Peer Community In
Evolutionary Biology

Determinants of population genetic structure in co-occurring freshwater snails

Trine Bilde and *Matteo Fumagalli* based on peer reviews by 3 anonymous reviewers

Jarne P., Lozano del Campo A., Lamy T., Chapuis E., Dubart M., Segard A., Canard E., Pointier J.-P., David P. (2021) Connectivity and selfing drives population genetic structure in a patchy landscape: a comparative approach of four co-occurring freshwater snail species. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Evolutionary Biology.
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Genetic diversity is a key aspect of biodiversity and has important implications for evolutionary potential and thereby the persistence of species. Improving our understanding of the factors that drive genetic structure within and between populations is, therefore, a long-standing goal in evolutionary biology. However, this is a major challenge, because of the complex interplay between genetic drift, migration, and extinction/colonization dynamics on the one hand, and the biology and ecology of species on the other hand (Romiguier et al. 2014, Ellegren and Galtier 2016, Charlesworth 2003).

Jarne et al. (2021) studied whether environmental and demographic factors affect the population genetic structure of four species of hermaphroditic freshwater snails in a similar way, using comparative analyses of neutral genetic microsatellite markers.

Specifically, they investigated microsatellite variability of Hygrophila in almost 280 sites in Guadeloupe, Lesser Antilles, as part of a long-term survey experiment (Lamy et al. 2013). They then modelled the influence of the mating system, local environmental characteristics and demographic factors on population genetic diversity.

Consistent with theoretical predictions (Charlesworth 2003), they detected higher genetic variation in two outcrossing species than in two selfing species, emphasizing the importance of the mating system in maintaining genetic diversity. The study further identified an important role of site connectivity, through its influences on effective population size and extinction/colonisation events. Finally, the study detects an influence of interspecific interactions caused by an ongoing invasion by one of the studied species on genetic structure, highlighting the indirect effect of changes in community composition and demography on population genetics.

Jarne et al. (2021) could address the extent to which genetic structure is determined by demographic and environmental factors in multiple species given the remarkable sampling available. Additionally, the study system is extremely suitable to address this hypothesis as species' habitats are defined and delineated. Whilst the authors did attempt to test for across-species correlations, further investigations on this matter are required. Moreover, the effect of interactions between factors should be appropriately considered in any modelling between genetic structure and local environmental or demographic features.

The findings in this study contribute to improving our understanding of factors influencing population genetic diversity, and highlights the complexity of interacting factors, therefore also emphasizing the challenges of drawing general implications, additionally hampered by the relatively limited number of species studied. Jarne et al. (2021) provide an excellent showcase of an empirical framework to test determinants of genetic structure in natural populations. As such, this study can be an example for further attempts of comparative analysis of genetic diversity.

References:

Charlesworth, D. (2003) Effects of inbreeding on the genetic diversity of populations. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358, 1051-1070. doi: https://doi.org/10.1098/rstb.2003.1296

Ellegren, H. and Galtier, N. (2016) Determinants of genetic diversity. Nature Reviews Genetics, 17, 422-433. doi: https://doi.org/10.1038/nrg.2016.58

Jarne, P., Lozano del Campo, A., Lamy, T., Chapuis, E., Dubart, M., Segard, A., Canard, E., Pointier, J.-P. and David, P. (2021) Connectivity and selfing drives population genetic structure in a patchy landscape: a comparative approach of four co-occurring freshwater snail species. HAL, hal-03295242, ver. 2 peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://hal.archives-ouvertes.fr/hal-03295242

Lamy, T., Gimenez, O., Pointier, J. P., Jarne, P. and David, P. (2013). Metapopulation dynamics of species with cryptic life stages. The American Naturalist, 181, 479-491. doi: https://doi.org/10.1086/669676

Romiguier, J., Gayral, P., Ballenghien, M. et al. (2014) Comparative population genomics in animals uncovers the determinants of genetic diversity. Nature, 515, 261-263. doi: https://doi.org/10.1038/nature13685

Reviews

Evaluation round #2

DOI or URL of the preprint: https://hal.archives-ouvertes.fr/hal-03295242
Version of the preprint: 2

Authors' reply, 30 August 2021

The final version of our article was deposited on HAL (version 3 available at https://hal.archives-ouvertes.fr/hal-03295242).

Decision by **Trine Bilde** and **Matteo Fumagalli**, posted 27 July 2021

minor revision

Dear Authors,

Thank you for submitting the revised version of the manuscipt. We are satisfied with the responses to the reviewer comments, and we kindly ask you to make a few minor corrections before we make the final recommendation. Please see the comments here:

1. Pantel et al citation is still ”submitted” in the text and bibliography while in the response the Author’s say it has been published. Can references to this paper be updated?
2. The sentence “Two correlations were significant in cases in which we did not expect a correlation, specifically, a negative correlation between size and connectivity and a positive one between stability and the density of favorable habitats” should be rephrased. We suggest something like “We observed two unexpected significant correlations, namely between size and connectivity (negative) and between stability and the density of favorable habitats (positive).”
3. Reference Otto (2021) is alphabetically wrongly placed in the bibliography.
4. ”recommander” should be ”recommender” in Conflict of Interests statement

Best regards
Matteo Fumagalli and Trine Bilde

Evaluation round #1

DOI or URL of the preprint: `https://hal.archives-ouvertes.fr/hal-03295242`
Version of the preprint: 1

Authors’ reply, 22 July 2021

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Decision by **Trine Bilde** and **Matteo Fumagalli**, posted 04 June 2021

minor revision

Dear Dr Jarne and co-authors

We are pleased that we have now received three reviews of your pre-print. The reviewers and we as co-handlers of your manuscript all enjoyed reading the pre-print, and that we would like to recommend minor revision.

All reviewers agree that your study is interesting and presents a very interesting and comprehensive study. The reviewers have provided several comments and useful suggestions on ways to improve the presentation. These mainly relate to improving clarity of various parts of the manuscript.

One potentially critical point was raised relating to the collinearity between predictors in some of the models, in addition to a question regarding whether an additional variable should be included in the analyses.

It should be fairly straightforward to address the comments in a revised version of the manuscript.

Best wishes
Matteo Fumagalli and Trine Bilde

Reviewed by anonymous reviewer 1, 12 April 2021

Review of the preprint ”Connectivity and selfing drives population genetic structure in a patchy landscape: a comparative approach of four co-occurring freshwater snail species” by Jarne et al.

The authors present an elegant approach to assess the distribution of genetic variation in Guadeloupe. They analyzed four co-occurring snail species with distinct mating systems and ecological traits. This allowed them to perform a comparative approach, evaluating similarities and idiosynchrasies in the obtained patterns. There are very few studies of this type, and it is important to note the great sampling effort, during several years, that made their study possible. The main strong points of their manuscript, in my opinion, are the solid methodology, in special the amazing sampling effort and the suite of appropriate analyzes applied; together with an Introduction containing relevant and updated research on the studied questions, and a Discussion very well written, considering both the expected and unexpected aspects of the obtained results. I see some opportunities to improve their manuscript, which I detail below:

Introduction

As I stated above, the introduction contains relevant and updated research on the studied questions and the motivation of the study is very clear. As a suggestion for improvement, I found the structure of this session somewhat confuse. There are several instances where the authors merge methods with the Introduction itself. For example, the start of the second (Lines 73-75), third (Lines 126-128) and fourth (Line 145-157) paragraphs. I believe some of these stretches would better fit in Mat&Met session. Some of this information could be condensed in the last paragraph of the Introduction, in the form of clear objectives and hypotheses (which are well organized in Table 1) that the authors are willing to test, to tackle the problems raised throughout their Introduction. This would make the Introduction much more clear and organized.

Methods

I believe that a figure containing the landscape properties (containing topgraphy or pond location and size, or any other aspect the authors believe is important) could be useful. This could be added to Figure 1 or to the Supplementary Material.

It is not clear by reading the methods when the genetically analyzed individuals were sampled (it gets somehow more clear in the Discussion, but could be better explained here too). Were they sampled throughout the years or in one specific season? If throughout the years, then the genetic statistics generated are including information of demographic/climatic events from different years. This is fine, but needs to be better stated. Also, how did you define invasion age given this inter-year sampling scheme?

I like the approach of comparing the results from different species, and the authors performed this with great detail and rigor. Yet, I still feel that some statistical analysis explicitly testing across-species correlations (i.e. including more than one species in the same analysis) with the environmental/demographic variables could be included, in addition to qualitatively comparing the results from different species.

Please provide your R scripts, especially for the linear models.

Discussion

The authors defend that an asymmetric island or a metapopulation model would be better suited for the studied species. Could this pattern affect the results of their mantel test? Moreover, I think the authors should consider the potential effects of IBD on their analyses of population structure and correlation with environmental factors. An extensive literature is available on such effects (for a review, see Meirmans 2015).

References

Meirmans, P.G. (2015), Seven common mistakes in population genetics and how to avoid them. Mol Ecol, 24: 3223-3231. https://doi.org/10.1111/mec.13243

Reviewed by anonymous reviewer 2, 14 May 2021

The manuscript ”Connectivity and selfing drives population genetic structure in a patchy landscape: a comparative approach of four co-occurring freshwater snail species” proposes a multi-species approach to detect how consistent the effects of environmental and demographic factors, as well as mating strategies, are across closely related species with similar ecologies and overlapping geographic distributions. The main conclusions are that mating systems and connectivity are the main predictors of neutral genetic variation and structure. I found the manuscript quite complete, though there are instances where I think it could use some re-writing so as to make it easier for readers to follow. My comments mainly address the form and I have some questions concerning choices in statistical analyses.

General comments:

Methods:

Line 357: You have chosen to run linear models to test the effects of the environmental factors on the observed genetic structure of populations/species. From Table S9, there exist correlations between these factors, but it is not clear to me whether this was accounted for in the linear models (I'm under the impression that it was not). I can understand the choice to look at each factor separately, but at the same time I think it pertinent to account for interactions between predictors of a linear model. Or have I missed something? If interactions/correlations were accounted for, could the code be made available somewhere?

Though it is not an environmental factor, as I read through the manuscript, it was not clear to me why the mating system was not included in the linear models. It would be interesting to show whether this trait overshadows any of the other predictors when it comes to the genetic structure, and to point out in which case it is not (if ever) the main predictor. Checking for correlations between it and the observed environmental factors may also provide some insight.

Results:

The results are presented in a detailed way, with main findings appropriately highlighted. However, the sheer density of information is overwhelming. I greatly appreciated the tables, that I found to summarise the results quite well, and was wondering whether the text could be organised differently so as to rely more on the readers' referral to the tables and make the reading lighter. There are also several instances when describing the results where the authors go back and forth between species. This left me utterly confused and I needed to re-read the text several times to untangle everything. Could there be a way to avoid this? Maybe describing each species separately then making comparisons (i.e. between sister species, selfing vs outcrossing, invasion ... but this could also just be done in the discussion as is already the case), or starting with the specific comparisons without going into the details of each species? Here the different layers of comparison are done simultaneously, and I personally had a tough time keeping up.

P23 line 36-37: This sentence is confusing since the results of the correlations are not mentioned further in the main text: ”It is less expected to find a negative correlation between size and connectivity and a positive one between stability and density of favorable habitats.” Maybe change it to something like: ”There were however unexpected correlations, notably, a negative correlation between size and connectivity and a positive one between stability and the density of favorable habitats.” On that last point, is stability expected to be negatively correlated with the density of favourable habitats? I would have thought that on the contrary, these two would be positively correlated. Would you mind explaining this?

Discussion:

P29 - line 161: What do you mean by ”selective interference” in this context?

P29 - line 180: ”As mentioned above, the four species differ in their colonization rate (not in extinction rates), but the difference is between the two families, not between selfers and outcrossers (Pantel et al., submitted). Since the difference is not between the two taxonomic families, it is likely that demographic extinction and colonization do not affect genetic variation strongly, as already shown in D. depressissimum (Lamy et al., 2012), but rather modulate the influence of the mating system." - You mention that the difference is between the two families then go on to say that it is not. Above it is that the difference is colonisation is between the two taxonomic families, so are the authors referring to demographic size in the second sentence? Please clarify.

Some minor comments:
P8 - line 184: 24 species were sampled?
P16 - line 331: the same effect as the first three
P29 - line 216: This dynamic

Reviewed by anonymous reviewer 3, 01 June 2021

The authors present a comparative analysis of population structure across four species of freshwater snails. The underlying questions concern the extent to which structure is determined by environmental features common to multiple species as opposed to species-specific factors that are species-specific. This question has broad interest but has rarely been studied using direct comparison, as the authors demonstrate with a survey of examples. The study system used here is ideal because of the defined and isolated region and the clearly delineated habitat patches. As the authors acknowledge, four species will not lead to very general conclusions but some interesting comparisons are possible (particularly between mating systems and between an invasive, expanding species and three native, more stable species). This study can also lead the way to further comparative approaches.

The Introduction does a very good job of defining the problem. The authors divide factors influencing neutral population structure into three categories: environmental factors, invasion dynamics (an example of an historical factor) and organismal traits. Of course, all of these factors will have effects. It would be helpful to be explicit about the quantitative nature of the question, i.e. to ask about the relative contributions of these factors. It would also be good to acknowledge immediately that they interact. For example, organismal traits can influence how each species experiences the same environmental factors.

The Methods section is also clear. I am not sure of the value of including the few samples from outside Grande Terre since we clearly expect different patterns between, as opposed to within islands. A modest number of microsat loci was used, but sufficient for the description of population structure. Since the loci used differed among species, some comparisons may be difficult (particularly for absolute diversity levels as opposed to patterns). Predictions are summarised in Table 1 and explained in the text. These are rather general and not directly connected to the measures of population structure derived here. This means that there is no explicit rationale for the choice of measures. A closer connection between the predictions and the variables used to test them would be helpful. On ll.340-341, the difference in predicted effect direction for P. acuta is not clear. On l.349, I would expect other things, not just site size, to influence long-term population size. Correlations among explanatory variables (Table S9) might influence the linear models, or their interpretation, and this possibility should be considered. The linear model description does not make it clear whether interaction effects were considered. Biologically, they might be expected, but their inclusion might make the models too complex.

The Results first present a summary of the patterns of variation and then consider the impacts of the explanatory variables, but without structuring by the three proposed factors. Not only were there correlations among explanatory variables but also there were strong correlations among measures of diversity and divergence. This suggests two things. First, that it may be possible to simplify the MS by focusing on the most informative variables rather than on multiple variables that measure more or less the same thing. I hesitate to suggest moving more information to SI, since this is already extensive, but that might be an option. Secondly, it makes one wonder about the potential to test multiple effects, especially when predictions are not clearly distinct.

Table 3 summarises effects in terms of significance, with connectivity being the major driver of both diversity and divergence. This is, perhaps, not very surprising. However, this comes back to the underlying question which, at least to my mind, should not be about whether these effects exist but rather about their relative contributions. The Yes/No answers in Table 3 seem poorly adapted to the latter question. Estimates of effect sizes would be preferable, if possible, perhaps with the redundant explanatory variables removed in order to focus on the three major factors.

The connectivity effect has been demonstrated previously for one of the 4 species. This species has also been shown to have a structure fitting an asymmetric island model. One issue is the extent to which this MS goes further. Model fitting does not seem to be possible for the other species, given the data available (and the likelihood of non-equilibrium for P. acuta). Nevertheless, the comparative approach that the authors advocate surely requires effect size estimates rather than only significance tests and it would be good to see this MS heading in that direction. The Discussion ends up being rather descriptive. That said, the logic is clear and the descriptions are interesting.

Use of English is generally good. I have commented only where the sense is unclear. However, some smoothing of the language might aid readability.

There is rather high reliance on the unpublished (parallel) paper by Pantel et al. (cited as ‘submitted’).