Dear Dr. Weinstein:  
  
  
The Editorial Board of The American Naturalist has reached a decision regarding your article, "Facilitation, not competition, in flowering timing in a diverse tropical hummingbird-visited plant community."  Your manuscript has been evaluated by two reviewers and by Dr. Jeremy Fox, one of our Associate Editors. After reading the manuscript, the reviews, and Dr. Fox's comments (pasted below), I regret that I find myself in agreement with the Associate Editor's recommendation that your paper be declined.  
  
I was interested to read about your work analyzing data on the flowering phenology and pollinator visitation patterns of a set of related co-occurring plant species to infer the potential roles of competition for pollinators and facilitation of pollination among these taxa. You apply a sophisticated set of analyses to an impressively large set of data and find patterns of flowering covariance consistent with interspecific facilitation of pollination rather than competition for pollinators. Dr. Fox and the reviewers recognize and appreciate a number of merits of your work, but they also identify serious concerns about the paper, including problems with the application of statistical methods, the omission of pertinent details of the analyses, and the potential for explanations other than pollinator facilitation to underlie the observed patterns of flowering covariance. The basis for these concerns is explained in detail in their comments. Although some of these issues might be  
resolved by revisions to the current paper, I agree with Dr. Fox and Reviewer 1 that neither the scope nor the novelty of the conclusions support the level of broad conceptual advance or synthesis we aim to publish in The American Naturalist. Thus, I consider it appropriate to decline the paper for further consideration here. Dr. Fox and both reviewers offer extensive insight into how you might refine the work and its presentation. I hope you will find this input useful for revising the paper for submission to a journal with a stronger focus on publishing empirical progress.   
  
As a result, I cannot accept your manuscript for publication. Because of space limitations, we can accept only 20% of submissions. We must emphasize the goals of The American Naturalist: to publish papers that are of broad interest to the readership, to pose a new and significant problem or introduce a novel subject to the readership, to develop conceptual unification, and to change the way people think about the topic of the manuscript. Unfortunately, this means that we must decline many good manuscripts that are worthy of scientific publication. Declined manuscripts are not eligible for resubmission in a revised form. I am sure that you will find this outcome disappointing. However, the helpful comments you’ve received here will no doubt be of assistance as you consider the next step for this manuscript. Thank you for thinking of The American Naturalist as an outlet for your work, however, and best wishes for your future research.  
  
Sincerely,  
  
Alice A. Winn  
Editor  
American Naturalist  
  
  
xxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxxx  
Associate Editor Dr. Jeremy W. Fox 's Recommendation  
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The ms uses a multilevel statstical model to estimate covariance in flowering phenology among 14 congeneric plant species in an Ecuadoran cloud forest, as a function of the degree to which they share hummingbird pollinators. It is assumed that if species that share pollinators flower at different times, it must be because they have evolved to avoid competition for pollinators and/or pollen contamination. Whereas if species that share pollinators flower at the same time, they must be doing so to maximize pollinator attraction, perhaps because patches of many open flowers attract disproportionately many pollinators. The authors argue that their results indicate that co-flowering species facilitate one another's pollination.  
  
The ms is framed around an issue of broad interest to Am Nat readers: species coexistence. The dataset is impressively large, and the analysis is statistically sophisticated. However, both reviewers raise serious concerns about the statistics, concerns that I share. Many details of the statistical model are omitted from the ms, and others are questionable. Perhaps some of these statistical issues are presentational rather than substantive, but the issues are numerous and serious and would need to be addressed in any revision.   
  
One of the reviewers, an expert on plant-pollinator interactions, also raises a number of serious concerns about the novelty and interpretation of the results. Having read the ms myself, I share these concerns. I recommend that the ms do more to place the results in the context of the previous literature and establish their novelty. Not merely methodological novelty, but novelty of the substantive ecological conclusions.   
  
I also have some comments of my own, of which #2 and #3 are most important:  
  
1. Fig. 3 shows the estimated phenological correlation matrices between the plant species, from models assuming that plants sharing pollinators tend to flower either at different times, or at the same time. It looks like each matrix is almost (but not quite) a rescaled negative of the other? That is, that the most positive estimated correlations in the left-hand matrix appear to be the most negative ones in the right-hand matrix? Is that right, and if so, is that an inevitable consequence of the model structure? Also, in Fig. 5, there are some notable cases in which the posterior prediction interval seems very broad relative to the spread of the training data, or else the training data fall far out in one tail of the posterior (examples include G. oblongicalyx in months 1-6, C. ciliata in months 6-12, G. quitensis in months 3-7, C. medicinalis in months 7-9, G. lateralis in months 5-7 and 10-12). On casual inspection, several of these cases seem to come from species  
estimated to have either very positive or very negative phenological correlations with other species in Fig. 3--is that just a coincidence? More broadly, how concerned should the reader be that the posterior prediction intervals often are quite broad and don't always line up all that well with the training data?  
  
2. A statistical model that assumes that plants sharing pollinators tend to flower at the same time only predicts flowering probability slightly better than alternative models (Fig. 4 right panel; the difference in mean discrepancy is only ~0.02 between the best model and the others). If I understand the model correctly, what the data in Fig. 4 are saying is that knowing which plants share which pollinators barely helps you predict plant flowering phenology at all. Is this correct? If so, it would seem to undermine the broad conclusions of the ms.   
  
3. There are other explanations for non-random patterns in plant flowering phenology besides those on which the ms focuses. Just because plant species that share pollinators tend to flower at the same time doesn't imply that they facilitate one another via pollinator attraction (or did so in the past). Nor do plant species that share pollinators but flower at different times necessarily flower at different times because they compete for pollinators (or competed for pollinators in the past). I believe the ms needs to be written in such a way as to make clear the distinction between the pattern being tested for, and the underlying mechanisms that might have given rise to that pattern. Referring to the pattern itself as "facilitation" is misleading.   
  
4. It is mathematically possible for the mean off-diagonal element of a correlation matrix to equal +1, but it's not mathematically possible for it to equal -1. Indeed, with a 14x14 correlation matrix, the mathematical lower bound on the mean off-diagonal entry is only slightly below zero. Does this mathematical constraint on the possible correlation matrices that could be observed not shape the interpretation of the data? For instance, even if there were very strong selection for 14 plant species to flower at different times so as to avoid competition for shared pollinators, the mean correlation between their phenologies couldn't possibly be much below zero--zero being the mean correlation you'd expect if species flowered independently of one another. Does this mathematical constraint explain why the "visitor repulsion" model predicts the test data about as well as the "time independent" model? And how does this mathematical constraint limit our ability to detect  
"repulsion" in plant species' phenologies?   
  
-Jeremy Fox  
  
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Reviewer #1:   
  
In this manuscript the authors use statistical modelling to assess whether the flowering phenology of 14 plant species in an Ecuador cloud forest are more consistent with competition or facilitation mediated by hummingbird pollinators. As I detail below, this study is rather limited in its scope, interpretation and implications, which limit its suitability for publication in the American Naturalist. It is also compromised by limited rationale, various aspects of the statistical model, and general presentation. Below, I provide the authors with suggestions for improving these aspects of their study.  
  
1) "we compare how well models of co-flowering repulsion and attraction predict flowering phenology of fourteen hummingbird-visited Gesneriaceae species in a diverse cloud-forest assemblage. Our primary goal is to identify non-random co-flowering association, and test whether this information improves predictions of co-flowering in a diverse tropical ecosystem.", lines 69-73 – As indicated by this statement from the last paragraph of the Introduction, the objective of this study is to discriminate whether the flowering phenologies of an assemblage of related plant species tend to be aggregated or dispersed relative to random expectations. The essential consideration concerning the fate of the submission is whether its publication would serve the goals of the American Naturalist. These "goals are to publish articles that are of broad interest to the readership, pose new and significant problems, introduce novel subjects, develop conceptual unification, and change the way  
people think". Whether flowering phenologies are dispersed or aggregated and the influence of interactions with pollinators in these patterns is a long-standing topic in pollination ecology (e.g., see review by Rathcke, 1983, pp. 305-329 in Real [ed.], Pollination Biology, Academic Press). Thus, the subject of this submission is not novel. Furthermore, as the submitted article solely describes and interprets patterns, it does not identify new problems or elaborate unifying perspectives.  Furthermore, that synchronous flowering promotes facilitation of pollination is a well-known feature of interactions between plant species (see recent review by Braun & Lortie, 2019, Perspectives in Plant Ecology, Evolution and Systematics 36: 33-40). Therefore, this manuscript will likely not alter perspectives on facilitation.  Given these characteristics, this manuscript does not align clearly with the goals of the American Naturalist.   
  
2) "we compare how well models of co-flowering repulsion and attraction predict flowering phenology of fourteen hummingbird-visited Gesneriaceae species", lines 69-71 – Not only do these species all belong to the same family, they belong to only six genera. Such closely related species could reasonably have similar flowering periods because of shared ancestry, rather than because of independent convergence. Nevertheless, the authors do not incorporate this possibility in their statistical analysis, nor do they considered in their interpretation.  
  
3) "The covariance among flowering species (C) is a function of the association distance among plant species (D), the strength of covariation () and a fixed decay in covariance () with increasing pollinator distance.", lines 146-148 – As "pollinator distance" is never defined I struggled to understand fully this aspect of the model; however, it seems that the authors consider hummingbird availability to be fixed, which then provides the context for plant phenology. If so, this depiction seems flawed, given both the extreme mobility of hummingbirds (i.e., beyond the scale of the study area) and their foraging flexibility, which allows them to feed opportunistically on whichever plant species is most rewarding at a given time.   
  
4) "the degree to which species interact can be modeled as a function of a degree of association. One association option for flowering is to use the overlap in pollinator visitation, as a proxy for the potential for pollen contamination", lines 63-65 – This approach relies on several assumptions for which the authors provide no supporting information. For both the plants and hummingbirds considered in this study, the unit of observation is species. However, heterospecific pollination (pollen contamination) requires that individual pollinators visit individual plants of different species interchangeably during individual foraging sequences.  If instead individual hummingbirds specialize temporarily on an individual plant species, plant species will not interact, no heterospecific pollination will occur, and synchronous flowering by different plant species will be cost free. Thus, despite the authors' claim that "(t)he mechanistic relationship between pollination facilitation  
and local diversity is unclear and depends on many variables" (lines 269-270), such mechanisms determine outcomes and their relegation to a blackbox raises concerns about the relevance of the authors' analysis and its interpretation.   
  
5) "We first modeled flowering phenology as a time independent model by dividing the flowering transect data into 6 elevations and 12 months. … This is akin to the null expectation with respect to time used in traditional randomization studies and as such served as the baseline for comparing the co-flowering models developed below.", lines 120-128 – A perennial issue with character displacement studies is to characterize the appropriate null model. The authors' choice is to propose that each species has a constant probability of flowering, regardless of the month.  This assumption proposes that plants flower regardless of the likely availability of pollinators in the study site, which makes no biological sense (too null to be meaningful). An alternative null model would allow the monthly flowering probability to vary in proportion to monthly hummingbird abundance visiting all plant species.  
  
6) "To estimate the probability of interaction among each hummingbird and plant species, we used a hierarchical Bayesian model that accounts for the differences in sampling among plants and captures the daily frequency of visitation between each bird and plant species in bloom (Weinstein and Graham 2017a). i,j,k,d ∼ (i,j,k)", lines 108-113 – What is the biological and statistical evidence that hummingbird visitation varied according to a Poisson distribution?  This would be remarkable for several reasons.  First, the visitation data were collected with cameras and likely included more 0 observations that expected from a Poisson distribution. Second, even without zero inflation, the distribution of pollinator visitation is usually over-dispersed compared to a Poisson distribution. At the least, the authors must provide statistical evidence supporting whatever distribution they use to characterize visitation. A similar concern applies to the authors' use of a multivariate  
normal distribution to characterize "the effect of other species in flower during that monthly transect" (lines 145-146).  As the authors fit their model to data, rather than using it to explore theoretical possibilities, using sampling distributions that accurately represent variation and covariate is essential.  
  
7) "we recorded 1324 interactions among 13 hummingbird species. The most common species was Aglaiocercus coelestis (n=421), and the rarest species included in the analysis was Urosticte benjamini (n=4). For additional information on this dataset see Weinstein and Graham (2017a, 2017b, 2018).", lines 102-105 – More information should be provided in the text of this manuscript explaining the temporal distribution of hummingbird visits, whether species are territorial or traplining, when the nesting season occurs, whether all species are present throughout the year, etc. In addition, more description of relevant characteristics of the study area (scale of sampling, seasonal variation in flowering conditions, etc) is needed. Such information will allows readers to understand the abiotic and pollinator context in which flowering phenology occurs.  
  
8) "For the attraction model we used omega=1 and lambda=2. These values ensure that the visitor overlap matrix has reasonable bounds, such that species with high visitor overlap tend to co-flower.", lines 158-160 – What is the consequence of this specific choice of parameter values for biological interpretation and the probability of detecting attraction versus repulsion?  
  
9) "All plants were not visited by the same hummingbird species, but those plants which share hummingbird visitors were more like flowering along the same elevation transect and during the same month. This result highlights facilitation in pollinator attraction as an important mechanism shaping hummingbird pollinated plant communities (Carvalheiro et al. 2014; Bergamo et al. 2017).", lines 261-265 – What is the basis of this extrapolation of results from a single tropical study area to all hummingbird-pollinated plant communities?  
  
10) "there are several potential evolutionary and ecological explanations for the observed lack of phenological staggering among species with overlap in pollinator niches", lines 284-286 – Given the complete lack of relevant information about the explanations presented in the 1.5-page paragraph that follows this statement, this discussion is unwarranted speculation.  
  
11) "Connecting natural history within local assemblages to hypothesized mechanisms of cooccurrence from biogeographic scales remains an ongoing challenge in community ecology.", lines 2-3; "Explaining the co-occurrence of related species in assemblages is a persistent challenge in community ecology", lines 20-21 – These sentences open the Abstract and Introduction, respectively, motivating the authors' study. In general, the best rationale for a scientific study is its relevant to biological systems, not the ignorance of biologists.  Therefore, these sentences should be replaced with statements identifying the relevance of species interactions for structuring species assemblages.  
  
12) "These explanations (competition and facilitation) represent competing hypothesis (sic) for flowering based on pollinator mediated repulsion (flowering at different times) and attraction (flowering at the same time) in local floral assemblages", lines 27-36 – Competition and facilitation are real processes, not explanations, that have both been widely demonstrated to influence assemblage structure. They become hypotheses only in the context of explaining the structure of specific assemblages.  
  
13) The notation used in this manuscript is very unhelpful, as the same symbols are used for different purposes. For example, Y is used to represent the number of hummingbird visits in "equation" 1, whereas in "equations" 2 and 3 it is a binary variable representing whether a plant flowered during a given month. Similarly, lambda has different meanings in "equation" 1 and the fifth line of "equation" 3.  
  
14) Several aspects of the authors' word usage are inaccurate:  
i) "hummingbird-visited plant community", title – A community includes all of the species at a site, not just one trophic level and certainly not just species from the same family.  The authors have studied an assemblage.  
ii) "Observed patterns of co-occurrence within a local community result from the fitness benefit of using a particular niche space versus the cost of having to share that space with other, often related, species", line 24-26 – The niche represents all of a species' interactions with the abiotic and biotic environment. Those interactions, and hence the niche, exist only if the species is present. Thus, this niche is not a space, nor can it be shared.  Nevertheless, the niches of different species can overlap, to the extent that they engage in similar interactions.  The important feature of niche overlap is interaction, not space.  
iii) "pollination services", line 4  
iv) "As we consider a broader range of plant species, visited by a wider array of taxa, the pattern of facilitation may increase, as the rewards for flowering simultaneously increase, but the potential costs of cross-pollination decrease", lines 275-277 – Costs of cross-pollination? Presumably the authors mean costs of heterospecific pollination.  
  
15) Keywords – Three of the keywords listed for this manuscript will be largely unhelpful as means of locating this study in a literature search.  
i) What is PGLMM? This acronym is not used or defined in the text.  I expect that this acronym will not be understood by most potential users.  
ii) Covariance and prediction – These two terms are too general to be useful as keywords. Furthermore, the authors do not specifically study covariance or prediction, they are simply features of their data or analysis, which is true for most ecological studies.   
  
16) References – This section needs through editing so that references are presented consistently and in a manner compliant with the Journal's style. Examples of problems from just the first five references include:   
i) Abrahamczyk and S. Renner. 2015. – Capitalize first letters of journal name.  
ii) Adler et al. 2018. – Delete (L. Comita, ed.)  
iii) Ashman et al. 2004 – Delete "Concep Ts & Synthesis Emphasizing New Ideas To Stimulate Research in Ecology", which identifies the section in the journal in which the articles published. Capitalize the first letter of only the first word of the article's title.  
  
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Reviewer #2:   
  
In manuscript 59255, the authors use time series data from a number of transects spanning ~1200 m in elevation to ask whether co-occurring species of Gesneriads (African Violets) tend to have similar or dissimilar flowering times. This question, which is of longstanding interest to ecologists, is matched with a strong dataset and a new statistical approach that have the potential to offer new insights.  
  
My overall take on this manuscript is that it has a lot of potential. The data are exceptional, and the goal of developing an hypothesis-testing framework that is more specific than classic null models is worthwhile. That said, there are a number of questions that I had about the methods used, and I am unconvinced that it is the best approach (or, equally, that if it is the best approach it is being implemented correctly). I do not want to be overly discouraging – with new and fairly complex methods it is often the case that authors need to be extremely clear to convince readers with a broad range of statistical backgrounds.   
  
Major concerns:  
My main concerns center on the statistical approach taken.    
First, in the set up of the statistics, there appears to be a critical step missing. In particular, the authors specify Y (line 113) as the number of visits of a plant by a hummingbird per day. This number provides a 'mean interaction matrix', which is then somehow used to calculate D, the mean similarity in partner choice. There are many ways to get from an interaction matrix to D, but the form of C (line 143) suggests that this similarity is constrained to be greater than (or equal to) 0. It is important that this step is clarified and transparent, as some similarity metrics would be inappropriate for this type of data.   
  
Second, it is unclear if and how the parameters lambda and omega were fit. On lines 158–161, it states that they were fixed. This seems to be a bizarre and arbitrary decision – allowing omega to vary essentially tells you how important pollinator overlap is to covariances (as omega -> 0, we would conclude that pollinator overlap has little or no influence on covariance in flowering time). On the same topic, if lambda is very low, we would conclude that any overlap is important, whereas if lambda is high we would conclude that only high pollinator overlap is important. To make this issue more confusing, line 162 states that informative priors were used for lambda – it seems like you mean fixed points with no distribution estimated, is that correct? My overall point here is that arbitrarily setting these robs us of this information and these inferences, and may lead to relatively poor fits to the data.  
  
Third, there are a number of issues with the presentation of the model that made it difficult for me to be certain that I understood what was being done. For example, the estimation of the interaction matrix seems to be fitting intercepts at the plant level (subscript j), but to fail to account for the species of plant. Because of this lack of clarity about plant vs species, it is unclear if the interaction matrix is a per capita interaction matrix, or somehow incorporates abundances into the calculation. Similarly, the subscript j appears to mean 'plant' in eq. 1 and 'transect' in the alpha term (line 126). The presentation of omega as a covariance is also confusing – it must be constrained to be between 0 and 1 for the multiplication of the identity matrix (line 142) to make sense, yet covariances are not constrained to this range. These inconsistencies make it difficult to know if I understand the underlying model.  
  
Fourth, it appears that each observation for a plant is used as an independent observation, but with camera and filming day included as (random?) effects. Does this fitting of camera and day capture some of the spatial/temporal variation in the data? It would seem hard to avoid doing so, but it isn't clear to me that you want that variation captured in random effects.    
  
Fifth, in the verbal set-up of null model (versus covariance model) approaches, the authors correctly point out some of the problems with null models – difficulty in knowing the exact hypothesis tested, challenges of incorporating patterns from the hypothesized process into the null, etc. What appears to be missing is a similar critique for their covariance model. For example, the structure of C causes the covariance among species to approach zero as distances among species in 'pollinator space' increases. If all species show positive covariances, wouldn't this approach lead to a false signal, simply because all species' covariances are predicted by 'high pollinator overlap' species and are not tested against 'low pollinator overlap' species (through the constraining of lambda?)? On a similar note, negative covariances among species are constrained as the number of species increases, whereas positive covariances are not – it is unclear how this approach accounts for that  
statistical phenomenon.   
  
Finally, it looks like the model has problems estimating when the observed = 0 (Fig. 5). For example, G. quitensis (months 3-7), G. oblongicalyx (months 1-5) and D. tenuis (months 11, 12 and 1). Why is this? What are the consequences of this fitting problem for the method used?  
  
  
Minor concerns:  
  
Line 22 – this argument is based on a misunderstanding of the mechanisms that promote or limit coexistence. Papers by Germain et al. (2016; Proceedings B) and Mayfield and Levine (2010, Ecology Letters) explain why closely related species may be more likely to coexist.  
  
Line 45 – '… and patterns of trait spacing,…' It is unclear what this means in this context. Please reword to something like, 'patterns of trait overlap among co-occurring species'   
  
Line 179 – '… computed the sum discrepancy'. From the figure, it looks like the mean discrepancy (otherwise it would scale positively with the number of observations).  
  
Line 235 – Fig. S3 was not in the manuscript (it ends at Fig. S1)  
  
Fig. 4 – it would be good to get an estimate of how much of an improvement this is (my sense is that it is not a huge improvement). Can you also present the odds ratio?  
  
Line 244 – is 'Error' mean discrepancy, or do you mean the error bars on the estimates given in the graph?  
  
  
  
  
  
EU GDPR required statement:  
  
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In compliance with data protection regulations, you may request that we remove your personal registration details at any time.  (Use the following URL: <https://www.editorialmanager.com/amnat/login.asp?a=r>). Please contact the publication office if you have any questions.