

Peer Review File

Manuscript Title: Trait-based sensitivity of large mammals to a catastrophic tropical cyclone

Reviewer Comments & Author Rebuttals

Reviewer Reports on the Initial Version:

Referees' comments:

Referee #1 (Remarks to the Author):

The authors used an impressive array of datasets to understand how large mammals respond to extreme climatic events, making use of a rare opportunity. The study is highly novel and extremely thorough in the scope of analyses conducted and the variety of responses tested, including the temporal scale from hours to years following the cyclone. The authors also place their findings within the broader ecological literature and test emerging hypotheses related to animal responses to tropical cyclones. Overall, an impressive and timely study that sheds new light on how we understand animal responses to extreme events. I do, however, have some comments that I hope will be useful to the authors in further strengthening their impressive study.

The number and variety of animal responses tested is a major strength of the work. However, as would be expected, some of the analyses and conclusions are more convincing than others. One of the most exciting analyses presented is that of the GPS telemetry. However, I also found it to be the least convincing due to the low sample sizes of collared animals, and also because the only real evidence from these data to suggest that smaller animals are more vulnerable than larger ones (the second hypothesis tested) comes from the bushbuck GPS data, for which the authors only had data from eight individuals, and only three of which died in the flood. I think these results are fascinating, but I wonder if they are overemphasized. The authors discuss them first in the manuscript, which makes sense given the increasing scales, but they also highlight them, but not others, when introducing the methods (line 72). The conclusions drawn from this relatively small dataset are, however, reinforced from the other, richer datasets (camera traps, dietary data, aerial censuses), which improves the certitude of the findings. I also understand that it is difficult to collar more animals than this at any one point in time and so I don't think this is a flaw in the study, but I would encourage the authors to consider placing less emphasis on these results, which could be achieved by not only calling out the GPS telemetry methods on line 72, and perhaps adding some statements about the limitations of these data to the study.

I was more convinced by the other analyzes, especially those investigating changes in diet and body condition, although more information is needed about when the body condition measurements were made (see my comment on the Supplementary Material below). I was also mostly convinced by the camera trap and census data, but I wondered about correlations between body mass and floodplain association. There are clear relationships between mortality and body size, and mortality and floodplain association, with smaller species and those associated with the floodplain being more vulnerable to flooding, but almost all small bodied species also showed high levels of association with the floodplain, whereas larger-bodied species did not (lines 144-148), so how can we

disentangle the effects of body size and habitat use (floodplain association), which are the two hypotheses tested? The two best performing models had just one of these two factors in them, but the difference in AIC between the models is small (0.96), and so we can't with confidence consider either one of these models to be better than the other. Some consideration and/or discussion of this point is needed.

The camera trap data are also generally convincing, but it would be helpful to add to the panels in Figure S9 a line denoted when the flood waters receded, and when animals could return to the area marked as "NEAR" (Figure S3 partly provides this information, but having it in Figure S9 will be helpful). Otherwise, I'm left questioning whether animals simply didn't go there because the area was flooded (or is this in fact the reason they don't go there?).

I also wondered about how many of the 30 surviving cameras were in the "NEAR" area? I'd assume that more in this area were damaged than in the other areas. Did this bias the results in any way?

Line 109 states that the GPS and camera trap data together indicate that body size was a key determinant of which animals survived the flood, but Figure S9 shows that waterbuck (the largest of the floodplain associated species) and not bushbuck (the smallest), showed the strongest response of moving away from the lake in the camera trap data. Should this statement be revised?

Lines 172-176 – Would carnivores also be robust to the cyclone because the quality of their diet not diminish as it did for herbivores? Also, would they benefit from scavenging on the abundance of carcasses? Carnivores generally do better during drought periods for similar reasons (higher mobility and increased prey vulnerability). I find it interesting that their response to the opposite climatic extreme (floods) are similar, perhaps suggesting that carnivores are generally more robust to extreme climatic events than herbivores.

Line 179-180 – Again, the issue of collinearity between body size and association with exposed habitats (the floodplain) is difficult to disentangle.

Supplementary Material:

Line 187 – I think reference 58 is the incorrect one here as it refers to a study system in Namibia, not Gorongosa, please check it.

Lines 522-524 – More information about how the body condition scores were recorded is needed. When were animals recaptured for body condition assessments? How long after the flooding was this done? Was it on the same animals as before the flood (to be able to make direct comparisons)? How many animals did the authors have repeat body condition scores for?

Figure S1 - How was floodplain association for each species measured?

Figure S10 – Will all readers know the identity of the species each silhouette represents?

Good work!

Andrew Davies

Referee #2 (Remarks to the Author):

Thank you for your submission to Nature. I enjoyed reading your manuscript and found it to be clearly written and well formulated. Your findings highlight the vast importance of collecting long-term monitoring data across a system to evaluate community-level responses. It's an impressive array of data, from GPS telemetry data to assess the movements of recovering animal populations, to camera traps and systematic animal surveys to evaluate population and distribution changes. I found your conclusions to be robust and supported by multiple forms of inference, one of the main strengths of your analysis. I also believe that your observational study will provide valuable information on community assembly, especially as it relates to the importance of ecological disturbance from extreme weather events that are becoming more frequent and more severe.

I have provided a few minor comments for you to address. My main comment, however, relates to how you compared shifts in daily home ranges at the onset of the cyclone. Kernel density estimates (KDEs) are known to be especially sensitive to small sample sizes and the amount of autocorrelation that exists (see Noonan et al. 2019 - A comprehensive analysis of autocorrelation and bias in home range estimation), which is impacted by the biology of the animal and the temporal interval of data collection. Spatial overlap also tends to be smaller when samples sizes are low, which makes me question if you are observing a true response to the cyclone or simply an artifact of the data and the analysis method being chosen. A few thoughts:

1) Can you justify why KDEs are appropriate in this case and why you have not considered frameworks (e.g., continuous time movement modeling) which incorporate the autocorrelation structure inherent in the data?

2) Can you extend the period of time in which you make comparisons? Rather than only comparing to the previous month, could you sample from multiple different time periods? I don't know the biology of all of these animals, but how stationary is a bushbuck home range over time? Do these dispersal events rarely occur, or is variability in dispersal common between individuals? Essentially, I am looking for further support that the changes in distribution are true effects and not just a result of the time period chosen.

3) It's unclear from the supplementary materials if the same time periods were compared. You write "We partitioned each individual's GPS locations into temporal bins that spanned (i) the month before the cyclone.... and (ii) 6 weekly bins after the onset of flooding.". My concerns is the comparison of the different temporal intervals, with the pre-cyclone period representing a full month of data, which is then compared to weekly data. Is this correct or am I misunderstanding how the pre-cyclone data were partitioned? Seems graphically that this was separated into weekly bins, but this is not clear in the text. Otherwise, there would be more variance among the weekly centroids than the monthly centroids. Please clarify.

4) Would it be possible to broaden your analysis to a longer time period of movements and include a

continuous predictor (such as the intensity of different storms or rain events)? This would be statistically 'safer' than a one-off treatment (i.e., one big storm), especially since all of the biases and variances are not being accounted for. It would potentially show in a more robust fashion how movements were impacted by average to extreme rain events.

I appreciate the opportunity to review your manuscript and hope these comments are useful in improving the content of your manuscript.

Sincerely,

Jared Stabach

Other Minor Comments:

Figures:

Fig. 1e - Marked Fig. 1e on line 90. Not marked in Figure (Only A-D marked).

Fig. 1d - Could you show where this area of interest is on Fig. 1c? A simple rectangle would suffice.

Fig. 2 - "All herbivores increased their selection for higher elevations and their avoidance of floodwaters, significantly so for bushbuck, kudu, and elephant." For 'elevation', yes, although the confidence intervals for elephant seem to overlap. For 'flood edge', however, the SSF coefficients for bushbuck don't represent a significant difference.

Supplementary Information

Line 184: Since you use step selection functions following instructions by Muff et al., I presume you included individual random effects. Please specify this information in the supplementary materials.

Line 193: The temporal interval of the GPS tracking device was different for each species (1-hr intervals for bushbuck, nyala, kudu, elephant; 3-hr intervals for lion and wild dog; 8-hr intervals for sable). Can you discuss how these different temporal intervals may impact your findings and/or comparability between species?

Line 397: Make sure to add doi.

Supplemental Figures:

Fig. S19 - "African wild dogs and lions increased their.....avoidance of flood waters after Idai". This is true for lion, but not wild dog based on the graph of coefficient estimates (perhaps marginally?). Seems no change to termite mounds and flood edge, although (as stated) a non-significant increase

in elevation.

Fig. S17 - Agree that lions are difficult to count and are underestimated. Also agree that this is a reliable index across years. But, I would say that "all" counts are underestimated, as undercounting bias is documented by multiple researchers, irrelevant of the species. A good example is the work conducted by Lamprey et al. comparing undercounting bias of rear-seat observers in wildlife surveys conducted in Kenya. Multiple other examples exist, including results from distance-based surveys. Like you say, a reliable index, but I recommend a slight edit/clarification to the text.

Line 239: 'fig. 19b' should be 'fig. S19b'.

Referee #3 (Remarks to the Author):

This is an extraordinarily well documented account of the impacts of Cyclone Idai on the larger herbivore of Gorongosa. I wish, though, that the findings were less obvious. It is completely intuitive that animals would seek higher ground and that less mobile species would suffer more than larger species (the old density-independent vs density-dependent dichotomy in life-history theory between small-bodied animals and large animals). While I completely agree with the authors in the need to document the impacts of rare events, the question is whether every well-documented perturbation merits publication in Nature. As well studied as this may be, it feels like an anecdote rather than an investigation into the general problem of when, say, extreme floods may or may not have larger impacts. For example, the Okavango swamps flood every year, animals routinely seek higher ground -- but do they show adaptations to these annual perturbations that the Gorongosa populations lacked? Hurricanes in the Caribbean influenced the morphology of island anoles; has the selective event in Gorongosa led to increased body size in bushbuck? As the authors imply, the ramifications of the Idai event will likely reverberate through this system for years -- something less obvious may yet emerge. For the moment, I think this paper fully merits consideration for Nature Ecology and Evolution.

Referee #4 (Remarks to the Author):

Walker et al., use spatial data and DNA metabarcoding to determine the effects of a severe climatic event on the large mammals of Gorongosa in Mozambique. This interesting study combines many techniques to better understand the potential effects and repercussions of such events that are only predicted to become worse and more frequent over time. Authors found that animals showed strong spatial responses, dietary responses, and numerical declines. In order to better conserve fragile ecosystems such as those in Gorongosa, information such as this is vital. I will state early on that I was asked to review the DNA metabarcoding portion of this manuscript, so this is where the majority of my comments center. I thought the manuscript was interesting, well written, and of broad interest. However, I have several comments regarding analyses and results which I think would strengthen the paper overall.

The authors make two main predictions: i) species in woody, higher elevation habitats are likely to

be more robust to cyclone Idai and ii) species robustness should be positively correlated to body size based on mobility and lower mass-specific metabolic rates. While I think these predictions are largely supported by the use of the spatial data, I think the authors could make better use of the DNA metabarcoding data to further support the second prediction; looking at the effect size of the cyclone on various dietary metrics may allow you to determine whether larger bodied animals are in fact more robust to such events in regards to diet as well as movement. For instance: Fig. S14. If you unpack this figure, what would the effect size be for each species? We know dietary richness is likely determined by body size, but is the effect of the cyclone greater for larger or smaller species, or is there no difference given species' size? The same could be considered when thinking about dietary turnover, is turnover between pre- and post-cyclone greater for smaller or larger species?

My next comment centers around the initial filtering of the data. Given the initial pipeline (e.g. removal of all sequences that were found to be highest in the control samples), were sensitivity analyses conducted to determine that sequences <1% RRA should be removed from carnivore and herbivore datasets to reduce the likelihood of false positives in the DNA metabarcoding data? Should the same threshold be used for both diet types? While RRA thresholds can be useful for removing false positives below a certain threshold, they can also introduce false negatives which has been shown to drastically influence diversity calculations in some datasets. I am interested to know whether the dietary DNA metabarcoding results hold regardless of the threshold selected. It is inevitable that rare taxa are also being removed by using such thresholds, but these rare taxa could paint an interesting picture; one could predict that rare taxa may or may not play an important role in the diets of large mammals after such an event (i.e., do species incorporate a greater number of rarer taxa into their diet following such an event, thereby increasing dietary richness beyond what is found currently?) Regardless, including better explanations as to why particular thresholds are used is warranted within the text for each dataset.

Line 122 authors wrote "After Idai, 123 herbivore diets tended to comprise a smaller proportion of grasses". When looking at fig. S13, ~55% of species (reedbuck, waterbuck, buffalo, oribi, elephant, impala) showed a decrease in the RRA of grasses in their diets during late-wet season, with these same species showing a similar pattern across the other two seasons. Can this result be unpacked in regards to species' traits or movement -- why do these species in particular show a greater decline in grass RRA compared to the other species?

In Fig. S12, the years 2016 and 2018 are lumped together under the same ellipses for the early dry season. But, given the variation between 2016 and 2018 in some species' NMDS plots, it is hard to discern whether 2016 and 2018 were treated as different years in the associated statistical models. This particular time period could give authors an idea as to the "natural" turnover of diets between years, but it is hard to determine whether the turnover between these years and 2019 could be considered to be within the "normal" range given the way the data are currently presented.

Smaller comments:

To aid the visualization of results, it could help to order plots from smallest to largest species (e.g. Fig. S12 and S13).

Line 126 to 128: What is the thinking behind why dietary niche differences among herbivore species were stronger in the post-cyclone early dry season compared to normal years?

Author Rebuttals to Initial Comments:

All references cited in this response letter are listed at the bottom of the document. Please note that we were unable to maintain a track-changes version of the manuscript, because we revised iteratively with successive edits from multiple co-authors (including modifications for style and clarity in addition to responses to reviewer comments). We have, however, tried to be thorough and precise in our responses below, citing line numbers in the revision where appropriate.

REFEREE #1 (REMARKS TO THE AUTHOR):

R1.1—The authors used an impressive array of datasets to understand how large mammals respond to extreme climatic events, making use of a rare opportunity. The study is highly novel and extremely thorough in the scope of analyses conducted and the variety of responses tested, including the temporal scale from hours to years following the cyclone. The authors also place their findings within the broader ecological literature and test emerging hypotheses related to animal responses to tropical cyclones. Overall, an impressive and timely study that sheds new light on how we understand animal responses to extreme events. I do, however, have some comments that I hope will be useful to the authors in further strengthening their impressive study.

We appreciate these positive comments and the very constructive and insightful suggestions.

R1.2—The number and variety of animal responses tested is a major strength of the work. However, as would be expected, some of the analyses and conclusions are more convincing than others. One of the most exciting analyses presented is that of the GPS telemetry. However, I also found it to be the least convincing due to the low sample sizes of collared animals, and also because the only real evidence from these data to suggest that smaller animals are more vulnerable than larger ones (the second hypothesis tested) comes from the bushbuck GPS data, for which the authors only had data from eight individuals, and only three of which died in the flood. I think these results are fascinating, but I wonder if they are overemphasized. The authors discuss them first in the manuscript, which makes sense given the increasing scales, but they also highlight them, but not others, when introducing the methods (line 72). The conclusions drawn from this relatively small dataset are, however, reinforced from the other, richer datasets (camera traps, dietary data, aerial censuses), which improves the certitude of the findings. I also understand that it is difficult to collar more animals than this at any one point in time and so I don't think this is a flaw in the study, but I would encourage the authors to consider placing less emphasis on these results, which could be achieved by not only calling out the GPS telemetry methods on line 72, and perhaps adding some statements about the limitations of these data to the study.

We understand this point and have revised the text to better contextualize the scope of inference from our GPS data. In accordance with the reviewer's suggestion, we have (i) removed the clause highlighting GPS telemetry when we introduce our methods (line 77 in the revised manuscript) which was superfluous and, we agree, overemphasized our reliance on GPS data; (ii) clarified that our sample of GPS collared animals was small, but that the results from those data align with other lines of evidence showing that small and floodplain affiliated species were most sensitive to the cyclone (lines 109-112); and (iii) added a statement to the Fig. 1 caption acknowledging the limitations imposed by a relatively small sample of documented mortality events (lines 367-368).

R1.3—I was more convinced by the other analyzes, especially those investigating changes in diet and body condition, although more information is needed about when the body condition measurements were made (see my comment on the Supplementary Material below). I was also mostly convinced by the camera trap and census data, but I wondered about correlations between body mass and floodplain association. There are clear relationships between mortality and body size, and mortality and floodplain association, with smaller species and those associated with the floodplain being more vulnerable to flooding, but almost all small bodied species also showed high levels of association with the floodplain, whereas larger-bodied

species did not (lines 144-148), so how can we disentangle the effects of body size and habitat use (floodplain association), which are the two hypotheses tested? The two best performing models had just one of these two factors in them, but the difference in AIC between the models is small (0.96), and so we can't with confidence consider either one of these models to be better than the other. Some consideration and/or discussion of this point is needed.

We appreciate the prompt to clarify these issues; in light of this comment and **R1.11**, we agree that our original presentation was not sufficiently clear. In fact, there was no correlation between body mass and floodplain association, as reported in Fig. S1 caption: Pearson's correlation test, $r = 0.04$, $df = 37$, $P = 0.80$ (in the original submission, we had mistakenly reported $df = 38$). In that analysis, we quantified the typical degree of floodplain association for each species using data from each of three systematic helicopter surveys spanning 5 years (2014, 2016, 2018) to capture inter-annual variability; each helicopter survey used the same methods to ensure comparability (details and data in Stalmans et al. 2019). We then followed Atkins et al. (2019) in calculating floodplain association as the proportion of individuals per species observed in treeless floodplain habitat (as delineated by Stalmans & Beilfuss 2008) in each survey. Hence, $n = 13 \text{ species} \times 3 \text{ surveys} = 39$ in the original regression. Triple-counting each species in this fashion is arguably pseudo-replication, but we thought that this was the most powerful way to test the lack of any relationship.

However, to harmonize this analysis with the metric of floodplain association reported in other analyses throughout the paper, we now report the correlation between body mass and **mean** floodplain association across all three 'normal' years, which gives an equivalent result ($r = -0.12$, $df = 11$, $P = 0.69$). This lack of correlation is robust to the use of several alternative methods for estimating floodplain association, including: (1) a more liberal definition of floodplain that includes the wooded floodplain-savanna margin (cf. Atkins et al. 2019, Walker et al. 2023; Extended Data Fig. 1b); (2) *log*-transforming body mass; and (3) excluding elephants, with their outlying body mass and intermediate floodplain association (all $|r| < 0.41$, all $P > 0.19$).

We have made several revisions to clarify these issues, which were deep in the supplemental materials of the original submission:

- We explicitly state the null relationship between body mass and floodplain association in the main text, with a callout to Extended Data Fig. 1 (lines 85-86).
- We more clearly specify the analytical procedure used to assess the relationship between body mass and floodplain association in both the methods and the Extended Data Fig. 1 caption (lines 857-861, 989-991).
- We include a synopsis of the methods used to quantify floodplain association in an earlier part of the methods (it was previously described in the penultimate paragraph of the manuscript under "Aerial wildlife surveys" but is now introduced on lines 516-518, which also makes it easier for readers to interpret the use of floodplain association as a predictor variable in our models).
- We have clarified the text previously on lines 144–148 (now lines 167-170) to eliminate the ambiguity that contributed to the reviewer's uncertainty as expressed in this comment.
- We also clarified our approach to quantifying and comparing nutritional condition, which is briefly mentioned in this comment; details are provided in our response to **R1.10**, below.

In response to the final point in this comment about the two univariate models of population trajectory: clarifying the null correlation between body mass and floodplain association should help to make clear that those two variables are not actually confounded, which addresses part of the reviewer's concern. To address the other part, about the similar relative support for the two models, we revised the main text to more precisely convey that the body-mass model does not dramatically

outperform the floodplain-association model ($\Delta AIC_c = 0.96$) despite explaining ~27% more variance ($R^2 = 0.28$ vs. $R^2 = 0.22$) (lines 173-175).

R1.4—The camera trap data are also generally convincing, but it would be helpful to add to the panels in Figure S9 a line denoted when the flood waters receded, and when animals could return to the area marked as “NEAR” (Figure S3 partly provides this information, but having it in Figure S9 will be helpful). Otherwise, I’m left questioning whether animals simply didn’t go there because the area was flooded (or is this in fact the reason they don’t go there?).

Good suggestion; we have amended this figure (now Fig. 2c) to include shaded areas showing the period during which areas that were dry before Idai remained inundated by flooding (March 15—May 31). This analysis shows that floodwaters displaced herbivores away from the lake (evidenced by sharply reduced detections in the ‘NEAR’ bin). Degree of displacement and rate of return varied; for example, impala detections recovered relatively quickly as the flood subsided, whereas warthog and waterbuck detections remained depressed into August, long after flooding had subsided (and coinciding with the rebound of understory productivity in that area; Fig. 3). We have revised the main text (lines 117-122) and the Fig. 2c caption (lines 391-393) accordingly to better contextualize these results.

R1.5—I also wondered about how many of the 30 surviving cameras were in the “NEAR” area? I’d assume that more in this area were damaged than in the other areas. Did this bias the results in any way?

Of the 30 surviving cameras, 8 fell in the “NEAR” bin, 12 in the “MID” bin, and 10 in the “FAR” bin. Thus, differences in camera survival across bins were not dramatic. We limited our analyses to detections from the 30 cameras that survived the cyclone, and discarded all data from cameras that did not, to avoid biasing our results by unbalanced sampling among cameras/years (lines 682-684). Note also that in our statistical models, which are the primary basis for inference, we treated ‘distance to lake’ as a continuous predictor variable (Supplementary Table 1); the categorization of cameras into discrete distance bins was arbitrary and purely to enable graphical presentation of the significant but difficult-to-intuit three-way interaction of cyclone occurrence, time since landfall, and distance to lake. In the original version of these visualizations, we had designated bins based on the entire camera trap grid ($n = 60$) which resulted in unequal numbers of surviving cameras in each bin. To assess whether this approach might bias visualization of the interaction term, we reproduced the graphs with an equal number of surviving cameras per bin ($n = 10$). The outputs are indistinguishable (compare Figs. A and B, below).

We have made the following revisions:

- We now report sample size as the number of surviving cameras when we discuss results from our statistical analyses (line 114), as opposed to the total number of cameras deployed across years, to clarify our approach.
- We have revised the figure (now Fig. 2c) to show the proportion of detections per camera-day based on an equal number of surviving cameras in each distance bin (i.e., Fig. B below); the associated inset maps of camera positions now show only the 30 surviving cameras instead of all 60. This figure also now includes shading to convey the duration of flooding, as per **R1.4**.
- Both in the Fig. 2c caption (lines 385-387) and methods (line 683-699), we clarify that we discretized distance to lake only to help visualize the three-way interactions in our statistical models, and that the statistical models used a continuous distance variable (not susceptible to bias from bin thresholds or sample-size imbalances) and are the primary basis for inference.

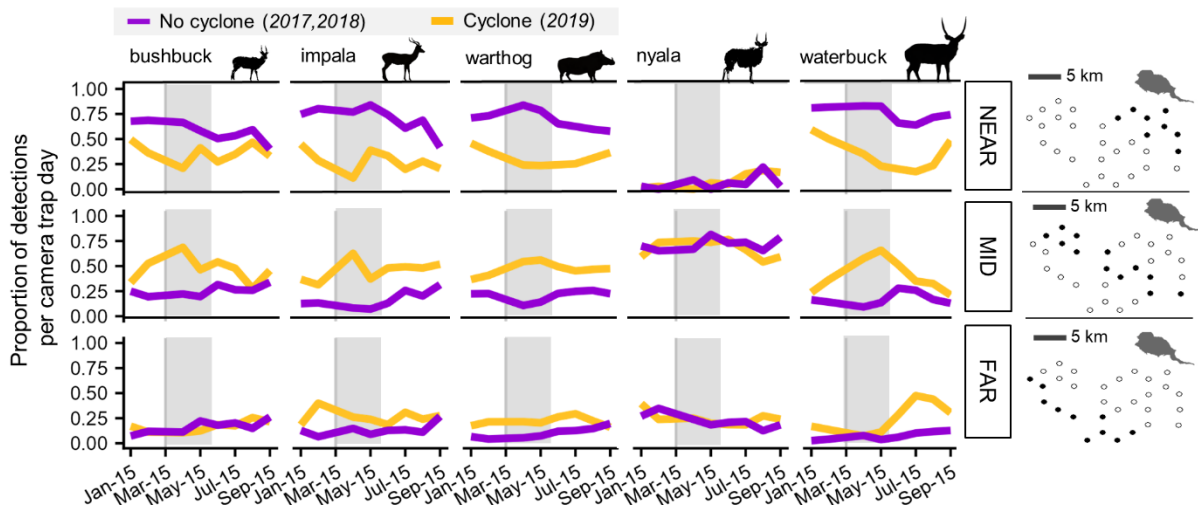


Fig. A. Distributional shifts (original binning). Here, the distance bins used for visualization are as per our original submission, with uneven numbers of surviving cameras per bin ($n = 8–12$). Cf. Fig. B, below.

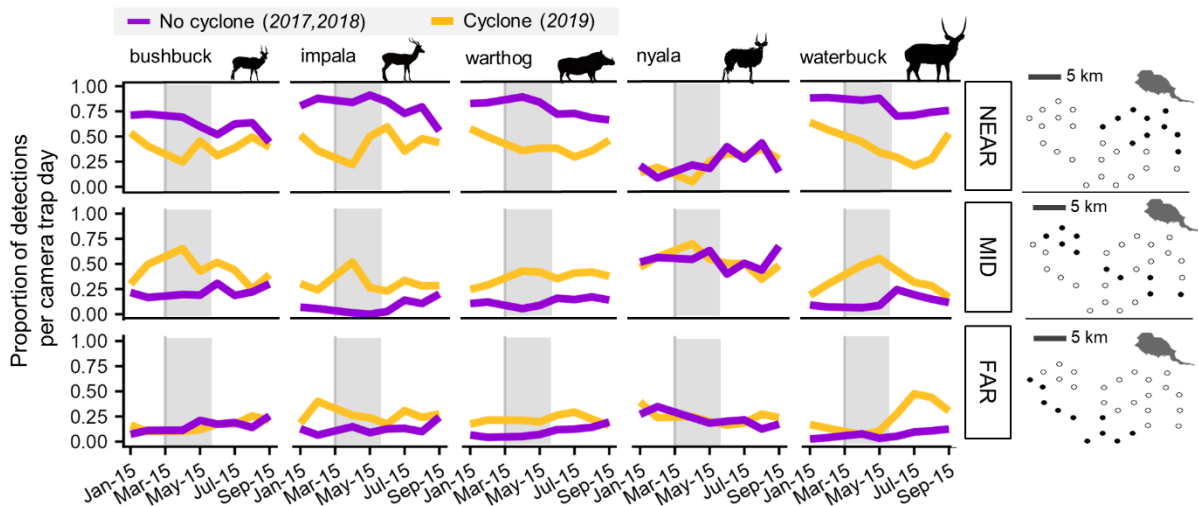


Fig. B. Distributional shifts (revised binning). Here, bin thresholds were assigned to obtain an equal number of cameras ($n = 10$) per bin, which does not detectably alter the visualization (cf. Fig. A). Because bins are used only to aid visualization of 3-way interactions in statistical models (given in Supplementary Table 1), we use this figure in the manuscript to minimize any concerns about uneven sampling (Fig. 2c).

R1.6—Line 109 states that the GPS and camera trap data together indicate that body size was a key determinant of which animals survived the flood, but Figure S9 shows that waterbuck (the largest of the floodplain associated species) and not bushbuck (the smallest), showed the strongest response of moving away from the lake in the camera trap data. Should this statement be revised?

The original statement was “Together, GPS-collar and camera-trap data indicate that body size, mobility, and behavioral flexibility were key for surviving the immediate aftermath of the cyclone.” This was based on our overall finding (based on all data streams) that large body size (~ mobility) and behavioral flexibility are factors enabling individuals to rapidly adjust their habitat use in response to the cyclone. But we agree that Fig. 2c in isolation provides equivocal support for this interpretation, and on reflection, a synoptic sentence is not necessary in this paragraph. We have

removed the sentence and instead finish the paragraph with a more specific description of the results (lines 119-122).

R1.7—Lines 172-176 – Would carnivores also be robust to the cyclone because the quality of their diet not diminish as it did for herbivores? Also, would they benefit from scavenging on the abundance of carcasses? Carnivores generally do better during drought periods for similar reasons (higher mobility and increased prey vulnerability). I find it interesting that their response to the opposite climatic extreme (floods) are similar, perhaps suggesting that carnivores are generally more robust to extreme climatic events than herbivores.

This is a great point, which we briefly alluded to in the previous submission, suggesting that “the abundance of unusually vulnerable and densely concentrated food” was among the factors differentiating herbivore and carnivore responses. In early drafts, we had unpacked this idea in more detail, precisely as suggested in this comment. We have revised accordingly (lines 199-203).

R1.8—Line 179-180 – Again, the issue of collinearity between body size and association with exposed habitats (the floodplain) is difficult to disentangle.

We have revised the text to make clear that body size and floodplain association were not correlated (**R1.3**).

R1.9—SI Line 187 – I think reference 58 is the incorrect one here as it refers to a study system in Namibia, not Gorongosa, please check it.

In fact, this was the intended reference. Tarnita et al. 2017 (ref. ⁷³ in the revision) included data from satellite imagery of *Macrotermes* spp. mounds in Gorongosa (their Fig. 1e,g and Extended Data Figs. 3, 4). The other reference cited in this sentence (Daskin et al. 2022, ref. ³¹) includes complementary data on mound distribution in GNP, based on LiDAR imagery. To avoid confusion, we have moved both references to the end of the sentence (line 617).

R1.10—SI Lines 522-524 – More information about how the body condition scores were recorded is needed. When were animals recaptured for body condition assessments? How long after the flooding was this done? Was it on the same animals as before the flood (to be able to make direct comparisons)? How many animals did the authors have repeat body condition scores for?

We appreciate the prompt to clarify our approach. Since 2014, we have collected a set of 11 individual-level body measurements as part of a long-term study of spiral-horned antelopes in GNP; our PCA-based approach for reducing those 11 measurements into two principal components (PC1 ~ body size, PC2 ~ nutritional condition) follows that described in previous publications (Atkins et al. 2019, Becker et al. 2021, Daskin et al. 2023, Walker et al. 2023) and is presented in Supplementary Tables 5 and 6. Measurements are from randomly sampled animals that were immobilized for GPS collaring in June–July of 2014, 2015, 2016, 2018, and 2019. Our GPS collars are remotely released when they enter low-battery status; we do not recapture individuals, in part to avoid adverse impacts on animals. Thus, our results reflect differences in the population-level distribution of body conditions before vs. after Idai, not change over time in condition of the same individual animals. Our sample size for each species in each year were, respectively: bushbuck, $n = 11, 11, 7, 13, 14$; nyala, $n = 7, 10, 6, 0, 4$; kudu, $n = 12, 9, 0, 18, 12$ (in 2016, we captured only bushbuck). Post-cyclone condition measurements were obtained 3 months after Idai (June 2019), by which time floodwaters had receded to pre-cyclone levels but forage availability was still lower than normal (Figs. 1b, 3 and Extended Data Fig. 2).

We have revised to clarify the nature of our comparisons and the timing of condition measurements relative to cyclone-induced flooding and forage depletion (lines 821-826, 841-843). We also now report sample sizes for each species×period (cyclone/non-cyclone) comparison in the Fig. 4f caption (lines 426-431).

R1.11—Figure S1 - How was floodplain association for each species measured?

We have clarified and elaborated on this point as detailed in response to **R1.3** above.

R1.12—Figure S10 – Will all readers know the identity of the species each silhouette represents?

Good point; this was an inadvertent omission (our other silhouettes are labeled). However, in reformatting the manuscript to meet *Nature*'s requirements (maximum of 10 supplemental display items), we eliminated this supplemental figure. The results visualized in this figure were ultimately redundant with the full quantitative report of camera-trap modeling in Supplementary Table 1, and indeed, we wish to direct readers' attention to the full analysis for reasons noted under **R1.5**.

REFEREE #2 (REMARKS TO THE AUTHOR):

R2.1—Thank you for your submission to Nature. I enjoyed reading your manuscript and found it to be clearly written and well formulated. Your findings highlight the vast importance of collecting long-term monitoring data across a system to evaluate community-level responses. It's an impressive array of data, from GPS telemetry data to assess the movements of recovering animal populations, to camera traps and systematic animal surveys to evaluate population and distribution changes. I found your conclusions to be robust and supported by multiple forms of inference, one of the main strengths of your analysis. I also believe that your observational study will provide valuable information on community assembly, especially as it relates to the importance of ecological disturbance from extreme weather events that are becoming more frequent and more severe.

We appreciate these positive comments about the execution and value of our study.

R2.2—I have provided a few minor comments for you to address. My main comment, however, relates to how you compared shifts in daily home ranges at the onset of the cyclone. Kernel density estimates (KDEs) are known to be especially sensitive to small sample sizes and the amount of autocorrelation that exists (see Noonan et al. 2019 - A comprehensive analysis of autocorrelation and bias in home range estimation), which is impacted by the biology of the animal and the temporal interval of data collection. Spatial overlap also tends to be smaller when samples sizes are low, which makes me question if you are observing a true response to the cyclone or simply an artifact of the data and the analysis method being chosen. A few thoughts:

We have now verified that using autocorrelated kernel density estimation (AKDE) produces qualitatively equivalent results that are robust to the temporal partitioning of our data, demonstrating a clear response to the cyclone. We provide a more detailed description of our additional analyses below.

R2.3—1) Can you justify why KDEs are appropriate in this case and why you have not considered frameworks (e.g., continuous time movement modeling) which incorporate the autocorrelation structure inherent in the data?

Our goal for this analysis was to test whether cyclone-induced flooding prompted a greater shift in space use than would be expected under typical conditions. We thus compared animals' displacement before vs. after Cyclone Idai with that observed over periods with no cyclone. We quantified displacement in two ways: (1) distance between the centroid of movements, and (2) proportional overlap of utilization distributions estimated via 95% fixed KDEs (Daskin et al. 2023). We appreciate that KDEs can yield negatively biased home-range estimates (Noonan et al 2019), but we do not expect this to bias our results because we used the same durations and sampling intensities to estimate individuals' ranges in both cyclone-impacted and typical periods.

However, we agree that accounting for the autocorrelation inherent in telemetry data produces more robust range estimates and can facilitate comparisons among species (Mueller et al. 2015). Thus, in the revision we use AKDEs conditioned upon the best-fitting continuous-time movement model to estimate utilization distributions (Fleming et al. 2016). For each partitioned GPS dataset (i.e., each before/after, cyclone/non-cyclone interval per individual), we identified the continuous-time movement model (Brownian motion, Orstein-Uhlenbeck process, or Orstein-Uhlenbeck foraging process) that best fit the data using AICc-based model selection (Mueller et al. 2015, Flemming et al. 2016). We then used this model, fit with the *fit_ctmm* function, to calculate the used range via 95% AKDE with the *hr_adke* function in the *amt* package in R (Singer et al. 2019). We have updated the discussion of our results (lines 107-109), methods (lines 650-665), and figures (Figs. 2b, 6b and Extended Data Fig. 6) to reflect this approach. Results and conclusions derived from AKDE do not qualitatively differ from those from derived from our previous KDE approach.

R2.4—2) Can you extend the period of time in which you make comparisons? Rather than only comparing to the previous month, could you sample from multiple different time periods? I don't know the biology of all of these animals, but how stationary is a bushbuck home range over time? Do these dispersal events rarely occur, or is variability in dispersal common between individuals? Essentially, I am looking for further support that the changes in distribution are true effects and not just a result of the time period chosen.

These are good questions, and we have addressed them with a series of additional analyses. To evaluate whether duration of the 'before' interval influenced the inferred change in distribution, we calculated the proportional overlap of ranges estimated via AKDE in each week after the cyclone made landfall with ranges during the week, month, two months, and three months before the cyclone (yellow lines in *Fig. C*, below). We used bushbuck as an exemplary species in these validation analyses because (1) they are the GPS-collared species that exhibited the most significant displacement after the cyclone (i.e., had the greatest potential for a Type 1 error stemming from non-cyclone-related variation in movements as mentioned by the reviewer), and (2) we had more years of GPS data for bushbuck than for any other species, which allowed us to characterize 'typical' movement behavior more thoroughly for bushbuck.

We first compared displacement after the cyclone to that observed among the same individuals ($n = 8$) earlier in 2019 (i.e., intervals before/after Feb.1st; *Fig. C, panel a*, purple lines). We then compared post-cyclone displacement of bushbuck to that observed in the same periods around March 15th in two non-cyclone years for which we had GPS data (*Fig. C, panel b*, purple lines; 2015, $n = 4$; 2020, $n = 8$). (Note, sample sizes of bushbuck for this analysis differ from those reported in **R1.10** because many collar batteries do not last from June/July until Feb/March of the following year.) In sum, we find that marked displacement of bushbuck after the cyclone was robust to duration of the 'before' time interval (1 week to 3 months) and to the baseline period used to define 'typical' behavior (earlier in 2019 vs. same time of year in 2015 and 2020) (Welch's two sample t-test: $t > -3.2$, $P < 0.02$ for all comparisons). We believe that the robustness of these relationships is likely consistent among other GPS-collared species for which we have less extensive baseline data. Additional analyses conducted in response to **R2.5** below support this

view: observed displacement of the 5 GPS-collared herbivore species was robust to whether post-cyclone movement was compared to ranges in the week or the month before Idai made landfall (see R2.5). Although space limitations prevent us including Fig. C in the manuscript, we have included a description of this validation analysis in our revised methods (lines 665-670).

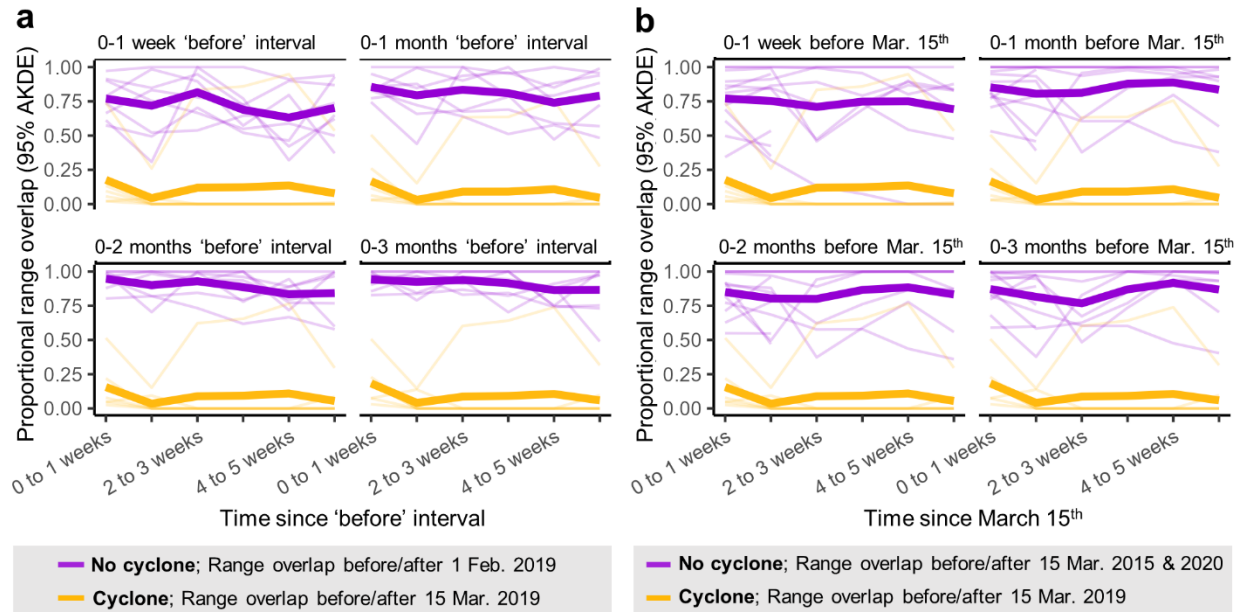


Fig. C. Inference about bushbuck home-range displacement is robust to how the ‘baseline’ is specified. (a) Immediately before Cyclone Idai, bushbuck ($n = 8$) exhibited high site fidelity; purple lines show overlap in range occupied before vs. after 1 February 2019 (thin lines, individuals; thick lines, average). After the cyclone, the same individuals ($n = 8$) vacated their prior ranges; yellow lines show range overlap before vs. after landfall on 15 March 2019. This conclusion holds regardless of whether prior range was estimated using 1 week (top left), 1 month (top right), 2 months (bottom left), or 3 months (bottom right) of GPS data. (b) Similarly, displacement before vs. after March 15 was far greater in 2019 (yellow, $n = 8$) than in years with no cyclone (purple; 2015, $n = 4$; 2020, $n = 8$), again regardless of the duration of the baseline interval.

R2.5—3) It's unclear from the supplementary materials if the same time periods were compared. You write "We partitioned each individual's GPS locations into temporal bins that spanned (i) the month before the cyclone.... and (ii) 6 weekly bins after the onset of flooding.". My concerns is the comparison of the different temporal intervals, with the pre-cyclone period representing a full month of data, which is then compared to weekly data. Is this correct or am I misunderstanding how the pre-cyclone data were partitioned? Seems graphically that this was separated into weekly bins, but this is not clear in the text. Otherwise, there would be more variance among the weekly centroids than the monthly centroids. Please clarify.

This interpretation is correct: we compared 6 weekly ‘after’ intervals to a month-long ‘before’ interval during both cyclone and non-cyclone periods. We also had defined the non-cyclone period differently among study species depending on availability of GPS data. For bushbuck, nyala, and kudu, we compared movement intervals before/after 15 March in two non-cyclone years (2015, 2020). For sable, elephant, wild dog, and lion, we compared intervals before/after 1 Feb. 2019 because those were the only GPS data available for those species.

We re-analyzed our data in light of this comment; as predicted by the reviewer, variance of our two response variables (proportional overlap and distance to prior range centroid) was marginally higher when we used a ‘week-to-week’ before/after comparison (proportional overlap: mean = 0.49, sd = 0.36; distance to centroid: mean = 3.52, sd = 5.51) than when we used a ‘month-to-week’

before/after comparison (proportional overlap: mean = 0.60, sd = 0.34; distance to centroid: mean = 3.69, sd = 5.09). Nevertheless, limiting our ‘before’ interval to a single week and changing the non-cyclone period to be consistent among species (before/after 1 Feb 2019) produced results consistent with those derived from our previous approach, underscoring the robustness of our inferences to choices about how to bin the data (see also **R2.4** and *Fig. C* for results of comparisons with additional ‘before’ period durations for bushbuck).

We agree that our original presentation of these results was unclear, and that our original analysis made distributional shifts less directly comparable among species than they could have been. We have therefore revised our methodology to define a consistent ‘non-cyclone’ period (before/after 1 Feb. 2019) among all species for which GPS data were available, and to compare 6 weekly ‘after’ intervals to a week-long ‘before’ interval during both the cyclone and non-cyclone periods (lines 650-670; *Fig. 2b, 6b* and *Extended Data Figs. 5-6*).

R2.6—4) Would it be possible to broaden your analysis to a longer time period of movements and include a continuous predictor (such as the intensity of different storms or rain events)? This would be statistically ‘safer’ than a one-off treatment (i.e., one big storm), especially since all of the biases and variances are not being accounted for. It would potentially show in a more robust fashion how movements were impacted by average to extreme rain events.

As noted in our responses to **R2.4** and **R2.5**, our inferences about animal movement are robust to several feasible alternative approaches, including using longer time periods to define ‘typical’ behaviors. Treating weather as a continuous variable is an interesting idea but not something we are able to do with the available data. Extreme weather events are, by definition, both uncommon and unpredictable, which is what makes the data in our study unique and valuable. Cyclone Idai was the most destructive storm on record in the Southwest Indian Ocean Basin and possibly the deadliest ever in the southern hemisphere (cf. 1892 Mauritius and 1973 Flores cyclones). 688 mm of rain fell in March 2019—more than the *annual* totals for 2011, 2012, 2015, 2016, and 2017, and fivefold more than a median wet-season month (*Extended Data Fig. 2*)—making 2019 by far the wettest year recorded in GNP (1874 mm, vs. median 877 mm and maximum 1479 mm since 1957).

Treating rainfall as a continuous variable is further complicated by nonlinearities in the expected wildlife response. In GNP, a predictable cycle of annual flooding governs spatiotemporal patterns of productivity and animal movements (Tinley 1977, Böhme et al. 2006). Low rainfall and flooding limits food availability for herbivores, and here we show that extreme deluges do the same. Thus, a >99th percentile event such as Idai can have qualitatively different effects from heavy but non-extreme rains. ‘Typical’ years in our study included both wetter than average (2018) and drier than average (2015-2016) periods, roughly bracketing the interquartile range of long-term annual rainfall, but contrasts in our study show that herbivore responses in these years were generally more similar to each other than any was to 2019 (e.g., *Figs. 4, 5* and *Extended Data Figs. 8–10*)—indeed, if anything, herbivore behavior after Idai was sometimes more similar to dry baseline years than to wet ones (e.g., *Fig. 4f* for bushbuck, *Extended Data Fig. 8* for waterbuck and buffalo).

For these reasons, we consider it most appropriate to treat Cyclone Idai as a categorical event. Although we acknowledge the limitations inherent in evaluating a one-off treatment, our study goes to unprecedented lengths in parsing the impacts of this extreme event on wildlife across scales and levels of organization (and is now even more rigorous thanks to reviewer feedback). As we discuss in response to **R3.1**, our study does ‘control’ to some extent for animals’ experience with disturbance: because GNP floods annually, we are able to isolate the impacts of an extreme and unseasonal event in a system conditioned by more predictable flooding. Last, while no events of similar magnitude to Idai have affected GNP in recent decades, such events are not uncommon at

regional to global scales, making it important to understand their impacts (Pruitt et al. 2019, Lin et al. 2020). As a case in point, just last month, Cyclone Freddy—the longest-lasting and highest-energy tropical cyclone ever recorded worldwide—hit Mozambique, passing both to the north and south of GNP. Evaluating continuous relationships between storm intensity and ecological impacts is an important goal that has been highlighted in recent calls for research on cyclone ecology (Pruitt et al. 2019, Lin et al. 2020), and we echo this call in our revision (lines 230-233).

R2.7—I appreciate the opportunity to review your manuscript and hope these comments are useful in improving the content of your manuscript.

Indeed they are very useful, and we appreciate the thoughtful and insightful feedback.

R2.8—Fig. 1e - Marked Fig. 1e on line 90. Not marked in Figure (Only A-D marked).

We have corrected this callout to Fig. 1d (line 99).

R2.9—Fig. 1d - Could you show where this area of interest is on Fig. 1c? A simple rectangle would suffice.

We have included rectangles in Fig. 1c denoting the area of interest, and we have added roads to Fig. 1d to facilitate spatial comparison between the panels.

R2.10—Fig. 2 - "All herbivores increased their selection for higher elevations and their avoidance of floodwaters, significantly so for bushbuck, kudu, and elephant." For 'elevation', yes, although the confidence intervals for elephant seem to overlap. For 'flood edge', however, the SSF coefficients for bushbuck don't represent a significant difference.

This is a fair point. The 95% confidence interval for selection of elevation by elephants before the cyclone is 0.9 – 1.1 and after the cyclone is 1.1 – 1.3, making the statistical significance marginal. We have revised the text for greater precision to reflect the non-significant increase in bushbuck avoidance of the flood edge and for greater precision in our interpretation of elephant selection for elevation (line 377-379).

R2.11—SI Line 184: Since you use step selection functions following instructions by Muff et al., I presume you included individual random effects. Please specify this information in the supplementary materials.

Correct, we did include per-individual random effects in our conditional logistic regressions and should have said so. We have included this information in our revised methods (line 636).

R2.12—SI Line 193: The temporal interval of the GPS tracking device was different for each species (1-hr intervals for bushbuck, nyala, kudu, elephant; 3-hr intervals for lion and wild dog; 8-hr intervals for sable). Can you discuss how these different temporal intervals may impact your findings and/or comparability between species?

Indeed, sampling intensity can affect estimates of home-range size (Swihart & Slade 1985, Silva et al. 2022) and patterns inferred from step selection functions (SSFs), depending on the temporal and spatial scale of the analysis (Thurgjell et al. 2014). However, our inferences about cyclone impact on movement behavior were all based on *within-species* comparisons of movements after Idai vs. in typical periods. Nevertheless, to ensure that our findings are robust to sampling interval, we ran an additional analysis in which we rarified all herbivore GPS data to an 8-hour fix rate (the least intensive regime) and re-fit SSFs to quantify herbivore selection for elevation, termite mounds, and flood edge in the two weeks before and after Idai using the procedure described on lines 611-637.

Results were largely consistent between methods; only the statistical significance (nonoverlapping CIs of before vs. after periods) of selection for elevation by elephant and nyala, and for flood edge by elephant, differed between the full and rarified datasets (Fig. D). We have retained the original analysis but now clarify in the Methods (lines 639-641) that differences in fix rate do not affect validity of our within-species analyses but do limit direct comparability among species.

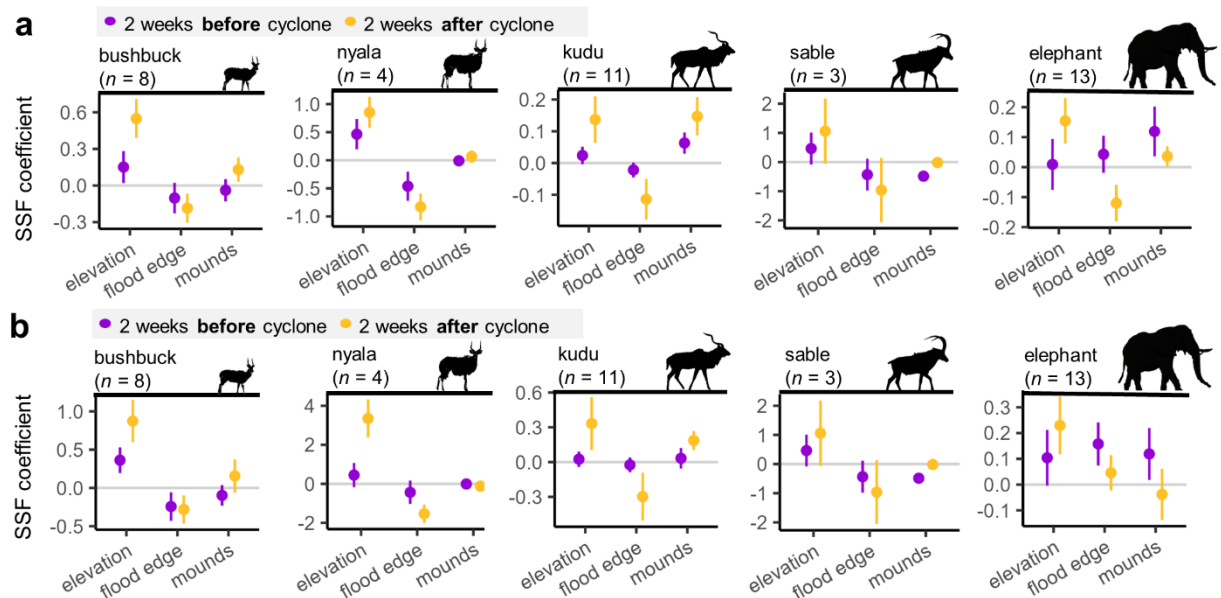


Fig. D. Coefficients and 95% CIs from step-selection functions (SSFs) are largely robust to sampling intensity. (a) Results from SSFs fit to hourly relocation data for bushbuck, nyala, kudu, elephant, and to 8-hr location data for sable, as presented in our original submission (revision Fig. 2a). **(b)** Results from SSFs fit to location data rarified to 8-hr intervals for all 5 herbivore species. The direction of change in movement patterns before vs. after cyclone is consistent between approaches. Statistical significance (nonoverlapping CIs between before/after periods) was also largely consistent, with three exceptions described above.

R2.13—SI Line 397: Make sure to add doi.

We have specified that we will add the doi for this database when the article is accepted (line 745).

R2.14—Fig. S19 - "African wild dogs and lions increased their.....avoidance of flood waters after Idai". This is true for lion, but not wild dog based on the graph of coefficient estimates (perhaps marginally?). Seems no change to termite mounds and flood edge, although (as stated) a non-significant increase in elevation.

This is correct, and we have revised our presentation of this result accordingly (lines 188-189, 447-450).

R2.15—Fig. S17 - Agree that lions are difficult to count and are underestimated. Also agree that this is a reliable index across years. But, I would say that "all" counts are underestimated, as undercounting bias is documented by multiple researchers, irrelevant of the species. A good example is the work conducted by Lamprey et al. comparing undercounting bias of rear-seat observers in wildlife surveys conducted in Kenya. Multiple other examples exist, including results from distance-based surveys. Like you say, a reliable index, but I recommend a slight edit/clarification to the text.

We completely agree. We have revised the wording on lines 1116-1124 (Extended Data Figure 10 caption) to retain the qualification about lions while also (1) explicitly noting that all count data are underestimates of true population sizes and should be viewed as minima and (2) emphasizing our reasons for confidence in the general reliability of these surveys (which include use of a helicopter with doors removed rather than fixed-wing aircraft, a data recorder/observer in the front seat, and 2 experienced observers on both sides of the aircraft in the rear seats, circling and/or photographing groups for more accurate counts when necessary, and surveying during the late dry season when tree canopy cover is lowest; Stalmans et al. 2019).

R2.16—Line 239: 'fig. 19b' should be 'fig. S19b'.

Good catch—we have moved this figure to the Main Text as Figure 6b.

REFeree #3 (REMARKS TO THE AUTHOR):

R3.1—This is an extraordinarily well documented account of the impacts of Cyclone Idai on the larger herbivore of Gorongosa. I wish, though, that the findings were less obvious. It is completely intuitive that animals would seek higher ground and that less mobile species would suffer more than larger species (the old density-independent vs density-dependent dichotomy in life-history theory between small-bodied animals and large animals). While I completely agree with the authors in the need to document the impacts of rare events, the question is whether every well-documented perturbation merits publication in *Nature*. As well studied as this may be, it feels like an anecdote rather than an investigation into the general problem of when, say, extreme floods may or may not have larger impacts. For example, the Okavango swamps flood every year, animals routinely seek higher ground -- but do they show adaptations to these annual perturbations that the Gorongosa populations lacked? Hurricanes in the Caribbean influenced the morphology of island anoles; has the selective event in Gorongosa led to increased body size in bushbuck? As the authors imply, the ramifications of the Idai event will likely reverberate through this system for years -- something less obvious may yet emerge. For the moment, I think this paper fully merits consideration for *Nature Ecology and Evolution*.

We are pleased with the Reviewer's generally favorable reaction to our study and the positive comments about the rigor and quality of the research. We also very much appreciate the skeptical comments about the 'surprise quotient' and the opportunity to clarify the nature and value of the advances in our paper. Although surprisingness is a subjective quality that readers will perceive differently (we are often impressed at how findings considered mundane by some readers are viewed as astonishing or controversial by others), the reviewer's feedback has helped us to articulate the significance of our work more clearly in the revision. We agree that our findings do not totally defy intuition, but that is different from being obvious. We also believe that the value of a contribution is measured along multiple axes, of which surprisingness is just one (and not the most important). For example, evolution by natural selection is completely intuitive, to an extent that there is an entire literature debating whether or not it is a tautology (e.g., Peters 1976, Bethel 1976, Gould 1976, Maddox 1991, Heller 1991, Weale 1991, Hunt 2014), yet its discovery was ground-breaking and there is (rightly) continuing interest in documenting its manifestations and understanding how it works (e.g., Exposito-Alonso et al. 2019, Groen et al. 2020, Campbell-Staton et al. 2021, Monroe et al. 2022, Klunk et al. 2022). In a related vein, the comment asks whether selection by Cyclone Idai has increased body size in bushbuck; we do not know, and it is worth investigating, but we do not immediately see why this result would be less intuitive than those presented in this study (indeed, the reviewer has already intuited it!). Below, we briefly expand on these arguments in relation to our study before detailing the revisions that we have made to address the reviewer's concern.

First, as to whether our results are surprising: We documented strong impacts of a cyclone on large mammals across levels of organization from individuals to the community, and across timescales from hours to years. We find support for a suite of specific mechanisms that link these scales: population-level effects reflect individual-level outcomes including direct mortality and displacement from flooding, along with food scarcity that prompted dietary shifts and changes in nutritional condition. Variation in these impacts was associated with body size and habitat affiliation, and also with trophic level (as noted in **R1.7**), which in turn predicted community-level change. Regulation of these impacts by body size extends the findings of what is to our knowledge the only other community-level study of cyclone impacts on animals—from a radically different system (lizards and spiders on 500-m² Bahamian islands that are fully inundated during cyclones; Spiller et al. 1998)—from islands to a continental ecosystem, across oceanic basins, and across nearly the full size spectrum of terrestrial animals (9 orders of magnitude from spiders to elephants).

We actually do not think any of these results is obvious a priori. It is obvious that seeking high ground in a flood should be adaptive, but we also show how some individuals were unable to do that (Fig. 1). Indeed, for most of our results, both the null hypothesis and one or more alternative hypotheses are highly plausible. Animals the size of ungulates and large carnivores might *all* be large and mobile enough to withstand the short-term effects of a cyclone, leading to null results. Mid-term effects mediated by forage might have been strongest for *larger* (rather than smaller) species, owing to their larger absolute requirements; in fact, recent studies make opposing predictions about whether large-bodied herbivores are more (Veldhuis et al. 2019) or less sensitive (Abraham et al. 2019) to climatic perturbations of forage. Alternatively, impacts might have been determined primarily by diet type and greatest among grazers, owing to disproportionate reduction of grass availability (cf. Abraham et al. 2019), yet diet type had negligible explanatory power in models of population trajectory (Supplementary Table 2). And even assuming some detectable effect of the cyclone at some level of organization, one can envision that the impacts might not have been appreciably associated with any of the predictors we tested. That they were, that we are able to trace connections across levels of organization to such an extent that it struck the reviewer as unsurprising, *and* that our inferences about body size and mobility harmonize with studies of Bahamian anoles, all seem to us highly noteworthy for a field that has long anguished over its inability to scale up, generalize, and predict (Lawton 1999).

In revisiting the manuscript in light of this comment, we saw that the presentation made the results seem rather cut and dried, which may have contributed to the reviewer's impression. In particular, our hypotheses as presented in the original submission did not reflect the fullness of our thinking heading into data analysis, or the plausible alternative hypotheses that we mention above. In our effort to economize, we also gave short shrift to both (1) the extent to which our study addresses key knowledge gaps that have been explicitly identified in prominent recent reviews on cyclone ecology and (2) the implications of our work for both the development of general theory and management interventions (discussed in the remainder of this response). In our revision, we have rectified these omissions (lines 51-65, 158-161, 199-203, 204-206, 215-219, 235-242).

Second, as to the value of advances in our study: The reviewer wonders whether “every well documented perturbation merits publication in *Nature*”. We suspect not (but defer to *Nature*'s editors), but we are also unsure what other studies the reviewer is referring to (perhaps the high-profile Caribbean anole studies, but most of that work is ~20 years old, and we are unaware of any parallel). We also stress that Cyclone Idai was not just a run-of-the-mill perturbation. Idai ranks at the top of many tragic lists—the deadliest storm on record in Africa and the Southwest Indian Ocean Basin (SWIO) and probably in the entire southern hemisphere (1,590 confirmed fatalities and >2260 missing; cf. 1973 Flores Cyclone), and also the most destructive storm on record in the

SWIO (\$3.3 billion damage). Given the increasing size and intensity of tropical cyclones (Lin et al. 2020), increasing frequency of landfalls with major intensity (Wang & Toumi 2022), increasing geographic range of cyclone occurrence (Pillay & Fitchett 2019) globally and in SWIO, it is crucial to understand the impacts of current outliers that could become the future norm (see **R2.6**).

The reviewer's question about Okavango is interesting but further underscores the importance of studying extreme events. Gorongosa—just like Okavango, Sudd, Kafue Flats, and several other globally important biodiversity strongholds in southern Africa—is governed by a predictable cycle of annual flooding that regulates spatiotemporal patterns of primary productivity and animal movements (Tinley 1977, Böhme et al. 2006). Accordingly, our study ‘controls’ for experience with/naïveté to flooding and shows that even communities in regularly flooded ecosystems are vulnerable to extreme flood events. This highlights the distinction between predictable, cyclical disturbances and the unpredictability of cyclone-induced disturbance (e.g., Palmer et al. 2022 on the influences of cyclical vs. irregular events on animal behavior). Indeed, it seems plausible that animals entrained by rhythmic disturbances of moderate intensity might be especially vulnerable to unpredictable, unseasonal extreme events—a possibility we now mention in the revision (lines 75-76, 211-215).

Last, we think that this comment implicitly underestimates (1) the novelty and scientific value of mechanistically understanding the impacts of cyclones across timescales and levels of biological organization and (2) the novelty, significance, and public interest of doing that for an assemblage of the world's largest terrestrial animals. While we appreciate the reviewer's compliments on the quality of our research, we have a hard time swallowing the suggestion that it “feels like an anecdote”. We would instead call it an extremely thorough effort not just to record a flashy set of outcomes in support of an hypothesis, but to actually *understand* how those outcomes emerged as the integrative product of processes operating at multiple scales. The reviewer seems to suggest that a comparative or macro-ecological approach would be more enlightening. Comparative and macro-scale analyses are indeed useful for detecting general patterns, but they are famously unable to reveal mechanisms, and mechanistic insight is essential for predictive power, developing general theory, and guiding interventions to assist species imperiled by global change.

Recent reviews on the hot topic of cyclone ecology have emphasized the logistical hurdles of building this knowledge base in even the most tractable study systems and have highlighted the resulting knowledge gaps. Among these are two papers in *Trends in Ecology & Evolution*:

- Pruitt et al. 2019 called for creation of a global consortium for tropical cyclone ecology to address “patchy geographic and taxonomic coverage (e.g., few animal studies)”, the “underrepresentation of key tiers of analysis (e.g., population and community ecology),” and “a lack of parallelism” across studies that “together weaken our ability to transcend the stigma of anecdote and to identify global patterns and rules.”
- Lin et al. 2020 noted that “cyclone ecology is biased towards the North Atlantic Basin” (14% of cyclones, 67% of published studies) and that this distorts understanding given that cyclone impacts differ both quantitatively and qualitatively across basins. Lin et al. also note that prior studies “do not explicitly address the role of ecological scale”; underscore the difficulty of linking across timescales; emphasize the importance of “looking at the impacts of cyclones with an emphasis on the linkages between and within levels of biological organization”; stress the need to identify predictors of resistance and resilience; suggest that “measurements should be taken shortly before and after a storm to limit the influence of other confounding factors”; note the extreme difficulty of doing all this; and conclude that “highlighting the links among scale-dependent processes in a cause-effect manner will improve mechanistic understanding of how cyclones alter ecosystems.”

Our study explicitly addresses all of the gaps and recommendations listed in these excerpts. We address scalability of cyclone impacts across scales of time, levels of organization, and variation in body size, and we identify trait-based correlates of species' robustness. The suite of mechanisms linking these scales not only yields a cogent mechanistic understanding of how this community responded to Cyclone Idai but also reveals parallels with patterns previously documented only in Caribbean anoles (Spiller et al. 1998). Although these two studies do not constitute a rule, our findings add considerable weight to Schoener and Spiller's (2006) suggestion that body size and mobility could form the basis of "a general theory of how climatic catastrophes affect ecological communities". We track how "effects of cyclones at the community [level] are mediated by the effects at the individual and species levels" (Lin et al. 2020) — to our knowledge, the first time that this has ever been done in any study of cyclone impacts on animals.

We believe that all of these features contribute to making our study exceptional. That we also focus on environmental drivers (extreme climate events) and taxa (large herbivores and carnivores) of inordinate contemporary interest in the context of global change should stimulate the interest of a broad readership of scientists from multiple disciplines, as well as the public and policymakers. By identifying correlates of vulnerability/robustness to extreme climate events in a disproportionately threatened fauna (Ripple et al. 2014, 2015), we lay groundwork for development of management plans to mitigate impacts on populations/species of concern. The translatability of our findings into a management context is not far-fetched given sophisticated monitoring and forecasting of major storms; plausible interventions might include driving at-risk animals away from at-risk locations using occupied or unoccupied aerial vehicles (as is done for mass game captures, Laubscher et al. 2015, Meagher 1989, Brinkman & Garcelon 2020) and/or providing supplemental food to help sensitive species withstand perturbations (Walker et al. 1987, Milner et al. 2014).

In summary, we have addressed the reviewer's concern in the revision in the following ways:

- (1) Contextualizing our results with alternative hypotheses (lines 55-60, 158-161, 201-203)
- (2) Emphasizing the novelty and value of our research, explicitly in light of key knowledge gaps identified by Lin et al. and Pruitt et al. (lines 61-65, 205-207, 215-219).
- (3) Elaborating slightly on the implications of our study for general size-based theory and management relevance (lines 235-242).

REFeree #4 (REMARKS TO THE AUTHOR):

R4.1—Walker et al., use spatial data and DNA metabarcoding to determine the effects of a severe climatic event on the large mammals of Gorongosa in Mozambique. This interesting study combines many techniques to better understand the potential effects and repercussions of such events that are only predicted to become worse and more frequent over time. Authors found that animals showed strong spatial responses, dietary responses, and numerical declines. In order to better conserve fragile ecosystems such as those in Gorongosa, information such as this is vital. I will state early on that I was asked to review the DNA metabarcoding portion of this manuscript, so this is where the majority of my comments center. I thought the manuscript was interesting, well written, and of broad interest. However, I have several comments regarding analyses and results which I think would strengthen the paper overall.

We appreciate these positive comments and the reviewer's insightful suggestions.

R4.2—The authors make two main predictions: i) species in woody, higher elevation habitats are likely to be more robust to cyclone Idai and ii) species robustness should be positively correlated to body size based on mobility and lower mass-specific metabolic rates. While I think these predictions are largely supported by the use of the spatial data, I think the authors could make better use of the DNA metabarcoding data to

further support the second prediction; looking at the effect size of the cyclone on various dietary metrics may allow you to determine whether larger bodied animals are in fact more robust to such events in regards to diet as well as movement. For instance: Fig. S14. If you unpack this figure, what would the effect size be for each species? We know dietary richness is likely determined by body size, but is the effect of the cyclone greater for larger or smaller species, or is there no difference given species' size? The same could be considered when thinking about dietary turnover, is turnover between pre- and post-cyclone greater for smaller or larger species?

These are excellent points. First, a tangential clarification: While it is intuitive that dietary richness should be an increasing function of body size, we have consistently failed to find any correlation between richness and body mass in ungulates; this null result has emerged in DNA metabarcoding studies both with (Pansu et al. 2022) and without (Kartzinel & Pringle 2020) a 1% RRA threshold (see **R4.3**), as well as in a global synthesis of herbivore and carnivore diets using a variety of methods (Hutchinson et al. 2022).

As for the main substance of this comment: We originally analyzed dietary protein content for spiral-horned antelopes (*Tragelaphus* spp.; Fig. 4f), showing that cyclone-driven shifts in diet quality were strongest and most consistently negative for the smallest species (bushbuck) and weakest/inconsistent for the largest (kudu). This analysis of 3 congeneric browsers is elegant because it controls for 'noise' resulting from variation in phylogenetically structured traits (Daskin et al. 2023; see also **R4.4**), but it is also limited, and we agree with the reviewer that it would be ideal to conduct a broader analysis of cyclone impacts on herbivore diet.

Accordingly, we analyzed the role of body size and floodplain affiliation in mediating cyclone impacts on a set of selected dietary variables that together encompass a wide range of functional implications: between-season dietary dissimilarity within species (i.e., turnover), plant family richness (i.e., dietary diversity), and mean digestibility (an integrative metric of quality that affects animals' ability to extract nutrients from plants). Statistical methods and results are summarized in the table below.

We found that small and/or floodplain-affiliated species exhibiting higher turnover, greater increases in diet breadth, and greater reductions in dietary digestibility. Despite variability in the seasonal manifestation of these effects (for which we can only offer ad hoc explanations), all significant effects were in the same direction and are broadly consistent with our larger findings that body size and floodplain affiliation influenced species' vulnerability to the cyclone. We discuss these results on lines 146–149 and have included the table as Supplementary Table 2.

Supplementary Table 2. Summary of cyclone-trait interactions for dietary metrics. For dietary dissimilarity (turnover, top row), we report results (coefficient $\pm$ s.e., *P*-value) of linear models containing the focal trait (body mass and habitat affiliation) as the only predictor; the response variable was each species' Z-score of dietary dissimilarity between the periods immediately preceding (November 2018) and following (April 2019) Cyclone Idai compared with that observed between seasons in non-cyclone years (as in Fig. 4a). For the other two metrics (family-level dietary richness, dietary digestibility), we report the cyclone $\times$ trait interaction from generalized linear mixed models containing fixed effects of year, focal trait, and their interaction, as well as per-species random intercepts. Models of dietary richness used a Poisson error distribution, models for digestibility used a Gaussian model and logit-transformed digestibility. Models for the early-dry season contained interaction terms for both of the non-cyclone years for which data were available (2016 and 2018).

Response	Season	Cyclone $\times$ Body mass	Cyclone $\times$ Habitat affiliation	Summary of cyclone impact
Dietary dissimilarity between seasons (turnover)	N/A	$\beta = -0.22 \pm 0.12$ <i>P</i> = 0.07	$\beta = 2.18 \pm 0.52$ <i>P</i> < 0.001	Higher turnover before vs. after cyclone (relative to normal inter-season variation) in floodplain-affiliated and small-bodied species
Family-level dietary richness	Late wet (Mar.–Apr.)	$\beta = 0.02 \pm 0.03$ <i>P</i> = 0.44	$\beta = -0.64 \pm 0.18$ <i>P</i> < 0.001	Cyclone increased dietary richness to a greater extent in floodplain-affiliated species relative to 2018
Family-level dietary richness	Early-dry (Jun.–Jul.)	$\beta = 0.01 \pm 0.03$ <i>P</i> = 0.59 (2016) $\beta = 0.01 \pm 0.03$ <i>P</i> = 0.66 (2018)	$\beta = -0.17 \pm 0.18$ <i>P</i> = 0.34 (2016) $\beta = -0.37 \pm 0.17$ <i>P</i> = 0.03 (2018)	Cyclone increased dietary richness to a greater extent in floodplain-affiliated species; this trend was qualitatively similar relative to both normal years, but stronger in 2018
Family-level dietary richness	Late dry (Oct.–Nov.)	$\beta = 0.07 \pm 0.03$ <i>P</i> = 0.006	$\beta = -0.29 \pm 0.2$ <i>P</i> = 0.15	Cyclone increased dietary richness to a greater extent in small-bodied species relative to 2018
Dietary digestibility	Late wet (Mar.–Apr.)	$\beta = -0.02 \pm 0.01$ <i>P</i> = 0.26	$\beta = -0.13 \pm 0.08$ <i>P</i> = 0.10	N/A
Dietary digestibility	Early dry (Jun.–Jul.)	$\beta = 0.002 \pm 0.02$ <i>P</i> = 0.89 (2016) $\beta = -0.01 \pm 0.01$ <i>P</i> = 0.55 (2018)	$\beta = 0.07 \pm 0.09$ <i>P</i> = 0.44 (2016) $\beta = -0.03 \pm 0.09$ <i>P</i> = 0.74 (2018)	N/A
Dietary digestibility	Late dry (Oct.–Nov.)	$\beta = -0.1 \pm 0.02$ <i>P</i> = <0.001	$\beta = 0.39 \pm 0.1$ <i>P</i> = <0.001	Cyclone flattened the negative scaling of digestibility with size and positive scaling of digestibility with floodplain affiliation, reducing diet quality in small-bodied and floodplain species relative to 2018

R4.3—My next comment centers around the initial filtering of the data. Given the initial pipeline (e.g. removal of all sequences that were found to be highest in the control samples), were sensitivity analyses conducted to determine that sequences <1% RRA should be removed from carnivore and herbivore datasets to reduce the likelihood of false positives in the DNA metabarcoding data? Should the same threshold be used for both diet types? While RRA thresholds can be useful for removing false positives below a certain threshold, they can also introduce false negatives which has been shown to drastically influence diversity calculations in some datasets. I am interested to know whether the dietary DNA metabarcoding results hold regardless of the threshold selected. It is inevitable that rare taxa are also being removed by using such thresholds, but these rare taxa could paint an interesting picture; one could predict that rare taxa may or may not play an important role in the diets of large mammals after such an event (i.e., do species incorporate a greater number of rarer taxa into their diet following such an event, thereby increasing dietary richness beyond what is found currently?) Regardless, including better explanations as to why particular thresholds are used is warranted within the text for each dataset.

This is a good point, and we understand (and generally agree with) the reasoning: use of arbitrary RRA thresholds reflects a tradeoff between precision and inclusivity, on the one hand, and the potentially biasing effects of low-abundance reads arising from erroneous sequences, on the other (Deagle et al. 2019, Littleford-Colquhoun et al. 2022a,b, Tercel et al. 2022, Wang et al. 2022). However, most metrics and inferences based on RRA should be relatively robust to inclusion/exclusion of rare reads, as they reflect the influence of more abundant mOTUs (with the obvious exception of richness), and it is also likely that ultra-low abundance reads contribute little to nutrition (even if their presence is ecologically interesting).

Previous work conducted in R.M.P.'s lab has taken different approaches to this issue. In studies from Kenya (Kartzinel et al. 2019, Kartzinel & Pringle 2020), we have avoided RRA thresholds, in part for reasons highlighted in this comment, and in part because we have a comprehensive local DNA barcode reference library including nearly all of the ~500 plant species known to occur in the area (Gill et al. 2019). Thus, we are able to filter out sequences that do not 100% match a local reference sequence, reducing the need for thresholds. In GNP, our local library is substantial, comprising ~250 common plant species (Pansu et al. 2019) and their functional traits (Potter et al. 2022), but it lacks many rare taxa (of an estimated ~650 in the study area); thus, many imperfect matches to the local database are undoubtedly real, and we use regional and global databases to identify mOTUs with <98% match to the local library (see Supplementary Information lines 112–115). This lowers our confidence in determining whether ambiguous low-abundance reads are genuine, and we have therefore erred on the side of using a 1% RRA threshold in GNP (e.g., Atkins et al. 2019, Branco et al. 2019, Guyton et al. 2020, Becker et al. 2021, Pansu et al. 2019 and 2022, Potter et al. 2022). For carnivore diet analyses, RRA thresholds may also reduce false positives arising from secondary predation (Deagle et al. 2019; but see, e.g., Wang et al. 2022 whose carnivore diet results were consistent across RRA thresholds ranging from 0.1% to 5%).

To address this comment, we re-ran analyses without the 1% threshold but with all other filtering parameters unchanged and confirmed that this did not alter our principal conclusions. Inferences about cyclone effects were qualitatively identical for the following responses when the threshold was removed: (1) intraspecific diet dissimilarity ('turnover'; Fig. 4a, Extended Data Fig. 7, Supplementary Table 2), (2) interspecific niche differentiation (Fig. 4d), (3) % grass consumption (Extended Data Fig. 8), (4) digestibility, digestible protein, food-plant height, Na, P, and lignin (Fig. 4b,c,f and Extended Data Fig. 9b-e), and (5) carnivore prey shifts (Fig. 6d,e). There were slight differences in strength of cyclone impact for a single response: food-plant height (stronger cyclone effect in the late dry season without threshold).

Perhaps unsurprisingly, the only response that differed markedly without the threshold was dietary richness (Extended Data Fig. 9a). With the threshold, the number of plant families per fecal sample was significantly higher in the cyclone year than in non-cyclone years in all seasons, but these differences evaporated when we removed the threshold. However, scrutiny of these results underscores the utility of the threshold for removing erroneous sequences. With no threshold, the mean number of unique plant sequences per sample increases from ~9 to ~840 (more than the number of species thought to occur in our study area), and the mean number of mOTUs per season across all herbivore species increases from 160 to an unbelievable 15,200 (which would amount to ~3.5% of all known terrestrial plant species). Mean plant family richness, the response variable in our study, increases from ~4 to ~54 (maximum 93). These clearly implausible numbers are obtained using our otherwise unadjusted filtering protocol, which retains sequences provided an >80% match to a reference database and bioinformatic designation as a dominant or singular mOTU (see Supplementary Information lines 54–56, 107–110, 115–117, 155–156), but even if we insist on 100% match to a local or global database (thereby omitting at least 28 plant species that we know **do** occur in our study area but have never been barcoded), we get 1195 unique sequences in November 2019—still roughly twice the maximum plausible number. So indeed, a 1% threshold drastically influences richness estimates, in large part by eliminating huge quantities of rare, erroneous reads.

Our interpretation of this exercise is that our results on dietary dissimilarity and quality are robust to the removal of the threshold because they are weighted by RRA, such that abundant sequences corresponding to heavily eaten plants drive the net result regardless of the addition of thousands of erroneous sequences present at very low abundance; by contrast, richness is sensitive because it is simply a count of all sequences detected at any abundance, such that the consistent ecological signal observed in ED Fig. 9a is drowned by vast numbers of false-positive reads that are equally likely to occur in any given sample.

There are endless possible variants of this exercise—stricter or laxer RRA thresholds, stricter or laxer thresholds for reference-database matching—but we have no objective basis for choosing among them or quantifying their offsetting advantages and disadvantages. If our local reference database for Gorongosa was comprehensive, we agree that the need for an RRA threshold would be diminished (though false positives still occur; Drake et al. 2022). Given that our local database is incomplete and most of our results are unaffected by the threshold, we retain our approach of using a 1% threshold in conjunction with our other bioinformatic filters and quality-control steps. This is consistent with our prior work in GNP (references cited above), and we also justify it on the grounds that plants contributing <1% of the DNA in a sample are unlikely to substantially influence net nutritional intake and fitness, which is ultimately most relevant to this study. Our choice of 1% as the threshold also aligns with the findings of Drake et al. (2021), who assessed RRA thresholds from 0.01% to 8% and found that false positives were only fully removed from mock communities at the highest thresholds were used (which also removed true sequences). For half of the datasets analyzed, Drake et al. identified 1% per sample as the optimal threshold to balance false-positive removal and true-positive loss (optimal thresholds for other datasets were ~0.35).

We have added text on Supplementary Information lines 125–131 to explain this justification, acknowledge the caveats of thresholding, and emphasize that our core conclusions are robust to this filtering decision. We have also reduced our reliance on our previously published work for describing methods and have accordingly expanded our methodological account in the revised Supplementary Information (Supplementary Information lines 2–164).

R4.4—Line 122 authors wrote "After Idai, herbivore diets tended to comprise a smaller proportion of grasses". When looking at fig. S13, ~55% of species (reedbuck, waterbuck, buffalo, oribi, elephant, impala)

showed a decrease in the RRA of grasses in their diets during late-wet season, with these same species showing a similar pattern across the other two seasons. Can this result be unpacked in regards to species' traits or movement -- why do these species in particular show a greater decline in grass RRA compared to the other species?

Those 6 species occupy intermediate positions on the grazer-browser spectrum, eating substantial quantities of both grasses and non-grasses ('mixed feeding'). The grazer-browser spectrum is universal in African savanna ungulates and is linked to variation in a suite of morphological and physiological traits (e.g., cranial anatomy, dentition, retention time, etc.; Codron et al. 2019). Mixed-feeding is seasonally variable; animals graze more in the wet season (when grass grows) and browse more in the dry season (presumably because they are less able to subsist on/compete for senescent grasses). By contrast, strict grazers (e.g., warthog, hartebeest, and wildebeest in GNP) rarely eat non-grasses and strict browsers (e.g., nyala, bushbuck, and kudu in GNP) rarely eat grasses, presumably also due to morpho-physiological and/or competitive constraints.

Our interpretation of the reviewer's observation is that mixed feeders were uniquely equipped to shift from grazing to browsing during the post-cyclone year of reduced grass availability in GNP. However, we note that even strict grazers in our study exhibited a decrease in grass consumption in the 2019 late dry season. Similar patterns have been observed during severe droughts (Abraham et al. 2019, Smit & Bond 2020), highlighting that the torrential rains of Cyclone Idai produced drought-like conditions of forage deprivation (see **R2.6**).

We have revised the text on lines 138-139 to clarify this interpretation.

R4.5—In Fig. S12, the years 2016 and 2018 are lumped together under the same ellipses for the early dry season. But, given the variation between 2016 and 2018 in some specie's NMDS plots, it is hard to discern whether 2016 and 2018 were treated as different years in the associated statistical models. This particular time period could give authors an idea as to the "natural" turnover of diets between years, but it is hard to determine whether the turnover between these years and 2019 could be considered to be within the "normal" range given the way the data are currently presented.

To clarify the specific uncertainty: this figure (now Extended Data Fig. 7) shows the non-cyclone years 2016 and 2018 using different markers, but the perMANOVA lumped these years. We included both non-cyclone years and differentiated the markers to (a) provide a more encompassing portrayal of the 'non-cyclone baseline' and (b) visualize the extent of 'normal' inter-annual turnover, but we combined them for statistical analysis to enable a far simpler analysis and interpretation. The null hypothesis being tested is '*no difference between cyclone and non-cyclone years*'; in this respect, lumping the non-cyclone years is (a) more straightforward than testing pairwise differences between years and (b) conservative in the sense that the non-cyclone baseline includes inter-annual variation (although it also increases sample size and hence statistical power).

More broadly: We agree that it is hard to define 'normalcy' given that there is dietary variation among years even without extreme events. In early drafts, we had included variants of a turnover figure (i.e., between-season dissimilarity) trying to convey what the reviewer alludes to. We have diet data for herbivores going back to 2013 and instinctively wanted to include *all* of the data to enable the most comprehensive portrait of 'normal' diets. The problem is that species are represented unevenly across most years and seasons. In 2013–2015 and 2017, we have data from varying subsets of species and seasons, and no data from the wet season when Cyclone Idai hit (e.g., waterbuck and warthog only in early-dry 2013; spiral-horned antelopes only in early-dry 2014; the five most common floodplain species in early-dry 2015 and early-/late-dry 2017; Guyton et al. 2020, Pansu et al. 2022, Daskin et al. 2022). In early-dry 2016, and routinely in all seasons in

2018 and 2019 (until COVID in early 2020), we analyzed the entire community. The uneven representation of species, seasons, and years precludes an unbiased community-level analysis using the full set of data, and our efforts to analyze/visualize turnover were unsatisfying and complicated; we settled on the NMDS in Extended Data Fig. 7 because it is unbiased and visually intuitive.

In light of this comment, and because we wish to have some visualization of compositional change in the main text, we revived the turnover figure. To show ‘normal’ dietary turnover for each species, we plot the distribution of Bray-Curtis dissimilarities between *all pairwise combinations* of non-cyclone sampling seasons in 2016 and 2018, both consecutive (e.g., wet vs. early dry 2018) and non-consecutive (e.g., wet vs. late-dry 2018). To show the cyclone impact, we plot turnover observed pre- vs. post-cyclone (late-dry 2018 vs. wet 2019). As predicted, intraspecific turnover after Idai was significantly greater than normal across all species (mixed-effects model with beta-error distribution with per-species random intercepts: $\beta_{Idai} = 0.53$, $SE = 0.16$, $P = 0.001$). For most species, dietary turnover after Idai was greater than or equal to that in any other comparison.

We retain the NMDS in Extended Data Fig. 7, with a clarified description to address the reviewer’s uncertainty (line 753-754, 1068-1069), and we include this new figure and analysis in Fig. 4a and on lines 134-136, 756-772. We believe this helps to address the upshot of the reviewer’s concern that “it is hard to determine whether the turnover between these years and 2019 could be considered to be within the ‘normal’ range given the way the data are currently presented.”

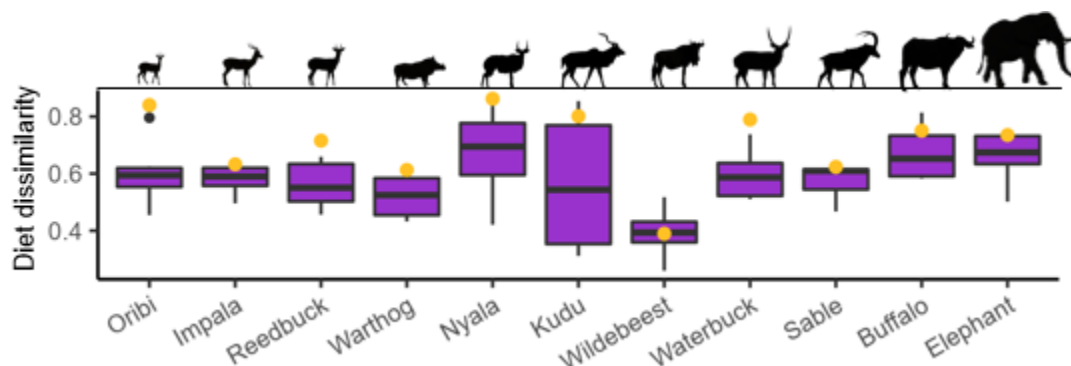


Fig. E. Dietary turnover (temporal dissimilarity within species) was higher than usual after Cyclone Idai. Seasonal changes in herbivore diets were significantly more pronounced after Idai (yellow; mean Bray-Curtis dissimilarity from Nov. 2018–Apr. 2019) than between seasons in non-cyclone years (purple; Bray-Curtis dissimilarity between all pairs of seasons in 2016 and 2018, consecutive and nonconsecutive; boxes, median and interquartile range; whiskers, minimum and maximum; dots, outliers; mixed-effects model with beta-error distribution and per-species random intercepts: $\beta_{Idai} = 0.53$, $SE = 0.16$, $P = 0.001$).

R4.6—To aid the visualization of results, it could help to order plots from smallest to largest species (e.g. Fig. S12 and S13).

This was in fact already the ordering of Extended Data Fig. 7 (formerly Fig. S12; species are from top left to bottom right in order of increasing body mass) and other figures where individual species are represented. For Extended Data Fig. 8 (formerly Fig. S13), we have retained the ordering from left to right based on decreasing grass RRA (which is the focus of the figure) because the figure is hard to read when ordered by body size.

R4.7—Line 126 to 128: What is the thinking behind why dietary niche differences among herbivore species were stronger in the post-cyclone early dry season compared to normal years?

Our thinking is that by reducing food availability (Fig. 3), the cyclone intensified interspecific competition, promoting dietary differentiation to alleviate it (Fig. 4d). Dietary differentiation should be particularly evident in the early-dry season after Idai because of the unusually long flooded period (flood extent in 2019 was above pre-cyclone extent until May 31st; Fig. 1; see **R1.5**), which meant herbivores were still crowded into higher elevation areas for a much longer period than usual, competing for the same limited amount of food. By the early-dry season, new herbaceous growth in the savanna, which likely allowed normal levels of niche partitioning in the late-wet season, was likely reduced leading to greater competition for food and interspecific partitioning of plants eaten. This view is consistent with evidence from ungulates (e.g., Gordon & Illius 1989, Pansu et al. 2022) and other taxa (reviewed in Schoener 1982) that when resources are abundant, species overlap in their use of a set of palatable foods, whereas when resources are limiting, palatable food is depleted and animals broaden their diets to include less preferred items. Under the latter conditions, competition should force individuals of a species to forage on plants that they have a relative advantage in harvesting and/or digesting, resulting in differentiation between species with different traits. This interpretation is also congruent with our finding that dietary richness was higher (Extended Data Fig. 9a) and multiple metrics of diet quality and nutritional condition lower (Fig. 4b-f, Extended Data Fig. 9b-e) in the year of Idai.

We have amended the text on lines 143–146 to clarify this interpretation.

Literature Cited

- Abraham, J. O., Hempson, G. P., & Staver, A. C. Drought-response strategies of savanna herbivores. *Ecol. Evo.* **9**, 7047-7056 (2019).
- Atkins, J. L., et al. Cascading impacts of large-carnivore extirpation in an African ecosystem. *Science* **364**, 173-177 (2019).
- Becker, J. A., et al. Ecological and behavioral mechanisms of density-dependent habitat expansion in a recovering African ungulate population. *Ecol. Monogr.* **91**, e01476 (2021).
- Bethell, T. Darwin's mistake. *Harper's* **252**, 70 (1976).
- Böhme, B., Steinbruch, R., Gloaguen, R., Heilmeier, H. & Merkel, B. Geomorphology, hydrology, and ecology of Lake Urema, central Mozambique, with focus on lake extent changes. *Phys. Chem. Earth* **31**, 745-752 (2006).
- Brinkman, M. P., & Garcelon, D. K. Applying UAV systems in wildlife management. Proceedings, 29th Vertebrate Pest Conference (2020).
- Condrón, D., Hofmann, R. R., & Clauss, M. Morphological and physiological adaptations for browsing and grazing. *The Ecology of Browsing and Grazing II*, Springer, Cham, 81-125 (2019).
- Daskin, J. H., et al. Allometry of behavior and niche differentiation among congeneric African antelopes. *Ecol. Monogr.* **93**, e1549 (2022).
- Drake L. E., et al. An assessment of minimum sequence copy thresholds for identifying and reducing the prevalence of artefacts in dietary metabarcoding data. *Methods in Ecol. & Evol.* **13**, 694-710 (2022).
- Deagle, B. E., et al. Counting with DNA in metabarcoding studies: How should we convert sequence reads to dietary data? *Mol. Ecol.* **28**, 391-406 (2019).
- Exposito-Alonso, M., et al. Natural selection of *Arabidopsis thaliana* genomes in present and future climates. *Nature* **573**, 126-129 (2019).
- Flemming, C. H., et al. Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data. *Ecol.* **97**, 576-582 (2016).
- Gill, B. A., et al. Plant DNA-barcode library and community phylogeny for a semi-arid East African savanna. *Mol. Ecol. Resour.* **19**, 838-846 (2019).
- Gordon, I. J., & Illius, A. W. Resources partitioning by ungulates on the Isle of Rhum. *Oecologia* **79**, 383-389 (1989).
- Gould, S. J. Darwin's untimely burial. *Natural History* **85**, 24-30 (1976).
- Groen, S. C., et al. The strength and pattern of natural selection on gene expression in rice. *Nature* **578**, 572-576 (2020).
- Guyton, J. A., et al. Trophic rewilding revives biotic resistance to shrub invasion. *Nat. Ecol. Evol.* **4**, 712-724 (2020).
- Heller C. Darwinism not tautological. *Nature* **351**, 600 (1991).
- Hunt, T. Reconsidering the logical structure of the theory of natural selection. *Commun. Integr. Biol.* **7**, e972848 (2014).
- Hutchinson, M. C., Dobson, A. P., & Pringle, R. M. Dietary abundance distributions: dominance and diversity in vertebrate diets. *Ecol. Lett.* **25**, 992-1008 (2022).

- Kartzinel, T. R., Hsing, J. C., Musili, P. M., Brown, B. R. P., & Pringle, R. M. Covariation of diet and gut microbiome in African megafauna. *PNAS* **116**, 23588-23593 (2019).
- Kartzinel, T. R., & Pringle, R. M. Multiple dimensions of dietary diversity if large mammalian herbivores. *J. Anim. Ecol.* **89**, 1482-1496 (2020).
- Klunk, J., et al. Evolution of immune genes is associated with the Black Death. *Nature* **611**, 312-319 (2022).
- Laubscher, L. L. et al. Non-chemical techniques used for the capture and relocation of wildlife in South Africa. *Afr. J. Wildl. Res.* **45**, 275-286 (2015).
- Lawton, J. H. Are there general laws in ecology? *Oikos* **84**, 177-192 (1999).
- Lin, T. C., Jogan, J. A., & Chang, C. T. Tropical cyclone ecology: a scale-link perspective. *TREE* **35**, 594-604.
- Littleford-Colquhoun, B. L., et al. The precautionary principle and dietary DNA metabarcoding: commonly used abundance thresholds change ecological interpretation. *Mol. Ecol.* **31**, 1615-1626 (2022a).
- Littleford-Colquhoun, B. L., Sackett, V. I., Tulloss, C. V., & Kartzinel, T. R. Evidence-based strategies to navigate complexity in dietary DNA metabarcoding: A reply. *Mol. Ecol.* **31**, 5660-5665 (2022b).
- Maddox, J. Is Darwinism a thermodynamic necessity? *Nature* **350**, 653 (1991).
- Meagher, M. Evaluation of boundary control for bison of Yellowstone National Park. *Wild. Soc. Bull.* **17**, 15-19 (1989).
- Milner, J. M., van Beest, F. M., Brook, R. K., & Storaas, T. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulate. *J. Wildl. Manage.* **78**, 1322-1334 (2014).
- Monroe, J. G., et al. Mutation bias reflects natural selection in *Arabidopsis thaliana*. *Nature* **602**, 101-105 (2022).
- Mueller, T., Olson, K. A., Leimgruber, P. & Calabrese, J. M. Rigorous home-range estimation with movement data: a new autocorrelated kernel-density estimator. *Ecol.* **96**, 1182-1188 (2015).
- Palmer, M. S. et al. Dynamic landscapes of fear: understanding spatiotemporal risk. *TREE* **37**, 911-925 (2022).
- Pansu, J., et al. Trophic ecology of large herbivores in a reassembling African ecosystem. *J. Ecol.* **107**, 1355-1376 (2019).
- Pansu, J., Hutchinson, M. C., Anderson, T. M., & Pringle, R. M. Generality of cryptic dietary niche differentiation in diverse large-herbivore assemblages. *PNAS* **119**, e2204400119 (2022).
- Peters, R. H. Tautology in ecology and evolution. *Am. Nat.* **110**, 1-12 (1976).
- Pillay, M. T., & Fitchett, J. M. Tropical cyclone landfalls south of the Tropic of Capricorn, southwest Indian Ocean. *Clim. Res.* **79**, 23-37 (2019).
- Potter, A. B., et al. Mechanisms of dietary resource partitioning in large-herbivore assemblages: a plant-trait-based approach. *J. Ecol.* **110**, 817-832 (2022).
- Pruitt, J. N., Little, A. G., Majumdar, S. J., Schoener, T. W., & Fisher, D. N. Call-to-action: a global consortium for tropical cyclone ecology. *TREE* **34**, 588-590 (2019).
- Ripple, W. J., et al. Collapse of the world's largest herbivores. *Sci. Adv.* **1**, e1400103 (2015).
- Ripple, W. J., et al. Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484 (2014).
- Schoener, T. W. The controversy over interspecific competition. *Am. Sci.* **70**, 586-595 (1982).

- Schoener, T. W., & Spiller, D. A. Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane. *PNAS* **103**, 2220-2225 (2006).
- Silva, I., et al. Autocorrelation-informed home range estimation: a review and practical guide. *Meth. Ecol. Evol.* **13**, 534-544 (2022).
- Singer, J., Fieberg, J. & Avgar, T. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol Evol.* **9**, 880-890 (2019).
- Smit, I. P. J., & Bond, W. J. Observations on the natural history of a savanna drought. *Afr. J. Range Forage Sci.* **37**, 119-136 (2020).
- Spiller, D. A., Losos, J. B., & Schoener, T. W. Impact of a catastrophic hurricane on island populations. *Science* **281**, 695-697 (1998).
- Stalmans, M., & Beilfuss, R. “Landscapes of the Gorongosa National Park” (Gorongosa National Park, 2008).
- Stalmans, M. E., Massad, T. J., Peel, M. J. S., Tarnita, C. E., & Pringle, R. M. War-induced collapse and asymmetric recovery of large-mammal populations in Gorongosa National Park, Mozambique. *PLoS One* **14**, e0212864 (2019).
- Swihart, R. K., & Slade, N. A. Influence of sampling interval on estimates of home range size. *J Wild. Manag.* **49**, 1019-1025 (1985).
- Tarnita, C. E., et al. A theoretical foundation for multi-scale regular vegetation patterns. *Nature* **541**, 398-401 (2017).
- Tercel, M. P. T. G., & Cuff, J. P. The complex epistemological challenge of data curation in dietary metabarcoding: Comment on “The precautionary principle and dietary DNA metabarcoding: Commonly used abundance thresholds change ecological interpretation” by Littleford-Colquhoun et al. (2022). *Mol. Ecol.* **31**, 5653-5659 (2022).
- Tinley, K.L., thesis, University of Pretoria, Pretoria, South Africa (1977).
- Thurfjell, H., Ciuti, S., & Boyce, M. S. Applications of step-selection functions in ecology and conservation. *Move. Ecol.* **2**, 4 (2014).
- Veldhuis, M. P., et al. Large herbivore assemblages in a changing climate: incorporating water dependence and thermoregulation. *Ecol. Lett.* **22**, 1536-1546 (2019).
- Walker, B.H., Emslie, R. H., Owen-Smith, N., & Scholes, R. J. To cull or not to cull: lessons from a southern African drought. *J. Appl. Ecol.* **24**, 381-401 (1987).
- Walker, R. H., et al. Mechanisms of individual variation in large herbivore diets: roles of spatial heterogeneity and state-dependent foraging. *Ecology* **104**, e3921 (2023).
- Wang, Q., et al. Assessing the diet of a predator using a DNA metabarcoding approach. *Front. Ecol. Evol.* **10**, 902412 (2022).
- Wang, S., & Toumi, R. More tropical cyclones are striking coasts with major intensities at landfall. *Sci. Rep.* **12**, 5236 (2022).
- Weile, M. E. Darwinism not tautological. *Nature* **351**, 600 (1991).

Reviewer Reports on the First Revision:

Referees' comments:

Referee #1 (Remarks to the Author):

The authors have incorporated all feedback from all reviewers in a thorough way, which, in my opinion, has led to an even stronger analysis and paper. I have no further comments and look forward to seeing the paper published.

Andrew Davies

Referee #2 (Remarks to the Author):

Thank you for your thorough review of comments made by four reviewers. Your review provides convincing evidence that findings are not due to artifacts/limitations of the data, with analyses that now incorporate the autocorrelation structure of the data. Not surprisingly, conclusions from your re-analysis match initial results. Thank you for the attention to detail. I have no additional comments and look forward to seeing your manuscript in print.

Referee #3 (Remarks to the Author):

While the revised paper does a better job of placing itself in the broader context of the relevant literature, I am still concerned (as were the other referees) by the tiny sample size upon which many of the conclusions were drawn. In contrast, the anole and invertebrate studies from the Caribbean involved 11-41 different islands/populations compared to only one site in Mozambique. My biggest concerns about this study are on the carnivore data: first, the paper relies on data from a single pack of African wild dogs and two "valid" lion collars (page 33 of the overall manuscript) during the weeks immediately after the cyclone. Second, both of these species were already reported as "rebounding" during the time of the study, so the mere fact that neither population declined during the cyclone is not terribly informative -- perhaps their growth would have been even higher in the absence of the catastrophic event. Wild dog dens would be highly vulnerable to flooding as would common denning sites for lions. Depending on the timing of a severe weather event, the authors might observe a more conspicuous impact on these two carnivores species. Thus, the bulk of my doubts centre on Figure 6, and its associated conclusions -- the wild dog diet in the immediate aftermath of Idai was based on only five prey-capture events, the lion diet on only 10 - these are minuscule sample sizes compared to the data collected from the herbivores. Thus I think it is highly inappropriate to claim that the carnivores were more "robust" than the herbivores -- an absence of evidence is not the same as evidence of absence.

And even with the herbivore data, Figure 2 is based on four collared nyala and three sable - if a single individual of either species had died, the results would have looked quite different. The higher mortality in the eight bushbuck resulted from the deaths of the smallest male and the two smallest females - were these animals fully grown? If not, might the difference with the remaining species be

due to the inclusion of three immature bushbuck whereas all the other species only included mature adults? Are age estimates available for the collared animals? Finally, nyala, impala, bushbuck, and warthog are all highly dimorphic -- were the females in these species more seriously affected by Idai than were the males? Why wasn't sex taken into account in the statistical analysis? Or were the sample sizes too small??

Referee #4 (Remarks to the Author):

The authors use an impressive dataset to understand the effects of Cyclone Idai, a severe climatic event, on the large mammals of Gorongosa. The dataset is vast and I believe the authors have done a good job with addressing concerns I had with the initial manuscript. First, authors analysed the role of body size and floodplain affiliation in mediating cyclone impacts on dietary turnover, dietary diversity, and mean digestibility and found that small and/or floodplain-affiliated species exhibited higher turnover, greater increases in diet breadth, and greater reductions in dietary digestibility. Second, authors conducted a sensitivity test to show that, in this instance, DNA metabarcoding results were relatively robust to changes in threshold parameters used. Finally, authors made changes to the wording of the manuscript that created greater clarity. Overall, I think this is a very nice paper that readers will find fascinating, as well as being a truly integrative piece of science.

Author Rebuttals to First Revision:

REFEREE #1 (REMARKS TO THE AUTHOR):

The authors have incorporated all feedback from all reviewers in a thorough way, which, in my opinion, has led to an even stronger analysis and paper. I have no further comments and look forward to seeing the paper published.

REFEREE #2 (REMARKS TO THE AUTHOR):

Thank you for your thorough review of comments made by four reviewers. Your review provides convincing evidence that findings are not due to artifacts/limitations of the data, with analyses that now incorporate the autocorrelation structure of the data. Not surprisingly, conclusions from your re-analysis match initial results. Thank you for the attention to detail. I have no additional comments and look forward to seeing your manuscript in print.

We are very pleased that Referees 1 and 2 approved of our revisions. We are grateful for the constructive and candid feedback we received on the initial submission, which helped enormously in refining the manuscript.

REFEREE #3 (REMARKS TO THE AUTHOR):

R3.1—While the revised paper does a better job of placing itself in the broader context of the relevant literature, I am still concerned (as were the other referees) by the tiny sample size upon which many of the conclusions were drawn. In contrast, the anole and invertebrate studies from the Caribbean involved 11-41 different islands/populations compared to only one site in Mozambique. My biggest concerns about this study are on the carnivore data: first, the paper relies on data from a single pack of African wild dogs and two "valid" lion collars (page 33 of the overall manuscript) during the weeks immediately after the cyclone. Second, both of these species were already reported as "rebounding" during the time of the study, so the mere fact that neither population declined during the cyclone is not terribly informative -- perhaps their growth would have been even higher in the absence of the catastrophic event. Wild dog dens would be highly vulnerable to flooding as would common denning sites for lions. Depending on the timing of a severe weather event, the authors might observe a more conspicuous impact on these two carnivores species. Thus, the bulk of my doubts centre on Figure 6, and its associated conclusions -- the wild dog diet in the immediate aftermath of Idai was based on only five prey-capture events, the lion diet on only 10 - these are minuscule sample sizes compared to the data collected from the herbivores. Thus I think it is highly inappropriate to claim that the carnivores were more "robust" than the herbivores -- an absence of evidence is not the same as evidence of absence.

We agree that it may be premature to draw conclusions about the relative robustness of carnivores given our sample sizes. The initial submission did not include the carnivore figure in the main text, and we added the possibility that "short-term impacts of extreme events may vary predictably with trophic level" in response to a comment from Referee 1. We have further qualified the presentation of these results and removed Fig. 6 from the main text (now Extended Data Fig. 8). The revised paragraph (i) is bracketed by clear caveats underscoring the limited sample sizes (lines 200-202, 215-216), (ii) specifies the sample sizes for known-fate data and movement analysis (lines 202-203, 206, and (iii) uses cautious language for interpretation ("consistent with", "appeared to shift", "detected no change"). To find a balance between Referee 1's observation—which is a valid and interesting hypothesis—and Referee 3's skepticism, the final sentence now reads "*While sample-*

size limitations temper our conclusions about the impacts of Cyclone Idai on carnivores, it is possible that short-term impacts of natural hazards on large mammals vary predictably with trophic level, and future research could test this hypothesis.”

R3.2—And even with the herbivore data, Figure 2 is based on four collared nyala and three sable - if a single individual of either species had died, the results would have looked quite different. The higher mortality in the eight bushbuck resulted from the deaths of the smallest male and the two smallest females - were these animals fully grown? If not, might the difference with the remaining species be due to the inclusion of three immature bushbuck whereas all the other species only included mature adults? Are age estimates available for the collared animals?

The inferences drawn from mortalities of collared animals were already carefully qualified and cross-validated by other data; we have subjected the manuscript to another round of intense scrutiny and are confident in both the rigor of our analyses and the fidelity of our presentation. We appreciate the prompt to clarify the age class of collared herbivores. While we were unable to obtain precise age estimates, because methods for aging individuals have not been validated for most of our study species (e.g., via analysis of cementum annuli, as used for deer), all GPS collars were deployed on adult animals. These assessments are made in the field based on measurements of body size, pelage coloration, horn/tusk growth, and tooth wear by teams with collective decades of experience in wildlife capture in Gorongosa and elsewhere throughout southern Africa; on rare occasions when we have inadvertently captured subadult individuals, we have not fit them with collars. We have revised the methods to clarify this point (lines 591-592, 1016-1017).

R3.3—Finally, nyala, impala, bushbuck, and warthog are all highly dimorphic -- were the females in these species more seriously affected by Idai than were the males? Why wasn't sex taken into account in the statistical analysis? Or were the sample sizes too small??

This is a fascinating question that we wish we were able to answer! Including sex as an index of intraspecific body size variation in our analyses would have been compelling, given that male and female body sizes differ substantially for most species in our study. However, we were unable to do this for several reasons. For GPS-collared species, sex-specific sample sizes were indeed too small to rigorously test for sex-based differences. For camera-trap data, sex and size cannot always be reliably established, depending on the species, image quality/completeness, and time of day. The same is true for fecal samples collected for diet analysis. Last, the aerial survey data do not include the sex of counted individuals, so we could not include sex as a predictor in analyses of long-term impacts of the cyclone.

REFEREE #4 (REMARKS TO THE AUTHOR):

R4.1—The authors use an impressive dataset to understand the effects of Cyclone Idai, a severe climatic event, on the large mammals of Gorongosa. The dataset is vast and I believe the authors have done a good job with addressing concerns I had with the initial manuscript. First, authors analysed the role of body size and floodplain affiliation in mediating cyclone impacts on dietary turnover, dietary diversity, and mean digestibility and found that small and/or floodplain-affiliated species exhibited higher turnover, greater increases in diet breadth, and greater reductions in dietary digestibility. Second, authors conducted a

sensitivity test to show that, in this instance, DNA metabarcoding results were relatively robust to changes in threshold parameters used. Finally, authors made changes to the wording of the manuscript that created greater clarity. Overall, I think this is a very nice paper that readers will find fascinating, as well as being a truly integrative piece of science.

We thank the Referee for this positive appraisal of our revision and for the helpful comments on the initial submission. We reiterate our gratitude to all four referees for their time, effort, and insight in helping us to improving our manuscript.