Weather explains inter-annual variability, but not the temporal decline, in insect biomass

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The author declares no competing interests.

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FD performed the analyses and did the figures and wrote the manuscript.

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The R codes to perform the analyses are provided as supplementary material.

**Data availability statement:**

The data are available with the original publication, [https://doi.org/10.1038/s41586-023-06402-z](https://doi.org/10.1038/s41586-023-06402-z%20).

# Main

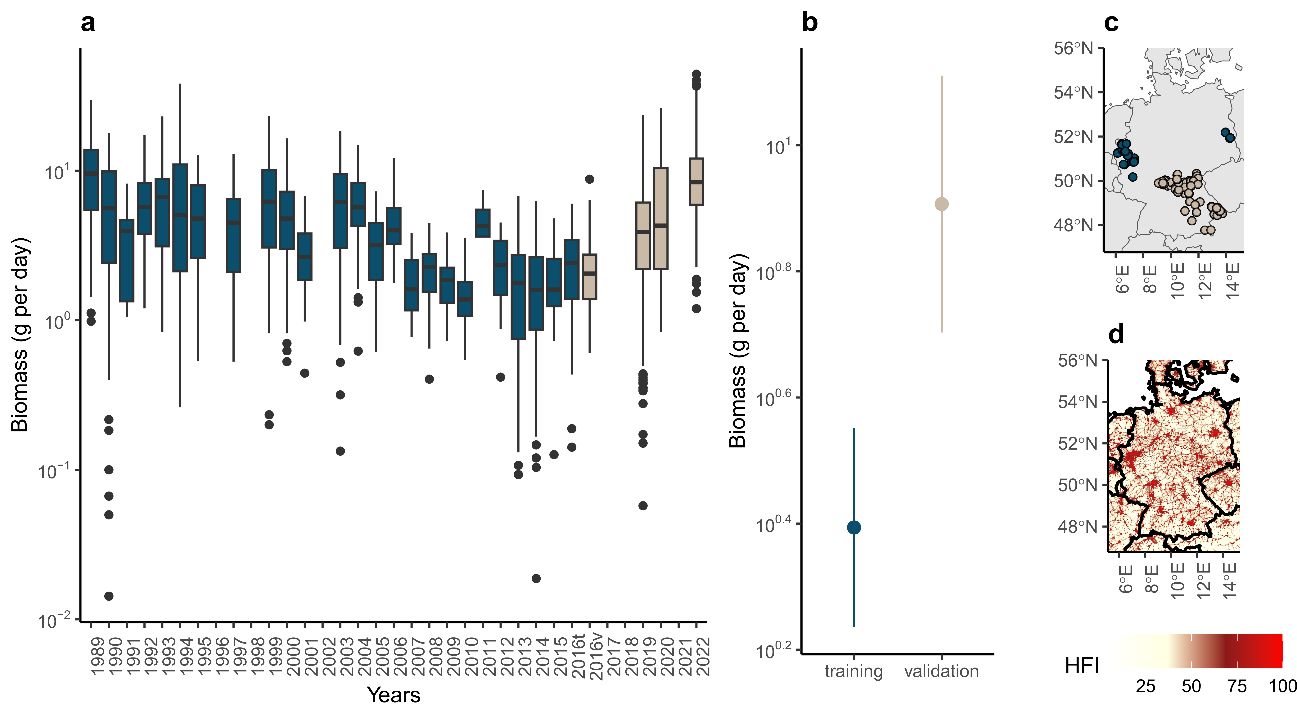
In a recent publication1, Müller *et al.* re-analysed, in light of new data, the dataset of the highly cited paper of Hallmann *et al.*2, who showed a strong decline in insect biomass in Germany between 1989 and 2016. Müller *et al.* first show that adding recently collected data (2016-2022) to Hallmann *et al.* time series, results in a non-significant decline in biomass between 1989 and 2022. Second, they present a re-analysis of the data from Hallmann *et al.* adding weather conditions as predictors and conclude that the temporal variations in insect biomass are explained by weather conditions only. Here I present arguments that explain why I think their analysis was unsuitable to draw such conclusions, because of the limitations of the dataset and because of flawed statistical analyses. More appropriate analyses produce a pattern opposite to the main message of Müller *et al.*: there is a significant temporal decline in insect biomass that is not explained by weather conditions and habitats conditions played a significant role in the observed decline.

## Interpretation of Figure 1 was misleading

First, figure 1 of Müller *et al.* is misleading because it exhibits two datasets collected on different geographic areas, as shown by their Extended Data Fig. 1, as a unique time series. The 1989-2016 data used by Müller *et al.* to fit their model were mostly collected in middle-west Germany, while the 2016-2022 data, used to validate the model, were collected in south-east Germany (Fig. 1). In the review process documentation available with the paper, Müller *et al.* stated that they have no reason to expect any difference between these two areas in terms of average insect biomass for two reasons: there is a strong overlap in biomass values on the unique year common to both datasets and previously they did not find any change in biomass between semi-natural and agricultural dominated landscapes. However, it would have been easy to test for a putative difference in average biomass of insects between the validation and training datasets before interpreting them together.

To test for it, we used a modified version of their log-gaussian General Additive model (GAM) to test for difference in biomass between validation and training dataset, while accounting for weather conditions, temporal trend, spatial autocorrelation, phenology and site-random effects. We found a significant and strong difference between both datasets (Fig. 1b), suggesting that both areas exhibit difference in average biomass that is likely to be driven by difference in the regional context, because it is not driven by the weather or the remaining temporal trend. Areas in which the data of Hallmann *et al.* were collected are more anthropized than the areas in which recent data were collected (Fig. 1b-c). This difference alone could explain the apparent increase in insect biomass in recent data.

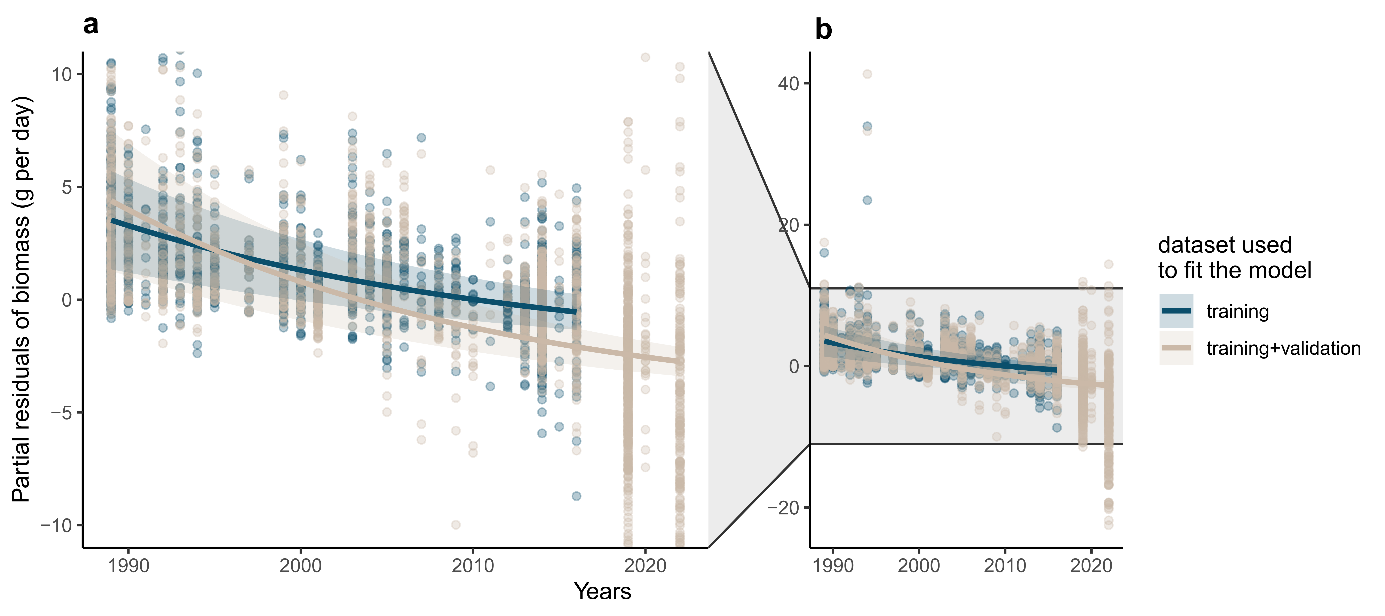
The use of two independent datasets to train and validate their model is a strength of Müller *et al.*’s work, but these datasets should not be compared with each other to extrapolate temporal trends without accounting for spatial differences. However, the authors take few precautions to interpret this heterogeneous time series: “*The temporal pattern of the compiled data shows that the linear decrease reported by Hallmann et al. throughout 2016 did not continue in more recent years, but instead biomass increased from 2016 until 2022, with highest values similar to those from the late 1980s reached in 2022 (Fig. 1).”*.

***Fig. 1: Misleading presentation of the initial and new datasets for insect biomass.*** *Data from Hallmann et al. (blue, training dataset in Müller et al.) and more recently collected data (beige, validation dataset in Müller et al.) were presented by Müller et al. on the same time series (a), while they exhibit different average biomass value (b) likely due to the fact that they were collected in different geographic areas (c). In (b) the average (±CI95%) estimated by a GAM is shown. In (d) I represented the Human Footprint Index (HFI, v2 1995-2004).*

## Weather conditions is not the only driver of temporal changes in insect biomass

Second, Müller *et al.* argue that weather conditions were the only driver of temporal changes in insect biomass, because when weather conditions were included in their model, the residuals exhibited no temporal trend (model 5 of their study). Such analyses clearly show that climatic conditions have a major impact on insect biomass but do not control for potential missing drivers of insect biomass, such as pesticides which are strongly suspected to cause insect decline3,4 but for which data are missing. One way to control for the potential effect of such missing press perturbation in statistical models analysing temporal variations is to include a time effect in addition to the effects of the other tested drivers, here weather conditions.

Simultaneously estimating temporal trend in insect biomass and effects of weather conditions, by adding a linear year effect to Müller *et al.*’s model, indicates that there is a significant decline in insect biomass over time (-4.0%.year-1) that is not explained by weather conditions (Fig. 2 and Table 1), while improving the fit of the model (lower AIC, Table 1). This temporal trend is not informative of the possible drivers of the temporal decline but indicates that insect biomass declined by 4% per year because of unknown factors.

When the additional recent dataset, used as a validation dataset in Müller *et al.* is included, the weather-independent temporal trend is even more negative (-4.8%.year-1) than with the dataset of Hallmann *et al.* only (Fig. 2). This suggests that the apparent increase in insect biomass between 2016 and 2022 (Fig. 1) was due to spatial heterogeneity in sampling or to weather conditions on those years.

***Fig. 2: The temporal trend in insect biomass is significantly negative when the effects of weather are accounted for.*** *Panel (a) is a zoom on the y-axis of panel (b), to improve readability, which is reduced by outliers. Both panels show the partial residuals of biomass, i.e. the amount of biomass not explained by other predictors, as a function of year, when using the training dataset only (blue, from Hallmann et al., 1989-2016) or the training and validation datasets together (beige, 1989-2022), to fit the model. Lines and ribbons show the model prediction and its 95% confidence interval.*

***Table 1: Model estimates and goodness of fit for the model of Müller et al. and for the modified version, with an additional linear year effect.***

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Variable | Model 5 from Müller et al. | | | Modified model 5 | | |
| Estimate | Stde | p-value | Estimate | Stde | p-value |
| Number of herb species | 0.0008 | 0.0011 | 0.4763 | -0.0022 | 0.0011 | **0.0377** |
| Number of tree species | 0.1174 | 0.0121 | **0.0000** | 0.0515 | 0.0143 | **0.0003** |
| Ellenberg value light | 0.1469 | 0.0646 | **0.0232** | 0.0529 | 0.0635 | 0.4051 |
| Ellenberg value temperature | -0.0351 | 0.0406 | 0.3867 | 0.0702 | 0.0408 | 0.0857 |
| Proportion of arable land | -0.3530 | 0.1108 | **0.0015** | -0.0808 | 0.1130 | 0.4746 |
| Proportion of forest | -0.1493 | 0.1139 | 0.1899 | 0.0630 | 0.1139 | 0.5803 |
| Proportion of grassland | 0.3484 | 0.1161 | **0.0027** | 0.2487 | 0.1129 | **0.0277** |
| Proportion of water | 0.2816 | 0.1479 | 0.0571 | 0.0364 | 0.1448 | 0.8016 |
| \**T* | 0.0814 | 0.0062 | **0.0000** | 0.0844 | 0.0060 | **0.0000** |
| \**P* | -0.0033 | 0.0008 | **0.0000** | -0.0025 | 0.0007 | **0.0007** |
| \**T* × *P* | -0.0001 | 0.0002 | 0.7482 | 0.0000 | 0.0002 | 0.8560 |
| \**T* ano. winter | -0.2943 | 0.0268 | **0.0000** | -0.1232 | 0.0321 | **0.0001** |
| \**P* ano. winter | 0.0339 | 0.0026 | **0.0000** | 0.0197 | 0.0030 | **0.0000** |
| \**T* ano. winter × *P* ano. winter | -0.0114 | 0.0025 | **0.0000** | -0.0021 | 0.0026 | 0.4187 |
| \**T* ano. April cur | 0.0820 | 0.0261 | **0.0017** | 0.0810 | 0.0237 | **0.0007** |
| \**P* ano. April cur | 0.0148 | 0.0016 | **0.0000** | 0.0068 | 0.0017 | **0.0000** |
| \**T* ano. April cur × *P* ano. April cur | -0.0028 | 0.0009 | **0.0036** | -0.0003 | 0.0009 | 0.7761 |
| \**T* ano. April prev. | -0.1082 | 0.0303 | **0.0004** | 0.0155 | 0.0301 | 0.6073 |
| \**P* ano. April prev. | 0.0021 | 0.0015 | 0.1477 | 0.0028 | 0.0014 | **0.0405** |
| \**T* ano. April prev. × *P* ano. April prev. | -0.0044 | 0.0008 | **0.0000** | -0.0014 | 0.0008 | 0.0932 |
| \**T* ano. month prev. | -0.0078 | 0.0119 | 0.5135 | -0.0059 | 0.0117 | 0.6134 |
| \**P* ano. month prev. | -0.0009 | 0.0004 | **0.0369** | -0.0001 | 0.0004 | 0.7498 |
| \**T* ano. month prev. × *P* ano. month prev. | -0.0006 | 0.0003 | **0.0419** | -0.0001 | 0.0003 | 0.7196 |
| Year | not included | | | -0.0411 | 0.0048 | **0.0000** |
| R2 | 0.6543 | | | 0.6661 | | |
| AIC | 13156.2570 | | | 13101.6760 | | |

*T*, temperature; *P*, precipitation; ano., anomalies; cur, year of sampling; prev., the month of the sampling day but in the previous year; Stde, Standard Error. Bold pvalues highlight significant effects (p-value < 0.05) and brightness of the color of the “Estimate” column is proportional to the magnitude of the estimate (red for negative and blue for positive effects).

## Habitat conditions played a significant role in the decline of insect biomass

Third, Müller *et al.* claimed 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. However, since weather conditions, as insect biomass, exhibits strong inter-annual variations, weather conditions could drive inter-annual variability in insect biomass without being the main driver of the long-term temporal decline observed by Hallmann *et al.*2. In contrast, habitats conditions measured here (number of trees, proportion of arable land in a 200m radius, etc.) are unlikely to exhibit strong interannual variations, and thus to explain inter-annual variability in insect biomass, but could be an important driver of the long-term trend.

To estimate the contributions of weather and habitat conditions in the long-term biomass decline, the temporal trend in partial predicts was estimated. Biomass was predicted according to weather conditions or habitat conditions only and the temporal trend in those values was calculated. The results show that weather conditions indeed played a role in the observed decline observed previously by Hallmann *et al.* (-1.4%.year-1, CI95%=[-1.57,-1.26]), but habitat conditions modelled by Müller *et al.* also played a significant role in that decline (-0.9%.year-1, CI95%=[-1.01,-0.78]). However, these contributions to the long-term decline in insect biomass are minors relative to the part of the decline that correlates more with time than with other included drivers, i.e. the remaining temporal trend (-4.0%.year-1) estimated by the year effect, as said previously.

One would also note the difference in the precision of modelling weather and habitat conditions. While weather conditions are modelled using 12 parameters, including time-lagged effects and interaction among variables, habitats conditions are modelled using 8 parameters, without time-lagged effects or interactions among variables. Some variables, extracted from Hallmann *et al.*, were based on a very coarse temporal resolution. For example, proportion of habitats within the 200m radius have been calculated from two sets of aerial images, taken in 1989–1994 and 2012–2015, and yearly values have been interpolated. Although it is a noble effort to model past habitat changes while there is almost no available data at such spatio-temporal scales, it's an illusion to believe that it captures all the effects of habitat conditions on insect biomass.

Among these variables none of them measure the effect of agricultural intensification, which has been documented as a cause of the insect plight3–5, and abundance changes in other taxa6. Thus, in contrast to what Müller *et al.* wrote, the significant temporal decline in insect biomass, independent from the effect of weather conditions and from modelled habitat conditions, could be explained by unmodelled temporal changes in habitat conditions. The conclusion “*temporal changes in habitat conditions played only a minor role*” in the temporal changes of insect biomass, is therefore surprising and unwarranted.

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***Fig. 3: temporal changes in weather and habitats conditions are linked to decline in insect biomass.*** *Biomass values predicted by weather (a) or habitat (b) conditions only, using the modified model presented in Table 1, as a function of the time. The temporal trend in those values (line) is the contribution of those conditions to the long-term temporal trend in insect biomass.*

## Conclusion

In writing this comment, I do not intend to tone down the effects of weather conditions on insect biomass; they are clearly demonstrated by Müller *et al.*’s analysis, and have been supported by other studies7,8. Analyses done by Müller *et al.* show that weather conditions strongly affect inter-annual variability in insect biomass, consistently with previous findings9–13, and that weather conditions could partially drive the observed decline in insect biomass. However, their analyses are not suited to state that weather conditions were the only driver of the observed decline, neither to affirm that habitats conditions played a minor role in that decline. Corrected analyses even show the opposite: most of the temporal decline in insect biomass remains unexplained by the available data and habitats conditions played a significant role in that decline. Such kind of illegitimate conclusions, minimizing the contribution of land use change in the long-term trend of insect biomass, can be strongly deleterious for biodiversity conservation.

With this comment, I would like to remind our modest ability to model complex ecological changes. Müller *et al.* push forward in the right direction in trying to understand the drivers of the temporal decline in insect biomass, using correlates for which causal mechanisms on the response variable are theorized. However, not accounting for the missing predictors, through a time effect, is likely to produce highly biased results. Assessing the relative importance of drivers requires models that simultaneously include all drivers in a similar way. Since most of the global change drivers exhibit high correlation with time, this remains a challenging task. Moreover, the effects of global change drivers likely depend on each other, e.g. the effect of climate change on insect abundance is mediated by land use8. I thus stress the need to be conservative in the interpretation of results, to prevent overinterpretation of analyses that often come with many limitations, especially when analysing large scale ecological patterns. Drawing conclusions that are not properly supported by statistical findings is likely to disrupt both the scientific debate and public outreach, with possible negative consequences for the trust in scientific results on important topics for societies.

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In a recent publication1, Müller *et al.* elegantly evidenced that weather variations had a strong impact on yearly variations in insect biomass using a training-validation approach with two independent datasets. While the training dataset was the one from the highly cited paper of Hallmann *et al.*2 showing a 75% decline in insect biomass in Germany between 1989 and 2016, the validation dataset was made of data collected between 2016 and 2022 in a different region of Germany. The joint presentation of the two datasets in their Figure 1 questioned the results found by Hallmann *et al.*2 as insect biomass increased in the recently collected data, reaching similar level than those of 1989. They further reanalysed the Hallmann *et al.*2 dataset adding weather conditions and habitat changes as predictors, a noticeable effort as past habitat change remains very rarely addressed. They conclude that weather conditions were the main driver of the temporal variations in insect biomass, that “*temporal changes in habitat conditions played only a minor role”*, and that when weather conditions are accounted for, the Hallmann *et al.* dataset do not present any significant decline in insect biomass. Here we explain why we think their analysis was unsuitable to draw such conclusions, and present alternative analyses we think more appropriate. Our analysis lead to opposite results, showing that there is a significant temporal decline in insect biomass not explained by weather conditions nor by past habitat changes, and that past habitat changes played a significant role in the observed decline, stronger than weather variations.

Müller *et al.* argue that weather conditions were the main driver of temporal changes in insect biomass, because when weather conditions were included in their model, the residuals exhibited no temporal trend (model 5 of their study). Such analyses clearly show that climatic conditions have a major impact on insect biomass but do not control for potential missing drivers of insect biomass, such as pesticides which are strongly suspected to cause insect decline3,4 but for which data are missing1. Estimating the temporal trend in the residuals is a hierarchical approach prone to bias since there is a known temporal trend in weather conditions due to climate change. The statistical fit, which seeks to explain as much variance as possible with the available variables, is likely to attribute any temporal change in insect biomass to temporal changes in weather conditions and habitat changes. As such, the absence of temporal trend in the residuals is not informative on the importance of non-modelled drivers. One way to control for the potential effect of such missing press perturbation in statistical models analysing temporal variations is to include a time effect in addition to the effects of the other tested drivers, here weather conditions.

Simultaneously estimating effects of weather conditions, habitat change and potential missing drivers by adding a linear year effect to Müller *et al.*’s model, indicates that there is a significant decline in insect biomass over time (-4.0%.year-1) that is not explained by weather conditions (Fig. 2 and Table 1) nor by past habitat change. It further improve the fit of the model (lower AIC, Table 1). The estimated temporal trend is not informative of the possible drivers of the decline but indicates that insect biomass declined by 4% per year because of unknown factors. Adding the recent dataset, used as a validation dataset in Müller *et al.*1, temporal trend independent of weather and habitat change is even more negative (-4.8%.year-1) than with the dataset of Hallmann *et al.*2 only (Fig. 2). This suggests that the apparent increase in insect biomass between 2016 and 2022 was due to particularly beneficial weather conditions on those years, as stated by Müller et al.1.

Müller *et al.* 1 also claimed that temporal changes in habitat conditions played a minor role in the temporal variations of insect biomass compared to weather conditions. However, since weather conditions, as insect biomass, exhibits strong inter-annual variations, weather conditions could drive inter-annual variability in insect biomass without being the main driver of the long-term temporal decline observed by Hallmann *et al.*2. In contrast, habitats conditions measured here (number of trees, proportion of arable land in a 200m radius, etc.) are unlikely to exhibit strong inter-annual variations, and thus to explain inter-annual variability in insect biomass, but could be an important driver of the long-term trend.

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One would also note the difference in the precision of modelling weather and habitat conditions. While weather conditions are modelled using 12 parameters, including time-lagged effects and interaction among variables, habitats conditions are modelled using 8 parameters, without time-lagged effects or interactions among variables. Among these habitat variables none of them measure the effect of agricultural intensification, which has been documented as a cause of the insect plight3–5, and abundance changes in other taxa6. As such, the significant temporal decline in insect biomass, independent from the effect of weather conditions and from modelled habitat conditions, could be explained by temporal changes in habitat conditions not covered by the selected variables.

In writing this comment, we do not intend to tone down the effects of weather conditions on insect biomass; they are clearly demonstrated by Müller *et al.*’s analysis and have been supported by other studies7,8. Müller *et al.* push forward in the right direction in trying to understand the drivers of the temporal decline in insect biomass, using correlates of drivers mechanistically linked to the response variable. However, not accounting for potential missing predictors, through a time effect, is likely to produce highly biased results. Assessing the relative importance of drivers requires models that simultaneously include all drivers in a similar way. Since most of the global change drivers exhibit high correlation with time, this remains a challenging task. Further, the effects of global change drivers likely depend on each other, e.g. the effect of climate change on insect abundance is mediated by land use8. We thus stress the need to be conservative when interpreting results of analyses that often come with many limitations, especially when analysing large scale ecological patterns. Drawing conclusions not adequately supported is likely to disrupt both the scientific debate and public outreach, with possible negative consequences on trust in science regarding on topical societal issues.