Peer Community In
Evolutionary Biology

Environmental and fitness landscapes matter for the genetic basis of local adaptation

Charles Mullon *based on peer reviews by 2 anonymous reviewers*

Fabien Laroche, Thomas Lenormand (2022) The genetic architecture of local adaptation in a cline. bioRxiv, ver. 4, peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.1101/2022.06.30.498280

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Natural landscapes are often composite, with spatial variation in environmental factors being the norm rather than exception. Adaptation to such variation is a major driver of diversity at all levels of biological organization, from genes to phenotypes, species and ultimately ecosystems. While natural selection favours traits that show a better fit to local conditions, the genomic response to such selection is not necessarily straightforward. This is because many quantitative traits are complex and the product of many loci, each with a small to moderate phenotypic contribution. Adapting to environmental challenges that occur in narrow ranges may thus prove difficult as each individual locus is easily swamped by alleles favoured across the rest of the population range.

To better understand whether and how evolution overcomes such a hurdle, Laroche and Lenormand [1] combine quantitative genetics and population genetic modelling to track genomic changes that underpin a trait whose fitness optimum differs between a certain spatial range, referred to as a "pocket", and the rest of the habitat. As it turns out from their analysis, one critical and probably underappreciated factor in determining the type of genetic architecture that evolves is how fitness declines away from phenotypic optima. One classical and popular model of fitness landscape that relates trait value to reproductive success is Gaussian, whereby small trait variations away from the optimum result in even smaller variations in fitness. This facilitates local adaptation via the invasion of alleles of small effects as carriers inside the pocket show a better fit while those outside the pocket only suffer a weak fitness cost. By contrast, when the fitness landscape is more peaked around the optimum, for instance where the decline is linear, adaptation through weak effect alleles is less likely, requiring larger pockets that are less easily swamped by alleles selected in the rest of the range.

In addition to mathematically investigating the initial emergence of local adaptation, Laroche and Lenormand use computer simulations to look at its long-term maintenance. In principle, selection should favour a

genetic architecture that consolidates the phenotype and increases its heritability, for instance by grouping several alleles of large effects close to one another on a chromosome to avoid being broken down by meiotic recombination. Whether or not this occurs also depends on the fitness landscape. When the landscape is Gaussian, the genetic architecture of the trait eventually consists of tightly linked alleles of large effects. The replacement of small effects by large effects loci is here again promoted by the slow fitness decline around the optimum. This is because any shift in architecture in an adapted population requires initially crossing a fitness valley. With a Gaussian landscape, this valley is shallow enough to be crossed, facilitated by a bit of genetic drift. By contrast, when fitness declines linearly around the optimum, genetic architecture is much less evolutionarily labile as any architecture change initially entails a fitness cost that is too high to bear.

Overall, Laroche and Lenormand provide a careful and thought-provoking analysis of a classical problem in population genetics. In addition to questioning some longstanding modelling assumptions, their results may help understand why differentiated populations are sometimes characterized by "genomic islands" of divergence, and sometimes not.

References:

[1] Laroche F, Lenormand T (2022) The genetic architecture of local adaptation in a cline. bioRxiv, 2022.06.30.498280, ver. 4 peer-reviewed and recommended by Peer Community in Evolutionary Biology. https://doi.org/10.1101/2022.06.30.498280

Reviews

Evaluation round #2

DOI or URL of the preprint: https://doi.org/10.1101/2022.06.30.498280
Version of the preprint: 3

Authors' reply, 08 December 2022

Download author's reply

Decision by Charles Mullon, posted 27 November 2022, validated 28 November 2022

Minor revisions

Dear authors,

Thank you for your response to the queries the reviewers and I made. I do not think it is necessary to ask reviewers to see your manuscript again. But before I recommend your preprint, there are a few points that need to be addressed (see below). I am sure this will be straightforward and so look foward to reading your updated manuscript soon.

Yours,

Charles.

Comments to authors:

1. (l. 246) "This requires simulating " The sentence is incomplete.

2. (l. 340) "i.e. sigma \sqrt\m\ / l = ..." Isn't there a square root of two missing on the left hand side of this equation? Otherwise equations 6 and 9 are inconsistent.

3. Equation 12b. How can alpha (as defined by equation 7b) depend on the mutant effect epsilon?

4. l. 375 "l_G < l" Shouln't it be "l_G < l<l_L(A)"?

5. Throughout, ”Gauss” –> ”Gaussian” (please be consistent).

Evaluation round #1

DOI or URL of the preprint: https://doi.org/10.1101/2022.06.30.498280
Version of the preprint: 2

Authors' reply, 17 November 2022

Download author's reply

Decision by Charles Mullon, posted 03 September 2022

Major revision

Dear authors,

Two expert reviewers have read your manuscript and based on their comments and on my own reading, I believe that some revisions are required before recommendation. In particular, I agree with both reviewers that parts of the mathematical analysis have to be more clearly explained and better connected to existing theory. I also agree that some of the notations should be revisited to align with more commonly used ones (e.g. for partial derivatives). I hope you find the reviewers comments and my own (below) useful in improving your manuscript. When you resubmit, please provide a point-by-point response to our queries.

All the best,

Charles.

Comments to authors (in order of appearance)

Around equation (4). I think it would be useful to specify that patches are large (to ignore random fluctuations within patches and consquences of kin competition) and that selection is soft (i.e. competition occurs within patches before dispersal).

l. 271-282 I found this section difficult to follow. Going to box 2 in Lenormand 2002 indeed helped, however I think it would be better if the manuscript did not rely so much on explanations given in another paper. One recommendation would be to express k and alpha in terms of parameters of the current model (in a way that is sufficiently general that it can apply to both fintess functions). This would help understanding the verbal definitions of k and alpha.

l. 288 and eq. (5) I guess the argument for invasion here is that second order effects can dominate first order effects. Spelling this argument out explicitly would be helful. Also, how do you ensure that you can still ignore third order effects?

l. 292 I recommend presenting the equation for k out of line, with its own reference. It may also be usful to write eq. 8 as a condition on pocket size l as later, many arguments are based on critical pocket sizes allowing for the invasion of locally adapted alleles (e.g Fig 5 and 7). The same holds for eq. 9.

l. 348 Could you please define Q_A and \bar\z\ more precisely?

Figure 6. There seems to be a mismatch between references in the main text to A and B and the figure legend. e.g. line 415, 6A is referred for Laplace but legend says it is Laplace.

l. 533. Please provide references for those ”previous models”.

Appendix.

Eq. A1. This linearized form for evolution in patch structured populations has been used in previous models (e.g. models of dispersal evolution by Lee Altenberg, see also Reinhard Burger's textbook). It would be useful to refer to those.

Eq. A3 Please explain what \bar\s\ is

Below Eq. A4. I found the explanation of what was being done a bit confusing. Why not say that you use Fourier analysis to solve eq. A4? Also refer to some works that have already used the regularity of lattice or stepping stone models (e.g. Francois Rousset's 2004 book)

Eq. between (A7) and (A8) please make sure the notation for entries of the matrix pi is the same throughout.

Below that equation, explain how you get lambda_2

End of that same page, please define s_1 and s_2 separately.

Top of before last page (page with equation A9). Please epxlain how you derived that first equation (with n \sigma_k on the right hand side).

Reviewed by anonymous reviewer 2, 02 August 2022

Laroche and Lenormand present an argument that shows the conditions for the concentrated architecture of alleles involved in local adaptation may be more permissive than previously thought, by analysing it in the context of a spatially explicit model. They also consider the impact of varying the shape of the fitness function. The manuscript explains the differing effects of two different shapes well, as well as the reasons the analytical methods may differ from the simulated results. I believe this work makes a valuable contribution to our understanding of the evolution of aggregated architecture.

My main concern with the manuscript is that I found parts of the methods and results are unclear or inaccessible, which made it difficult to follow and reproduce. In particular:

- I suggest making the arrival to Equation 2 more understandable. I expect this is not a technique many readers (myself included) will be familiar with.
- I am unfamiliar with and expect most readers to be also be unfamiliar with, the delta notation introduced in Equation 5 which isn't explained in text. If I had to guess, it's the partial derivative with respect to the second variable, and then z substituted back in? The notation is used extensively throughout so I believe it would be well worth explaining this or using alternative, more standard, notation. I struggled to work it out initially, because lambda(z,z) looks like it should equal 1.
- L267-268: I understand the parameters s_i and t_i as far as "this is what pops out the exponential when we differentiate w_i", but a placing within a biological context (if they have one) would improve the accessibility of the paper. The names chosen make them look like selection coefficients.

Some justification of the simulation parameters used would improve the manuscript.

For example, the juvenile migration rate is 0.5; I don't have much expertise of models with limited dispersal, but this seems an incredibly high value.

Other points:

Main text needs proof reading throughout.

Figures: Legends and within-figure text require proofreading. Perhaps merge Figures 5 and 7 for easy comparison without flicking between figures, and so they can share a legend. I suggest keeping a consistent order Laplace/Gauss or Gauss/Laplace across figure panels (and throughout the manuscript) for ease of comparison.

Figure 4 L812: Can you include what it is you want the reader to find in the text in the legend?

Table 1: Main text uses “n” for number of patches, rather than “X” as in table.

L236-237: Citation missing for this invasion approximation?

Reviewed by anonymous reviewer 1, 14 August 2022

“The genetic architecture of local adaptation in a cline” addresses how adaptation to a new habitat occurs at a quantitative trait. The model assumes several patches organised in a circle, a proportion of which are in the “ancestral” habitat and another in the “new” habitat, each habitat having it’s own phenotypic optimum. Migration occurs between the patches at a fixed rate. The authors explore how the fitness function, the size of the second habitat, and migration influence the strength of mutations (strong or weak) that are recruited during the adaptation process, and how these mutations are distributed along the genome (clustered within the same genomic region or not). Their main findings are that clustering of mutations is indeed favoured in a large range of parameter values.

The paper is well thought out and well written, I enjoyed reading it, despite my limited understanding of the underlying mathematics in the analytical part of the model. I find the approach quite elegant, with a relatively “simple” scenario to answer a very complex question. I mean this in a very positive sense – the authors have proposed a model with but a few parameters and found a way to analyse and present the results in an intuitive way. The comments I have are minor and should be quite easy to see to.

Comments:

Abstract:

line 23: “spatially continuous space” seems awkward … “continuous space” would seem sufficient, unless I have missed something. But on that note, I had understood the patches to be discrete, which could lead to some confusion on the use of “continuous space”, but I can’t think of a better way to phrase it. Maybe a “continuous habitat space/range”?

Introduction:

line 107: rewording suggested “At one extreme, if a single mutation that confers perfect adaptation can occur, indirect…”

line 146: “1-dimensional” □ “one-dimesional”

Methods

As a non-mathematician, some notions were difficult to follow. I am quite aware that it is impossible for me, and readers such as myself, to gain detailed knowledge of the whole process behind the derivations (I have given up on trying to understand the Fourier transform in sufficient detail), but some hints on how it works could be useful. My greatest challenge (that can be remedied), which I think should be explained by adding a line or two is the measure of aggregation (starting line 224). It was not initially intuitive to me as to why a square signal would translate as a “low frequency signal”. Is it because these approaches based on spectral analyses are temporal? Hence a square signal in a spatial context, concentrated only on a part of the genome, would be translated as a weak temporal signal?

line 220: Out of curiosity: why the choice of the last 75% of simulation time? is it an arbitrary choice?

lines 267-268: It would be appropriate to specify that w’ and w” (lines 267-268) are first and second derivations of (if I understood correctly) the Fourier transform.

line 276: “characteristic length” (sensu Slatkin 1973) – can more information be given? I’m not sure what this means., since it is crucial to the understanding of k (which I have only been able to understand in a very superficial way)

Results

line 327: Missing “.” before “Hence”

Figures: I was very grateful for Figures 1-4, thank you! They made the understanding of the model intuitive.
- Figure 5 is a bit information heavy, and the dotted lines may need to be made more visible (thicker?). I suggest that the vertical line be removed completely from panels A and C, as they are not very visible, make it a bit difficult to follow what is on those panels and are in any case represented on panels B and D. This will also aid in shortening the legend, which as is, was slightly confusing to read.

Discussion

line 519: rewording “the optimal value”

General: There are some small residual language mistakes that are easily corrected. I had started a detailed correction, but then realised it was too time consuming and could more easily and efficiently be done by having someone directly make the changes in the document. There are small recurring mistakes, such are missing or too many s’s and the’s, as well as “same … than” (“same … as” – “different … than”). Some are also present in the appendices.