Reply to: More evidence is needed to show that heritability and selection are not associated

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REPLYING TO J. Brommer *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-019-0989-9> (2019)

We agree with Brommer¹ that identifying the best possible environmental proxy is crucial for drawing reliable inferences about genotype-by-environment interactions (GEI), that is, genetic variation in reaction norm slopes. This is, however, not feasible for many traits. Thus, researchers may be faced with the decision to refrain from analysing GEI altogether or, alternatively, follow the approach of using the environment-specific phenotypic means ($\bar{Y}$) as a proxy, which was criticized by Brommer. We cannot, however, fully follow the specific criticism outlined by Brommer.

First, while we agree with the structure of the presented path diagram, we think the logic of the given example is flawed. It is, of course, true that if E (and only E) affects both $\bar{Y}$ and the proxies (prE_{i-n}), and if the correlation between E and $\bar{Y}$ ($r_{E,\bar{Y}}$) and the correlation between $\bar{Y}$ and a proxy for E ($r_{\text{prE}_i,\bar{Y}}$) are 0.6 and 0.42, respectively, then the correlation between E and its proxy (r_{E,prE_i}) becomes 0.7 and hence higher than $r_{E,\bar{Y}}$. This follows from a simple path analysis. However, we dispute the logic of fixing $r_{E,\bar{Y}}$ and $r_{\text{prE}_i,\bar{Y}}$ and effectively letting r_{E,prE_i} become a function of these as done in this example. As, according to the path diagram, E (and only E) affects both $\bar{Y}$ and prE , $r_{\text{prE}_i,\bar{Y}}$ is a function of $r_{E,\bar{Y}}$ and r_{E,prE_i} . The result of the numerical example given by Brommer hence depends on setting r_{E,prE_i} to a higher value than $r_{E,\bar{Y}}$ and does hence not show that r_{E,prE_i} necessarily has to be higher than $r_{E,\bar{Y}}$.

Second, Gienapp² could show using simulations that using environment-specific phenotypic means ($\bar{Y}$) as a covariate yielded results comparable to using the true—but unknown—driver of plasticity (E) and also outperformed all proxies, except the ones very closely correlated with E . Furthermore, he could show mathematically that the correlation between $\bar{Y}$ and E ($r_{E,\bar{Y}}$) approaches unity for sufficient sample sizes. This depends, however, on the assumption that the driver of plasticity (E) determines a sizeable proportion of the total phenotypic variation in the trait. If the total phenotypic variation of the trait depends to a large extent on other environmental variables, $\bar{Y}$ is no longer a reliable proxy of E , but in this case E itself explains only a small proportion of the phenotypic

variation. Detecting GEI in response to E will hence become difficult and any correlation between selection and heritability will have small evolutionary consequences. Consequently, while we agree that the power of some analyses in Ramakers et al.³ may have been limited—as discussed there—we are still convinced that if sizeable GEI had been present in the majority of datasets, we should have been able to demonstrate it.

Received: 27 June 2019; Accepted: 20 August 2019;
Published online: 23 September 2019

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Acknowledgements

We thank M. Morrissey for his input in the discussion.

Author contributions

J.J.C.R. and P.G. drafted the manuscript; A.C. and M.E.V. critically reviewed the manuscript.

Competing interests

The authors declare no competing interests.

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