FORUM

A re-evaluation of hemispheric asymmetries in herbivory: a response to Kozlov & Klemola 2017

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Summary

1. Kozlov & Klemola (Journal of Ecology, 105, 2017: 000-000) argued that our conclusion about hemispheric asymmetries in herbivory is not supported after the replacement of data points extracted from Moles & Westoby (Oikos, 90, 2000: 517–524.).

2. To re-evaluate the asymmetries in herbivory, we analysed the revised dataset according to Kozlov & Klemola’s (2017) suggestion, as well as the dataset used in Kozlov et al. (Global Ecology and Biogeography, 24, 2015: 1126–1135.).

3. All the analyses showed that herbivory decreased with latitude only in the Northern hemisphere, but in the Southern hemisphere, herbivory showed no relation to latitude. Model selection showed that in both datasets, hemisphere is a key determinant of herbivory, with Southern hemisphere having higher levels of herbivory than the Northern hemisphere.

4. Synthesis. Based on currently available data collected from publications, we found evidence for hemispheric asymmetries in herbivory. This conclusion is unlikely to change even when the controversial data points are replaced.

Key-words: biotic interactions, climate, growth form, herbivory, latitude, plant defense–herbivore interactions

Recent studies have triggered continuous debates on the solidity of the widely accepted latitudinal herbivory hypothesis that predicts herbivory will decrease with latitude (Anstett et al. 2016). After making a synthesised analysis of the published data on herbivory, we found the hypothesis was only supported in the Northern hemisphere and, in general, the Southern hemisphere has significantly higher levels of herbivory than the Northern hemisphere (Zhang, Zhang & Ma 2016). When some data points in the dataset were replaced and a different statistical model was used, Kozlov & Klemola (2017) argued that our conclusion about hemispheric asymmetries in herbivory were not supported. Kozlov & Klemola’s (2017) key concerns lie in two points: (i) the use of data points, including the loss of whole branches with all associated leaves (LLA\_{total}) from Moles & Westoby (2000) overestimated the level of herbivory in the Southern hemisphere. Kozlov & Klemola (2017) argued that these data should be replaced by other estimates that excluded this loss of branches (LLA\_{total}); and (ii) A full model should be used in the data analyses that includes latitude, hemisphere, and their interaction as explanatory variables.

We used the data points that included the loss of whole branches with all associated leaves (LLA\_{total}) from Moles & Westoby (2000) based on Turkotte et al.’s (2014) published dataset that stated clearly the herbivory was caused by ‘Insecta (general)’. Nevertheless, we tend to agree with Kozlov & Klemola (2017) that it is unlikely that the loss of entire branches is attributable to insect herbivory. Accordingly, using the dataset revised by Kozlov & Klemola (2017), we retested the following hypotheses: (i) the Southern hemisphere has higher levels of herbivory than does the Northern hemisphere, and (ii) herbivory decreases with latitude only in the Northern hemisphere. We also re-analysed Kozlov et al.’s (2015) dataset, as Kozlov & Klemola (2017) stated that this dataset was more uniform than ours because it included only background losses of the foliage of adult woody plants to insects. For this dataset, we used only the data points on leaf damage caused by all herbivores (n = 1477) extracted from published literature because only these data are comparable to ours.

To keep consistent with the methods used in Kozlov & Klemola (2017), all herbivory data were ln(1 + sqrt(x)) transformed before data analyses, and data points that could not be attributed to a single plant species were treated as missing values (n = 22 for our dataset and n = 122 for the dataset derived from Kozlov et al. 2015). Because different models...
We agree with Kozlov & Klemola (2017) that a full model that includes latitude, hemisphere, and their interaction as moderators of herbivory is more suitable for testing hemispheric asymmetries in herbivory. One basic statistical principle in data analysis is that moderators should be independent of each other in the same model. But in both of the two datasets, the absolute latitude of the study site differed significantly between the two hemispheres (Fig. S1, Supporting Information). Therefore, the full model obviously violates the basic requirement of data analysis due to the structure of the datasets, and this may lead to confusing results. We adopted two methods to deal with this problem. First, model simplification based on the Akaike information criterion (AIC value) was conducted in addition to the full model. We assumed that models with $\Delta$AIC $\leq 2$ are considered to be equally likely, and larger values indicate a lack of fit and lower explanatory power relative to the best model (Burnham & Anderson 2004). Secondly, we tested the latitudinal herbivory hypothesis separately between the two hemispheres.

The results showed that the two datasets had quite similar patterns in herbivory (Figs 1–4). When hemisphere was used as the only explanatory variable, the dataset of Kozlov et al. (2015) also showed that the Southern hemisphere had higher herbivory compared to the Northern hemisphere, which is consistent with the results from Kozlov & Klemola (2017).
significantly higher levels of herbivory than did the Northern hemisphere ($F_{1,302} = 8.67, P = 0.0035$).

For our dataset, in the full model, none of the three variables showed significant effects on herbivory (Table 1), and the results differed from those of Kozlov & Klemola (2017). In our full model, the slope estimated for the herbivory-latitude relationship in the Northern hemisphere was $-0.0037$ ($t = -3.06$, d.f. $= 275, P = 0.0024$), indicating a significant negative relationship between herbivory and latitude in this hemisphere. But for the Southern hemisphere, the estimated slope was $-0.0005$ ($t = -0.17$, d.f. $= 275, P = 0.8671$), indicating no correlation between herbivory and latitude in this hemisphere.

For the dataset of Kozlov et al. (2015), only latitude showed a significant relationship with herbivory (Table 1). In the full model, the slope estimated for the herbivory-latitude relationship was $-0.0046$ ($t = -4.04$, d.f. $= 302, P < 0.0001$) in the Northern hemisphere, which supports the prediction of the latitudinal herbivory hypothesis. But in this model, the slope estimated for the herbivory-latitude relationship in the Southern hemisphere was $-0.0033$, with no significant difference from zero ($t = -1.30$, d.f. $= 302$.)
was nonsignificant (Fig. 4). Therefore, the general pattern based on the two datasets also suggests that herbivory is unlikely to decrease with latitude in the Southern hemisphere.

Kozlov & Klemola (2017) stated that their “original data” on insect herbivory in Kozlov et al. (2015) showed no evidence of the existence of hemispheric asymmetries in herbivory. In fact, as Kozlov et al. (2015) noted, the herbivory level in the “original data” was much lower than that in the published data. The level of herbivory based on their “originally collected” data points not only showed no difference between the two hemispheres but also showed no relationship with latitude (see the results in Kozlov et al. 2015). There are substantial differences in the patterns of the data that came from the two different sources (Kozlov et al. 2015). In fact, Kozlov et al. (2015) had noticed this difference, and the data of the two sources were analysed separately in their study. Considering the “original data” were collected “by persons who were not aware of the hypothesis being tested” (Kozlov et al. 2015), and based on our own field experiences, people tend to choose intact leaves when they know nothing about the use of these leaves. This might be why these data showed different patterns compared to the data collected from publications. Nevertheless, based on the currently available published data, we could not predict that herbivory will decrease with latitude in the Southern hemisphere.

A recent study suggested that leaf life span might be an important factor in explaining hemispheric asymmetries in herbivory (Zhang, Zhang & Ma 2017). Compared to the Northern hemisphere, the Southern hemisphere floras are typically dominated by evergreen species (Peppe et al. 2011). A relatively longer leaf life span could lead to a higher level of herbivory accumulation (Zhang, Zhang & Ma 2017). Therefore, we suggest that herbivory and possible differences in key functional traits of plants between the two hemispheres should be evaluated in further studies.

It should be declared that both the datasets have limits in testing the hemispheric asymmetries in herbivory because the geographical ranges of the study sites are highly imbalanced between the two hemispheres. Latitude can only explain a marginal proportion of the variation in herbivory (Zhang, Zhang & Ma 2016), and this may be a reflection of the various methods used in measuring herbivory (Anstett et al. 2016). Further standardised methods in measuring herbivory should be developed for testing the latitudinal herbivory hypothesis.

In general, our analyses showed that the latitudinal hypothesis was only supported in the Northern hemisphere. Based on the currently available published data, we found no evidence to predict that herbivory will decrease with latitude in the Southern hemisphere. More studies in the Southern hemisphere, especially those conducted at high latitudes, are needed for our understanding of the latitudinal variations in herbivory.

Authors’ contributions

S.Z. analysed the data and wrote the manuscript; Y.Z. and K.M. revised the manuscript.

Acknowledgements

This work was supported by National Natural Science Foundation of China (31370451, 31300368).

Data accessibility

All data and SAS code are uploaded as online Supporting Information.

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Received 16 March 2017; accepted 13 June 2017
Handling Editor: Emily Lines

Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. The absolute latitude of the study sites in the Northern and Southern hemisphere based on the revised dataset from Zhang, Zhang & Ma (2016) (Z’s dataset) and Kozlov et al. (2015) (K’s dataset).

Data S1. Zhang et al.’s (2016) data and associated SAS script.

Data S1a. Kozlov et al.’s (2015) data and associated SAS script.