

Interactive comment on “Faunal carbon flows in the abyssal plain food web of the Peru Basin have not recovered during 26 years from an experimental sediment disturbance” by Tanja Stratmann et al.

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We respond to each of the issues identified by Reviewer #2 as follows:

General comments: General comment 1: I feel the naming of sites within the DISCOL experimental area that were not directly ploughed as ‘undisturbed’ misleading. Although not ploughed, such sites will still likely have experienced disturbance in the form of settlement of re-suspended sediments; a projected impact of deep-sea mining noted by the authors on page 2, line 26 of the manuscript. This is an issue which

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should be discussed in the manuscript but is not presently recognised. Our response: We agree with Reviewer #2 that the naming we adopted from previous DISCOL publications was misleading and therefore changed it in the revised manuscript to ‘inside plough tracks’ which corresponds to the former ‘disturbed sites’ and ‘outside plough tracks’ corresponding to the previous ‘undisturbed sites’.

General comment 2: The authors describe the DISCOL experiment as a ‘simulated small-scale deep-sea mining experimental disturbance’ (Page 2 lines 7-8). However, no nodules were removed during the DISCOL experiment, and in this way, amongst others, DISCOL was not a perfect simulation of disturbance caused by deep-sea mining. How the results of this study may differ if nodules are removed from the sediment deserves discussion. Our response: We agree that nodules were not removed, but most epifauna utilize the nodules that protrudes from the sediment and the ploughing did mix the nodules into the sediment. So, we reason that for epifauna that are dependent on nodules as hard substrate there is no difference between removing the nodule or ploughing it into the sediment as in both cases the nodule disappears from the sediment surface. We therefore added the following two sentences: “This hypothesis could not be tested directly, because nodules were not removed in this experiment, but only ploughed into the sediment. However, the disappearance of nodules from the sediment surface will likely have the same effect on sessile epifauna that depend on nodules as hard substrate independently of the method by which the nodules disappeared.” Additionally, we describe more specifically which type of disturbance were created during the DISCOL experiment in the Introduction: “A 10.8 km² circular area (Figure 1) was ploughed diametrically 78 times with an 4 m wide plough-harrow; a treatment which did not remove nodules, but disturbed the surface sediment, buried nodules into the sediment and created a sediment plume (Thiel et al., 1989).”

General comment 3: A glaring omission to the LIM analysed in this manuscript is the lack of microbial and meiofaunal data. It is explained in the manuscript that this is because of insufficient data (page 3, lines 10-11). This is understandable, but the impact

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this lack of microbial and meiofaunal data may have had on the analyses conducted deserves discussion in the 'Model limitations' section of the manuscript. Our response: We added this short statement to the 'Model limitations' section: "A notable omission is the lack of data for microbes and meiofauna throughout the times series, hence our C cycling models only resolve C cycling by macro- and megafaunal compartments." However, we cannot further state whether the trend changes when microbial data are added because this would be pure speculation.

General comment 4: Another limitation of this study is the lack of baseline sampling – a 'Pre-Disturbance' time point. Such a time point would give a better indication of the 'undisturbed' ecosystem state against which all post-disturbance time points could be compared (especially PD0.1). Clearly it is not possible to obtain this data now, but this lack of baseline data requires discussion. At present it is only noted in the legend of figure 6. Our response: We briefly mention this in the introduction ("Therefore, the food-web models presented in this work cover post disturbance 1989 (no adequate pre-disturbance sampling took place) to 2015 and contain only macrofauna, invertebrate megafauna and fish.") and discuss it in more detail in the 'Model limitation' section of the discussion: "Pre-disturbance samples and samples from reference sites were not collected for all food-web compartments. We therefore lack a baseline to which the 'outside plough track' food web at PD0.1 could be compared to assess the impact that the disturbance effect had on sites outside the plough tracks."

General comment 5: Throughout the manuscript, the high values of community metrics obtained for the PD3 time point are noted frequently – highest biomass, highest faunal C ingestion, highest respiration, highest macrofaunal contribution, lowest faeces contribution to total C outflow etc. However, no attempt is made to explain this observation. Similarly, on multiple occasions, 'natural variability' is noted amongst observations. I find it surprising that no attempt has been made to identify the variable(s) that may be driving this variability, even qualitatively. If quantitative analyses to this effect are not possible, the manuscript would still benefit from greater discussion of this natural vari-

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ability. Our response: The aim of our study was to test Jumars' predictions on ecosystem recovery after deep-sea mining with real data. We therefore do not consider our 'Feeding-type specific differences in recovery' section of the discussion an adequate place to discuss natural variability. However, we address this issue in the 'Model limitations' section now (page 10, lines 11-13): "we cannot determine whether the high biomass and carbon flows at PD3 were due to the onset of the positive (La Niña) phase of the El Niño Southern Oscillation (Trenberth, 1997), a phenomenon which is known to lead to a comparatively high POC export flux in the Pacific Ocean (e.g. Station M; Ruhl et al., 2008)."

General comment 6: Whilst the use of Jumars' (1981) paper to structure the discussion of this manuscript is an excellent idea, I feel that the quality of this discussion could be improved. For example, on page 11, line 28 it is stated that "...Jumars' (1981) predictions for subsurface deposit feeders could not be tested...". In the 'Specific Comments' section, I have given some suggestions of simple analyses which could be used to test Jumars' predictions more effectively. Our response: We appreciate these suggestions and address them below.

General comment 7: Finally, whilst the quality of language used in this manuscript is satisfactory, many sentences, particularly in the discussion section could be re-written to improve the flow of the manuscript (e.g. the first sentence of section 4.1). Our response: We improved the manuscript using the detailed textual corrections from Peter Jumars and the specific comments by Reviewer #2. We also modified the first sentence of section 4.1.

Specific comments for the abstract: Specific comment 1: The title is rather long and could be improved to increase the impact of the manuscript. I suggest something like 'Abysal plain faunal carbon flows remain depressed 26 years after a simulated deep-sea mining disturbance'. Our response: We accept the suggestion of the new title.

Specific comment 2: It is not immediately clear upon a first read-through of the ab-

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stract that LIM were produced for all points in the time-series, rather than just at PD26 (as the title may suggest). Please make this clearer. Our response: We rephrased the sentence as follows: “We used this unique abyssal faunal time series to develop carbon-based food web models for each point in the time series using the linear inverse model (LIM) approach for sediments subjected to two disturbance levels: 1) outside the plough tracks, not directly disturbed by plough, but probably suffered from additional sedimentation and 2) inside the plough tracks.”

Specific comment 3: Percentages – is it possible to give some sense of variability around these values? Our response: It would only be possible to present standard deviations or standard errors for flow values, but not for the biomass at PD26, since no replicates are available for megafauna estimates. For consistency, we therefore decided not to report any variability around the percentages in the abstract. However, standard deviations or standard errors are reported in the main text and figures/ tables.

Specific comment 4: At nearly 400 words, the abstract would be improved by more a concise wording. Our response: We shortened the abstract following the advice of both reviewers.

Specific comments for the introduction: Specific comment 5: The description of the DISCOL experiment (page 3, paragraph 1) could be clearer. Perhaps a figure illustrating the areas ploughed/not ploughed would help. Also, I feel it would be better for only a short introduction to the DISCOL experiment to be included in the Introduction section, with a more detailed description being reserved for the ‘Methods’ section. Our response: We added a figure showing the plough tracks inside the DISCOL experimental area, but we like to keep the focus of the ‘Methods’ section on the food-web models instead of describing the DISCOL experiment in more detail. Moreover, the DISCOL is described in detail in the referenced papers Thiel and Schriever (1989) and Bluhm (2001).

Specific comment 6 (Page 3, paragraph 2): It is good to introduce the basics of LIM in

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the Introduction section. However, the current text is perhaps a little too technical for this section. I suggest moving the more technical aspects of this paragraph to a new paragraph in the Methods section. Our response: We moved the more technical parts of the paragraph to a new subsection in the method part and combined it the former Method section 2.4.

Specific comment 7: I would like to see the aims of this study, and perhaps some hypotheses (e.g. based on Jumars (1981)), stated more explicitly at the end of this section. Our response: We rephrased this section and explicitly state the three aims of our study.

Specific comments for the methods section: Specific comment 8: It would be useful for the reader to know how many box cores were collected from ‘disturbed’ and ‘undisturbed’ sites at every time point, not just the PD26. This could be easily detailed in a table, which could also detail surface area of seabed surveyed for megafauna. Alternatively, the locations of all box cores collected over the 26-year study period could be plotted (color-coded for date of collection) on the figure I proposed above illustrating the DISCOL experimental mining disturbance regime. Our response: The requested data were already available in our original submission in Supplement 2, but we now also include them in Table 1. We decided, however, against plotting sampling stations on the map because several stations are taken so closely together that symbols would overlap considering the scale of the map.

Specific comment 9 (Page 4, line 8): Only three box cores were collected from disturbed sites for PD26. This is a very low level of replication, and something which should be discussed in the ‘Model Limitations’ section. Our response: We understand this comment, but logistical reasons underlie this low replication. The box corer was not equipped with video guidance and could therefore not be positioned exactly within the 8-m plough tracks. As a result, only three of the boxcores hit the targeted tracks and could be allocated to the category “inside plough tracks”. The remaining boxcores in the DISCOL experimental were conservatively assigned to “outside plough tracks”.

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Owing to the ship time available for this type of sampling it was not possible to pursue further attempts to hit the plough tracks.

Specific comment 10 (Page 4, paragraph 1): It seems strange that such an effort was made to analyse the same number of images for 'disturbed' and 'undisturbed' sites for megafauna, but there was no corresponding effort to analyse the same number of box cores for 'disturbed' and 'undisturbed' sites. Was an effort made to standardise megafaunal sampling effort for the other post-disturbance time points to that of PD26? Our response: The low number of box core replicates was addressed above. We did not attempt to standardize megafaunal sampling to other post-disturbance time points because camera systems also differed between the cruises PD0.1, PD0.5, PD3 and PD7. Additionally, selective sampling which was used during the cruises prior to the PD26-cruise make standardization almost impossible and we therefore included also comparisons of samples from the same sampling event, i.e., samples from outside the tracks vs. samples from inside the tracks (e.g. Fig. 6).

Specific comment 11 (Page 4/5): Conversion of biomass into carbon content; I would like to know exactly what the conversions used were, if possible. These could be included in a supplementary materials file. Our response: As mentioned in the Methods section 2.2, individual macrofauna organic C values were obtained by direct measurements on an elemental analyzer, so no conversion factors were applied. Conversion factors for megafauna are presented in Supplement 1.

Specific comment 12 (Page 5, line 20): No details are given of the conversion used for cnidarian/ poriferan biomass to carbon content. The authors should elaborate on the use of the Tilot (1992) paper. Our response: We did not elaborate on how the cnidarian/ poriferan biomass was converted to carbon content because we directly adopted the carbon content data from Tilot's PhD thesis (1992), in which she described in detail in the section on 'Estimation des biomasses sur les différents sites d'études' (p.289 onwards) how she determined the biomasses at the specific sampling sites in the Clarion-Clipperton Fracture Zone.

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Specific comment 13: The section detailing biomass to carbon content conversion would be made clearer by greater consistency in the use of the term 'biomass' to mean either the total weight of individuals, or the total carbon weight of individuals. Our response: To improve the understanding of this specific section and other parts of the manuscript, we now refer to a compartment biomass as 'carbon stock' and use the term 'biomass' only for the organic carbon content of individual organisms.

Specific comment 14 (Page 6, lines 4-9): What literature was used to determine the coarse feedings guilds assigned to other taxa? Our response: A list with references is provided in Table 2.

Specific comment 15 (Page 6, lines 7): It is stated that "...a further detailed classification of the macrofaunal polychaetes..." was made. However, this further detailed classification seems only to additionally subdivide deposit feeding polychaetes into surface/subsurface categories. Could this division not be made with a little effort for all invertebrate macrofauna and megafauna? Our response: The subdivision of macrofaunal polychaetes was based on polychaete families for which detailed descriptions are available in Jumars et al. 2015. All other fauna were 'only' identified to higher taxon-level and a more specific classification in feeding types is therefore not possible/reliable.

Specific comment 16 (Page 7 line 23 to page 8 line 9): Why was 'Hedge's d' used here rather than t-tests or their non-parametric equivalent? This should be clarified. Our response: We used the effect size 'Hedges' d', because this is commonly used in meta studies/ analysis to compensate for the fact that we have different sample sizes for different size classes, disturbance levels and sampling events (see e.g. Koricheva, Gurevitch and Mengersen. 2013. Handbook of Meta-analysis in Ecology and Evolution. Princeton University Press).

Specific comments for the results: Specific comment 17 (Page 8, lines 21-23): This comparison of the change in % biomass difference between disturbance treatments

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from PD0.1 to PD3 is verging on discussion. I suggest moving it to the Discussion section. Our response: We report here solely data on the contributions of specific feeding types to total biomass and we therefore believe that this fits better in the Results than the Discussion.

Specific comment 18 (Page 8, lines 24-26): Why is 'absolute weighted Hedge's d |d+|' reported here when on page 8, lines 6-9, Hedge's d is explained in a different form? This is confusing for the reader as page 8 lines 6-9 suggests that values greater than ~0.8 represent strong effect sizes, but the results given on page 8 lines 24-26 report small values associated with the metric and the authors describe these as 'indicating a strong experimental effect'. Our response: Hedges' d is used to compare differences carbon stocks of the same food-web compartment, e.g., megafauna deposit feeders outside vs. inside plough tracks from PD0.1. In contrast, absolute weighted Hedges' d |d+| compares the sum of all carbon stocks from outside vs. inside plough tracks from e.g. PD0.1. Hence, the absolute weighted Hedges' d |d+| is the summary statistic of Hedges' d. For a comparison of the effects sizes for each individual compartment (Hedges' d) and summarized over all compartments (absolute weighted Hedges' d), both types of Hedges' d are presented in tables in Supplement 3.

Specific comments for the discussion: Specific comment 19 (Page 9, line 28): Suggest changing "...compared to the undisturbed sediment after 26 years" to "...compared to the undisturbed sediment 26 years after experimental mining disturbance". Our response: We rephrased the sentence as follows: "the sum of all carbon flows in the food web was still significantly lower inside plough tracks compared to outside plough tracks 26 yr after experimental mining disturbance."

Specific comment 20 (Page 10, lines 1-23): I feel the authors are somewhat under-selling the conclusions of their manuscript by placing a model limitations section so early on in their Discussion. This could be moved to later in the manuscript, perhaps to just before the conclusions. Our response: We considered to move this section, but we do think that this is warranted at the beginning of the Discussion because this allows

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the reader to put our results that are discussed later on into perspective of the study limitations.

Specific comment 21 (Page 11, line 7): I am confused why the authors are discussing changes in fish respiration over long time periods (3 years) at undisturbed sites. The predictions of Jumars (1981) would be better tested by considering changes in respiration at disturbed sites very soon after the disturbance (e.g. PD0.1). I note that no fish were detected at disturbed sites at PD0.1, so simply put, this hypothesis cannot be tested with this data set. Our response: We removed the discussion about respiration during PD3 and concentrate on PD0.1 as follows: "The author also predicted that the density of mobile scavengers, such as fish and lysianassid amphipods would rise shortly after the disturbance in response to the increased abundance of dying or dead organisms within the mining tracks. In fact, experiments with baits at PAP and the Porcupine Seabight (NE Atlantic) showed that the scavenging deep-sea fish *Coryphaenoides armatus* intercept bait within 30 min (Collins et al., 1999) and stayed at the food fall for 114 ± 55 min (Collins et al., 1998). Therefore, the absence of fish inside plough tracks during PD0.1 and PD0.5 could be related to a lack of prey in a potential predator-prey relationship (Bailey et al., 2006). However, because of the relatively small area of plough tracks (only 22% of the 10.8 km² of sediment were ploughed; Thiel et al., 1989), the low density of deep-sea fish (e.g., between 7.5 and 32 ind. ha⁻¹ of the dominant fish genus *Coryphaenoides* sp. at Station M; Bailey, Ruhl and Smith, 2006) and the high motility of fish, this observation is likely coincidental."

Specific comment 22 (Page 11, line 28): "Hence, Jumars (1981) predictions for sub-surface deposit feeders could not be tested...". Indeed, it would be easier to test Jumars' predictions if a PD0 time point was available. However, would it not be possible to test whether there is a significant difference in the density of subsurface deposit feeders at PD0.1 between the disturbance categories? Under Jumars' predictions, we would expect the density of sub-surface deposit feeders to be much reduced at 'disturbed' sites relative to 'undisturbed' sites at this time point. Our response: We thank

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Reviewer #2 for the suggestion how to test Jumars' (1981) predictions for subsurface deposit feeders. We used the Hedges' d and compared its development over time to investigate the recovery of subsurface deposit-feeding polychaetes: "Hence, Jumars' (1981) predictions for sub-surface deposit feeders are difficult to test, provided the natural fluctuations in PolSSDF densities that were used to calculate carbon stock. However, Hedges' d for PolSSDF was $|1.47|$ at PD0.1 and decreased steadily to $|0.66|$ at PD7 (Supplement 3), indicating a very strong experimental effect after the disturbance event and a constant recovery over time."

Specific comment 23 (Page 11/12, lines 30-6): The authors state Jumars' prediction that surface deposit feeders will be more drastically impacted by mining activities than sub-surface deposit feeders. However, they do not test this prediction, instead comparing deposit feeder ecosystem functioning to that of 'omnivores, filter- and suspension feeders and carnivores'. Please explain why. It would be possible to investigate the relative changes in surface and sub-surface deposit feeder contributions to ecosystem functioning between 'disturbed' and 'undisturbed' sites. Our response: We combined the sections on surface and subsurface deposit feeders into one section also following the advice given in specific comment 22 and compare these two feeding types.

Specific comment 24 (Page 12, lines 15-16): "After 26 years, the relative difference in the filter and suspension feeding respiration rate was still 80%". I assume that this refers to the difference in respiration rate of filter and suspension feeders between the disturbance categories? The current text is ambiguous and could be interpreted as the difference in respiration rate between filter and suspension feeders. It is also unclear whether an 80% difference means that respiration rates at 'disturbed' sites were 80% lower than at 'undisturbed', or that respiration rates at 'disturbed' sites were 80% of those at 'undisturbed'. Our response: We added the following phrase to improve the clarity of the sentence: "suspension feeding respiration rate between outside plough tracks and inside plough tracks".

Specific comment 25 (Page 12, lines 18-19): "...indicating a slow recovery of this feed-

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ing group". I'd argue that compared to Jumars' predictions this apparent recovery rate is relatively fast! Our response: Indeed, when compared to Jumars' predictions this recovery rate is fast, however, in comparison to other feeding types, the recovery rate is rather slow.

Specific comment 26 (Page 12, lines 23-24): The authors complain here and elsewhere about natural variability in values making it difficult to isolate disturbance-related trends. However, the authors make no effort to identify or even simply discuss the key environmental factors which may be driving this variability. Our response: See our response to general comment 5.

Specific comment 27 (Page 12, lines 20-28): This summary paragraph is unnecessary. Our response: We removed the summary paragraph.

Specific comment 28 (Page 13, lines 5-6): "In contrast, filter and suspension feeders did not recover at all...". This sentence is too strongly worded. The authors state on page 12, lines 13-15, that "Directly after the initial DISCOL disturbance event, the respiration rate of filter and suspension feeders at the disturbed sediment was only 1% of the respiration rate of this feeding type at the undisturbed sediment" and on page 12, lines 15-16, that "After 26 years, the relative difference in the filter and suspension feeding respiration rate was still 80%". Whilst I agree that the respiration rate of filter- and suspension feeders is still clearly depressed at 'disturbed' sites relative to 'undisturbed', even 26 years post-disturbance, there clearly has been some recovery - perhaps even more so than might be expected! Please re-word this sentence to soften your conclusions. Our response: We rephrased the sentence as follows: "In contrast, filter and suspension feeders recovered less and the relative difference in respiration rate was 79%."

Specific comment 29 (Page 13, line 7): The authors state that "...[ecosystem functioning] has not recovered 26 years after the experimental disturbance". However, there is clearly some evidence of recovery. Please could the authors change this statement

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to "...[ecosystem functioning] has not fully recovered 26 years after the experimental disturbance"? Our response: We rephrased the sentence accordingly.

Specific comments for tables and figures: Specific comment 30 (Table 1): Please explain what 'n' stands for. Is this the number of taxa analysed, or the number of individuals used to estimate taxon-specific biomass etc.? Our response: We added the following sentence to the legend of the table: 'n' refers to the number of individuals used to estimate taxon-specific biomasses.

Specific comment 31 (Figure 1): There is a lot of information on this figure, and the overlap in error bars make it especially difficult to read. One option would be to plot each group separately, although this would result in a large number of graphs. Alternatively, this information may be more clearly presented as a table (as per Table 2). Why are there no error bars for the PD26 bars? Our response: This point was also addressed by Peter Jumars (Reviewer #1) and we therefore decided to present the figure without error bars which represent standard deviation and report the standard deviations together with the means in Supplement 2.

Specific comment 32 (Figure 4): Why are there no error bars on figure 4a? Are they simply too small to see? Our response: The error bars that symbolize the standard deviations of the flows are indeed very small but were included now in Figure 4a.

Technical corrections for abstract: Page 1, line 27: I, and most others, consider fish as megafauna. Please explain why they are treated separately to the other megafauna. Our response: We separated fish from invertebrate megafauna because of differences in their metabolic rates. To stress that megafauna in our study only includes invertebrate megafauna, we added 'invertebrate' to megafauna throughout the manuscript.

Page 2, line 12: The word 'occasionally' is used twice in same sentence. Our response: We removed the second 'occasionally'.

Page 2, line 20: Yttrium is typically considered a rare earth element. Our response:

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We took yttrium out of the list.

Page 2, line 25: One could argue that there's not really such a thing as food-rich surface sediments on the deep seafloor. Our response: Though the deep-sea is extremely food-limited, the surface sediments still contain comparatively more (labile) carbon than subsurface sediment.

Page 3, line 2: '10.8 km² large circular area' – 'large' is not required. Our response: We deleted 'large'.

Technical corrections for methods: Page 4, line 21: 'could' should be used, not 'can'. Our response: We changed the wording accordingly.

Technical corrections for the discussion: Page 9, line 23: Suggest changing 'evolution' for 'change over time'. Our response: We changed the wording accordingly.

Page 9, line 27: Put in comma after "...role of the various feeding types in the carbon cycling differs", and after "...was significantly lower". Our response: We added commas accordingly.

Page 11, line 28: "Hence, Jumars (1981) predictions..." should be 'Hence, Jumars' (1981) predictions...'. Our response: We changed it accordingly.

Page 11, line 34: "...deposit feeders seem to have advantages during the recovery from the DISCOL disturbance experiment...". Relative to whom? Our response: To address specific comments 22 and 23, we removed this part of the text.

Technical corrections for figures and tables: Figure 1: 'Figure 1' is actually referred to in the text after 'figure 2' is. Swap around the order of these figures – i.e. 'figure 2' should be renamed 'figure 1', and vice versa. Our response: We renamed the figures accordingly.

Figure 2: Inconsistent spelling of faeces here and throughout the manuscript. Figure legend line 7 "...yellow-dashed arrow indicate..." should be '...yellow-dashed arrow

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indicates...'. Incorrect use of 'due to' here and throughout the manuscript. Please change to 'because of' or 'as a result of'. Our response: We changed it accordingly.

Figure 5: Is it possible to subscript the x-axis post-disturbance times – e.g. PD0.1, for consistency with the rest of the manuscript? Our response: We adjusted the figure accordingly.

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