PCIEvolBiol

Submission of a revised version

Dear Recommender and reviewers,

We thank you for your comments and your patience, we are happy to submit a revised version of our preprint article "**Spatial autocorrelation and host anemone species drive local components of fitness in a wild clownfish population"**
We are glad to have revised the article by closely following the recommender's and referees' comments, which greatly improved its scientific value.
We clarified the contribution of our study to spatial ecology, in particular when considering the spatial autocorrelation of fitness components, and considered all comments, in particular those about statistical analyses and results associated with the model averaging, which we removed accordingly, and the approach used to take spatial autocorrelation into account.

The version 2 (revised version) of the preprint, data, code for scripts of statistical analyses that were conducted in R, figures, and supplementary information can be found on https://zenodo.org/doi/10.5281/zenodo.12763868

Please note that we uploaded versions of the revised paper: a "clean" version of the manuscript and a "track changes" version that shows changes made to the text in blue and locates every referee's comment in the margin (if text was removed, then it does not appear).

Looking forward to hearing from you.

Please find below a point by point response to the comments:

Response to the recommender's - Pierre de Villemereuil - comments

Thank you for your constructive comments which allowed us to improve our article.

Comment #1 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.
Response #1 We have read through the text and nuanced the narrative to clarify the contribution of our paper. We agree that there is nothing new into conducting a spatial ecology study and did not want to reader to think that. The same is true when it comes to evaluating the spatial autocorrelation of phenotypic traits, which I was already doing more than twenty years ago. The contribution of our paper lays into its application to a particular

type of variation; a local component of fitness that informs us about the ability of fish populations to self-recruit.

*Comment #2 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").*
Comment #3 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.
Response #2 and #3 We simplified the text in agreement with your comment, and those of the reviewers. The revised version of the article benefits from less focus on the adaptive potential. It is no more misleading and keeps the reasoning closer to our work on the spatial autocorrelation of fitness components. As a result, the first two paragraphs became one and the sentences at the origin of these two comments were removed.

Thank you for your constructive comments which allowed us to improve our article.

Response to reviewer 1's - Stefan Vriend – comments

Thank you for your constructive comments which allowed us to improve our article.

Comment #4 (continuous numbering of the comments of all reviewers) Adaptive potential. As you put your study in context of adaptive potential, I had imagined that, after reading the Abstract and Introduction, the analysis would include a temporal component, and that you would assess how clownfish recruitment (probability and number) would respond to changes in the environment. I want to stress that I think that adding an explicit spatial component to an analysis of LRS is interesting and elegant by itself. However, it might be misleading to provide this work in context of adaptive potential, which hinges on this dimension of change, which is not part of your analysis. I therefore suggest putting the work more in context of spatial autocorrelation (as is done elsewhere in the Introduction) and less so of adaptive potential, or, alternatively, include time in the analysis.
Response #4 We simplified the text in agreement with your comment and the comments of the other reviewer and the recommender. The focus on the adaptive potential was removed in the revised version of our article because it was misleading. We still outline the global importance of the ability of species to adapt in the introduction, but without going into much details, only so that we can introduce the interest of analyzing selection mechanisms. As a result, the revised version of the introduction is closer to our work on the spatial autocorrelation of fitness components.

Comment #5 LRS. Interesting that the unit of your LRS measurement is the "recruit" rather than the classically used "offspring". This choice makes sense in relation to the importance of self-recruitment for population persistence as you highlight in L107-108). Up until the Methods section (L175 and further), it was however not clear to me that you defined LRS in such a way. I suggest emphasizing this in the Abstract and Introduction. In particular, in L75-

82, where you provide a definition of LRS that does not match yours, the manuscript would benefit from citations to other studies that have focused on a recruit-based LRS.

Response #5 We agree and modified the text accordingly to better define LRS in our study as being based on recruits, from the start, in the introduction. We hope to have clarified this aspect. For a mutual understanding, we must outline here that there is often no real difference between records of offspring and recruits in most studies based on long term surveys of wild populations. This is because individual LRS estimates are produced from an observational or genetic pedigree. This pedigree is built with potentially breeding individuals captured on site. In other words, they mostly have the same type of data than us. We somehow could have dropped the term recruit but want to make sure that there is a clear understanding of what was analyzed in this study. We therefore gave a more precise definition of LRS that links our use of the term recruit to the classical use of the term offspring.

Comment #6 Model averaging. I appreciate that you recognise the issue with putting too much faith in any single model and instead draw conclusions from multiple candidate models through model averaging. However, if I interpret the description of the model averaging procedure used in this study (as described in L235-242) correctly, this form of model averaging can be flawed whenever there is multicollinearity among the predictor variables in the candidate models. That is, predicted responses based on the average of regression coefficients [incorrect] will not be the same as the average of predicted responses for each candidate model [correct] (see Cade, 2015, Ecology, https://doi.org/10.1890/14-1639.1). That is, the former will not take into account the covariance structure of predictor variables, whereas the latter will. So, if I understood your methods correctly, multicollinearity in your predictor variables (which is often the case in ecological studies) might be problematic for interpreting your results. One possible way forward, as highlighted by, e.g., , is standardising the parameters. In cases where this does not suffice, model averaging predictions (rather than coefficients) will solve many of the issues (also highlighted here: https://atyre2.github.io/2017/06/16/rebutting_cade.html).

Response #6: We thank the reviewer for their considerations regarding the numerous issues that may arise from multicollinearity among variables. In fact, all variables (both ecological variables and the principal components of PCNM) were standardized before fitting the models. We actually forgot to mention it in the Material & Method section. This important step is now included in the text.

Minor comments:

Title: I believe that the title covers the content of the study well, but I wonder whether it should rather read "spatial autocorrelation and host anemone species drive variation in local components offitness…". *or another word that indicates a 'change'. Data accessibility statement: Thank you for providing the scripts to Zenodo. However, the data files seem to absent. Could you add these, so that one could run the scripts?*

Response: Done

L43-46: I find this sentence hard to read. What do you mean with "within the habitat variable" and "global habitat information"? Please clarify.

Response: We changed the text to: "Whether the host anemone species, geographic location, density or depth contributed to LRS remains however unknown because they were combined into a unique variable", which should clear the issue.

L46-48: What do you mean with "local components of fitness" here? Self-recruitment could also be seen as a component of fitness? Or does this refer to LRS? Please clarify.
Response: Self-recruitment is a population process whereas "components of fitness" was used here to call for individual variation in reproductive success. We see why our wording could be misleading and clarified this point. We changed the text to: Here we tested whether it is the ecology or the spatial distribution of clownfish that shaped the individual variation of a local fitness component, which would affect the population self-recruitment process and ultimately the maintenance of this wild population.

L52-54: The conclusion that your findings "imply that this clownfish population is susceptible to human-induced [...] modifications ..." does not seem to follow logically from the findings as presented in L49-52. That is, there is no mention of 'human-induced modifications' in any of the study's aims and or findings. Please make the link between the findings and conclusive sentence more explicit.
Response: We modified the text and removed "natural or human induced" to clarify the point made. Our conclusion is drawn from the lines 49-51: "We found that the host anemone species had an impact on wild clownfish LRS independently from their spatial distribution. The spatial distribution nevertheless had an impact on its own, as reflected by the spatial autocorrelation of LRS". In a nutshell; the host anemone species and spatial distribution drive variation in fish LRS. Their modification would therefore logically impact the clownfish population.

L57: I suggest replacing "wild populations resilience" by either "The resilience of wild populations".
Response: the text was modified accordingly

L58: Just a thought whilst reading this sentence: perhaps it will provide some context to the reader if you would relate 'adaptive potential' to other widely used terms and synonyms, such as 'adaptive capacity' and/or 'adaptive plasticity'.
Response: In fact, following your previous comment, we removed some text on the adaptive potential rather than adding more information. We do not want to confuse the reader on the aims of the paper by discussing too much about the adaptive potential of populations in the introduction. Our approach participates to better understanding the ecological mechanisms shaping components of fitness in a wild population. However, we did not estimate adaptive plasticity.

L59: "by means of"
Response: As a result of previous comments; this sentence no longer present in the text

L62-63: What do you mean with "harbouring adaptive potential"?
Response: As a result of previous comments; this sentence no longer present in the text

L68-82: Very clear paragraph!
Response: Thank you, we nevertheless modified the text to make it even clearer in accordance with other comments outlining that we put too much emphasis on introducing notions about the adaptive potential where the focus of our paper is more on mechanisms shaping fitness variation

L89-91: I suggest removing this sentence. The next sentence (starting with "Previous work...") would follow well from the previous sentence (starting with "Coral reef fish...").

Response: Done

L93: What do you mean with "that it can be achieved"? I suggest rephrasing this sentence so that it explicitly states what Salles et al. 2020 achieved.
Response: As a result of the simplification of the introductory text on the adaptive potential, suggested in previous comments, this part of the sentence was removed.

L106: What is the rationale behind a percentage of 50%?
Response: We clarified the link between a self-recruitment of 50% in the population and LRS, which measurement is based on recruits, and cited the corresponding reference.

L108-111: I take from this statement that Salles et al. 2020 already found out what the ecological drivers of LRS variation in this system are. How is this different from your goal to "disentangle different ecological sources of variation in LRS…" (L104)? L120-134: Strong paragraph.
Response: They identified the effect of the habitat which was a unique variable combining different factors such as the anemone species or depth. This is already more than what most studies do. Here, we went further and disentangled the role of the various ecological variables previously combined within the notion of habitat, and analyzed their spatial autocorrelation effect. We modified the text to mention this information, which we hope will clarify this aspect.

L131-139: In these lines, you use "spatial dependency", "spatial distribution", "spatial scale", and "spatial structure", and it is not clear to me whether some of them are used as synonyms or how they relate to one another.
Response: "structure" was not necessary and was removed. The "word "spatial" was removed before "scale". The other words "dependency" [between variables], distribution [of a variable] are self-explanatory. We hope that this will clear this concern.

L135-142: I appreciate that you compare you spatially explicit model to a model without spatial autocorrelation.
Response: Thanks

L136: What do you mean with "depth"?
Response: We don't mean nothing more than depth, ie, the vertical distance from the surface to the bottom, when using the word depth

L145-173: Very clear description of the study system.
Response: Thanks

L181-182: Please provide a rationale for this choice here, or should I read L184-185 as such?
Response: We clarified the rationale for this choice in the text: "This choice was made to adapt LRS to the group hierarchy of clownfish breeders and to be a sensible measurement of the relative ability of clownfish individuals to participate to the population self-recruitment."

L195-199: Why did you choose a radius of 200 meters instead of, for example, the mean or the maximum (recruiting) distance?
Response: We agree with you that we could have chosen the mean distance between recruits and their parents (254m). We chose the closest round number in hundreds that would be a

shorter distance for the sake of clarity and efficient analysis. The maximum distance between recruits and their parents would not have been relevant to express the local environment around the focal anemone. More precisely, as mentioned in the materials and methods, we choose a radius of 200 meters around the focal anemones for 3 reasons: 1) the mean distance between self-recruits and their parents was around 250m, 2) 47% of recruits are located at less than 200m from their parents and 3) the mean distance between anemones were around 400m. All these features suggest a potential effect of the local environment around the focal anemone on the probability of self-recruiting. The distance of 200m was chosen because it was a good compromise to express the "local" environment around the focal anemone.

L199-204: What is the maximum distance that a recruit could potentially travel? In other words, could the difference between recruiting distance and between-anemone distance rather be a result of physical constraints?
Response: The maximum distance between a recruit and their parents was 662m in this population (note that this does not reflect the maximum distance larvae could travel). The mean distance between each anemone and all the other anemones was 388m. 26% of recruits have been found beyond this distance (from their parents). These numbers suggest that there are no (absolute) physical constraints. This information can be visualized in supplementary information 1.

L204-210: To what extent are individuals with S. gigantea as a focal anemone more spatially constraint in where they can recruit? I imagine that shallow waters (or the shore itself) will inevitably force individuals to recruit to deeper depths.
Response: we would not use the word "inevitably" because the currents that drive dispersal may be complex. We acknowledge this higher probability below in the text : "larvae may recruit on deeper anemones than their anemones of birth (Buston et al. 2012), we expected that the probability to produce self-recruits increases as the depth of host anemone of parents decreases, independently from the species of the anemone." We'd rather not discuss this aspect in more details because it would be speculative.

L209: In L191 you introduce "focal anemone", but here you use "parental anemone". Please stay consistent in the choice of terms.
Response: We simplified the wording used here, and removed the word "parental" from the text elsewhere, sometimes replacing it with "focal" when appropriate.

L213: I suggest citing R as well.
Response: We added the reference accordingly

L217: I interpret your zero-inflated model as a zero-inflated Poisson because you refer to Poisson in L214, but it would be clearer if you could specify that here.
Response: We added this information in the text.

L227: "Because no ecological variables were…"
Response: done

L252-255: Why did you choose to use discrete lags rather than a continuous distance measure in your correlograms?

Response: This is a regular spatial autocorrelation approach. Spatial autocorrelation is always calculated within a range of distances. When the spatial correlogram is built, similarity among neighbors estimated per range of distances is plotted against a gradient of these distance ranges. Using a "continuous" distance measure would result in the impossibility to build the correlogram because there would not enough data per distance unit.

L266-267: Why did you choose to truncate the distance matrix?
Response: This is the standard approach for the PCNM approach. See Dray et al. 2006 (https://doi.org/10.1016/j.ecolmodel.2006.02.015) for a complete description of this method, or Bo rcard and Legendre 2002 (https://doi.org/10.1016/S0304-3800(01)00501-4) for a complete justification of the truncated distance matrix.

L310-318: Would it not be more natural and/or easier interpretable to put your results in terms of the probability to self-recruit and the probability to produce a (self-)recruit rather than the probability to not self-recruit and not produce a recruit?
Response: The zero-inflated Poisson model predicts the probability to have a 0 (vs. any positive number), which corresponds here to the probability of not self-recruiting. We chose to keep the brute estimates from the model because it is unclear whether transforming the probability to have a 0 into the probability to have a 1 would be right because the effect of factors (e.g., the year of sampling) on the probability to not self-recruit may not be similar when applied to 1 minus the probability to not self-recruit.

L328-331: I think it would be easier to read this section if you would describe the results in terms of "X times more likely" rather than "X the odds".
Response: We corrected the text to explicitly indicate the probability to not self-recruit in our population and its variation for fish living on *S. gigantea*.

L342-344: There only seems to follow one component following "a unique combination of", but one would expect at least two, so I suggest rephrasing. Perhaps something like "Our spatially explicit analysis of long-term monitoring data from a wild clownfish population revealed…".
Response: done

L344-345: Maybe a bit more nuance would be justified. Your study clearly highlights the difference between the spatial and non-spatial models in terms of the number of recruits produced, but for the probability of (not-)recruitment, there is only one effect that seems different.
Response: we toned down this aspect in accordance with the reviewer's comment

L353-354: What do you mean with "at all scales" and how could the reader check this assertion?
Response: The Egs included in the spatially explicit model (and generated with the PCNM) describe all the scales at which LRS is autocorrelated. This is a property of the PCNM itself, as explicitly mentioned L246-250 and L255-258 in the Material & Method section.

L419-431: It would be great if you could elaborate on the (ecological) consequences of this finding. Why would individuals have a better recruitment probability in S. gigantea? In

addition, what other differences between the two locations where the anemones occur could explain the difference in recruitment probability?
Response: we agree; this is why we took the time to elaborate on these hypotheses are detailed in the next paragraph

L434: Some text appears in red.
Response: Thanks for indicating that issue, now sorted. It will appear in blue in the version where we indicate changes made in the revised text but will appear in black in the clean version of the revised manuscript

L478-483: Interesting. This is exactly the type of environmental change I refer to in my first main point and had expected to be part of the study after reading the context of adaptive potential. As climate change is not part of your study in any shape, I suggest removing the sentence starting with "More investigations are…".
Response: done

L484-486: This feels rather out of the blue, mostly because it is the first time you mention "long-distance dispersal" (Interesting nonetheless!). I suggest rephrasing the ending of the conclusion section so that it better fits with the conclusions of your work.
Response: We removed this sentence

Figure 1: Please specify the x and y axes. Please increase the size of the text and the plot itself to increase readability.
Response: This Figure is a map of the anemones around Kimbe Island that includes the geographic scale. In order to avoid any confusion with a graph, we added the North direction. Also, we increased the size of the text and the points.

Figure 2: The text and labels of this figure seem dragged out of proportion. Please fix this to increase readability.
Response: done

Supplementary figure: Please increase the text size to increase readability.
Response: done

Response to reviewer 2's - anonymous – comments

Thank you for your constructive comments which allowed us to improve our article.

Comment #7 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.
Response #7: We modified the text of the results and discussion sections accordingly to improve the connection between our results and biological interpretation. In particular, we toned down the discussion about the impact of using the spatially explicit model. Although our comparison of the two models showed that the spatially explicit model contributed new insights, we agree that the biological interpretation was not drastically modified.

- How the spatially explicit model changed the results was already presented in the results: “The inclusion of Egs affected the magnitude, the sign and the confidence intervals of averaged estimates both in terms of probability of not self-recruiting and the count number of recruits produced” and “Egs increased the degree of fit of the model with an improvement of adjusted R^2 of 0.18 (the non-spatial and the spatially explicit model explained respectively 16% and 34% of the variance in LRS) and a drop of AIC of 183. This AIC drop means that the inclusion of the 29 Egs significantly improved the degree of fit of the model without over-parameterizing the model”.
- Similarities and differences found between the two approaches were already presented in the result section, in particular for the “year of sampling” and the “ecological” effects on LRS.

Comment #8 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.
Response #8: We removed most of the text on the adaptive potential (first two paragraphs are now only one paragraph) and clarified the text of the introduction to avoid misguiding the reader. The emphasis of this paragraph is now put on the explanation of the LRS.

Comment #9 I think the underemphasized aspect of the study is the difference in variance explained between the adjusted R2 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?
Response: although we agree that environmental effects that were not measured in this study and were spatially autocorrelated might explain the difference between the R^2 of the two models, we do not think that we should elaborate further on this broad topic aspect in the paper because we want to avoid speculation.

Specific comments
Comment #10 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.
Response #10: we agree and modified the text to simplify its content in order to avoid any confusion between the general context of the study and its aims. We reduced the text on the adaptive potential because it is not the focus of our paper. We also clarified some aspects because this introductory text should be understandable on its own without the need to add definitions.

Comment #11 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.

Response #11 As a result of other comments, we removed the definitions of the adaptive potential, and only introduce its global importance as part of the general context of the study, while our focus is made on spatial autocorrelation

Comment #12 Line 69-71: Does environmental variation always reduce the response? I think it would not always reduce the response.
Response #12 As a result of the simplification of the introductory text on the adaptive potential, this sentence was removed

Comment #13 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, LJN, 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.
Response #13 We totally agree. This reference had been lost in translation over the long writing journey of this article. It is now cited.

Comment #14 Line 38- 39: To date, only a few studies have quantified the LRS across multiple generations in wild marine species.
Response #14 Text was modified accordingly.

Comment #15 Line 40-42: Because of a long-term sampling effort, such information is available for a population of the …
Response #15 Text was modified accordingly.

Comment #16 Line 42: What does PNG refer to? It is not clear to me.
Response #16 Papua New Guinea, the text was modified accordingly

Comment #17 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.
Response #17 This is indeed from previous work. Text was modified accordingly

Comment #18 Line 48-49: Our state of the art spatially explicit analysis disentangled the role of these factors.
Response #18 This is similar to what's written in the text. The issue was likely linked to using the words "state of the art". We therefore removed them.

Comment #19 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).
Response #19 We modified the text accordingly

Comment #20 Line 57: Wild populations resilience to worldwide anthropogenic changes is….
Response #20 This is similar to what's written in the text. We modified the sentence so that it reads better: "The resilience of wild populations to environmental change is closely linked to their ability to adapt"

Comment #21 Line 89-91: What possibility? It isn't clear from this sentence what possibility you are referring to? Please consider clarifying.
Response #21 As a result of the simplification of the introductory text on the adaptive potential, suggested in other comments, this sentence was removed

Comment #22 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 adaptivie potential/fitness/additive genetic variance of fitness? Is it credible intervals? I'm not following the logic of what was accomplished?
Comment #23 Line 93-95: What also showed? Previous work? Please be specific in this sentence.
Response #22 #23 As a result of the simplification of the introductory text on the adaptive potential, suggested in other comments, parts of this sentence were removed. The revised version of this sentence should be clearer as it addresses directly the findings of a previous study on clownfish LRS variation.

Comment #24 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
Response #24: Done

Comment #25 Line 102-105: In what case? In the case of the Hendry et al. (2018) manuscript?
Response #25: The sentence as rewritten and the "in this case" referring to the absence of genetic variation for fitness mentioned in the former sentence was replaced by "When little or no genetic variation for fitness is found,".

Comment #26 Line 108: As mentioned earlier, A previous study outlined that the habitat of the breeders -definted 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 a breeders host anemone and the lagoon where they love."
Response #26: Done

Comment #27 Line 120: Is it spatial autocorrelation that generates similarity or is it shared environmental features that are measured by spatial autocorrelation?
Response #27: Our wording was awkward, we clarified the text. To answer your question: Shared environment effects may or may not be measured by spatial autocorrelation.

Comment #28 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 …..
Response #28: The text was modified accordingly:

Comment #29 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 clow fish, and (ii) to compare this spatially explicit model to a spatially naïve model to quantify the potential biased 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.
Response #29: Done

Comment #30 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.
Response #30: Done

Comment #31 Line 167-169: Is there any error rate is this size measuring method for sex and reproductive status? Is it always the relatively largest fish that is female?
Response #31: Indeed, the largest fish is always the dominant and the dominant is always female.

Comment #32 Line 227: Because no ecological variables was to expected predominantly…
Response #32: we modified the text to avoid cutting the verb infinitive

Comment #33 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.
Response #33: done

Comment #34 Figure 2: Could you label the intervals with their associated depths?
Response #34: done

Comment #35 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?
Response #34: We added text to clarify these aspects: "it is the best method to remove spatial autocorrelation, independently from its direction and its strength (relaxing the assumption of isotropy and stationary)".

Comment #36 Line 265: This colon should introduce a list separated by commas as above.
Response #36: done

Comment #37 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.
Response #37: Done, replaced by « altered »

Comment #38 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.
Response #38: We agree that the sentence was awkward and used strong wording. We toned down the sentence and modified the text accordingly with the reviewer's comment. We now outline that the spatially-explicit model outperformed the non-spatially-explicit model. How the biological interpretation would differ between the two approaches is mentioned and developed later in the text, so that we did not added text here about this difference to avoid redundancy.

Comment #39 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.
Response #39: We agree, the corresponding text was removed

Comment #40 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 brough 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.
Response #40: Text was modified accordingly. We mentioned the reviewer's idea about the interest of identifying the source of spatial autocorrelation but we did not want to speculate as to what this source of variation would be because many untested hypotheses could explain spatial autocorrelation (clownfish directed dispersal, habitat choice, habitat linked coral cover, density of food, link with anemone's ecology in terms of dispersal, movement, food, survival, etc.)

Comment #41 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.
Response #41: the model averaging approach was replaced by full models following the request of ref 3, we nevertheless toned down the conclusive aspect of the text

Comment #42 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.
Response #42: done

Comment #43 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.
Response #43: The wording was toned down

Comment #44 Line 485: space between self and recruitment.
Response #44: This text was removed following reviewer1's comment

Comment #45 In number of recruits the intercept is not bolded as all other estimates with confidence intervals that do not overlap zero.
Response #45: done

Comment #46 Consider increasing the dpi of the figures for higher quality figures.
Response #46: we have used the same resolution than for past articles

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Response to reviewer 3's - anonymous – comments

Thank you for your constructive comments which allowed us to improve our article. I tried to separate the text of your report in numbered comments to facilitate the response. I hope it will be suitable.

Comment #47 the current manuscript models LRS in a wild population. As a consequence, there are various components to both the ecological and sampling process that need to be accounted for with an appropriate statistical model, which here includes the presence of many zeros as well as a spatially structured sampling design. The discussion has a large focus on the spatially explicit modeling, and consequences of lacking to account for the spatial properties of the sampling process. This is briefly done by comparing the results of a spatially explicit model and a model that does not account for such properties. There is also a paragraph in the introduction with that angle, though the introduction is generally more biologically focused.
Response #47 As noticed, the whole point of the manuscript is take into account spatial autocorrelation, which is relatively rare the study of Lifetime Reproductive Success data from long term surveys. The interest of the study comes from applying spatial autocorrelation to a biological study of LRS. Indeed, wild population LRS comes with many zeros, which is taken into account in the analysis by using a zero inflated approach of the data. The introduction has now changed a little and following other reviewers' comments, we reduced the text on the adaptive potential, which makes more of the focus on the interest of using a spatially explicit approach of LRS in a wild population.

Comment #48 Overall, I do not agree with many of the statements made with respect to the analysis, nor do I find the analysis particularly novel (which, to be clear, is fine). Including spatial components in statistical models is mainstream in biology and many of its empirically focused subfields. However, the present study attempts to convince the reader that the modeling is groundbreakingly novel, complex or "state of the art".
Response #47 As mentioned above, the interest of the paper lies in combining spatial autocorrelation and ecological analysis of LRS in wild populations which is original, even more so in marine fish populations, but we did not make claims about conducting a groundbreaking approach in the paper. We never attempted to sell the use of spatial

autocorrelation as groundbreaking. We read through the text to make sure that no text could be interpreted this way anymore.

Comment #49 My primary recommendation is to shift that focus and to bring the study more in line with its biological narrative.
Response #49. As mentioned above, the introductory text about adaptive potential was reduced so that the focus is more on the spatial autocorrelation/LRS/wild population interesting combination.

Comment #50 The attempt to convince Biologists that not accounting for the consequences of spatially structure designs is also not new, and since it is based on a single study, and is not exhaustively discussed, distracts from the main narrative of clownfish lifetime reproductive success.
Response #50. We did not attempt to convince biologists that using spatial autocorrelation was new! I used spatial autocorrelation on phenotypes more than twenty years ago and am aware of this lack of novelty. The narrative is not a focus on the LRS, it is on using a spatially-explicit study of LRS data from a wild population long term survey. We think this point is now clearly presented in the paper.

Comment #51 In the discussion the authors state that the inference drawn from their study would have been negatively impacted if it had not accounted for its spatially structured design in the analysis, but insufficiently go into detail as to in what ways it would be different, for a study focused on the consequences of spatially structured sampling designs in evolutionary biology.
Response #51. We agree and outlined this aspect throughout the manuscript.

Comment #52 My second major comment relates to the difference between data and model. In various places the authors confuse properties of the data with (violations in) assumptions of their statistical model. In the results (for example) it is stated that the data follow a Poisson distribution where the sample mean of the data is used as estimator for the first moment of a Poisson distribution. However, in one of the following sentences the authors state that there are excess zeros relative to that same Poisson distribution. Generally, the authors use properties of the raw data to motivate their choice of statistical model, without verifying if those choices indeed are required due to assumption violations in the statistical modeling approaches that they apply. This is the case both for the zero-inflated component, as well as the spatially structured design. Hence, I would like to see more evidence of violated residual assumptions for a Poisson GLM (violation of non-independence of observations as well as deviation from Poissonanity), before the authors move to a spatially structured zero-inflated Poisson GLM. Generally, the authors should be aware of the difference between calibrating a model for prediction, and calibrating a model for inference. A model that predicts well is rarely suited for performing inference. While the authors seem to be interested in performing inference, the methods they apply are mostly suitable for performing predictions. AIC is a information criteria that finds models that predict well, and modelaveraging is usually very suitable to find a model that predicts well but is rarely useful for inference (to support this statement I have also included a link to a recent preprint by Ben Bolker below, but I encourage the authors to further study this issue). My suggestion is to remove the model-averaging component from this study entirely; for inference the full model often has considerably better properties.
Response #52. We agree with the reviewer’s comment and therefore replaced our model averaging approach by a full model. We do not want to engage in a neverending debate but nevertheless invite the reviewer to reflect on the « considerably better propoerties that the full model offers for inference », because a model that predicts is also a models that infers properly the parameters, a model averaging approach offers some specific advantages, and both type of approaches provided us with similar results.

Comment #53 This combines well with my suggestion in the following paragraph. On a more technical note, the authors fit a GLM with eigenvectors from the neighbourhood matrix included as predictors. Consequently, the eigenvectors and associated slope parameters are treated as fixed-effects. Usually, unmeasured effects (such as spatial effects) are treated as random instead of fixed. A more appropriate approach might be 1) to treat the slopes of the eigenvectors as random effects coming from the same distribution, or 2) use a spatially distributed random effect instead (note: this is implemented for ZIP models in the glmmTMB R-package amongst others). Personally, I would advice the authors to go with the second approach as it allows for a more explicit relationship between distance of sampling units and counts (in terms of an autocorrelation function) and it circumvents the issue of sensitivity of the analysis to the number of included eigenvectors, which I consider an unresolved issue to the approach the authors have taken.

Response #53. We think that it would be a mistake to consider our Egs as random effects. The reason for using a variable as a random effect is generally to test for a global effect rather than comparing the relative effect of its different modalities, and to control for its variation by estimating the variance among blocks (a random effect is typically a discrete variable with more than 5-6 blocks), without losing many degrees of freedom. Here, both these issues do not apply. By using a random effect, we would save only one degree of freedom and would estimate variance across a continuous variable, which would make no sense for these eigenvectors. Further, more throrough information supporting our reply can be found on this blog article by Brian McGill (https://dynamicecology.wordpress.com/author/brimcgill/), or this page on GLMM by Ben Bolker et al. (https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#should-i-treat-factor-xxx-as-fixed-or-random).

Comment #54 Finally, the authors mention that the dataset is the result of long-term sampling, but no other mention to a temporal component is made. It would be nice (but not completely necessary) if the temporal nature of the dataset could be elaborated on a little bit in reply to this review.

Response #54. The data is Lifetime Reproductive Success, it is in itself the result of the long term survey, we do not see what "temporal component" the referee would like us to mention. We mentioned the duration of the survey and the life cycle of the fish.

Detailed comments

l40: The first few sentences outline a knowledge gap, so I suggest to rewrite this sentence in a way that makes clear that this study addresses that.

Response: We modified the sentences accordingly

l42: I suggest (in the entire paper) to avoid such vague references as "here" or "there" as it tends to be confusing to the reader. Explicitly name the object/place that you reference, please.

Response: done throughout the entire paper

l44-46: This sentence is relatively ambiguous. Please improve along the lines of "However, habitat can in fact be understood as comprised of various components . . . , so that the exact driver of LRS is unclear".

Response: the sentence was clarified: "Whether the host anemone species, geographic location, density or depth contributed to LRS remains however unknown because they were combined into a unique variable"

l48-49: "state of the art" feels like overselling what is in practice a spatially structured GLM.

Response: we removed these words. This was a misunderstanding as we thought this was meaning something in the line of "typical", "usual", "proof-tested"

l57: changes -> change.
Response: done

l59: mean -> means, changes -> change.
Response: In accordance with comments from other reviewers, this text was removed

l60: please avoid the use of "parameter" is a non-statistical context here.
Response: done

l67: this statement implies in this article adaptive potential is "directly estimated", but how exactly is not clear to me. If it is directly estimated, I would like to see that explained more clearly in the manuscript. If it is not, this sentence should be removed.
Response: sentence was removed, and the whole paragraph simplified to drive the focus away from the adaptive potential, which was misleading about the aims of the study.

l75-82: good sentence.
Response: Thanks

l87: affect -> affects.
Response: Done

l89: I am not sure what maintenance means in this context.
Response: We clarified the text by using "conservation"

l90: unclear what "most" refers to; most clownfish researchers?
Response: this sentence was removed for the sake of clarity

l93: an odd place to mention "statistical framework" here, it feels again like overselling the modeling in this study.
Response: this sentence was modified and these words removed for the sake of clarity

l102: I am not sure what the authors refer to with "in this case".
Response: The sentence as rewritten and the "in this case" referring to the absence of genetic variation for fitness mentioned in the former sentence was replaced by "When little or no genetic variation for fitness is found,".

l103: here -> in this study.
Response: Done

l108: "a previous study".
Response: This sentence was modified on the basis of other reviewers' comments and these words removed

l113-116: this is an ambiguous sentence, please rewrite. For example, what is "relative detailed contribution"?
Response: We changed the sentence to: "The relative contribution of the anemone species, its depth and the local density in anemones to the LRS of clownfish remains unknown to date. Knowledge of this relationship would improve our understanding of clownfish ecology and adaptation to their complex habitat"

l125: "450ha" not information that is of interest here; the introduction can be relatively high level and broad.

Response: we removed it

l127-128: I consider pseudo replication and spatial autocorrelation as two separate issues. Indeed, both result in non-independence of observations, but that is about all that these issues have in common. The "Haining" reference is a whole book, please cite more specifically: is there a specific page or chapter that the authors want to refer to perhaps?

Response: We agree with you, spatial autocorrelation and pseudo replication are not the same issue. Pseudo replication was mentioned here as the consequence of not taking into account spatial autocorrelation. This point is clearly mentioned L127-128. We removed the Haining reference, and replaced it by an academic article (Hurlbert 1984)

l129: "a ..24 studies", I do not see the relevance of this information for the introduction.

Response: we disagree because we think that it is important to mention the number of studies used to conduct a meta-analysis and therefore kept this information

l120-134: I find this a lot of text to say "we fitted a GLM".

Response: We find this comment surprising as the text (L120-134) mentions the statistical issues when spatial autocorrelation is ignored. We believe this is central to our paper.

l213-214: this statement is problematic. There is a difference between distribution of data and the calculation of its sample mean, and the assumed distribution of a model and its estimator for the first moment of the assumed distribution. Please revise.

Response: We removed the "poisson distribution" term and replaced the previous sentence by "In this population, the mean of individual LRS was 1.27 (± 2.32) and reached a maximum of 20 self-recruits".

l214: is this "maximum" of 20 the possible upper bound for the number of self-recruits? I.e., is the Poisson assumption of an upper bound at infinity unrealistic for this application?

Response: We are surprised by this comment. Technically, the upper bound of anything in nature being "infinite" is unrealistic… "20" represents the maximum LRS observed in our population.

l215-217: the authors first state that the data follow a Poisson distribution, but then state that it actually does not (excess zeros relative to a Poisson process). Please correct this.

Response: We removed the first statement that the data follow a Poisson distribution.

l217-221: the authors seem to confuse 1) excess zeros in the data, and 2) the need to account of those excess zeros in the model because the Poisson assumption is violated as shown by (e.g.,) residual diagnostics. I would advice the authors read Warton (2005): Many zeros does not mean zero inflation: comparing the goodness-of-fit of parametric models to multivariate abundance data, and rethink this paragraph. I would also request that they include residual diagnostics (with randomized quantile residuals, the DHARMa Rpackage will return this for ZIP models fitted with glmmTMB).

Response: We thank the reviewer for this interesting reference. Actually, we followed the same approach used in Warton (2005): We compared the goodness of fit of a Poisson model vs. a zero-inflated model. Because the AIC of the zero-inflated model was more than 100 smaller than the Poisson model, we chose this model. Following your advice, we now use the glmmTMB package to fit our model, and then we use the DHARMA residuals simulations. The diagnostics did not support any strong deviation of the residuals.

l221-223: I do believe that is true, but AIC finds the model that predicts best, not the model that is best for inference or provides the most valid inference. Hence, I do not find this statement very convincing and would advice the authors to take a difference approach to motivate their choice of a zero-inflated model, which is more aligned to their goal of ecological inference instead of prediction.
Response: Following Waront (2005), we strongly think that comparing models on the basis of their AIC is a good method. AIC comparison has been extensively used to choose among models, which is exactly what we did to choose between a Poisson model and a zero-inflated model.

l239-240: the authors at length discuss the repercussions of fitting a non-spatial model to data that suffer from spatial structuring, but include non-spatial models in their model-averaging. I suggest to rethink this.
Response: we are surprised by this comment of the reviewer. Of course that we included the non-spatial model in the model averaging procedure. The whole process was about comparing the non-spatial model to an explicit spatial model. Anyway, following the reviewer's comment, we do not use anymore model averaging approach.

l252: I am a fan of such a "simple" approach of just visualizing the distribution of counts to convey the issue of spatial structuring, but from fig 1A it is not apparent to me that this dataset indeed suffers from spatial structuring. What I would expect to see is that points more closely together have higher counts than points further away. Generally, I do see a divide between the left and right sides of the figure; the counts on the right side seem higher, but it would be good if this is further elaborated on by the authors.
Response: Surprising comment since on the next line, we formally mention that we conducted a correlogram in order to test if our dataset is spatially structured…

Generally, Figure 1A misses scales; it is difficult to read (surrounding geographical context is missing).
Response: Again a surprising comment since the scale is clearly indicated on the map.

l252-255: OK, the figure is clear but it is not clear what model the RHS is retrieved from, and thus does not clarify if the spatially explicit terms in the model are necessary.
Response: We did not understand what is RHS and are surprised by the way the comment is formulated since the reviewer is "not a fan of abbreviations".

l263: I am not a fan of abbreviating terms unnecessarily, or in ways that are not frequent in the various branches of ecology or statistics, as here. It does not improve the readability of the text, in fact it (usually) makes for a text that is harder to read through, espeically when used in combination with other abbreviations that the reader might be unfamiliar with (for me here: LRS). A 11 letter word is abbreviated to a 3 letter word, and one that is only used in a limited section of the text (mostly the methods). I suggest to use "eigenvectors" as usual.
Response: this comment pushes a personal view that is not coherent with the wording used by the reviewer in the previous comment, and is not shared by many reviewers who often ask to use widely acknowledged abbreviations such as LRS and Egs.

l278: covariate -> covariates.
Response: Done

l289-290: the authors do not state how they calculated Moran's I. I suppose this was on the residuals of some model (not clear which model from the whole subset of models, or if it is from the final model-averaged solution), but which type of residual is not stated.

Response: Moran's indexes have been estimated on the residuals from a model linking the response variable (LRS) and the Egs only. This is now clearly mentioned in the legend of Figure 2.

l293: as I think I understand from another part in the text (I admit, I may misunderstand), the "spatial model-averaging procedure" included models without eigenvectors from the neighborhood distance matrix. This seems odd, as the authors (at length, in the introduction) describe the fact that biases might be introduced to estimates when not accounting for spatial autocorrelation in a model when that is required. In essence, the authors use a method that they admit in the manuscript to be biased.
Response: It does not matter anymore because we do not use the model averaging procedure. This was indeed a misunderstanding. We had compared a non-spatial procedure vs. a spatially explicit procedure in order to evaluate the effect of spatial autocorrelation when ignored.

l303-306: I have no idea what these sentences mean or are trying to convey. I would suggest an alternative, but struggle with that too. So, I broadly suggest for the authors to rewrite these sentences.
Response: We rephrased this sentence to clarify the message.

l318-319: This interpretation is incorrect; the Poisson process can also generate zeros, so this statistic that is retrieved from the zero-inflated component of the model is correctly interpreted as "the probability that fish will not produce a self-recruit not due to the Poisson process" or similar.
Response: We agree but did not used the formulation that you proposed, which would have weighed down the text.

l327-328: this is a sentence for in the methods.
Response: We disagree and think that this back transformation needs to be mentioned in the result section for the sake of the continuity of the logical narrative.

l335: remove "however"; the meaning of the sentence remains the same.
Response: Done

l344-345: It is not clear to me how the inference in this manuscript would be different if the authors would not have included the spatial terms in their model. This statement is probably true, but the authors could try to better connect it to their own results.
Response: We clarified this sentence accordingly, which now reads: "the spatially-explicit model outperformed the non-spatially-explicit model, so that ignoring spatial autocorrelation affected the estimates of our zero-inflated model"

l363-364: This is not a convincing statement. There are few ecologists/evolutionary biologists or statisticians that would be surprised that including 29 additional variables in a model explains more variation.
Response: We are surprised by this comment which we fail to understand. We could not identify what this comment was based on. The fact that including 29 additional variables (previously selected) increase the explained variation of a model is indeed obvious. We never mentioned that it was surprising.

Appendix
Figure 1: these are not statistical distributions (densities) these are histograms of data.
Response: thank you for noticing this error in the supplementary information, which we corrected

Zenodo repository

- *Available in review portal under "data for results" but does not seem to actually include data*
- *Please include scripts as R files, not as text files*
- *The data availability statement notes that Rdata files are available in the zenodo repo, yet all I can see is scripts and the manuscript*
- *Please provide scripts that use the RData files instead of the raw data, if the raw data will not be deposited anywhere*
- *Please trim the package lists; lme4 is loaded (and lmerTest) but not used in the script as far as I can tell*
- *Note that although some model objects are called "glmm" these are in facts glms without random effects*
- *try to run: does it work? file paths anywhere? a-b runnable?*
- *self-contained?*

Response: we have run through the Zenodo files and made sure to correct any issue, the format and the name of files remains at our discretion…