





# Peer Community In Evolutionary Biology

## Is our best measure of fitness correlated with environment? A study in an orange clownfish population.

**Pierre de Villemereuil**  based on peer reviews by **Stefan Vriend**  and 2 anonymous reviewers

Pascal Marrot, Cécile Fauvelot, Michael L. Berumen, Maya Srinivasan, Geoffrey P. Jones, Serge Planes, and Benoit Pujol (2024) Spatial autocorrelation and host anemone species drive variation in local components of fitness in a wild clownfish population. Zenodo, ver. 3, peer-reviewed and recommended by Peer Community in Evolutionary Biology.

<https://doi.org/10.5281/zenodo.13806778>

Submitted: 01 August 2023, Recommended: 24 September 2024

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Getting a clear definition of fitness for a particular evolutionary biology question is a complex challenge, fraught with pitfalls and misconceptions (Orr, 2009; Walsh & Lynch, 2018). In longitudinal surveys of wild populations, lifetime reproductive success (LRS) is generally considered the best measure of individual fitness (Bonnet, 2022). However, it is important to bear in mind that LRS is only a (noisy) measure of the realised success, relying on a substantial amount of assumptions (e.g. with regard to generation overlap, Walsh & Lynch, 2018), not a direct measure of fitness.

In a study on the clownfish, Marrot et al. (2024) studied the spatial and ecological drivers of lifetime reproductive success. To do so, they analysed a 10-year long survey on over 300 anemones harbouring clownfishes, and used a genetics-based pedigree to infer the LRS of each individual. Using a characterisation of the micro-habitat provided by each anemone, they used the anemone species, density and depth as ecological drivers and spatial-autocorrelated models to study more general (and undefined) spatial drivers.

The authors found that LRS was influenced by a significant amount by the spatial structure of the population, and, to some extent, by the anemone species harbouring the clownfish individuals. Together, they explain a substantial proportion of the individual variation in LRS.

While the actual determinants of spatial variation of LRS in this (and other) species remain understood, this study highlights an important aspect of measuring fitness in wild populations using LRS: it is particularly noisy and subject to environmental variation. This certainly does not mean that LRS is a bad proxy for fitness, it

is still among the best measure of it we can have access to. However, it highlights how carefully we should thread when analysing it. Especially, spatial auto-correlation of LRS, combined with population structure within a population, would lead to genotype-environment correlation for fitness, which is likely to bias predictions of response to natural selection and would be extremely difficult to estimate (Falconer & Mackay, 1996).

### **References:**

Pascal Marrot, Cécile Fauvelot, Michael L. Berumen, Maya Srinivasan, Geoffrey P. Jones, Serge Planes, and Benoit Pujol (2024) Spatial autocorrelation and host anemone species drive variation in local components of fitness in a wild clownfish population. Zenodo, ver.3 peer-reviewed and recommended by PCI Evol Biol <https://doi.org/10.5281/zenodo.13806778>

Bonnet, T., Morrissey, M. B., de Villemereuil, P., Alberts, S. C., Arcese, P., Bailey, L. D., Boutin, S., Brekke, P., Brent, L. J. N., Camenisch, G., Charmantier, A., Clutton-Brock, T. H., Cockburn, A., Coltman, D. W., Courtiol, A., Davidian, E., Evans, S. R., Ewen, J. G., Festa-Bianchet, M., ... Kruuk, L. E. B. (2022). Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science*, 376(6596), 1012–1016. <https://doi.org/10.1126/science.abk0853>

Falconer, D. S. and Mackay, T. F. C. (1996). *Introduction to quantitative genetics* (4th ed.). Benjamin Cummings.

Orr, H. A. (2009). Fitness and its role in evolutionary genetics. *Nature Reviews Genetics*, 10(8), 531–539. <https://doi.org/10.1038/nrg2603>

Walsh, B. and Lynch, M. (2018). *Evolution and selection of quantitative traits*. Oxford University Press.

## **Reviews**

### **Evaluation round #2**

DOI or URL of the preprint: <https://doi.org/10.5281/zenodo.12763868>

Version of the preprint: 2

### **Authors' reply, 20 September 2024**

Dear PCI Evolutionary Biology managing board, dear recommender Dr. Pierre de Villemereuil, dear reviewers,

Please find below our point by point response to all the comments on the v2 of the our article entitled Spatial autocorrelation and host anemone species drive variation in local components of fitness in a wild clownfish population.

Our version 3 of the article takes into account all these comments and shows in blue the changes made to the text, and a clean version. All files, including data and R protocols are deposited on ZENODO with the following DOI : 10.5281/zenodo.13806778

Regards,

For the authors, Benoit Pujol

Comments by Pierre de Villemereuil

Dear authors,

I have now received two reviews, both from original reviewers. Both reviewers appreciated the changes in the new version of the manuscript and are happy for it to be recommended. However, they had very minor suggestions for increasing the quality of the manuscript before recommendation.

Thus, I invite the authors to consider the minor suggestions from the reviewers and submit an updated version for recommendation.

>Thank you for your evaluation, we have taken into account all the comments of the reviewers.

Review by Stefan Vriend, 07 Aug 2024 10:18

I congratulate the authors on this revised version of the manuscript. The authors addressed all my comments in a satisfactory way, and I am also satisfied with their responses to comments made by other reviewers. Though, I feel urged to say, that in some cases, I was a little taken aback by the tone in which the responses were written (or, at least, perceived by me).

>Thank you for your comments that improved the quality of our manuscript. From our perspective, we simply took into account all your comments and described how in our point by point response with a very neutral and factual tone. Please be assured that there was no other intention.

I think that reframing the manuscript increased its focus. Adding more refinement in the interpretation of results and comparison of methods have strengthened the manuscript. I think that the conclusion of the manuscript is still slightly overemphasized (referring to L447-449), but I accept that this can also be a choice of style.

>Thank you for your comment, we agree and removed "undoubtedly strongly" from our conclusion to adopt a more neutral and factual style.

I want to congratulate once again the authors with their work.

>Thanks again for your comments that contributed to improving the MS

Some very minor comments remain:

L40, L79, L149: "long-term" instead of "long term".

>Done

L61: "Effective evaluation of this ability is successfully integrated in conservation strategies (Funk et al. 2019)".

>Done

L213: R version 4.0.3 was not released in 2024 but in 2020.

>Done

L228: Do you mean explanatory variables?

>Indeed, we modified the text accordingly

L228-229, L315: Species names are not italicised.

>Done

L325, L391: Elsewhere in the manuscript you write "spatially explicit".

>Done

L380-382: This sentence is somewhat confusing. Perhaps something like: "The biological mechanisms that underlie this pattern of spatial autocorrelation remain unknown to date. Yet/however/[pick your word], identifying them would improve our understanding of clownfish LRS and self-recruitment."

>Done

L511: Floating Bonnet.

>Done

Review by anonymous reviewer 1, 01 Sep 2024 19:54

I appreciate the authors clarification of their methods and justification of their approach in this revision of the article. I have only a few minor comments to be addressed.

>Thank you for your comments. They contributed to improve the quality of the MS.

Line 95-96: Perhaps an important clarification is that it is a small proportion of the variation that is attributable to genetic variation. I think you could argue that Bonnet et al. 2022 found substantial genetic variation (at least enough that in theory could contribute to some demographic change?).

>We modified the text accordingly

Line 99-100: I think you can remove the first part of this sentence. I think we rarely identify the ecological drivers, not only when little or no genetic variation is found.

>Done

Line 188: Be specific with the word "This". It is not clear what exact concern you are referring to here.

>We clarified by replacing "this concern" by "The focus on the habitat of breeders rather than larvae"

Line 371: Be specific with "This". What is in line?

>Done, we replaced by "this result is original because..."

## Decision by **Pierre de Villemereuil** , posted 10 September 2024, validated 10 September 2024

Dear authors,

I have now received two reviews, both from original reviewers. Both reviewers appreciated the changes in the new version of the manuscript and are happy for it to be recommended. However, they had very minor suggestions for increasing the quality of the manuscript before recommendation.

Thus, I invite the authors to consider the minor suggestions from the reviewers and submit an updated version for recommendation.

Best Regards,

Pierre de Villemereuil

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## Reviewed by anonymous reviewer 1, 01 September 2024

I appreciate the authors clarification of their methods and justification of their approach in this revision of the article. I have only a few minor comments to be addressed.

Line 95-96: Perhaps an important clarification is that it is a small proportion of the variation that is attributable to genetic variation. I think you could argue that Bonnet et al. 2022 found substantial genetic variation (at least enough that in theory could contribute to some demographic change?).

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Line 371: Be specific with "This". What is in line?

## Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.5281/zenodo.8198952>

Version of the preprint: 1

### Authors' reply, 17 July 2024

[Download author's reply](#)

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### Decision by [Pierre de Villemereuil](#) , posted 20 October 2023, validated 20 October 2023

#### **Please provide a revision according to the reviewers' feedback**

Dear authors,

I have now received the comments on three complementary reviewers on your papers, who provided detailed feedback. One of the reviewer is rather trained in spatial statistics, while the two others are evolutionary ecologists. There is a gradient of reception from the reviewers, from quite enthusiastic to skeptical about the novelty of the approach. I believe that, although spatial ecology is certainly not new, we are indeed lacking studies that are accounting for spatial auto-correlation, which does make the study interesting for a broad audience. At the same time, I believe the manuscript could work out better by being more nuanced, see many interesting comments from the reviewer in that regard.

Finally, I agree with the reviewers that the part about the adaptive potential in the introduction is a bit misleading regarding the scope of the paper and could be removed. Especially, (a measure of) the adaptive potential is the *\*additive genetic\** variance of fitness, not its total variance (which is rather named "opportunity for selection"). Also, the description of the Price paper is a bit too simplistic: as explained by Price (by the way, did you mean the 1972 paper about Fisher's equation?), the name "environmental" is quite a misnomer here, because "deterioration of the environment" for Fisher has as much to do with recomputation of the breeding values from one generation to the next, as it has to purely environmental effects.

Please consider the feedback from all reviewers, especially the ones about the presentation of the results and the ones about the statistical analyses (notably the bits about model averaging and accounting for spatial auto-correlation) to revise and submit a new version of the manuscript.

Best regards,

Pierre de Villemereuil

[Download the review](#)

## Reviewed by anonymous reviewer 1, 09 October 2023

### General comments and overview

Marrot et al. provide an interesting study examining the impact of accounting for spatial autocorrelation on our interpretation of ecological variables that affect lifetime reproductive success in a wild clownfish population. Overall, I think the set of the study is interesting and a worthwhile pursuit, but I think the authors overemphasize the impact of their results on the biological interpretation. In the writing of the results and the discussion sections I find there is a disconnect between the results provided and the authors interpretation of those numbers. I think a stronger manuscript would emphasize both the similarities and the differences found between the two approaches. Or the authors need to provide stronger evidence that the spatially explicit model drastically changes the results.

The introduction could be improved to better guide the reader to understanding environmental drivers of LRS. Currently, there is a lot of emphasis on adaptive potential, and I'm not sure this manuscript really address this concept.

I think the underemphasized aspect of the study is the difference in variance explained between the adjusted R<sup>2</sup> for both models. It seems to suggest that there is missing information that results in spatial autocorrelation and explains some variation in LRS. What are the hypotheses for this? Is it just many hard to measure environmental variables that are shared in proximity? How do we begin to understand it?

### Specific comments

Please consider my comments below that range from small and specific to broader suggestions for manuscript.

Line 58-67: This section is not convincing. Many of the definitions are unclear. What does it mean to "respond positively by mean of phenotype or molecular changes to the environmental demand? What is the environmental demand? I'm don't think you've outlined what you are defining as adaptive potential. Please consider being more specific in your definitions.

Further, many of these citations show responses to climate change, I don't know if the demonstrate that populations with adaptive potential are coping with climate change? Again, it is unclear to me what you mean by "cope" and "adaptive potential" in this circumstance.

Line 68-69: I think this is a second definition of adaptive potential, but it might be better to be more specific and clearer in your 1st definition (Line 58) and instead here note how adaptive potential is/can be measured? I also think there might be some important nuance missed here, but I could be wrong. I think here you are referring to the additive genetic variance of fitness, but I think this measures the rate of adaptive genetic change and not necessarily the adaptive potential.

Line 69-71: Does environmental variation always reduce the response? I think it would not always reduce the response.

Line 78-82: It seems pretty important to reference Bonnet et al. (2022) in this paragraph.

Bonnet, T, Morrissey, MB, de Villemereuil, P, Alberts, SC, Arcese, P, Bailey, LD, Boutin, S, Brekke, P, Brent, L, JN, Camenisch, G, Charmantier, A, Clutton-Brock, TH, Cockburn, A, Coltman, DW, Courtiol, A, Davidian, E, Evans, SR, Ewen, JG, Festa-Bianchet, M, de Franceschi, C, Gustafsson, L, Höner, OP, Houslay, TM, Keller, LF, Manser, M, McAdam, MG, McLean, E, Nietlisbach, P, Osmond, HL, Pemberton, JM, Postma, E, Reid, JM, Rutschmann, A, Santure, AW, Sheldon, BC, Slate, J, Teplitsky, C, Visser, ME, Wachter, B & LEB Kruuk. (2022) Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science* 376(6596): 1012-1016.

Line 38- 39: To date, only a few studies have quantified the LRS across multiple generations in wild marine species.

Line 40-42: Because of a long-term sampling effort, such information is available for a population of the ...

Line 42: What does PNG refer to? It is not clear to me.

Line 42: -43: Is this from previous work or from this study? I think, it should be clear from the summary alone.

Please consider rewording as below.

Previous work on the wild orange clownfish near Kimbe Island suggests that there is little adaptive potential and that variation in LRS is mainly driven by a breeder's habitat.

Line 48-49: Our state of the art spatially explicit analysis disentangled the role of these factors.

Line 52-64: Our findings imply that this clownfish population is susceptible to human-induced or natural changes in the spatial distribution and local assembly of anemone species. (Please correct to clownfish if it is the spatial distribution of clownfish that matters...but it is not completely clear to me from the current summary as written).

Line 57: Wild populations resilience to worldwide anthropogenic changes is....

Line 89-91: What possibility? It isn't clear from this sentence what possibility you are referring to? Please consider clarifying.

Line 91-93: Again, it is unclear what "it" is referring to in this sentence. Measuring fitness? Collecting pedigree data? Measuring additive genetic variance of fitness? Please clarify.

What about this work is convincing us that we are accurately measuring adaptive potential/fitness/additive genetic variance of fitness? Is it credible intervals? I'm not following the logic of what was accomplished?

Line 93-95: What also showed? Previous work? Please be specific in this sentence.

Line 99-100: Again, important to consider the Bonnet et al. (2022) reference above and perhaps this reference below.

The quantitative genetics of fitness in a wild seabird M Moiron, A Charmantier, S Bouwhuis  
Evolution 76 (7), 1443-1452

Line 102-105: In what case? In the case of the Hendry et al. (2018) manuscript?

Line 108: As mentioned earlier, A previous study outlined that the habitat of the breeders -defined as the combination of their host anemone species and the lagoon where they live - contributes most to the variation in LRS...

Consider rewriting as, "In this system most of the variation in LRS is explained by a breeders host anemone and the lagoon where they live."

Line 120: Is it spatial autocorrelation that generates similarity or is it shared environmental features that are measured by spatial autocorrelation?

Line 128-130: A meta-analysis conducted on 24 studies using linear regressions found that on average model coefficients were biased by ~25% when spatial .....

Line 135: Please consider the rewritten paragraph below to improve clarity.

There are two main aims of this study: (i) to build a spatially explicit model estimating the effect of environmental features on the LRS of clown fish, and (ii) to compare this spatially explicit model to a spatially naïve model to quantify the potential bias induced by spatial dependency. To accomplish these aims we used a

geostatistical method that takes into account spatial autocorrelation at multiple spatial scales to disentangle the relative contribution of these effects independently from their spatial structure. Overall, we expected these effects to be overestimated when spatial autocorrelation is not taken into account.

“these effects” should be replaced by exactly what you mean when you say these effects. I think you mean the effects of anemone species, local density, and depth.

Line 163: “fishes” usually is the plural for multiple species, while fish is used for the plural of a single species. I think you are counting multiple individuals of clown fish here and not surveying other fish species.

Line 167-169: Is there any error rate in this size measuring method for sex and reproductive status? Is it always the relatively largest fish that is female?

Line 227: Because no ecological variables were to be expected predominantly...

Line 235: Colon should be used to introduce a list.

Please consider the following rewrite to correct.

The model-averaging method is based on three steps: (i) the generation of all possible sub-models from the set of predictors of interest, (ii) the selection of the AIC-based 95% best models (leading to 106 spatially explicit models and 13 non-spatial models, see geostatistics below), and (iii) the averaging of estimates from predictors among all selected models weighted by Akaike weight of each model that includes the corresponding predictor. Here our zero-inflated model included ten variables (the effect of our five variables on the probability that fish will not produce a self-recruit and the count number of recruits produced by breeders), leading to 1032 models generated.

Figure 2: Could you label the intervals with their associated depths?

Line 257-261: You mention the choice of this method is based on the literature, but what about this approach is favourable? Can you be specific about what aspect of performance you are referring to?

Line 265: This colon should introduce a list separated by commas as above.

Line 293: Examining table one the point estimates differ, but almost all confidence intervals overlap and the estimates seem to be in the same direction. I think you should avoid using the word affected...especially in the results section because there isn't much difference in the interpretation or the estimates themselves.

Line 344: I don't really see any evidence for the strong wording in this manuscript for this statement? Almost all of your estimates are similar (overlapping confidence intervals) between the two approaches. Please consider being more specific in exactly the biological interpretation that would differ between the two approaches (e.g. the effect of *S. gigantea*). I think this would be a more credible interpretation of the results.

It might be more convincing to evaluate whether the spatially-explicit model outperforms prediction of LRS.

Line 376: In our analysis, only the effect of life span....

I don't see any evidence for this in your results? How are you concluding that only life-span was unaffected by spatial auto-correlation? Please define how you are defining differences between the approaches in your



methods.

Line 399: Please consider rephrasing to “Only a few examples from wild plant and animal populations indicate that spatial...

I think it would be worthwhile including in the discussion a paragraph on what exactly spatial autocorrelation is biologically. Sure, there are not many studies that use your approach, but there are certainly many studies that have show that different environmental conditions might affect selection or genetic variation. I think this is an interesting aspect of the study that could be brought to the forefront of the manuscript. You are finding that some of the variation is explained by spatial autocorrelation, and it seems we just don't have a grasp on this environmental features.

Line 419-431: Your exclusion of depth is not the most convincing evidence that depth plays no role in the number of recruits. RI is still high and the confidence intervals for the estimates for each model overlaps.

Line 438-440: Please consider the following rewording. However, anemone bleaching cannot explain our results because evidence suggests that bleaching affects all anemone species with the same magnitude (Hobbs et al. 2013) and no anemone bleaching event was reported over the duration of the survey.

Conclusion: Overall, I think the wording just needs to be toned down. I don't think the results provide as strong a contrast as your interpretation suggests. Please provide stronger evidence for the dramatic differences if you disagree.

Line 485: space between self and recruitment.

In number of recruits the intercept is not bolded as all other estimates with confidence intervals that do not overlap zero.

Consider increasing the dpi of the figures for higher quality figures.

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