Peer Community In Ecology

Pollination-herbivory by weevils claiming for recognition: the Cinderella among pollinators

Juan Arroyo *based on peer reviews by* ***Susan Kirmse***, ***Carlos Eduardo Nunes*** *and 2 anonymous reviewers*

Julien Haran, Gael J. Kergoat, Bruno A. S. de Medeiros (2022) Most diverse, most neglected: weevils (Coleoptera: Curculionoidea) are ubiquitous specialized brood-site pollinators of tropical flora. HAL, ver. 2, peer-reviewed and recommended by Peer Community in Ecology. https://hal.inrae.fr/hal-03780127

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Since Charles Darwin times, and probably earlier, naturalists have been eager to report the rarest pollinators being discovered, and this still happens even in recent times; e.g., increased evidence of lizards, cockroaches, crickets or earwigs as pollinators (Suetsugu 2018, Komamura et al. 2021, de Oliveira-Nogueira et al. 2023), shifts to invasive animals as pollinators, including passerine birds and rats (Pattemore & Wilcove 2012), new amazing cases of mimicry in pollination, such as "bleeding" flowers that mimic wounded insects (Heiduk et al., 2023) or even the possibility that a tree frog is reported for the first time as a pollinator (de Oliveira-Nogueira et al. 2023). This is in part due to a natural curiosity of humans about rarity, which pervades into scientific insight (Gaston 1994). Among pollinators, the apparent rarity of some interaction types is sometimes a symptom of a lack of enough inquiry. This seems to be the case of weevil pollination, given that these insects are widely recognized as herbivores, particularly those that use plant parts to nurse their breed and never were thought they could act also as mutualists, pollinating the species they infest. This is known as a case of brood site pollination mutualism (BSPM), which also involves an antagonistic counterpart (herbivory) to which plants should face. This is the focus of the manuscript (Haran et al. 2023) we are recommending here. There is wide treatment of this kind of pollination in textbooks, albeit focused on yucca-yucca moth and fig-fig wasp interactions due to their extreme specialization (Pellmyr 2003, Kjellberg et al. 2005), and more recently accompanied by Caryophyllaceae-moth relationship (Kephart et al. 2006).

Here we find a detailed review that shows that the most diverse BSPM, in terms of number of plant and pollinator species involved, is that of weevils in the tropics. The mechanism of BSPM does not involve a unique

morphological syndrome, as it is mostly functional and thus highly dependent on insect biology (Fenster & al. 2004), whereas the flower phenotypes are highly divergent among species. Probably, the inconspicuous nature of the interaction, and the overwhelming role of weevils as seed predators, even as pests, are among the causes of the neglection of weevils as pollinators, as it could be in part the case of ants as pollinators (de Vega et al. 2014). The paper by Haran et al (2023) comes to break this point.

Thus, the rarity of weevil pollination in former reports is not a consequence of an anecdotical nature of this interaction, even for the BSPM, according to the number of cases the authors are reporting, both in terms of plant and pollinator species involved. This review has a classical narrative format which involves a long text describing the natural history behind the cases. It is timely and fills the gap for this important pollination interaction for biodiversity and also for economic implications for fruit production of some crops. Former reviews have addressed related topics on BSPM but focused on other pollinators, such as those mentioned above. Besides, the review put much effort into the animal side of the interaction, which is not common in the pollination literature. Admittedly, the authors focus on the detailed description of some paradigmatic cases, and thereafter suggest that these can be more frequently reported in the future, based on varied evidence from morphology, natural history, ecology, and distribution of alleged partners. This procedure was common during the development of anthecology, an almost missing term for floral ecology (Baker 1983), relying on accumulative evidence based on detailed observations and experiments on flowers and pollinators. Currently, a quantitative approach based on the tools of macroecological/macroevolutionary analyses is more frequent in reviews. However, this approach requires a high amount of information on the natural history of the partnership, which allows for sound hypothesis testing. By accumulating this information, this approach allows the authors to pose specific questions and hypotheses which can be tested, particularly on the efficiency of the systems and their specialization degree for both the plants and the weevils, apparently higher for the latter. This will guarantee that this paper will be frequently cited by floral ecologists and evolutionary biologists and be included among the plethora of floral syndromes already described, currently based on more explicit functional grounds (Fenster et al. 2004). In part, this is one of the reasons why the sections focused on future prospects is so large in the review.

I foresee that this mutualistic/antagonistic relationship will provide excellent study cases for the relative weight of these contrary interactions among the same partners and its relationship with pollination specialization-generalization and patterns of diversification in the plants and/or the weevils. As new studies are coming, it is possible that BSPM by weevils appears more common in non-tropical biogeographical regions. In fact, other BSPM are not so uncommon in other regions (Prieto-Benítez et al. 2017). In the future, it would be desirable an appropriate testing of the actual effect of phylogenetic niche conservatism, using well known and appropriately selected BSPM cases and robust phylogenies of both partners in the mutualism. Phylogenetic niche conservatism is a central assumption by the authors to report as many cases as possible in their review, and for that they used taxonomic relatedness. As sequence data and derived phylogenies for large numbers of vascular plant species are becoming more frequent (Jin & Quian 2022), I would recommend the authors to perform a comparative analysis using this phylogenetic information. At least, they have included information on phylogenetic relatedness of weevils involved in BSPM which allow some inferences on the multiple origins of this interaction. This is a good start to explore the drivers of these multiple origins through the lens of comparative biology.

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https://doi.org/10.1111/plb.12889

Reviews

Evaluation round #1

DOI or URL of the preprint: https://hal.inrae.fr/hal-03780127
Version of the preprint: 1

Authors' reply, 16 February 2023

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Decision by Juan Arroyo, posted 24 December 2022, validated 26 December 2022

Haran's et al 2022 preprint merits a revision

Decision about the manuscript by Julien Haran, GaelJ. Kergoat, Bruno and A.S. de Medeiros. Most diverse, most neglected: weevils (Coleoptera: Curculionoidea) 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. 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). 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". L. 176-179 seem to be contradictory.

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. 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). 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. 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. 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..." Other minor issues: or the meaning of "recent phytocentric studies on tropical pollinators" (L. 151), why phytocentric? perhaps it is better "tropical pollination"? Why do you consider that weevils "passively pollinating..." (L. 194) What do you mean specifically here for tripartite interactions? (L. 1052). 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). 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).

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.

Reviewed by Susan Kirmse, 15 October 2022

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.

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. 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. 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. 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. 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.

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

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?

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

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

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 insect-tophilous 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.

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

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

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

L 167: Really all plant-weevil pollination mutualisms?

1. A wide spectrum of mutualistic interactions

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

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

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

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

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".

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

L 329: Are flower buds and fruits inside chambers?

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

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

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

3. Economic importance and conservation

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

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.

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".

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

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 & Dufaÿ 2003
Barfod et al 1987
Chomicki et al. 2020
Couvreur & Baker 2013
Franz 2007
Franz NM & O'Brien 2001
Haran et al. 2022
Haran et al. 2020a
Hsiao & Oberprieler 2020
Kirmse & Chaboo 2020
Küchmeister et al. 1998
Marshall 933a
Mora-Urpí et al. 1997
Núñez-Avellaneda et al. 2017
Saunders 2012
Scariot et al. 1991
Silberbauer 1990
Syed et al. 1981
Valente et al. 2019
Vaurie 1968

Reviewed by anonymous reviewer 1, 22 November 2022

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 theis 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 ambicious. The manuscript is too long and hard to be 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.

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Reviewed by Carlos Eduardo Nunes, 17 November 2022

General comments to authors and editors

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

Specific comments to authors

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 stablish mutualistic interactions in certain circunstances, 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.

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

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Reviewed by anonymous reviewer 2, 01 December 2022

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.

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.

L124: polenn, no S

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

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).

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.

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.

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.

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.

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.

(***)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.

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

(***)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.

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).

(***)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.

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

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.

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.

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

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.

(***) 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.

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.

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.

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.

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

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.