. Up to date, it is not clear if or to what extent BSPM has impacted this transition. Instead, it should be focused on the advantages of animal/insect pollination.

We agree with the reviewer that wind-BSPM is not a particularly relevant transition. We start the text with anemophily -> pollination by generalist animals -> pollination by specialized animals -> BSPM -> weevils as a strategy to highlight the context in which specialized pollinators might emerge in more general terms. We consider this as a strategy to engage a broader readership more acquainted with generalist pollinators and perhaps temperate environments.

Approaching weevil pollination from a taxonomic angle (animal/insect/beetle/weevil) may seem as less general by some readers that we would like to reach (ignoring relevant information is one of the causes for the lack of knowledge on weevils engaged in BSPM, as we highlight in the text). Therefore, we believe that approaching the subject from a functional angle (insects -> BSPM -> BSPM weevils) may have a higher success in generalizing the points we make.

L 115-116: This is questionable: generalist pollinators may have preferences and can show flower constancy.

This is true: generalist pollinators with behavioral flexibility may be functionally specialized in specific contexts. But they are still able to choose from a variety of food items, resulting in different dynamics (e. g. Inter-specific competition for pollinators). In the introduction we have tried to be as concise as possible in order to avoid diluting the message. In the revised version, we have modified the corresponding sentence to add more nuance:

L. 117: "*The latter limits the efficiency of generalist pollinators, as they are not constrained to actively seeking out specific plants (Whitehead 1968; Bawa 1990; but see Wolowski et al. 2014).*"

Readers are also referred to the third reference for contrasting examples.

L 117-121: It is questionable if most insect pollinators are specialized or rather generalized flower visitors. There are also arguments why even more generalist pollination systems are maintained in tropical forests.

We agree that there is a debate about the relative importance of specialized vs generalized pollination syndromes in the tropics. Our point is not to contribute to the debate here, but only to tell the reader that systems including specialized pollinators are widespread in tropical biomes (see the cited references: Gottsberger 1986; Bawa 1990; Renner & Feil 1993; Ramirez 2004; Maruyama et al. 2013; Vizentin-Bugoni et al. 2018; Guy et al. 2021). We expect that many readers will have a view on pollination that is strongly influenced by the more diverse generalist pollinators in temperate regions (i.e. bees), so it is important to emphasize that patterns may be different in the tropics.

L 125: Are these really rewards or could it be considered as trade offs?

Good point, the meaning of this is not always clear (semantically but also ecologically, see section 2.3.4). Here we have only employed terms commonly and historically used in the field of brood-site pollination mutualism. In any case, pollinator rewards in general impose some cost on plants (e.g. nectar production) so we do not see breeding sites as substantially different not to be treated as a reward.

L 167: Really all plant-weevil pollination mutualisms?

Thank you for pointing this point, indeed, we are only focusing on BSPM here, the sentence has been reworded:

L. 168: "*The aim of this review is to provide a synthetic overview of all plant-weevil **brood-site pollination mutualisms** described to date.*"

## **1. A wide spectrum of mutualistic interactions**

L 193: Not all weevils have a narrow host range.

The weevil lineages discussed in this sentence (tribes developing in seed/flowers at larval stages) are generally mono- or oligophagous (see Caldara et al. 2014 for a review). We have clarified this statement to avoid misunderstanding:

L. 192 “Weevils **in these clades** generally visit flowers when feeding on pollen and ovipositing in buds, ovaries and fruits where larval development occurs (Oberprieler et al. 2007; Caldara et al. 2014).”

L 228: Perhaps the kind of PNC could be explained shortly.

This is a critical point, as many of the relationships discussed in this review are based on PNC in absence of direct evidence of BSPM. We think it is important to discuss our approach in detail, and other reviewers have asked for more detail on this. We have tried to keep this information as concise as possible in the introduction, the details on the approach have been presented in a “Material and Methods” section available in Appendix 1.

L 232: Does it refer to all plants or to palms? This should be better explained.

We refer here to all interactions, please see sentence above:

“Importantly, the majority of weevils engaged in BSPM show a marked pattern of phylogenetic niche conservatism (PNC) at the genus level (Table 1, & Table S1 & appendix 1)“.

L 278: Adaptations of the flowers to cantharophily could involve different beetle families.

We have reworded this sentence to clarify this statement:

L. 275: “Overall, BSPM with weevils has been demonstrated experimentally in 12 of the 22 plant families involved in this mutualistic system, with the remaining 10 families suggested based on both PNC of weevil genera and **traits of floral structures associated with cantharophily.**”

## **2. Reciprocal adaptations**

### **2.1 Plant adaptations to BSPM by weevils**

Most of these adaptations mentioned can be found in any kind of beetle pollinated flower or can be found in insect pollinated flowers in general; better “plant traits associated with BSPM”.

The subtitle was replaced by “2.1 Plant traits”. The first part of this section indicates that these traits are related to those encountered in cantharophily in general.

L 317: Larger floral structures attract greater numbers of many flower visitors not only weevils (see resource concentration hypothesis).

We agree with this, but in the specific case discussed in this section (Annonaceae flowers and Cyclanthaceae inflorescences, see references), these pollinators happen to be weevils. We rephrased to make the statement more general:

L. 328: *"Field observations and experiments on various Annonaceae flowers and Cyclanthaceae inflorescences show that larger floral structures attract greater number of pollinators (Gottsberger 1999; Franz 2007a), revealing that this floral trait has been independently selected to increase weevil attraction and pollination."*

L 329: Are flower buds and fruits inside chambers?

Thank you for pointing out this mistake, the buds have been removed from this list as well as the fruits. The latter refers to the orchids *Diachea* that do not form typical flower chambers.

L 341-344: Do staminodes provide shelter and protection?

Yes, see observations on weevil behavior in Franz (2007a) and Armstrong & Irvine (1990).

L 370-371: This applies to Cyclocephala scarabs as well (though they are not brood-site pollinators); IR (abbreviation).

We clarified that this applies to other insects by rephrasing. Infrared has been written in full.

L. 380: *"This phenomenon is postulated to act as an attractant for weevil and **other beetle pollinators,**"*

L 420: There are also generalist nocturnal flower visitors and specialized diurnal visitors.

We agree, the corresponding hypothesis has been deleted.

### **3. Economic importance and conservation**

L 848: While plant-weevil BSPM probably emerged to balance pollination constraints: this is highly questionable.

This statement has been nuanced in the revised version of the manuscript:

L. 891: *"More generally, while plant-weevil BSPM probably emerged to balance **some** pollination constraints in tropical biomes, it is also a risky evolutionary"*.

We refer here to pollination limitation, a constraint that has been demonstrated in several BSPM systems involving weevils (Franz 2007a; Nunes et al. 2018).

#### **Figures:**

Figure 1: The expected numbers are based on what? The number of species within a plant genus in concordance with niche conservatism? I recommend explaining this better.

The 'expected numbers' are those inferred on the basis of PNC. In the following sentences we explain briefly the approach and refer to the method (Appendix 1) for more details.



L. 279. “Most of the plant families reported here contain at least one experimentally verified case of BSPM; however, for the plant families highlighted with an “\*”, BSPM interactions are postulated based on the phylogenetic niche conservatism of the weevil genera involved (see method in appendix 1).“

Figure 2. Geographical distribution of weevil lineages: the weevil lineages (e.g. Molytini, Brentidae) are more widely distributed: I suggest specifying, for instance, “geographical distribution of known BSPM in relation to weevil lineages”.

The caption has been reworded as follow:

L. 292: “Geographical distribution of brood-site pollination mutualism (BSPM) involving weevil lineages and estimates of knowledge gaps”.

Figure 4. Better?: Dorsal habitus of weevils ...

The caption has been modified accordingly.

### References:

The following references should be checked in the text and in the reference list, and there are a few mistakes in the alphabetical order in the reference list.

Anstett & Dufay 2003 XX reference in the text corrected

Barfod et al 1987 XX this reference does not appear in the manuscript, it is only quoted in the database (Table S1). It was removed from the reference list of the main text.

Chomicki et al. 2020 XX year in the reference list corrected

Couvreur & Baker 2013 XX order of authors names checked

Franz 2007 XX reference specified for the two papers published this year (a,b)

Franz NM & O'Brien 2001 XX quote in the manuscript corrected

Haran et al. 2022 XX reference specified for the two papers published this year (a,b)

Haran et al. 2020a XX “a” removed in the manuscript (unique reference)

Hsiao & Oberprieler 2020 XX correct date (2022) double checked

Kirmse & Chaboo 2020 XX order in reference list corrected

Küchmeister et al. 1998 XX reference added to the manuscript

Marshall 1933a XX “a” removed for this single reference

Mora-Urpí et al. 1997 XX reference deleted

Núñez-Avellaneda et al. 2017 XX transferred to the references associated with Table S1

Saunders 2012 XX recte : Saunders 2020 : checked in all the text Silberbauer-Gottsberger

Scariot et al. 1991 XX transferred to the references associated with Table S1

Silberbauer 1990 XX correct name "Silberbauer-Gottsberger" added

Syed et al. 1981 XX correct publication date (1982) verified.

Valente et al. 2019 XX reference added to the manuscript

Vaurie 1968 XX transferred to the references associated with Table S1

## Reviewer 2 anonymous

Reviewed by anonymous reviewer, 22 Nov 2022 19:57

additional minor comments here :

[https://ecology.peercommunityin.org/stream\\_pdf/t\\_reviews.review\\_pdf.aa45809c79e5b7ea.5072657072696e7420486172616e20657420616c2e205265766965772077656576696c20706f6c6c696e6174696f6e2074726f706963735f5265762e706466.pdf](https://ecology.peercommunityin.org/stream_pdf/t_reviews.review_pdf.aa45809c79e5b7ea.5072657072696e7420486172616e20657420616c2e205265766965772077656576696c20706f6c6c696e6174696f6e2074726f706963735f5265762e706466.pdf)

The manuscript bring a very interesting revision on the role of weevils beetles as pollinators in rainforests. They bring some ideas regarding phylogeny of weevils and their respective host plants. Besides of great importance to help to put this group of insects in the "hall of fame of pollinators", I think that the idea is very ambitious. The manuscript is too long and hard to follow. The authors describe many names of plants and weevil, but there is no information regarding the site of occurrence. Should be interesting if the authors could put this information in the table 1. I did not found the supplementary table.

Thank you for the constructive comments on our article. The manuscript is indeed long, but we have done our best to make it as concise as possible, with a detailed plan to make the ideas as organized and easy to follow as possible. The subject matter covers a lot of aspects (ecology, evolution, systematics, etc) and it is difficult to reduce the text without removing critical points. We assume that a review is the ideal place to develop long and complex ideas, but we are open to discuss if specific points seem unnecessary.

We have decided to illustrate our arguments with many detailed examples and several comments in this first round of review specifically asked for more details in several sections. We think it is appropriate to give detailed examples with scientific names in this review as 1) it reinforces the arguments on the importance of BSPM involving weevils (not just a concept, there are documented examples) and 2) it will help the reader to find his study of interest into the "bush" of papers published on this topic.

The geographic location of the systems discussed was indeed missing in several cases. We have added relevant indications where necessary (e.g. see the sections on Cycads and Eupomatiaceae in section 1). In the last subsection of section 1, we have better described the overall distribution of the discussed interactions. Figure 2 is an attempt to provide an overview of the distribution range of the lineages listed in Table 1.

Table S1 was not attached to the first submission due to format constraints of the preprint (size and format issues). We will try to attach it for this revised version. We can also send it directly under request.

Specific comments:

L. 32- and bees as the most important.

Bees are indeed a major group of pollinators, and we mention this in the introduction (see section starting by “*Of the neglected lineages (...)*”). In the abstract we have tried to be concise and focus on brood-site pollination mutualism, which is the aim of this review.

L. 45- This is more common for scarab beetles, no?

Indeed, these characteristics are not limited to weevils and have been described for several beetle-based pollination systems, including scarabs. In order to keep the abstract concise, we do not elaborate on this idea in detail, and we only refer to cantharophily in general:

L. 43: “*Plants engaged in weevil-mediated pollination are generally of **typical cantharophilous** type exhibiting large, white and fragrant flowers or inflorescences and they also show specific structures to host the larval stages of their specialist pollinators. Another characteristic feature is that flowers often perform thermogenesis and exhibit a range of strategies to separate sexual phases, either spatially or temporally*”.

This statement is also developed in section 1 (plant traits):

L. 312: “*Flowers and inflorescences of plants engaged in BSPM with weevils generally **display typical traits related to cantharophily (beetle pollination)** and remarkable convergent morphologies, physiologies, phenology and reproductive strategies. All these characteristics enhance the attractiveness of flowers to weevils, provide them with food rewards, and sometimes protect them from predators; they also improve pollen transfer to weevil integuments and play a role in weevil pollinator selection and retention, thereby improving pollination efficiency.*”

L. 308- This is only for plants from rainforest? Because there is many species of Asteraceae, Eriocaulaceae and Cyperaceae, that have BSPM and have single flowers or small flowers

This section refers to the weevil-based BSPM only, we have not included characteristics of other systems to avoid “diluting” the message:

L. 321: “*A first **major characteristic for weevil-pollinated plant lineages** is that they tend to display large flowers or inflorescences (Figure 1).*”

Table 1- Should be interesting if you include a row with the location of occurrence of the species. For example: Amazon rainforest, Brazil, or Rainforest of Congo...

We have tried to make this information available and easy to read in Figure 2. Readers can see the correspondence of the distribution via the names of the weevil lineages (see captions in the bottom right of the figure). We find this an appropriate approach to condense the extensive information about the geographic locations. We have made an addition to the caption of Table 1 to clarify this point:

L. 307: “*Table 1. Synthetic list of known plant-weevils BSPM systems. See Table S1 for details on species-specific interactions, species authorship, tissues for larval development, presence of cryptic lineages and corresponding reference list. See figure 2 for geographic distribution of the weevil lineages involved in BSPM.*”

## Reviewer 3 Carlos Eduardo Nunes

Reviewed by Carlos Eduardo Nunes, 17 Nov 2022 18:11

General comments to authors and editors

additional minor comments here :

[https://ecology.peercommunityin.org/stream\\_pdf/t\\_reviews.review\\_pdf.b66e78b1ef3052c9.5072657072696e7420486172616e20657420616c2e205265766965772077656576696c20706f6c6c696e6174696f6e2074726f706963735f7265765f4345504e2e706466.pdf](https://ecology.peercommunityin.org/stream_pdf/t_reviews.review_pdf.b66e78b1ef3052c9.5072657072696e7420486172616e20657420616c2e205265766965772077656576696c20706f6c6c696e6174696f6e2074726f706963735f7265765f4345504e2e706466.pdf)

Dear Authors and Editors,

In this manuscript, the authors present a thorough review, extremely rich in details and insights. The manuscript is well succeeded in providing good evidence to support the point featured in the title. The authors make it clear to the reader what and where are the knowledge gaps, paving a long avenue for future research on the topic.

Notwithstanding, the paper can be improved by the addressing of minor issues and corrections (listed in the attached pdf). Moreover, I have a couple of specific comments related to the weevil-pollination system I am more familiar with (listed below and in the pdf). Thereby, I recommend the publication after Minor Revision.

I have no concerns in publicizing my identity as a reviewer if the policy of this publication platform allows.

Best regards,  
Carlos E. P. Nunes

Thank you for your positive appreciation of this study and for the detailed and insightful comments made on several points of the study. All comments have been taken into account, details on the corrections/additions made are provided below.

#### Specific comments to authors

Line 603 (2.3.1. Larval host specificity): Regarding host attraction specificity, Nunes et al. (2016, reference below), describe the attraction of *Montella* weevils to 2-methoxy-4-vinylphenol emitted by *Dichaea pendula*. Curiously, the *Montella* species attracted to *Dichaea pendula* in the populations studied is not able to complete its cycle on most of the flowers the the weevils pollinate as the plant is self-incompatible and female weevils only perform self-pollination. The active-pollinating *Montella* weevils, were found to complete their cycle in *Dichaea cogniauxiana*, a self-compatible species in which weevils proved to achieve successful flower fertilization. Thus, in this orchid-weevil system, the breeding system of the plant is essential to determine the mutualistic character of the plant-insect association.

Nunes, C. E. P., Peñaflor, M. F. G. v., Bento, J. M. S., Salvador, M. J., & Sazima, M. (2016). The dilemma of being a fragrant flower: the major floral volatile attracts pollinators and florivores in the euglossine-pollinated orchid *Dichaea pendula*. *Oecologia*, 182(4), 933–946. <https://doi.org/10.1007/s00442-016-3703-5>

Line 184: This sentence refers only to plant lineages, so we have purposely not addressed the emergence of other groups of organisms. We also kept the sentence “rise to dominance” as it depicts clearly what we meant: angiosperms diversified and became dominant at that time scale (see details in the references quoted: Dilcher 2000; Magallón & Castillo 2009; Benton 2010).

Line 184: “*Syagrus*” has been corrected and checked throughout the text. The spelling of names in the table has been double checked as well.

Line 418: “orchid” has been added to the exceptions. Thank you for pointing this out.

Line 603: Regarding host attraction specificity, Nunes et al. (2016), describe the attraction of *Montella* weevils to 2-methoxy-4-vinylphenol emitted by *Dichaea pendula*. Curiously, the *Montella* species attracted to *Dichaea pendula* in the populations studied is not able to complete its cycle on most of the flowers the the weevils pollinate as the plant is self-incompatible and female weevils only perform self-pollination. The active-pollinating *Montella* weevils, were found to complete their cycle in *Dichaea cogniauxiana*, a self-compatible species in which weevils proved to achieve successful flower fertilization. Thus, in this orchid-weevil system, the breeding system of the plant is essential to determine the mutualistic character of the plant-insect association.

Nunes, C. E. P., Peñaflor, M. F. G. v., Bento, J. M. S., Salvador, M. J., & Sazima, M. (2016). The dilemma of being a fragrant flower: the major floral volatile attracts pollinators and florivores in the euglossine-pollinated orchid *Dichaea pendula*. *Oecologia*, 182(4), 933–946. <https://doi.org/10.1007/s00442-016-3703-5>

This is a very interesting point that we missed during the literature review process. We have added a sentence in the relevant section and added the corresponding reference to the list:

L. 654: *“Also, in the Montella weevils actively pollinating Dichaea cogniauxiana, the adult visit the flowers of another orchids species (D. pendula), but can only perform their life cycle in the former due differences in self-compatibility of reproductive system (Nunes et al. 2016).”*

lines 771-777: Here it is important to note that Nunes et al. (2018) observed similar Montella weevils (Bariditae, Conoderinae) ovipositing on the ovaria of orchid flowers. Some of the species actively pollinated the flowers they used, being thereby able to establish mutualistic interactions in certain circumstances, while other species did not pollinate the flowers they used, acting only as florivores. This raises the question of whether the active pollination behaviour is ancestral or not among the Montella genus, a group apparently specialized in the orchid family. Thus, I suggest that in your review you explore more the questions of where, when, and in which ecological context, active pollination behaviour evolved in weevils.

Thank you for the detailed explanations. We have reworded the sentences associated with the 2018 paper based on your suggestions. Regarding the question of the ecological context promoting the emergence of pollination behavior, this is indeed a very stimulating question, but we can only formulate hypotheses at this stage (there is no paper dealing specifically with this question). These questions and hypotheses are listed in the section 5.2.2 “Evolutionary trajectories: when, why and how?”. For your information, we are in the process of completing a separate paper on this topic, with new insights into the life strategies of weevils that favored the shift toward brood-site pollination mutualism.

Line 802: What about the dates of origin of the specific groups of palms Derelomini pollinate? Are they more ancient too? Do you have this more specific information? If so, please provide it briefly here.

This is a good point, but there is no specific clade of palms that Derelomini pollinate (e.g. see the phylogenetic tree in Baker et al. 2011 and other Baker’s papers). These interactions have been described in palm clades spread across most of the palm family tree.

## Reviewer 4 anonymous

Reviewed by anonymous reviewer, 01 Dec 2022 16:09

### OVERVIEW

This review about the diverse and overlooked curculionid beetles as specialised brood-site pollinators is a relevant, timely, informative and thought-provoking piece. It is very well written throughout, scholarly referenced, well documented. By flashing the spotlight towards weevils as specialist brood-site pollinators, this paper contributes to shifting the 'tradition' of ignoring weevils in flowers because they are bad pollinators or even flower enemies. I think this review could inspire future research in a so far highly overlooked area of pollination biology. I only have two main concerns: 1) the lack of details on the procedures/methods to estimate the

expected numbers of weevil BSPM yet to be found which the authors report and plot in Figure 1. Documenting in detail the methods used to produce these estimates 'de novo' (not reviewed from the literature) is crucial for science rigour and repeatability. 2) Quantitative evidence is often lacking with many comparisons and arguments very often relying only on verbal comparisons or statements, hence quantitative evidence (numbers, data) is needed to strengthen a few arguments. The rest of my comments are mainly suggestions to improve the flow and clarity of particular paragraphs, adding more context or diving further into the details of some aspects to give a more rounded opinion or an overview rather than just valuable case-study findings, as well as some minor edits to the figures and legends.

I would strongly endorse the manuscript, pending the two major concerns voiced above and detailed below (marked with “\*\*\*\*”) are revised.

Thanks for your positive comments on this manuscript and very useful suggestions on several critical points. All concerns and comments have been taken into account, a point-by-point response is provided below:

## COMMENTS

L46: Consider rewording to spatially and temporally. In my opinion, that jargon is more often used and sometimes it helps readers to give them the common/keywords to help them link concepts rapidly.

Thanks for this suggestion, the sentence has been modified accordingly.

L124: pollen, no S

This mistake has been corrected.

Figure 1. What does the purple box stand for? Not mentioned in the legend. Why is it coloured differently?

This box had a different color because it corresponds to a distinct subfamily within the CCCMS clade. We have kept the contrast, but replaced the purple by blue to avoid misinterpretation.

Figure 2. Really nice figure condensing lots of information. But I think the y-axis of the barplots needs to be labelled in the figure, even if briefly due to space constraints (# relationships).

Thanks for this suggestion: “species nb” has been added as a label for the y-axis. The explanation has also been included in the caption.

L351-362: The phrase 'in an opaque cloth' comes as a bit of a surprise. I think context about the experiment should be given before in this paragraph to continue with an easy-read and fluid manuscript.

Indeed, we have reworded as follow to clarify the sentence:

L. 367: *“In contrast to those experimentally shaded by an opaque fabric”.*

L373-374: Thermogenic activity is not maintained once insects enter flowers--> It would be nice to have a few more lines deepening the knowledge and details on this very niche topic.

This sentence has been reworded to give more details on the context of this thermogenesis:

L. 383: *“but this is likely not the case for weevils since thermogenic activity is usually correlated with short phases of attraction/repulsion and is not maintained during the interim phase when individuals stand on flowers or are enclosed in floral chambers”.*

We have deliberately not given more details on circadian cycles, morphology etc ... as these topics are developed in other subsections of section 2.1.

L379-380: Temperature increases can also repel insects from the flowers.--> Again a few more lines with further details on this would be greatly appreciated. It is a fairly niche and unknown topic by most, as the authors' title points out.

See answer of the comment below.

L374-380: This paragraph gives examples of flower temperature being used to attract and repel insects, but no overview statements is provided, and so these can seem as two contradicting sentences. I think giving more details in each of the cases (attract/repel) will help, as stated in the comments above. But also, perhaps giving an overarching statement explicitly stating that indeed, temperature can be used to +/- pollinators and so overall enhancing pollination efficiency via pollinator relocation (?) would be a good way of tightening this paragraph. Perhaps it can even make a punchier topic sentence.

We agree, so we have reworded this section to give more detail on this important aspect (including examples of specific study cases):

L. 389: *“In several systems (Carludivicoideae-Derelomini; Zamiaceae-Belidae), the first peak of thermogenesis associated with the attraction phase of the weevils is followed, after an interim phase of several hours, by a second peak where weevils leave the inflorescences (Franz 2007a; Teichert et al. 2018; Salzman et al. 2020). These second peaks of thermogenesis coincide with the staminate phase and probably act as repellent or as an aid for improved take-off that favors weevil departure once they are covered in pollen (Teichert et al. 2018). This kind of push-pull mechanism where weevils are successively attracted and then repelled during the circadian flowering cycle promotes pollinator movement between plant congeners and thus cross-pollination (Salzman et al. 2020).”*

If my above interpretation is correct, then it maybe implies that some beetles like it hot and some species like cooler? So are there species-specific differences in temperature preferences? Might be nice also adding something about the implications of these for speciation. Or perhaps it is that flowers go beyond or below the common threshold of 'acceptable temperature' to repel weevils? Really curious to know more about this and I think other readers would be too.



For the first point, not really, the species attracted and repelled are the same, but the plant uses some peaks to attract and others to repel. This is probably clearer in the new layout of the section (see above). For the second point, yes, it is likely that the temperature threshold differs (second peak slightly higher in temperature). This has been demonstrated in the cycad-thrips system, but not in systems involving weevils to our knowledge, so we decided not to develop this aspect in detail in this review.

(\*\*\*)L427-428: Really thought-provoking observation/fact. I am eager to see more research on this in the near future! But just wanted to make sure this 'all' is a quantitative fact. Perhaps it would be good to make a more quantitative statement, such as 'of the ### of plants with BSPM, so far all plant species have separate sexes, which is striking given that the vast majority of plant species have joint sexes.' or something along those lines.

We have made this statement clearer in the text, with the percentage of species involved and gave more context on dioecy to reinforce the message:

L. 444: *“A remarkable feature of plant lineages engaged in BSPM with weevils is the separation of sexes. About 95% of the species recorded in this review show a physical or functional dioecy, a feature yet rare in the plant kingdom in general.”*

Format: Page numbers have been muddled up when figures come in.

Page numbers have been corrected.

(\*\*\*)L483-486: I think this statement needs to be toned down and reinforced with quantitative evidence available so far. Toned down: are there any empirical or direct evidence of the magnitude of selection operating on the camouflage of weevils in flowers? If so, please provide it. Otherwise, very valid observation but needs to be toned down further, perhaps stating that there is actually no quantitative evidence so far (inviting for research) and strengthening the valid observational argument with the proportion or % of cases showing flower camouflage. Same for how this pattern is more prevalent in diurnal species, claiming it as an hiding adaptation. Adding quantitative evidence available so far of % of camouflaged diurnal species versus % camouflaged nocturnal ones will really strengthen this.

The message has been toned down, as suggested:

L. 504: *“Overall, there **seems** to be a selective pressure to mimic floral substrates as suggested by the various examples of strongly converging phenotypes among unrelated species associated with the same host plant (e.g., *Derelomus pallidus* and *Ebenacobius rectirostris* on *Euclea racemosa*; Haran et al. 2022b; Figure 4A, B), **but whether these phenotypes really provide an advantage to escape predation has not been formally explored**. Interestingly, patterns of mimicry are **generally** found in species active during the day on inflorescences, with little or no space to hide (i.e. most *Derelomini* associated with *Areaceae* or *Ebenaceae*). Conversely, weevil lineages that remain hidden in floral chambers or inflorescences during the day, the integuments are **usually** pale brown or reddish in color, and they do not specifically match floral substrates (e.g., in *Cyclanthura*; *Ochyromerini*; Figure 4C, F).”*

L497: Are these pollen-carrying morphologies exclusively found in BSPM weevils? More comments on this would be helpful to understand whether this may be adaptations that evolved over the BSPM interactions, or whether they were pre-existing features which now serve a new function under BSPM (exaptations).

We have clarified this sentence; setae are indeed widespread in weevils:

L. 519: “A series of putative pollen-carrying morphologies are found in weevils engaged in BSPM. Most of these lineages have species with erect setae on their body surface (Haran et al. 2020, 2022a; Dao et al. 2023). **Hair or scale cover on integument are widespread in weevils, so these may represent instances of exaptation. However, their peculiar size or arrangement in some lineages acting as brood-site pollinators led to suggestions that they could have evolved to enhance pollen transport (Syed et al. 1982).**”

(\*\*\*)L546: Really nice powerful argument, but again it would benefit from some quantitative statement. It would good to compare weevils flight abilities to those of stereotypically good pollinators such as honeybees or native bees or hoverflies. Not an exhaustive comparison, just a couple of hard data to back up this argument that their flight abilities are as good or even better than those of 'gold' pollinators.

We could not find a single experimental study testing the maximum flight distances of a weevil engaged in BSPM. We have added a sentence to explain what is known on this:

L. 590: “Weevils engaged in BSPM likely have 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). **This is supported by experimental data in other small weevils, which are capable to fly up to kilometers in flight mills (McKibben et al. 1998; Evenden et al. 2014) and by our own experience in collecting specimens on isolated hosts, suggesting that they can move over long distances (J. Haran and B. de Medeiros pers. obs.).**”

L559-561: So many push-pull tricks using the same cue in these interactions! Interesting :)

Yes, it is remarkable that such divergent plants have apparently converged on similar “solutions” to cope with weevil pollination !

L761-764: I do not think the authors have actually stated or summarised why this costly form of pollination which can destroy 80% of seeds in some cases is evolutionarily stable and maintained. They refer to other case studies as examples, but as a review article, this comment needs to be spelled out in this paragraph. Why is this maintained? What have these other studies concluded? Please review this here.

Thanks for this warning, we have double-checked the manuscript and reworded the sentence appropriately:

L. 786: “Such a benefit is, however, less evident when the flower buds or seeds are destroyed during the larval development of the weevils, and sometimes it even results in a sharp reduction in the fitness of the host. For example, brentids in the genus *Antliarhinus* are ovule

*parasites that can destroy up to 80% of the seeds of their cycad host Encephalartos. Despite this, adults have been shown to contribute 10% to the cross-pollinating their host (Donaldson 1997). “*

Is this related to promoting cross-pollination over selfing? Do we know anything about the ploidy levels of plants who pay high costs? I expect plants with lower ploidy to be more susceptible to inbreeding depression from selfing or geitonogamy than plants with higher ploidy levels.

This is a very interesting thought. We are not aware of any work linking ploidy levels and reliance on weevil pollination for cross-pollination. We will keep this idea for future research. In the context of the review, we do not address this point to avoid overly speculative statements.

L77-792: Really cool transitions to cheaters! Looking forward to future research on the arms race examples of this to come.

An exciting idea indeed, although determining precisely who is a pollinator and who is a cheater is very time consuming. Applying these questions on an entire group of weevils would be a lifetime research project !

L940-944: Not clear to me what the intended comparison between neo and paleo tropical species actually is. Please reword to spell this comparison clearly. This is one of the few paragraphs which are hard to read through. Perhaps use some of the concluding sentence as a topic sentence, saying that the only known specialised pollinators of Annonaceae are in the paleotropical regions, and none have yet. Not clear to me if these relationships have not been described or they are not specialised.

We have tried to rework this section to make it clearer:

*L. 988: “). This set of interactions requires further investigations in this region since the weevil lineages involved remain unidentified and possibly include undescribed lineages (the pollinators of Annonaceae reported (Ochyromerini) are exclusively paleotropical; Alonso-Zarazaga & Lyal 1999).”*

(\*\*\*) L970-980: Not enough (almost no information) detail is given on how the PNC-derived estimates of expected weevil BSPM systems are obtained or calculated. A detailed, repeatable account of such methods is required, either in the main text or referenced as a supplementary, but such procedures are certainly essential for this paper and are currently missing.

The method and details on how the estimates were calculated are provided in Appendix 1 and reference to this supplementary material has been cited in the text.

L1024-1041: Are these weevils hard to identify to species level? (Like some flies which are famously hard to identify for requiring careful examination of the fly genitalia). Are there abundant and suitable keys? I guess the answer to all these is no, but these issues should also be spelled out as part of the 'resistance' or challenges to taxonomic identification.

Yes, see details on the complexity of the groups in section 2.3.3. Furthermore, many genera have simply never been formally treated (taxonomic revision) and a large number of species are still awaiting description. We have made this clear in the sentence:

L. 1075: *"A better understanding of the diversity and functioning of plant-weevil BSPM systems requires detailed studies of the corresponding interactions (Fenster et al. 2004), but also of the identity and boundaries of the species involved. To date, too many plant-weevil BSPM studies have a focus on plants and poorly account for pollinator identity. **This is partly due to the complexity of the taxonomy in these groups (species complexes, small sized species) but also to taxonomic shortfalls.**"*

In this case, then perhaps DNA is the best tool, no? I perceive some anti-DNA id sentiment in this paragraph, when my thought as a non-beetle expert on this would be that DNA would be very helpful is taxonomic id is challenging. If that anti-DNA sentiment is not the authors' opinion, consider rewording this slightly. If it is your opinion, then it is well communicated.

We did not intend to give an anti-DNA message here, much of the review highlights the progress made by molecular tools in understanding of BSPM and all the co-authors are familiar with these approaches. On the contrary, we specifically advise to use DNA barcoding when taxonomic expertise is not available:

L. 1086: *"When expertise is not available, we strongly recommend producing at least one DNA barcode sequence for each weevil morphospecies involved in a system and depositing it on international databases"*

That said, we have reworded one of the sentences to make it clear that the recommendations to clarify the taxonomy of these groups include molecular tools.

L. 1083: *"Taxonomic descriptions are essential prerequisites for any study of pollination in the highly specialized plant-weevil BSPM systems, and this effort must be made with the relevant expertise of trained taxonomists using **an integrative approach based on morphology and molecular tools** (Toon et al. 2020; Engal et al. 2021)."*

L1051: I would consider replacing the word relationships with interactions here and throughout the document. Again, just because it is a triggering keyword in evolutionary ecology.

"Relationships" has been replaced by "interactions" in all the text.

L14061-1063: Discuss more concretely what genomic research questions; this sounds a bit vague, a bit too much hand-waving.

This sentence has been deleted, as genomic data can only be considered as a tool to answer the questions suggested in section 5.2.2.

L1065-1073: I do not think this paragraph adds anything new or central or specific. I suggest deleting it. The Anthropocene is challenging for all living creatures and no particular example is given here for its special relevance for weevils BSPM.

This section has been deleted. Some elements relating to the evolution of BSPM in a context of human-induced disturbance have been transferred to the previous section.