# Time is not a meaningful ecological predictor of insect biomass

## Reply to Duchenne: Weather explains interannual variability, but not the temporal decline, in insect biomass

Jörg Müller[1,2], Torsten Hothorn[3], Ye Yuan[4], Sebastian Seibold[5,6,7], Oliver Mitesser[1], Julia Rothacher[1], Julia Freund[1], Clara Wild[1], Marina Wolz[1], Annette Menzel[4,8]

[1] Field Station Fabrikschleichach, Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashüttenstrasse 5, 96181 Rauhenebrach, Germany

[2] Bavarian Forest National Park, Freyungerstrasse 2, 94481 Grafenau, Germany

[3] Epidemiology, Biostatistics and Prevention Institute, University of Zurich, Zurich, Switzerland

[4] Technical University of Munich, Ecoclimatology, TUM School of Life Sciences, Hans-Carl-von Carlowitz Platz 2, 85354 Freising, Germany

[5] Technical University of Munich, TUM School of Life Sciences, Ecosystem Dynamics and Forest Management Research Group, Hans-Carl-von Carlowitz Platz 2, 85354 Freising, Germany

[6] Berchtesgaden National Park, Doktorberg 6, 83471 Berchtesgaden, Germany

[7] TUD Dresden University of Technology, Forest Zoology, Pienner Strasse 7, 01737 Tharandt, Germany

[8] Institute for Advanced Study, Technical University of Munich, Lichtenbergstrasse 2a, 85748 Garching, Germany

We very much appreciate that our article has stimulated discussion in the scientific community. We are particularly pleased that by disclosing all the data and R codes necessary for the analysis of the original study by Hallmann et al.[1] and our recently published data[2], it was possible to independently reproduce and scrutinize numerical results in detail. However, we not only disclosed raw data and R code but also the detailed documentation of the entire review process (https://static-content.springer.com/esm/art%3A10.1038%2Fs41586-023-06402-z/MediaObjects/41586_2023_6402_MOESM2_ESM.pdf). As several of the points criticized in the reply have already been extensively discussed and dealt with there, but not referenced in Duchenne's comment, the author might have overseen this resource of information. Furthermore, his initial link (https://www.nature.com/articles/s41586-021-03871-y) to our paper and data leads to a different article.

We therefore summarize our responses related to the specific points of criticism below:

**(1) Duchenne criticized that Figure 1 of Müller et al. is misleading because it exhibits two datasets collected on different geographic areas, as a unique time series.**

We want to note that the data of Hallmann et al.[1] are not a standardized time series with repeated measures at all sites over time, but many of the sites differed between years, and the sampling intensity varied over time. The intention why we showed the two data sets in one figure was to show the raw data used for training and validation. In addition, Duchenne did not mention that the training and validation data showed a large overlap at the intersecting year 2016. This overlap is easy to recognize once training and validation data are plotted side-by-side with appropriate color-coding. Temporal patterns and trends can only be deferred from models, which account for the heterogeneity in the data. Our validation data are from a geographically adjacent region, roughly in between the two regions represented in the training data, and thus, they even homogenize the overall spatial data distribution. The reviewers of

our paper also followed this reasoning (see Peer Review File). We therefore consider the assessment as "misleading" to be inappropriate.

**(2) Duchenne criticized our claim that weather conditions are the main drivers of the temporal changes in insect biomass, whereas temporal changes in habitat conditions played a minor role only.**

Here, we would like to refer once again to our R code. Contrary to what Duchenne claims, temporal changes occur also in local and landscape habitat conditions (e.g., changes in Ellenberg values over time). We compared the effects of these changes to the effects of weather conditions in models 7a and 7b. Our statement, “temporal changes in habitat conditions played only a minor role“ is based on these statistical results. This was discussed during the review process and finally approved by the reviewers.

**(3) Duchenne criticized that we argue that weather conditions were the only driver of temporal changes in insect biomass because after including weather conditions in the model, there was no temporal trend. Here, he considers our hierarchical approach as highly biased.**

We disagree with this criticism for the following reasons. First, Hallmann et al.[1] have already, and very clearly, demonstrated the existence of a negative trend over time. However, as in many scientific disciplines, time is not a meaningful ecological predictor. Instead, time is operating as a proxy for more cryptic other causal relationships (e.g., linearly increasing atmospheric $CO_2$ concentrations). Therefore, temporal trends always require further research on the underlying mechanisms explaining the temporal patterns. Including time (as a linear fixed effect) simultaneously in the model without any hypothesis about the mechanisms is not useful in trying to explain the trend. Just like the use of a random effect on year (see here the discussion in the article as well as in the Peer Review File), the hypothesis-free use of time also leads to the absorption of variance in the temporal term (known as “spatial confounding”

in the spatial statistics literature, see Peer Review File for references). Therefore, we decided to a priori identify the time windows for weather and weather anomalies that are potentially relevant for insects in a strictly hypothesis-driven approach. Of course, there are likely other additional relevant time windows that may improve the model, but we aimed to follow an a priori hypothesis-driven approach rather than data mining searching for the time windows that provide the best fit. Since our data are publicly available, of course further explorative analyses are possible (see discussion in the Peer Review File). However, we would argue that such analyses would need to define appropriate validation strategies. Here our main contribution, the validation of our model using independent new data, has been completely ignored in Duchenne's discussion. The partial negative linear time effect postulated in his re-analysis does not seem to be well aligned with the raw data (Fig. 1) and was not validated properly on independent data.

It has to be noted that observational data as presented in Hallmann et al.[1] and in our study[2] do not allow identification of causal effects, at least not without making very strict assumptions. Different exploratory analyses can therefore be expected to lead to substantially different results. This fact was demonstrated in a recently published study[3] examining the reproducibility of scientific results. More than 200 biologists analyzed the same sets of ecological data and got widely divergent results, not because of differences in the environment, but because of scientists' analytical choices.

**(4) Appropriate interpretation**

At the end of the reply, Duchenne's argumentation switched from biomass to biodiversity, which we think is not appropriate since biomass is not the same as species richness and also responds differently to drivers. For example, insect biomass has been found to be similar in agricultural and seminatural areas, whereas species diversity is lower in agricultural areas[4]. Moreover, declines in species number in grasslands were modulated by cover of arable fields

in the surrounding landscape, but not of biomass[5]. We thus recommend arguing more precisely and in a more differentiated way, as we did in our paper. Ultimately, complex drivers influence insect populations. Correlative analyses, especially with ecologically irrelevant predictors, such as time, do not help to understand the effects of global change on insects and will not enable us to predict the future. Thus, any correlative study calls for further effort to replace explanatorily weak by stronger predictors.

## References


1 Hallmann, C. A. *et al.* More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *Plos One* **12**, e0185809, doi:10.1371/journal.pone.0185809 (2017).

2 Müller, J. *et al.* Weather explains the decline and rise of insect biomass over 34 years. *Nature*, doi:10.1038/s41586-023-06402-z (2023).

3 Oza, A. Reproducibility trial: 246 biologists get different results from same data sets. *Nature* **622**, 677-678, doi:10.1038/d41586-023-03177-1 (2023).

4 Uhler, J. *et al.* Relationship of insect biomass and richness with land use along a climate gradient. *Nature Communications* **12**, 5946, doi:10.1038/s41467-021-26181-3 (2021).

5 Seibold, S. *et al.* Arthropod decline in grasslands and forests is associated with drivers at landscape level *Nature* **574**, 671-674, doi:10.1038/s41586-019-1684-3 (2019).