ECOLOGY LETTERS

Ecology Letters, (2018) doi: 10.1111/ele.12972

TECHNICAL COMMENT

Using connectivity to identify climatic drivers of local adaptation: a response to Macdonald *et al.*

Jérôme G. Prunier[1]* and Simon Blanchet[1,2]

Abstract

Macdonald *et al.* (Ecol. Lett., 21, 2018, 207–216) proposed an analytical framework for identifying evolutionary processes underlying trait-environment relationships observed in natural populations. Here, we propose an expanded and refined framework based on simulations and bootstrap-based approaches, and we elaborate on an important statistical caveat common to most datasets.

Keywords

climate, connectivity, local adaptation, habitat choice, bootstrap, collinearity, structure coefficients.

Ecology Letters (2018)

INTRODUCTION

Macdonald *et al.* (2018) proposed an appealing analytical framework to identify evolutionary processes underlying trait-environment relationships (TERs) observed in natural populations. It is based on the visual inspection of the graphical distribution of two summary statistics (β-weights *Benv* and *Bint*; see Fig. 1 in Macdonald *et al.* 2018) that are also used to compute another summary statistic (*L*) described as an index of local adaptation. As stated by the authors, this framework is 'embryonic' and exposed to several caveats. Here, we nurtured this embryo by refining the original graphical framework, by proposing an appropriate test for each statistic, and by elaborating on an important statistical caveat common to most empirical datasets.

REFINING MACDONALD *ET AL.*'S FRAMEWORK

There is no theoretical foundation to expect that a case study would fall *strictly* within one of the three graphical categories proposed by Macdonald *et al.* When traits are independent, we rather expect summary statistics related to each trait to be scattered in all quadrants from the biplot. The specific pattern observed in Macdonald *et al.*'s empirical case study occurred because some of the traits covaried negatively (e.g. CTmax and CTmin), and obviously showed opposite TERs (notably with Tmin, Tmax and AMT). To refine the framework, and illustrate the graphical scope of possibilities, we numerically simulated data under basic scenarios (see Appendix S1). Simulations showed that independent traits can theoretically fill the entire *Benv*-*Bint* biplot and that each TER can be considered independently (Fig. 1a). In many situations, we also identified discrepancies between simulated processes and processes identified according to the sole interpretation of *L* and/or β-weights, which shows that the framework also has limits that must be seriously considered when applied to real data (Fig. 1a; see also Fig. 1c). To limit potential biases and to make the interpretation of *L*, *Benv* and *Bint* more objective, we designed a bootstrap procedure to estimate 95% confidence intervals (CIs), and hence to take into account the uncertainty associated with each statistic. This refined approach (Table 1; Fig. 1b) permitted directly inferring processes underlying each TER *independently*, even when a single trait and single environmental variable are considered. With this approach, TER can be considered as null, driven by phenotypic plasticity, or by local adaptation (Fig. 1b and c, Table 1 for details). Situations where *Bint* is non-null but *Benv* is null indicate that TER does not exist at intermediate levels of connectivity (Appendix S2) but does exist at low/high levels of connectivity, which may indicate that (mal)adaptation may covary nonlinearly with connectivity (Appendix S3). A solution to interpret ongoing processes in such situations is to plot predicted trait values obtained from the fitted model against explanatory variables (Aiken *et al.* 1991; Appendix S3).

A CAUTIONARY NOTE ABOUT MULTICOLLINEARITY

As it is based on the interpretation of β-weights, this framework relies on the assumption of non-collinearity among predictors. As stated by the authors, covariation between environmental variables and connectivity must be limited to correctly interpret the data. Collinearity is a major issue in ecology (Dormann *et al.* 2013; Prunier *et al.* 2015) and we here reiterate this warning, and explain further how this can bias interpretation in such a context. When an environmental variable is highly correlated to connectivity, it is tricky to statistically determine whether TER is actually impacted by connectivity or non-linearly related to the environmental variable (Appendix S4). Though frustrating, a reasonable procedure is to disregard environmental variables that strongly correlate with connectivity ($|r| > 0.7$, Dormann *et al.* 2013). Beyond this threshold, it is extremely risky to tease apart putative underlying processes. Solidly-grounded biological reasons can

[1] *Station d'Écologie Théorique et Expérimentale (UMR 5371), Centre National de la Recherche Scientifique (CNRS), Université Paul Sabatier (UPS), 2 route du CNRS, 09200 Moulis, France*

[2] *Laboratoire Evolution & Diversité Biologique (UMR 5174), UPS, CNRS, Ecole Nationale de Formation Agronomique, 31062 Toulouse Cedex 4, France*

**Correspondence: E-mail: jerome.prunier@gmail.com*

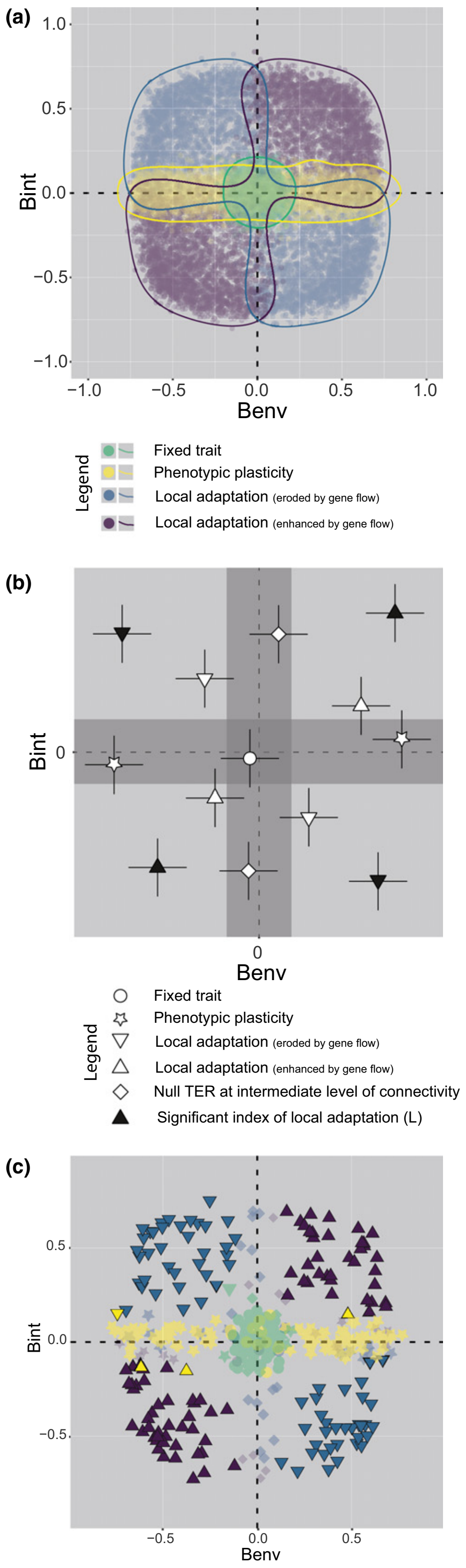

Figure 1 (a) *Benv*-*Bint* scatterplot of 20 000 simulated TERs (5000 per scenario). Solid lines encompass 99% of TERs for each scenario as delimited by a smoothed Kernel density surface. Overlapping areas indicate that different processes may lead to similar TERs. (b) The Macdonald's framework expanded (See figure 1 in Macdonald *et al.* 2018 for a comparison). Depending on 95% confidence intervals about *Benv*, *Bint* and *L*, any TER may be identified as fixed (null *Benv*, *Bint* and L*)*, resulting from phenotypic plasticity (null *Bint* and *L*) or from local adaptation, either eroded or enhanced by gene flow (non-null *Bint* and *L* index). Situations where *Bint* is non-null but *Benv* is null are indicative of a trait driven by local adaptation but showing null TER at intermediate levels of connectivity. Black symbols indicate an expected non-null *L* index while empty symbols indicate an expected null *L index*. (c) *Benv*-*Bint* scatterplot of 400 additional simulated TERs (100 per scenario). Drivers of TER were identified according to 95% CI based on our bootstrap procedure, as shown in panel b. Faded colours indicate that the L index of local adaptation was null, according to 95%CI. Colours as in panel a; symbols as in panel b. Results indicate that our procedure is robust, although a few TERs simulated under a scenario of phenotypic plasticity were found to be driven by local adaptation.

Table 1 Possible interpretations of Trait-environment relationships depending on 95% confidence intervals about observed values of *Benv* and *Bint*. 0: lower bound of the 95% confidence interval is negative whereas upper bound of the 95% confidence interval is positive; +: lower bound of the 95% confidence interval is positive; –: upper bound of the 95% confidence interval is negative

		Benv		
		–	0	+
Bint	–	Driven by Matching habitat choice (Local adaptation enhanced by gene flow)	To be investigated graphically	Driven by Local adaptation (eroded by gene flow)
	0	Driven by Phenotypic plasticity	Null	Driven by Phenotypic plasticity
	+	Driven by Local adaptation (eroded by gene flow)	To be investigated graphically	Driven by Matching habitat choice (Local adaptation enhanced by gene flow)

of course be invoked to orientate conclusions, but given that the method proposed by MacDonald *et al.* is purely correlative and hence subject to artefacts, we argue that biologists should be cautious and refrain from interpreting (or even running) regressions when collinearity between the environment variable and connectivity is too high. Furthermore, collinearity can induce severe distortion in β-weights (Thompson & Borrello 1985), which may prevent proper interpretation of the summary statistics. We advocate the concomitant interpretation of both β-weights and structure coefficients (Thompson & Borrello 1985; Appendix S5) to evaluate the possible distortion of interaction terms (*Bint*) when $|r| < 0.7$ (Ray-Mukherjee *et al.* 2014; Prunier *et al.* 2015).

RE-ANALYSING MACDONALD *ET AL.*'S DATASET

We re-analysed Macdonald *et al.*'s dataset using a random intercept model and our proposed bootstrap procedure (see Appendix S6 for R-scripts). The scatterplot was very similar to Fig. 1 in Macdonald *et al.*, but 95% CI indicated that some TERs -considered as driven by local adaptation by

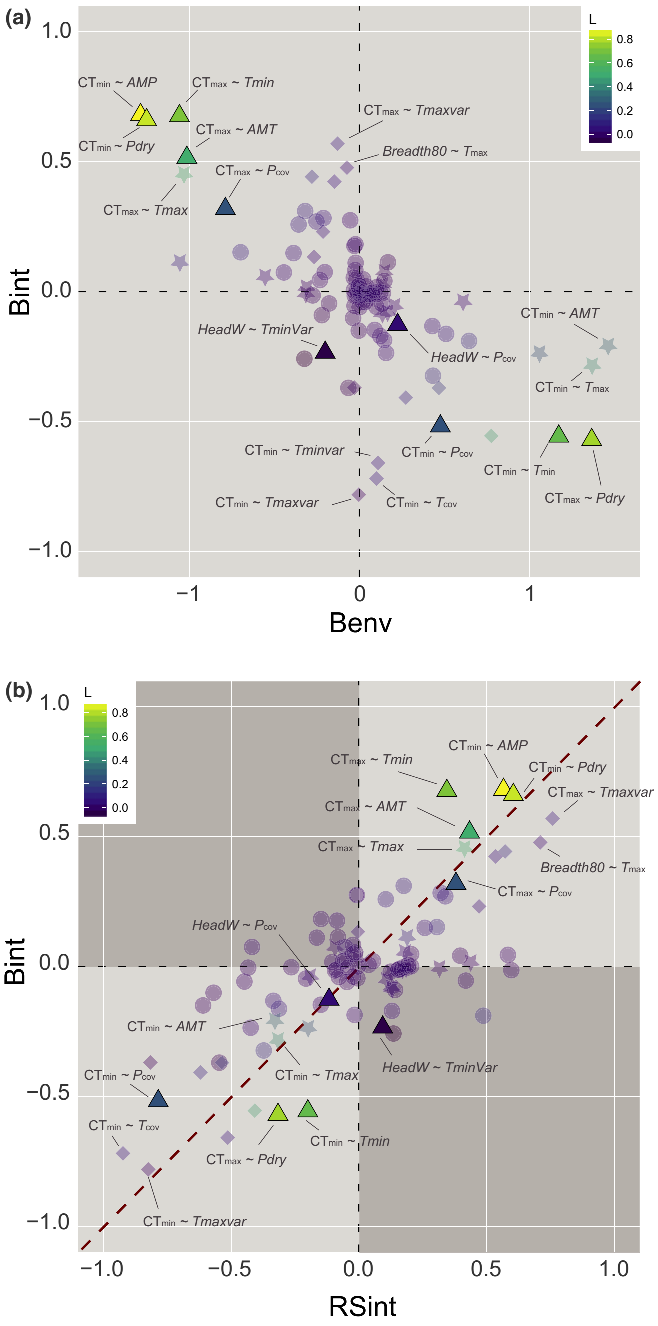

Figure 2 The Macdonald's empirical dataset revisited. Symbols are the same as in Fig. 1b and indicate whether a TER was found to be driven by plasticity or by local adaptation while taking uncertainty in the model estimates into account. Colours indicate values for the *L* index of local adaptation. Faded colours indicate that the L index was not different from 0 according to 95% CI. (a) Scatterplot showing the results of 99 linear nested mixed effect models run to assess the putative driver of each TER (See figure 3 in Macdonald *et al.* 2018 for a comparison). (b) Scatterplot showing the distortion in *Bint* estimates due to multicollinearity, when compared to structure coefficients *RSint*. In the absence of collinearity, *Bint* and *RSint* are supposed to be similar and corresponding TERs to line up along the red dashed 1:1 slope. Severe distortion (sign reversal) occurs within dark grey quadrants, and concern 36 out of 99 TERs in Macdonald *et al.*'s dataset. These 36 TERs are therefore to be disregarded.

Macdonald *et al.*- were actually more likely to be driven by plasticity (Fig. 2a). On the contrary, we identified some additional TER (though null at intermediate levels of connectivity), as well as two TER with low but non-null L-values to be driven by either local adaptation or matching habitat choice. Nevertheless, investigating structure coefficients indicated that 36 out of the 99 TERs (including a TER identified as resulting from matching habitat choice) were associated with a reversal in the sign of *Bint*, and that additional distortions in *Bint* occurred in several TERs (Fig. 2b), which indicate multicollinearity issues (Ray-Mukherjee *et al.* 2014). To sum up, we confirmed most of Macdonald *et al.*'s interpretations but our refined framework allowed to rule out several spurious correlations, as well as to confidently identify additional TERs as driven by local adaptation.

DATA ACCESSIBILITY

Prunier and Blanchet (2018): Using connectivity to identify climatic drivers of local adaptation: a response to Macdonald *et al.* (R-scripts). figshare. Fileset. https://doi.org/10.6084/m9.figshare.6067406.v2. BenvBintBootstrap.R: This R-script implements the expanded Macdonald's framework as proposed here. It may be used to compute *Benv* and *Bint* beta weights, *RSint* structure coefficients, as well 95% CI about *Benv* and *Bint* as obtained from bootstrap. BenvBintBootstrapPlot.R: This R-script can be used to plot outputs from the BenvBintBoostrap.R function. InteractionPlot.R: This R-script can be used to get both a fan-representation and a surface-representation of a first-order interaction.

REFERENCES

Aiken, L.S., West, S.G. & Reno, R.R. (1991). *Multiple Regression: Testing and Interpreting Interactions*. SAGE Publications, Newbury Park, Calif.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G. *et al.* (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46.

Macdonald, S.L., Llewelyn, J. & Phillips, B.L. (2018). Using connectivity to identify climatic drivers of local adaptation. *Ecol. Lett.*, 21, 207–216.

Prunier, J.G., Colyn, M., Legendre, X., Nimon, K.F. & Flamand, M.C. (2015). Multicollinearity in spatial genetics: separating the wheat from the chaff using commonality analyses. *Mol. Ecol.*, 24, 263–283.

Prunier, J.G. & Blanchet, S. (2018). *Using connectivity to identify climatic drivers of local adaptation: a response to Macdonald et al. (R-scripts). figshare*. Fileset. 10.6084/m9.figshare.6067406.v2.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D.W., Slotow, R. & Hamer, M. (2014). Using commonality analysis in multiple regressions: a tool to decompose regression effects in the face of multicollinearity. *Methods Ecol. Evol.*, 5, 320–328.

Thompson, B. & Borrello, G.M. (1985). The importance of structure coefficients in regression research. *Educ. Psychol. Meas.*, 45, 203–209.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Tim Coulson
Manuscript received 26 March 2018
Manuscript accepted 30 March 2018