

Answers to reviews on submitted article "Efficient sampling designs to assess biodiversity spatial autocorrelation: should we go fractal?" by F. Laroche

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Dear recommender and reviewers,

Thank you very much for your time and effort in evaluating the previous version of the manuscript "Efficient sampling designs to assess biodiversity spatial autocorrelation: should we go fractal?". I have carefully addressed all your suggestion of modifications and complementary analysis. Briefly, changes brought in the revised version include :

- (i) a deeper analysis of average design performance across a range of autocorrelation ranges ;
- (ii) more realistic profiles of the environmental covariate ;
- (iii) an analysis of the practicality of sampling designs ;
- (iv) more references to contemporary literature on the topics of fractal designs, virtual ecology and spatial autocorrelation assessment and a synthesis of general guidelines for empiricists implied by our results ;
- (v) a more detailed presentation of the code associated to the study.

You may refer to my point-by-point answers to reviews appended below for details. I hope that these changes will bring answers to most of your comments on the previous version of the manuscript.

Yours sincerely,

Fabien Laroche

Point-by-point answers to comments made by the recommender, Pr. E. Goberville

Dear Dr. Laroche,

Thank you for submitting your article titled "Efficient sampling designs to assess biodiversity spatial autocorrelation: should we go fractal?" to PCIEcology. We have now received feedback from two referees, and I would like to express my gratitude to both referees for their thorough and insightful review of your manuscript. I share their opinion regarding the relevance of your study and its significant contribution to the existing literature, as well as the importance of providing access to the code for ensuring reproducibility of the analyses. However, before your study can be considered for publication, some revisions and clarifications are necessary.

The first referee noted that your article addresses a pertinent subject but highlighted a lack of references to recent research in the field. It is strongly recommended to include credible sources to support your arguments and enhance the credibility of your article.

We added five references tightly related to our topic, covering : (i) the application of virtual ecology principles (Thiele et al.), (ii) the need to jointly consider scales and gradients when designing a sampling strategy (Guo et al.) ; (iii) the general interest of fractal designs for long-term studies (Ewers et al.) ; (iv) the performance of fractals to study pathogen aggregation (Ferrandino et al.) ; (v) additional evidence that can partially remove the confounding effect between exogenous and endogenous sources of autocorrelation (Bonada et al.). One of these references was suggested by reviewer 2.

Additionally, the referee encourages you to delve deeper into specific aspects of your analysis by providing concrete examples or case studies to substantiate your viewpoints.

Among the references cited above Thiele et al. and Bonada et al. are applied studies, while Guo et al. and Ewers et al. are reviews that cover many case studies. We referred to them, as well as to other concrete and applied virtual ecology studies (like Bijelvelde et al. or Perret et al.) throughout the text. We emphasize the main practical implications of our work in a new figure 10 that provides concrete, overarching guidelines. We clearly acknowledged in the revised manuscript (ll. 556-561) that our study aims at pointing general principles that empiricists should have in mind, while case-by-case virtual ecology studies remain necessary for practical implementation.

The second referee acknowledges the commendable aspects of the article, including the methodology of defining hybrid and fractal patterns and the use of the Pareto front method to examine trade-offs. Overall, the referee provides valuable feedback regarding the need to consider multiple variables/species,

We deeply modified our study, adding new analyses (e.g. Figure 8) to address the question of multiple species.

the practicality of sampling designs,

We added a whole new section of results regarding the practicality of sampling designs, where we compared the minimum spanning path length of fractal and grid as suggested by reviewer 2 (see result section « Spanning path length of grid versus fractal designs »). We also insisted more on the practical advantages of fractals in our conclusion (ll. 618-621) and mentioned that point in abstract (ll. 33-34)

and the choice of environmental variables.

We generalized the shapes of environmental covariates considered in the study, as detailed in a new method section (section « Methods - Modeling the observed variable »). Those shapes are illustrated in Figure 3.

Further exploration of these aspects is encouraged to improve the practical applicability of the study.

We kindly request that you take these comments and suggestions into consideration during the revision of your article. Please submit a revised version of your manuscript, incorporating the referees' remarks. Additionally, we would appreciate a detailed response letter addressing how you have addressed the referees' comments.

Thank you for your valuable contribution to our scientific journal, and we look forward to receiving your response.

Best regards,
Eric Goberville

Point-by-point answers to comments made by reviewer 1, Pr. N. Yoccoz

Despite the recognized importance of sampling design, at least for researchers with an interest in statistical questions, it is remarkable that so few empirical studies in ecology are in fact designed according to well-defined objectives and some forms of random or systematic sampling. If one takes the example of species distributions, most studies use “available” data which are most often derived from opportunistic sampling or some form of hybrid designs (e.g. random design initially but with some nonrandom selection of final units linked for example to accessibility or observer availability). Many approaches have then been developed to account for this lack of design, but their robustness is often unclear. Clearly it would be preferable to start with a good sampling design.

This paper investigates different designs – random, grid, fractal (multiple scales) – and their efficiency when autocorrelation can be seen either as a “nuisance” and a parameter of interest. It is based on extensive simulations, and using a model-based approach for estimation. The conclusions are that fractal designs are seldom efficient. The scripts for running the simulations are available, but I did not run the simulations to check the results.

This is an interesting contribution for researchers working on sampling design, as it explicitly addresses different objectives (i.e. not “just” estimating population size, or an environmental effect). I could add that a specific difficulty with autocorrelation from a statistical point of view is that it may be hard to distinguish between a “real” autocorrelation due for example to intrinsic processes such as dispersal and the effect of a spatial covariate having an autocorrelation with the same range (i.e. it is not just an issue of bias but also of identifiability).

We agree that the statistical analysis cannot discriminate between an endogeneous process generating autocorrelation in the response biodiversity variable and an exogeneous effect of a hidden covariate that would harbour a spatial structure similar to the former effect. Models including both scenarios to perform some selection would necessarily suffer from unidentifiability. External additional evidence can be generated to support the limited dispersal interpretation though, especially in multispecific studies, when for instance the range of autocorrelation covaries with known dispersal traits of species. We added a sentence about this with a reference in introduction (ll. 48-51), when introducing the interpretation of spatial autocorrelation in terms of limited dispersal.

As one often does not know what are the effects and range of environmental covariates, it is not obvious how sampling should be done. This paper addresses some of the issues associated with autocorrelation and estimating effects of covariates, and

perhaps the author should emphasize the importance of making simulations to assess different designs depending on study objectives. Simulations are useful not just for assessing different design as is well done in this paper, but also because it forces the researchers to specify objectives, both in terms of ecological questions and in terms of what can be realistically expected in terms of precision/bias.

We fully agree with this statement. We added a sentence with practical examples in introduction mentioning the importance of performing simulations and virtual studies (ll. 55-62). We also clarified that our study is conceptual, and that implementing the principles that were identified here requires case-by-case virtual studies (ll. 556-561).

Point-by-point answers to comments made by reviewer 2, Pr. R. M. Ewers

This manuscript explores the ability of different sampling designs to estimate levels of spatial autocorrelation for a given sampling effort (number of sample points). Designs are categorised into two groups – regular grids where proportions of the points have been moved to random locations, and fractals (patterns that are self-similar across a range of spatial scales). The methods are split into two ‘problems’: Problem 1 explores whether sampling schemes can recover the spatial autocorrelation value of a single variable. Problem 2 adds in one of two environmental covariates – a linear and a u-shaped gradient. Browsing rev 1 on bioRxiv, I think the inclusion of an environmental covariate was a new addition, and given the results I think this was a good decision.

There is a lot to comment the paper. The methods for defining the hybrid and fractal schemes is great and provides a really nice framework for future studies to follow. I also really like the pareto-front method of examining the trade-offs between estimating μ and σ .

Thank you for these positive feedbacks.

I have 3 high-level comments, and a few general comments, mainly related to the studies generalisability to real-world scenarios:

1) The idea of sampling for more than one variable/species is not considered and barely discussed; [...]

We agreed, we modify our study and added new analyses (Figure 8) to clearly put our results in perspective with multi-taxonomic studies. Our general strategy was to provide an average view of designs performance across a broad range of autocorrelation, which provides a way (among others) to quantify to versatility of designs across a potentially wide range of target taxa.

The last sentence of the abstract states “The interest of designs with a clear hierarchical structure like fractals may stand out more clearly when studying biological patterns with contrasted spatial structures across scales”. This is a really important point, as

In the quoted sentence, we were actually referring to the fact that a univariate response variable can harbour more complex variograms than the one considered in our study, which makes autocorrelation to exponentially decrease with distance according to a single scale parameter. The response variables could harbour a spatial structure with heterogeneous patterns at different scales resulting from distinct processes. We develop this idea at ll. 624-632 in our conclusion and mention it in abstract(ll. 31-32).

in the vast majority of cases researchers will be simultaneously sampling multiple variables that have differing spatial autocorrelation structures (eg topographic wetness index vs annual precipitation) or multiple species where body size/dispersal ability/home range sizes can differ by orders of magnitude (eg wrens vs eagles, or whole saproxylic beetle community in the author’s own example). However, at the moment it is only tagged on to the very final paragraph of the conclusion!

We agreed with the reviewer’s comment. We now provide a global assessment of sampling designs across a broad range of possible autocorrelation ranges, hence introducing the idea that a design can be confronted to a wide range of taxa with contrasted autocorrelation patterns. This lead to deep changes in discussion. For instance, we now refer to this multi-taxonomic perspective in Introduction (ll. 91-95) and in discussion at ll. 471-475, and ll. 572-582.

The importance of the fractal design (or other cluster patterns) is that it can investigate a range of

spatial scales simultaneously – a good example is the SAFE project in Borneo which has implemented the fractal design (see <https://www.safeproject.net/info/design> and its hundreds of outputs on thousands of different species, functions and processes). All are sampled under a unified network that means patterns and processes across different scales can be directly linked to each other in space, and that makes multi-taxa studies easier. See Ewers (2011) <https://doi.org/10.1098/rstb.2011.0049> for the original description of the project, and also the Ecological Fractal Network (<https://ecofracnetwork.github.io/>) which has implemented the protocol across the northern hemisphere.

We agreed and mentioned in Introduction (ll. 91-95) the important interest of fractal designs as versatile strategies potentially well suited for long-term designs where many questions will be investigated at a time. We referred to Ewers et al (2011) there, as a good entry point on this question.

It would be worth a more rigorous exploration in the discussion, if not it's own analysis (for example, you could look at a set of as values and examine which designs perform best across all of them, or which design has the 'least bad' worst-case).

We followed this advice. We chose a range of as values and explored the average rank of errors of designs as explained in methods at ll. 237-248, presented in results in Figure 8 and commented discussion at ll. 471-486, ll. 521-528, ll. 547-553, ll. 564-582.

2) The practicalities of implementing a mostly random design is also not considered; [...] the number of sampling points is only one measure of effort. Having implemented the fractal design myself in an Amazonian rainforest forest scenario (ie where trails have to be cut to reach each point) it is fairly similar to implementing a grid system, and getting around them efficiently is pretty straightforward as well. Any random points however, become quickly impractical as special trails have to be cut in random directions and distances to individual points, and not something I would ever recommend doing from a practical day-to-day viewpoint. For example doing a simple travelling salesman solution to the examples given in figs 1 and 2 we can see that the fractal designs are much more efficient, apart from against truly random (not a surprise as that doesn't sample up to the edges). However, we can see how difficult it would be to implement something truly random in the field. An acknowledgement of this impracticality would be useful.

We thank Dr. Ewers for this excellent suggestion about reporting the performance of designs in terms of traveling salesman problem. We added a new section to the manuscript where we clearly show the interest of fractals on that matter (ll. 410-423), and we mentioned this fact in the conclusion (ll. 618-621) and in the abstract (ll. 32-34).

3) the environmental co-variables are too similar and don't necessarily reflect the scales most biologists sample at. In terms of problem 2 and the effect of an environmental covariate, it is hard for me to assess how representative the scenarios are, because I struggle to visualise their effects on the response variable. However, with this caveat, my thoughts would be:

- I really consider the two environmental variables as essentially the same – both are monotonic with a single peak in the landscape, only the 'u-shaped' variable the peak is centred on the centre of the study area, and the 'gradient' is centred on the edge. This scenario only really equates to either climate scales at continental extents, or variables at very small extents (tens of metres). I don't think they really reflect the variables (soil, hydrology, vegetation etc) and extents most ecologists work with, which will be patchy within the landscape.
- the U-shaped variable (fig. 3) is the absolute sub-optimal scenario for the fractal design, given that it is centred on the exact centre of the fractal design, where sampling effort is not present, and it is exactly radial, so that the points closest to the centre all have exactly the same information.

I would personally prefer to see variables which have multiple peaks within the study area. However, without seeing what the effect of the environmental variables has on variable of interest, it is hard for me to say whether it is worthwhile exploring a wider range of patchiness.

We have considerably diversified the types of environmental covariates in our analysis, as presented at ll. 175-179, and Figs 3 and 6. However results could still be presented in two broad categories : monotonic environment covariates in space versus, non-monotonic profiles with peaks located within the area of study.

Although it took a good 6-8 hours to run it on my computer, I can confirm that I get the same results figures when running the code. However, I found the code made available to the reviewers almost uninterpretable as it is completely unformatted, multiple objects defined on single lines, little to no annotations etc. So I am unable to review whether the code is doing what is described in the manuscript.

We embedded all the code in a markdown file that more carefully presents the generation of results, available at <https://zenodo.org/record/8420366>

[...]

General comments

- Following on from the previous point, what would really help me would be some visualisation representations of the variable under different as values, and their interactions with the environmental variables in fig. 3. The key here is how 'patchy' they are in relation to dmin and I personally find it hard to do this when only presented with as values.

We added this type of visualization in our presentation of code, on the online repository <https://zenodo.org/record/8420366> (see table of contents there).

- As I mentioned, the pareto-front method of examining the trade-offs is excellent. Figs 5, 7 and 8 are a really nice way of visualising this. In fact, I would like to see them expanded – at the moment each only shows 1 value of as but it would be easy to show, say, 5 values using 5 panels in a row for each figure.

We followed this advice and generalized this mode of presentation in our new figures 4 and 6.

- However, for figs 5, 7 and 8, please use a different colour scheme to separate the fractal and hybrid designs, as you have used blue and red for the small-large range values in other plots.

Since we do not other, less useful plots anymore, we stuck with red and blue here.

- Similarly, you could consider incorporating figs S1 and S3+4 into figs 4 and 6 respectively – I found myself flicking between the two repeatedly to the point where I ended up copying and pasting them together. Fig. 1 and 2 could be combined into a single figure if necessary to make the space.

Given the deep modification of figures in the manuscript, these comments do not apply any more.

- The Discussion and Conclusion are really long, almost 3000 words, and could do with some trimming (eg lines 496-511 could easily be lost).

We seriously shortened the discussion and conclusion (now c.a. 2300 words), centering the text around few key messages.

- In general, there are quite a few wording issues throughout. I won't find them all, but I noted down some at lines 56, 71, 163, 210, 317, 428, 486-9, 499, 517, 539. Perhaps worth getting a fresh pair of eyes to check it through. Try and keep consistent ordering throughout – in the text it is generally hybrid then fractal, but the figures are fractal then hybrid.

- Lines 221-244 – Should most of this not be in the Methods section? And potentially some of up to lines 284 as well?

We agreed that an important part of this section was actually superfluous details of calculus, and moved to appendix. However, key elements like (i) the expression of estimation errors in a design and (ii) the asymptotic properties of these errors at low and high autocorrelation ranges are important outputs of the analysis that should stay in results. The subsection is now substantially shorter than in the previous version of the manuscript.

Lines 70 – I think this should be fig. 2?

Yes it was, we corrected.

Line 74-77 – This paper didn't really show that 'fractal designs lead to estimating higher values of autocorrelation range than an intensive control design' – rather that for a given sampling effort it could recover patterns on average more similar to the control than other designs.

Thank you for this clarification, we modified the text accordingly (ll. 82-85).

Line 118 – please reference R, and any other key packages as a huge amount of work goes in to making them freely available for users.

I did.

Fig. 4 legend – I think it is 'red shows the fraction of these designs that are eliminated when introducing the other type of design in the comparison'?

We carefully checked the caption of Figs 5 and 7 regarding color code.

Fig. 5 legend and other places – I am not sure 'browsing' is the best wording. Perhaps 'traversing' or 'tracking'?

Done

Fig. 6 – I think the bottom right panel should be labelled as Hybrid rather than Fractal?

Yes, I corrected in what is now figure 7.

Line 615 – I strongly disagree that implementing designs with random points is easier than fractals (which are essentially a series of straight lines).

We removed this statement. As mentioned earlier, we now provide more arguments showing the practical interest of fractals, based on a traveller salesman analysis.