

Point-by-point response to the referees' comments

We are grateful to Professor Arroyo and the three reviewers for their constructive comments and suggestions for improving our manuscript. Below, we provide a point-by-point response to all their comments; our responses are numbered and highlighted in blue.

Professor Juan Arroyo, recommender:

Dear Dr. Torices,

As a member of PCI in Evolutionary Biology I was asked to manage your preprint in order to get it recommended in this platform

“Architectural traits constrain the evolution of unisexual flowers and sexual segregation within inflorescences: an interspecific approach”

Three competent colleagues made insightful reviews from different, albeit complementary fields, and their comments are available to you. I consider, like reviewers, that the preprint has a high value to be recommended by PCI Evol Biol, but at the same time, I consider that many of the comments and concerns raised by the reviewers are worth to be taken into account and responded properly. These reviews, albeit anonymous, and your responses will be posted in PCI Evol Biol portal. Since the reviews are made from different perspectives, I strongly believe that considering them in your response and/or revised manuscript will greatly enhance its quality and the readership of the final preprint.

I also would add some specific minor comments from my own side:

1. Given the very particular nature of the inflorescence type in your study, I would consider including some indication in the title. It might be adding “...in Asteraceae”, “flower heads”, “compact inflorescences”, etc. As the authors mention in their Discussion, it remains to be proved what is the case in other kind of inflorescences, specially those being sparse.

1. We believe Asteraceae is only an example of a general phenomenon and we would prefer to keep the title as it is. We have now modified the last part of the discussion to make a stronger case for the generality of an influence of inflorescence architecture on sexual specialization and segregation, illustrated here using Asteraceae.

2. Please, consider to do an extra review of the English, I found some typos (e.g. line 76 “later”) and format of the reference list (some journal titles are not italicized, similarly to some species names, among others). Reference by Funk et al. 2009 is published by IAPT?. Please, consider that a preprint is a publically available text and that PCI Evol Biol does not support proof correction.

2. We have carefully reviewed the whole MS to clean it out of typos and to fix any mistake in the reference list. Regarding Funk's et al. 2009 book, yes, it seems weird, but it was published by the IAPT.

3. Line 134. I have some doubt about the meaning of “phylogenetic gradient”.

3. We meant that evolutionary transitions between sexual systems in Asteraceae likely happened from an hermaphroditic ancestor to monoecy through a gynomonocious intermediate. This common evolutionary pathway occurred towards the increasing of floral sexual specialization. We have reworded this sentence, though, to clarify this statement. (L139-142).

4. Lines 186-188. A sample of 97 species might be low or high enough depending on its representativeness. It would be important to add more information in Table S1, for example adding the subfamilies, and the rough distribution of species. For those readers non-familiar

with systematics of Asteraceae, a supplementary figure with the position of the sampled species in the Asteraceae tree would be very useful. I also wonder why four genera were represented by more than one species (particularly *Vernonia*). Did you think that there were within genus variability?, but this is not discussed in the manuscript. Is the tree used including within genus variability?

4. We have updated the supplementary Table S1 including the information of the subfamily and the rough distribution of each species. In addition, we have detected that the numbers indicated in M&M and in this table did not match. Some of the species sampled were not included in the last analysis because they were not part of any phylogenetic hypothesis. We have removed them from Table S1, and updated the numbers. Thus, the final number of species is 91 instead of 97. We also included a new Supplementary Figure S1 to show the position of sampled species in the Asteraceae supertree. Finally, we have included a brief statement of our sampling representativeness in M&M (L195-206).

In our sampling approach, we tried to include as many different lineages as possible from different parts of the evolutionary tree of this vast family. We sampled then specimens from 26 tribes and 7 subfamilies (including the most diverse ones such as *Carduoideae*, *Mutisioideae*, *Asteroideae*, *Cichorioideae*, and the “*Heliantheae* alliance”, but also the early divergent subfamily *Barnadesioideae* which is the sister clade of the rest of the family). We put a strong emphasis in sampling hermaphroditic and gynomonoeious representatives at the early and late diverging lineages. Hermaphroditism is the ancestral condition in the family and also for most of the early diverging lineages (see the new Supplementary Figure S1). But once gynomonoeicy evolved at the origin of the subfamily *Asteroideae*, it persisted as the ancestral condition for most of the tribes of this clade. Thus, we sampled basal and derived hermaphroditic and gynomonoeious species to take into account the different evolutionary history of ancestral and derived hermaphroditic and gynomonoeious species in this family. All monoecious species were always derived from gynomonoeious lineages in the subfamily *Asteroideae* where all monoecious species evolved in this family with very few exceptions and thus, we did not follow the same procedure for them.

Regarding those four genera with more than one species, we sampled several species of those genera where there was phylogenetic evidences of paraphyly. This was the case for four genera as the editor noted: *Vernonia*, *Inula* (x2), *Senecio* (x2), and *Dasyphyllum* (x2). In the case of *Vernonia*, many of the species sampled are considered now different genera. To avoid confusion, we have used the new genera names for those *Vernonia* in those cases in which these new names have been accepted. So, we did not search within genus variability. As it can be expected in a large group as Asteraceae, within genus variability can be high for some genera, and null for others, and it would require another sampling scheme.

5. Line 374. Although I like the arguments raised by the authors, I consider that there is a possibility to test if geitonogamy (i.e. selfing) avoidance (as stated by Harder & Barrett 1995 considering pollinator movements) is involved by correlating SI data (as from Ferrer et al. 2007, cited by the authors) with your data, if possible. Incidentally, do you have wind-pollinated species in your data set? this information could be also useful in your Table S1.

5. We explored this suggestion by asking Miriam Ferrer for the data she used in her paper in 2007. Unfortunately, we have not been able to communicate with her. Nevertheless, we agree with the Editor and see that the combination of both, the SI data set and our inflorescence data set would allow explicitly testing hypotheses about the effect of the SI on the evolution of inflorescence traits in this family.

It is quite likely that most of the sampled species are pollinated by biotic vectors. However, as we do not have data to support it, we prefer not to use this information in Supplementary Table S1. Otherwise, we are sure that no species with unisexual capitula, as happens with some wind-pollinated species in this family, were included in this sampling.

Reviewer #1:

This study examines whether sexual specialization (evolution of unisexual flowers within inflorescences) is related to architectural constraints conditioning the availability of resources for fruit and seed production. Authors proposed that the architecture of the inflorescence affects the availability of resources for early and late flowers within inflorescences affecting the expression of sexual specialization. In turn, this mechanism will result in higher sexual specialization among those species with stronger architectural constraints (larger difference between outer and inner fruits and seeds). The study used a comparative approach with a sample of 70 species of Asteraceae which have flowers grouped in capitula and present different levels of sexual dimorphism at the inflorescence level (from cosexual hermaphroditic flowers to monoecious unisexual flowers). Overall, the manuscript is clearly written and easy to follow. Methods, and Results are nicely presented and support the main conclusions. I do have, however, a couple of points for further improvement of the presentation and discussion of the results.

1. Lines 61-75: I believe it might be important to consider those selection pressures that can operate upon variation in fruit size within infructescence. For instance, dimorphism and strong variation in seed size in desert Asteraceae has been recorded as a strategy to deal with unpredictable environmental conditions (see Venable studies with desert species). In the absence of a significant pattern related to sexual specialization, this can be an alternative explanation.

6. We agree with the reviewer and we believe that, if possible, it would be important to consider those selection pressures that could favour fruit size variation within infructescences. Although it has been suggested that fruit size variation within inflorescences can be higher in those species growing under environments with low predictability of abiotic conditions, this has not been tested yet. For instance, we do not think that there is strong evidence showing that fruit size variation in desert areas is higher than in other environments. In fact, in Asteraceae, large fruit size variation within heads has been shown in many species not distributed in desert regions such as *Senecio jacobaea* (McEvoy, 1984), *Crepis sancta* (Imbert et al., 1997), *Leontodon autumnalis* (Picó & Koubek, 2003), *Leontodon longirostris* (Ruiz de Clavijo, 2000), *Leontodon saxatilis* (Brändel, 2007), *Tragopogon porrifolius* (Torices & Méndez, 2010), *Anacyclus clavatus*, *A. valentinus*, and *A. homogamos* (Torices et al., 2013), *Galinsoga parviflora* (Rai & Tripathi, 1982, 1987), and also observed in crops such as *Helianthus annuus* (Alkio et al., 2003) where conditions commonly are highly homogeneous.

We agree that the strong selection for having high fruit size variation within infructescence could reduce fitness differences through the female function between outer and inner flowers and thus limit the evolution of sexual segregation. However, one of the well-known examples of heterocarpy in Asteraceae, *Calendula arvensis*, has unisexual female and male flowers in their heads. This interesting idea deserves further systematic research.

2. Lines 76-78: The following two reasons relies on the expectation that resources for fruit production are limited. Although this is a general expectation widely accepted, it would be useful to support this assumption with published evidence that added unlimited resources and still found positional effects on fruit size. This will indicate a true positional constraint. In addition, if differences in fruit size disappear under unlimited resources, then resource limitation will be the major constraint. Could you please provide more support for this central assumption of your work. This will add to your main conclusion posted at the end of the Abstract.

7. The number of papers addressing resource limitation of reproduction in plants is very high but, for some reason, Asteraceae have not been targeted in this kind of studies (in a quick search of MM reference list of 83 papers). That resource limitation influence seed production in Asteraceae can, however, be inferred from other kind of studies such as the cost of floral display, performed by Andersson (1999, 2001) or our own experimental study of positional effects on seed mass (Torices & Méndez, 2010). In these studies, increasing watering or removing rays/flowers increased the seed mass, showing that flowers within a capitulum are competing for limited resources.

3. Lines 445-446: I would consider that modularity may increase within individual variance reducing the power to detect patterns at higher levels of organization.

8. If this is the case, our study succeeded in finding relevant patterns in the presence of this large amount of noise. Of course, the best way to avoid this effect of within individual variance is to target similar positions of the modules sampled. In our case, the gradient in resources occurred in the capitulum and we targeted inner and outer flowers in the capitula. In other inflorescence architectures, basalmost and distalmost flower positions could be targeted for sampling. We do not see a major obstacle due to modularity; studies should carefully consider the architecture of the plants to be included in interspecific comparisons.

4. Line 465: I would expect also that different inflorescence type may impose differences in the magnitude of architectural constraints and FSD.

9. Exactly. A very promising research line would be a joint analysis of the evolution of architectural constraints and inflorescence architecture in a comparative framework. In the same way as inflorescence architecture constraints FSD in ecological time, FSD could (in evolutionary time) constraint inflorescence architecture. This certainly deserves further research and it is in our list of pending tasks for the future, using a family in which inflorescence architecture shows variation (not the case in Asteraceae).

Reviewer #2:

This study explores the idea that sexual specialization is driven by resource allocation and architectural constraints in angiosperms (i.e., that male-only flowers evolve as a response of having insufficient resources to develop seed). Generally, I found this study to outline a clever approach, with its use of herbarium specimens and phylogenetic comparisons. My criticisms are that:

(1) I think they could have outlined the mechanism a bit better (i.e., it hinges on trade-offs in resource allocation in plants that make new resources throughout the growing season - many would argue that if the resources are replenished through photosynthesis, then a trade-off is unlikely to exist)

10. Extensive research during the 1970s and 1980s has already settled that growth and reproduction in plants is not limited by photosynthesis but by mineral nutrients (Bloom et al., 1985; Aerts & Chapin, 2000). Photosynthesis in terrestrial plants is positively related to leaf N content (Field & Mooney, 1986), and nutrient deficiency can even compromise photosynthesis (Dietz & Harris, 1997). In this sense, our hypothesis relies on well-established facts of plant resource economy. We believe it is not needed to reiterate this factual basis.

, and (2) at times, I struggled with parts of the methodology although I think all of that confusion could be ironed out with more information. I outline below where I felt more information or a more thorough treatment of alternative hypotheses is needed.

Line 122-124: Overall, I found the Introduction to be very well-written and a pleasure to read. Some of the sections could use more clarity however. E.g., here, I found it confusing that they state that a negative association between size and number could obscure patterns. It seems to diminish the approach. I suggest rewording to end on how you can deal with this confounding pattern.

11. Thank you for pointing this out. We have modified the last part of this paragraph to clarify our point on the necessity of using flower density rather than the number of flowers per inflorescence as a measure of flower/fruit resource competition within inflorescences.

Line 194: Flower density seems a bit of a problematic metric, being constructed from inflorescence size and number of flowers per inflorescence. I would need more convincing that it isn't confounded with flower size.

12. The reviewer is right that flower density is likely confounded with flower size. Actually, we observed that flower density was, as otherwise expected, negatively correlated with fruit size (Fig. 3c). However, this relationship between flower/fruit size and flower density is not problematic for the goals and analyses of our study. In fact, this relationship with flower/fruit size is one of the advantages of flower density. In this study we aimed to assess whether inflorescence traits (namely, inflorescence size, number of flowers, and flower density) were associated with different levels of floral sexual specialization and sexual segregation within inflorescences. Our main hypothesis is that inflorescence traits can correlate with resource differences between flowers within the same inflorescence because of an increase of competition by resources among flowers/fruits.

To assess this idea, flower density represents a better inflorescence description than other inflorescence traits such as inflorescence size or flower number per inflorescence. For instance, a decline in inflorescence diameter or a higher number of flowers do not necessarily have to impose a higher resource competition among flowers. Therefore if the decline in inflorescence size goes hand in hand with a decrease in either flower size or number, and the increase in the number of flowers triggers also an increase in both inflorescence and flower size.

By contrast, flower density takes into account at the same time inflorescence size and flower numbers, and we also know how it affected fruit size. This was the reason why we used flower density as a covariate in our analyses comparing fruit size of female and bisexual flowers. In fact, the omission of flower density as a covariate in this analysis did not allow to observe fruit size differences between flowers with different sex (Table S5).

For all these reasons, we do not see problematic that flower density can correlate with flower size.

Line 199: Please provide data on how the fruiting heads of Asteraceae “usually” retain the size and structure of the inflorescence. Some of your conclusions hinge on this claim.

13. Unfortunately, we do not have any quantitative data to support this claim. After several years observing flowering and fruiting heads of hundreds of species of this family, we observed that commonly the receptacle, the basal part of the head where flowers and fruits are inserted, is commonly kept by plants, even after they die. As we do not have any systematic data on the potential shift on inflorescence size and structure, we have added a sentence remarking this assumption (L219-220).

Line 204: What is “good” conservation status?

14 We meant here that fruiting heads remained intact and thus fruits were at the original positions within their heads (L222-223). We have modified the wording of this sentence.

Line 204: “For each species, one specimen was selected” - how was this one specimen chosen? Was it randomized?

15. No, it was not randomized. Sampling herbarium material faces strong constraints priming conservation of the specimen sampled against any other consideration. So, we always removed a head from those specimens in which this removal represented the least damage possible for the specimen. We have added this explanation in the text (L223-226).

Line 212: descriptions of fruit size from the projection seems unnecessarily vague. I’m assuming you got a measurement of fruit area (please state this, if so).

16. We have modified this sentence to state that we measured fruit area (L233)

Line 259: It was not clear to me why phylogenetic reduced major axis regressions were conducted with phyloRMA and also phylo.RMA

17. We used `phyl.RMA` from `phytools` package. To avoid the misleading we have removed any mention to `phyloRMA`.

Line 262: There is a great deal of attention to fruit size in this paper yet it is odd that there is so little on flower size. Are flower size and fruit size not correlated? Small flowers will likely make small fruits which will diminish the size differences between early and late fruits I expect. Large flowers (will have large fruits) yet may be selected to increase pollinator visitation. These alternative hypotheses are explored later in the manuscript only in the sense of flower number and its effects on selfing rate. Flower density seems to be used as a type of proxy for flower size (with an implied trade off between size and number) but I didn’t see this explicitly treated in any way (other than the mention that flower size and fruit size are roughly the same, with no data to back this up).

18. The functional meaning of flower size in Asteraceae should be considered cautiously. Contrarily to other angiosperms, in this family flowers are not the attraction unit. Instead, flowering heads and even sometimes secondary aggregations of flowering heads are the common pollination unit in this family. Thus, an increase in flower size not always has to be translated in higher pollinator visitation, if that increasing, for instance, co-occur with a decline in the number of flowers per head.

The attractiveness of the head can thus be enhanced by increasing the number of flowers per head and frequently by producing ray florets in the outermost positions, which usually have strong effects on floral visitors.

Besides, flower size is not necessary to test the main hypothesis posed in this MS. Our hypothesis relies on the availability of resources at different flower positions. We could have assessed this hypothesis using flower size differences between different flower positions within inflorescences, yet fruit size rather than flower size is usually a better estimation of resource availability. Fruit production requires a much higher mass and nutrient allocation than corolla and primary sexual floral components. Therefore, fruit size can be more easily resource-limited than flower size and in this way fruit size may show signatures of resource deprivation with higher likelihood than flower size.

Line 313: I found the results interesting but thought that habitat and growing environment were likely confounding variables. The hypothesis being tested seems to operate only if you can imagine preemption of resources as the growing season comes to an end. Does it not likely matter where these species are growing (i.e., in environments with short or long growing seasons?). Therefore, I'm not sure that it's helpful that the species comes from different continents and biomes as stated earlier.

19. We are not sure how the habitat and growing environments can affect our results. The evolution of gynodioecy and dioecy have happened across different lineages of Asteraceae which are distributed in different continents and environments (Torices et al. 2011). Our hypothesis is related to architectural effects at the inflorescence level rather than resource status at the individual level. So, we expect that the effects we are assessing are independent from the environment the species occupies.

Reviewer #3:

Torices and collaborators in the manuscript entitled "Architectural traits constrain the evolution of unisexual flowers and sexual segregation within inflorescences: an interspecific approach" test the hypothesis that inflorescence architecture may impose a constraint on resource availability for late flowers, which may potentially lead to different optima in floral sex allocation and unisexuality. They expect that inflorescence traits increasing the difference in resource availability between early and later flowers would be phylogenetically correlated with a higher level of sexual specialization. They have performed comparative analyses of inflorescence traits (inflorescence size, number of flowers and flower density) to test this hypothesis in the Asteraceae family (including different levels of sexual specialization: hermaphroditic, gynodioecious and dioecious species). Their main results are that dioecious species had significantly denser inflorescences and species with denser inflorescences showed greater differences in the size of early and late fruits (this was used as a proxy of resource variation between flowers). Finally, they concluded that floral sexual specialization may be the consequence of different floral sex allocation optima driven by the sequential development of flowers that results in a persistent resource decline from earlier to later flowers.

The authors present an interesting case study to investigate. The topic of the paper is interesting and novel. In general the paper is well written, the analyses appear well executed and the main conclusions are well argued for. The authors provide substantial data and analyses for addressing the questions posed. The strengths of this manuscript include the well-developed motivating question and the ideal study group of organisms to test the hypothesis.

However, they are a number of major and minor issues that need to be justified (listed

below). I will try to provide suggestions on how the manuscript could be substantially improved and how these issues could be handled.

1. Number of inflorescence per individual. This is an issue that needs to be at least discussed. I understand that probably there are species that will produce many inflorescences per individual and other species will produce one inflorescence per individual. I think the paper would gain if the authors discuss how it could affect their conclusions.

20. We have modified the third paragraph of the discussion to include the relationship between the number of inflorescence per individual (L404-424). The number of inflorescences in Asteraceae can vary extraordinarily since in this family you can find From small herbs displaying only solitary or few large head per individual to large shrubs or trees with large aggregations of small heads (Torices & Anderberg 2009).

2. Sampling. The authors have highlighted the very high species richness of family Asteraceae. They have only included 100 species in this study. The authors should discuss how these species are distributed in the family. And how their very low sampling of the Asteraceae lineage could affect their conclusions.

21. See our comment 4.

3. Intraspecific variation. They have measured only ca. of one herbarium sample per species. I would like to know how the intraspecific variation has been estimated and whether or not it has been included in their phylogenetic comparative method analyses.

22. We have not incorporated intraspecific variation within our phylogenetic comparative method analyses.

4. Authors have used Likelihood Ratio Test for model selection. AIC and other criteria have been proved to provide better results.

23. We have checked that AIC values comparisons always agreed with the results of the LRT. As model selection in our analyses comprised only two models (OU vs. BM), we think that Likelihood Ratio Test (LRT) provided a more direct way of showing the comparison between these two models.

5. The phylogeny they have used was published in 2005 (over ten years ago) with a calibration from a paper from 2010. During the last decade it has been an exponential improvement of phylogenetic and divergence estimates methods. In the last years many new studies has been published with better estimates of divergence time in all branches of the tree of life, including the family Asteraceae (see Time Tree of Life here <http://www.timetree.org/>). I wonder whether or not the phylogeny and branch lengths estimates could be significantly improved.

24. We understand that given the speed on publishing new dating estimations for divergence events in an increasing number of clades could give the impression that to use a supertree published in 2005 and dated in 2010 would be a wrong decision because we could miss some new data. However, we are not sure that using last published papers on this large group will always significantly improve dates of divergence events. The phylogeny and the calibration of this phylogeny published in 2010 includes only taxonomic evidence which has been discussed and agreed by a large community of systematic botanists of this family. This means that this phylogenetic relationships are sustained by strong phylogenetic evidences which has been scrutinized by a large community of experts.

Timetree site, otherwise, includes new published dating data that can be hard to assess by not expert people. One example is the recent paper suggesting an older origin of Asteraceae (Barreda et al. 2016). The taxonomic placement of the fossil pollen grain utilized in this paper has been criticized by other experts in this family (Panero et al. 2016) and thus it might require further scrutiny or at least additional evidence.

For all these reasons we believe that the most conservative approach is to use the phylogenetic hypothesis receiving the highest support from the community of experts since we are unable to assess the quality of new published papers.

6. I like the phylogenetic comparative methods approach that authors have used. But I think they could be significantly improved. They have used BM and OU models. However, they have only used an OU model with a single optimum. This model might be used with two, three, four, five, etc. optima. The data seem to suggest that the best models could have two or three optima. Including analyses with two and three optima OU models (one for each of the sexual specialization: hermaphroditic, gynomonocious and monoecious species) would significantly improve the manuscript.

This paper was the first to show this approach: Butler, M. A., & King, A. A. (2004). Phylogenetic comparative analysis: A modeling approach for adaptive evolution. *American Naturalist*, 164(6), 683-695. doi:10.1086/426002. They are many examples in the literature using this several optima approach. See these three examples among many: Nürk, N. M., Michling, F., & Linder, H. P. (2018). Are the radiations of temperate lineages in tropical alpine ecosystems pre-adapted? *Global Ecology and Biogeography*, 27(3), 334-345. doi:10.1111/geb.12699. Schmitz, L., & Higham, T. E. (2018). Non-uniform evolutionary response of gecko eye size to changes in diel activity patterns. *Biology Letters*, 14(5) doi:10.1098/rsbl.2018.0064. Zanne, A. E., Pearse, W. D., Cornwell, W. K., McGlenn, D. J., Wright, I. J., & Uyeda, J. C. (2018). Functional biogeography of angiosperms: Life at the extremes. *New Phytologist*, 218(4), 1697-1709. doi:10.1111/nph.15114.

25. We completely understand this suggestion. In fact, we used the “ouch” approach in a preliminary assessment of the hypothesis tested in this MS, included as a chapter of the Ph Dissertation of the first author. In that analysis, we used different optima for modelling the evolution of inflorescence traits under hermaphroditic, gynomonocious and monoecious lineages. That was possible because we used a small clade within Asteraceae, the tribe Inuleae, in which we have also previously explored sexual system evolution in more detail (Torices & Anderberg 2009).

We discarded this approach now when we moved up to assess this hypothesis using the whole family because we believe that for using these OU models with several optima, it is important to have a good completeness of the phylogenetic history of the studied clade. This includes both the phylogenetic relationships but also good knowledge of the selective regimes. Sadly, our sampling represent a tiny proportion of the whole diversity of Asteraceae, and thus we cannot trust in the optima scenarios that should be imposed for these multiple optima OU models. These scenarios would unquestionably be built with a lot of missing information, and so, they will be very unrealistic.

Nevertheless, it is important to highlight that our results found by the “ouch” approach for the tribe Inuleae totally agree with the results presented in this pre-print. The optimum values inferred for the density of flowers were associated to the degree of sexual specialization. Hermaphroditism showed the lowest value, while the highest density value and lowest fruit size was associated to monoecy. In other words, using the ouch approach we also observed that monoecious species showed the highest

degree of competition among flowers and fruits within the same capitulum and the lowest fruit size.

Therefore, we believe that despite the simplicity of the evolutionary models assumed in the phylogenetic comparative methods, our results are robust.

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