Peer Community In
Evolutionary Biology

# A new approach to identifying drivers of local adaptation

***Ruth Arabelle Hufbauer*** *based on peer reviews by* ***Ruth Arabelle Hufbauer*** *and* ***Thomas Lenormand***

Stewart L. Macdonald, John Llewelyn, Ben Phillips (2017) Using Connectivity To Identify Climatic Drivers Of Local Adaptation. Missing preprint_server, ver. Missing article_version, peer-reviewed and recommended by Peer Community in Evolutionary Biology.
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Local adaptation, the higher fitness a population achieves in its local "home" environment relative to other environments is a crucial phase in the divergence of populations, and as such both generates and maintains diversity. Local adaptation is enhanced by selection and genetic variation in the relevant traits, and decreased by gene flow and genetic drift. Demonstrating local adaptation is laborious, and is typically done with a reciprocal transplant design [1], documenting repeated geographic clines [e.g. 2, 3] also provides strong evidence of local adaptation. Even when well documented, it is often unknown which aspects of the environment impose selection. Indeed, differences in environment between different sites that are measured during studies of local adaptation explain little of the variance in the degree of local adaptation [4]. This poses a problem to population management. Given climate change and habitat destruction, understanding the environmental drivers of local adaptation can be crucially important to conducting successful assisted migration or targeted gene flow. In this manuscript, Macdonald *et al.* [5] propose a means of identifying which aspects of the environment select for local adaptation without conducting a reciprocal transplant experiment. The idea is that the strength of relationships between traits and environmental variables that are due to plastic responses to the environment will not be influenced by gene flow, but the strength of trait-environment relationships that are due to local adaptation should decrease with gene flow. This then can be used to reduce the somewhat arbitrary list of environmental variables on which data are available down to a targeted list more likely to drive local adaptation in specific traits. To perform such an analysis requires three things: 1) measurements of traits of interest in a species across locations, 2) an estimate of gene flow between locations, which can be replaced with a biologically meaningful estimate of how well connected those locations are from the point of view of the study species, and 3) data on climate and other environmental variables from across a species' range, many of which are available on line. Macdonald *et al.* [5] demonstrate their approach using a skink (*Lampropholis coggeri*). They collected morphological and physiological data on individuals from multiple populations. They estimated connectivity among those locations using information on habitat suitability and dispersal potential [6], and gleaned climatic data from available databases and the literature. They find that two physiological traits, the critical minimum and maximum temperatures, show the strongest signs of local adaptation, specifically local adaptation to annual mean precipitation, precipitation of the driest quarter, and minimum annual temperature. These are then aspects of skink phenotype and skink habitats that could be explored further, or could be used to provide background information if migration efforts, for example for genetic rescue [7] were initiated. The approach laid out has the potential to spark a novel genre of research on local adaptation. It its simplest form, knowing that local adaptation is eroded by gene flow, it is intuitive to consider that if connectivity reduces the strength of the relationship between an environmental variable and a trait, that the trait might be involved in local adaptation. The approach is less intuitive than that, however – it relies not connectivity per-se, but the interaction between connectivity and different environmental variables and how that interaction alters trait-environment relationships. The authors lay out a number of useful caveats and potential areas that could use further development. It will be interesting to see how the community of evolutionary biologists responds.

***References:***

[1] Blanquart F, Kaltz O, Nuismer SL and Gandon S. 2013. A practical guide to measuring local adaptation. Ecology Letters, 16: 1195-1205. doi: [10.1111/ele.12150](`https://doi.org/10.1111/ele.12150`)

[2] Huey RB, Gilchrist GW, Carlson ML, Berrigan D and Serra L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. Science, 287: 308-309. doi: [10.1126/science.287.5451.308](`https://doi.org/10.1126/science.287.5451.308`)

[3] Milesi P, Lenormand T, Lagneau C, Weill M and Labbé P. 2016. Relating fitness to long-term environmental variations in natura. Molecular Ecology, 25: 5483-5499. doi: [10.1111/mec.13855](`https://doi.org/10.1111/mec.13855`)

[4] Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. The American Naturalist 173: 579-588. doi: [10.1086/597611](`https://doi.org/10.1086/597611`)

[5] Macdonald SL, Llewelyn J and Phillips BL. 2017. Using connectivity to identify climatic drivers of local adaptation. bioRxiv, ver. 4 of October 4, 2017. doi: [10.1101/145169](`https://doi.org/10.1101/145169`)

[6] Macdonald SL, Llewelyn J, Moritz C and Phillips BL. 2017. Peripheral isolates as sources of adaptive diversity under climate change. Frontiers in Ecology and Evolution, 5:88. doi: [10.3389/fevo.2017.00088](`https://doi.org/10.3389/fevo.2017.00088`)

[7] Whiteley AR, Fitzpatrick SW, Funk WC and Tallmon DA. 2015. Genetic rescue to the rescue. Trends in Ecology & Evolution, 30: 42-49. doi: [10.1016/j.tree.2014.10.009](`http://dx.doi.org/10.1016/j.tree.2014.10.009`)

# Reviews

## Evaluation round #1

DOI or URL of the preprint: **10.1101/145169**
Version of the preprint: 1

### Authors' reply, 24 August 2017

**Download author's reply**

### Decision by **Ruth Arabelle Hufbauer**, posted 28 June 2017

**Revise**

Dear Dr. Macdonald and colleagues,

I really like your basic idea for refining hypotheses regarding local adaptation without doing reciprocal transplants – it is clever and makes a potentially important conceptual advance, which has excellent potential for application. If you are able to address the points made in the reviews, some of which are fairly substantial issues, I would consider recommending it on PCI Evol Biol (i.e. this is a decision akin to "major revision"). The Thomas Lenormand pointed out that clines can arise from historical/biogeographic events, and not reflect local adaptation, phenotypic plasticity or behavioral tracking. In addition to the four other concerns presented, make sure not to loose track of that. I hope you find the PCI process valuable. Thank you for submitting your work for review.

Best, Ruth Hufbauer

### Reviewed by **Ruth Arabelle Hufbauer**, 28 June 2017

I really like your basic idea for refining hypotheses regarding local adaptation without doing reciprocal transplants – it is clever and makes a potentially important conceptual advance. The issue/meaning of connectivity is a challenge. Given your knowledge of the biology of this species, it seems reasonable to think that your calculation of connectivity may indicate actual movement, and thus gene flow. But what if it doesn't (for your species, or for others who would like to try this approach)? A bit of discussion about that is warranted.

I also find some of the ways that the main idea is described confusing. In particular, Figure 1, and the text describing it, could be made clearer, I think. Please see specific comments below. As you state, often, plastic responses to the environment are of inherent interest themselves. It might be more compelling to frame the paper as being not about identifying local adaptation (which you may not be able to actually do), but as being about distinguishing among local adaptation, plastic responses to the environment, and behavioral tracking of the environment.

Best, Ruth Hufbauer

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Figure 1 The axes are a bit opaque. If I understand correctly, the x-axis is the correlation between an aspect of the environment (e.g. temperature) and a trait (e.g. wing span). So, -1 would mean that as temperature increases, wing span decreases and +1 would mean that as temperature increases, so does wing span. Correct? It would be nice to have something more easily interpretable than "environmental coefficient" as a label. Even just adding trait back in so that it reads "Environment-trait correlation" would be better. In the legend, be sure to describe it fully, such as: The correlation coefficient between an environmental variable and trait values."

The y-axis title is also confusing to me. Line 126 makes one expect it will be simply connectivity, but it is clearly not.

To me, a graph of the following sentence ("Environment-trait correlations that are strong, but which are also weakened by connectivity, are indicative of environment-trait correlations that have arisen through local adaptation.") suggests a different graph in several ways. (1) Connectivity is in this case more the explanatory variable than the envt-trait correlation, so that should be the X-axis. (e.g. see line 142 "increased connectivity diminishes the correlation" – as you yourselves say, it's the connectivity that is potentially the causal factor) (2) Can't the axis be simply connectivity, not 'environment-connectivity interaction coefficient'? (I still don't quite grasp that interaction coefficient at this point in the paper, though maybe that will come clear as I read further). (3) Connectivity can run from 0 (unconnected) to 1 (highly connected). No negative is needed. Simpler! (4)

Similarly, I don't think that the sign of the environment-trait correlation matters. A graph with zero correlation to highly correlated (either positively or negatively) also would be more simple.

I've sketched – the end result (three simple lines) is similar, but to me, much easier to interpret. To me, something like that would be much easier for the reader to interpret.

line 155 – the ideas in this paragraph are great.

line 169 – rather than 'axes' I would recommend 'aspects of the climate'

line 252 – ok, here I see more what is meant by the interaction between environment and connectivity. Taking into account size (SVL) and sex, this model allows you to look at whether environment influences the trait (Benv), and whether that influence depends upon connectivity (Bint). I think that graphically, simply having 'connectivity' on the axis is still more straightforward. If there are good reasons to keep it as the Bint value, I think that this needs to be explained conceptually more thoroughly and clearly prior to presenting figure 1.

Is L necessary? You don't use it in any figures, or present it, just mention it briefly. Also 'L' is typically used for genetic load. If you keep this concept in, I think it should become more integral to the paper, and perhaps be changed to LA for local adaptation.

311 – Does this pose a problem? – running linear models with variables that are highly correlated violates the assumption of independence. I like the discussion of the biological meaning of such potential correlations in the discussion (e.g. around line 433), but I still think that a mention of why violating the assumption of independence is not a problem is warranted.

Figure 3 is interesting. I find it surprising that there are not some traits that are plastic. Is it the choice of traits? What would happen, if, for example, you evaluated size (something more likely to be plastic) as your response? Do you get the expected lack of correlation for that trait?

317 – Less short hand would be more readable. E.g. Understanding correlations between the environment and traits will…

## Reviewed by **Thomas Lenormand**, 27 June 2017

General comment

This paper proposes to exploit the fact that local adaptation is eroded by gene flow to detect traits, and the causal climatic variables, involved in local adaptation. As the authors argue, this pattern of erosion can help distinguishing local plastic response (supposedly not influenced by gene flow) from that of local adaptation. In principle, this is indeed a good idea (although plasticity also can present some degree of local adaptation). In practice, however, the methodology may be much trickier to elaborate than what the authors propose (see four major comments on the method below). Historically, phenotypic clines have always been difficult to interpret because of plasticity. However, this is not the only issue. Another difficulty is that many clinal patterns can arise due to biogeographic / historical patterns unrelated to local adaptation. Here, having a control (i.e. neutral differentiation) is necessary to make conclusive evidence. The paper should not entirely bypass this difficulty.

Comments on the method

The first issue is that the method proposes to measure the effect of gene flow by a measure of connectivity. Apart from the fact that connectivity may not be a good surrogate of dispersal, a more serious issue is that the effect of gene flow is not that of dispersal per se. Maladaptation only occurs when gene flow brings in genes that are not locally well adapted. Being highly connected to populations presenting the same traits/genes is not a problem. Being little connected but to very differentiated populations can lead to strong maladaptation. Connectivity does not matter that much. What matters is the genetic composition of the migrant pool compared to the local one. Hence the method proposed can be very misleading.

A second issue is that connectivity is simply measured as a local characteristic of the environment, just like any other climatic or soil variable. Finding an effect of connectivity may thus simply reflect that connectivity is partially correlated to another variable causing a plastic response (i.e. connectivity correlates with an environmental variable that influences the traits, possibly in a plastic way). Hence, with the method proposed, it is impossible to rule out that plasticity explains all the patterns. In principle, it should be easy to check for such spurious effect. For instance, any other climatic variable could be used as a second covariate (mimicking the role of connectivity). It would be then be important to show that such analysis does not result in similar outcome. By substituting other climatic variables to connectivity (and repeat the analysis) would allow to present a baseline distribution of the effect of a second covariate (e.g. on local adapt score, or on the strength of relationship as illustrated on Fig. 3) and see whether the effect of connectivity really stands out. Finally, even if it does stand out, it could still be possible that it is caused by the structure of hidden correlations and plasticity effects alone (e.g. for variables not included in the dataset).

A third issue is that the interpretation can be very unclear. For instance, trait optimum may not vary linearly with climatic variables. Further, there is a problem of interpretation in the statistical model, which depends on the choice of intercept. Comparing all the effects based on slopes requires that the mean of environmental values (which depends on the distribution of sampled locations) matches with the position where gene flow from the right and left cancel each other. This is highly unlikely to occur by chance. Another difficulty in the interpretation is that gene flow is expected to attenuate, not reverse, the trends.

A fourth issue relates to the fact that the method considers one environmental variable after another. Even considering only linear effects, there is no reason that the direction of adaptation align along any one of these axes. The linear combination of variables that are relevant for adaptation may be in a different direction for the projection in 1D. More generally, it is very difficult to see how the choice of climatic variables was guided. This is entirely arbitrary and it can completely miss the important ones (this is a general and difficult problem, not only in this paper).

Thomas Lenormand