

Disturbance and recovery: a synthesis of microbial community reassembly following disturbance across realms

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Abstract

Disturbances alter the diversity and composition of microbial communities, but whether microbiomes from different environments exhibit similar degrees of resistance or rates of recovery has not been evaluated. Here, we synthesized 86 time series of disturbed mammalian, aquatic, and soil microbiomes to examine how the recovery of microbial richness and community composition differed after disturbance. We found no general patterns in compositional variance (i.e., dispersion) in any microbiomes over time. Only mammalian microbiomes consistently exhibited decreases in richness following disturbance. Importantly, they tended to recover this richness, but not their composition, over time. In contrast, aquatic microbiomes tended to diverge from their pre-disturbance composition following disturbance. By synthesizing microbiome responses across environments, our study aids in the reconciliation of disparate microbial community assembly frameworks, and highlights the role of the environment in microbial community reassembly following disturbance.

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Data statement: Accession numbers for the datasets included in this study are included in the supplementary data of this article, and are publicly available. Code used for sequence processing and null modelling is publicly available at <https://github.com/drcarrot/DisturbanceSynthesis>, and code used for statistical analyses is publicly available at <https://github.com/sablows/microbiome-disturbance>. Both repositories will be combined and archived at Zenodo upon acceptance.

Novelty statement: We compare the recovery of disturbed microbial communities across 86 aquatic, mammalian, and soil time series by measuring richness, compositional dispersion, and compositional turnover over time. We find that patterns of community reassembly in microbiomes are environment-specific, reconciling existing, environment-specific hypotheses of microbiome responses to disturbance. This is the first study to explicitly compare microbial community reassembly across environments within time scales that are relevant to bacterial life histories.

ABSTRACT

Disturbances alter the diversity and composition of microbial communities, but whether microbiomes from different environments exhibit similar degrees of resistance or rates of recovery has not been evaluated. Here, we synthesized 86 time series of disturbed mammalian, aquatic, and soil microbiomes to examine how the recovery of microbial richness and community composition differed after disturbance. We found no general patterns in compositional variance (i.e., dispersion) in any microbiomes over time. Only mammalian microbiomes consistently exhibited decreases in richness following disturbance. Importantly, they tended to recover this richness, but not their composition, over time. In contrast, aquatic microbiomes tended to diverge from their pre-disturbance composition following disturbance. By synthesizing microbiome responses across environments, our study aids in the reconciliation of disparate microbial community assembly frameworks, and highlights the role of the environment in microbial community reassembly following disturbance.

INTRODUCTION

Disturbances to ecological communities (i.e., externally imposed forces that cause mortality or stress to at least some of the members in the community) represent a critical process that influences the diversity and composition of taxa in those communities (Rykiel 1985). The resistance, resilience and invariance of communities following disturbances over time (Clark *et al.* 2021) provide insight into how ecological communities reassemble in the face of natural and anthropogenic disturbances, which are growing in frequency and magnitude (Newman 2019). The study of metacommunity assembly seeks to understand how taxa co-occur in local communities and the regions in which they are embedded, and how this varies through time, such as in the face of external perturbations (e.g., (Leibold & Chase 2017).

There are a multitude of ways to quantify how metacommunities respond to, or recover from disturbance, each of which gives insights into different parts of the community assembly process (overviewed in Figure 1, see also (Philippot *et al.* 2021). First, we can measure summary variables such as taxa richness in a given locality immediately following the disturbance, which gives us a picture of the resistance of the community to disturbance. Over longer periods of time following the disturbance, measuring richness can lend insight into the recovery of the community. Across both aquatic and terrestrial ecosystems, richness is found to decline at local scales after disturbance (Murphy & Romanuk 2014), and similar patterns have been observed in microbial communities (Shade *et al.* 2012a). However, richness can also increase if competitively dominant

taxa are more strongly depressed by the disturbance (Kondoh 2001), or in microbes, if the disturbance involves the addition of novel taxa (e.g., with sewage sludge amendments to soil (Ho *et al.* 2017). Over longer time scales, richness may either fail to fully recover (at least within the period observed; e.g., (Pilla *et al.* 2020), recover fully (Hillebrand & Kunze 2020), or even be higher following disturbance (Hartmann *et al.* 2015).

Second, we can measure compositional variation among local communities following disturbance. Compositional **dispersion** can be taken as an indicator of beta-diversity (Anderson *et al.* 2006). Following disturbance, dispersion can decrease, for example, if only a subset of taxa can persist and/or priority effects are reduced (Chase 2003, 2007). Alternatively, dispersion can increase, for example, if different taxa are favored due to stochastic differences in which taxa persist following disturbances (Debray *et al.* 2021). In microbial ecology, this observation of change in dispersion following disturbance has been well documented (e.g., (Zaneveld *et al.* 2017).

Third, we can measure to what extent community composition recovers following disturbance. The tendency of the community to return to its pre-disturbance conformation, or to tend away from this original conformation over time (i.e., distance from undisturbed controls) can be quantified via **turnover**. Given enough time, we might expect the same taxa that dominated prior to a disturbance to recover to their original abundances (Philippot *et al.* 2021). However, under some circumstances (e.g., strong or long disturbances, invasion (Ratajczak *et al.* 2017; Amor *et al.* 2020), it is also possible that the disturbance could permanently alter dominance patterns in the community (e.g., (Seekatz *et al.* 2015; Khan *et al.* 2019). Using a null modelling approach, it is possible to further partition observed changes in dispersion and turnover into compositional and richness changes (Chase *et al.* 2011) and shed light on the processes driving microbial community recovery.

Evidence for the effect of disturbance on the dispersion and turnover of microbial communities is mixed and environment-dependent. For example, the recovery of disturbed animal-associated microbiomes has been studied in relation to host health. It has been suggested that the microbiomes of sick hosts generally exhibit greater dispersion than healthy or undisturbed microbiomes (Zaneveld *et al.* 2017), but experimental research has found that disturbance can either reduce (Lavrinienko *et al.* 2020) or increase dispersion in host-associated microbiomes (Neely *et al.* 2021), and that this pattern is dependent on the time since disturbance (Ferrenberger *et al.* 2013). Across environments, microbiomes have been shown to recover towards (negative turnover, e.g., (Shade *et al.* 2012b; Jurburg *et al.* 2017), or to drift away from (positive turnover, e.g., (Shaw *et al.* 2019), their pre-disturbance compositions. Among other factors, different microbial habitats have varying degrees of spatial and temporal heterogeneity, microbial species pool sizes, and resource availability, which may affect community reassembly processes and result in different patterns among environments. For example, animal gut microbiomes have relatively low diversity (Thompson *et al.* 2017) and are dispersal-limited due to the host physiology, likely affecting the recovery of diversity. In contrast, soil microbiomes are extremely diverse, but poorly connected (Vos *et al.* 2013), likely affecting local dispersal and recolonization following disturbance.

Studying the responses of microbial communities through a metacommunity assembly lens (Leibold & Chase 2017) can yield a generalized understanding of how microbial communities assemble following disturbance across environments, which is a pressing question in microbial ecology (Philippot *et al.* 2021). Unique characteristics of microbes, including rapid evolution (Niehus *et al.* 2015), extreme taxonomic richness (Shoemaker *et al.* 2017), functional redundancy (Curtis & Sloan 2004), and dormancy (Locey *et al.* 2020) may result in deviations from the patterns observed in eukaryotic systems.

A better understanding of how microbiomes assemble following disturbance could also aid in the development of treatments of diseases in plants and animals, allow us to anticipate the effect of environmental change on the soil biota, and contribute towards developing novel practices for microbiome management (Konopka *et al.* 2015). To assess commonalities and differences in microbiome disturbance responses across environments, we performed a synthetic analysis of each of the responses discussed above (richness, dispersion and turnover) in the short and long term response to disturbance in aquatic, mammal-associated, and soil microbiomes.

Given the rapid rates of compositional turnover in many microbiomes (Kenney *et al.* 2020), we focused on studies that repeatedly sampled the microbiomes within 50 days post disturbance.

MATERIALS AND METHODS

Dataset selection

Using Google Scholar and Web of Science (a list of keywords is available as Supplementary Materials), we collected studies from each system where an experimental disturbance was imposed and 16S rRNA gene amplicon sequencing datasets were available. Specifically, we chose studies, which : 1) were sequenced in Illumina or IonTorrent platforms; 2) sequenced the v3-v4 regions of the 16S rRNA gene; 3) were published after 2014; 4) repeatedly sampled microbial communities following a discrete disturbance or environmental change; 5) included samples from before the disturbance (i.e., controls), at least one sampling within a week after disturbance, and at least one sampling within a month after disturbance; and 6) included experimental triplicates (i.e., three samples per time point). Criteria 1-3 ensured that the sequencing techniques were comparable between studies, and avoided the biases associated with sampling different regions of the 16S rRNA gene (Yang *et al.* 2016). Whether shifts in community composition occur at similar rates across environments is seldom compared using empirical data. Criteria 4-6 ensured that the time scales were comparable between time series, that the effects of environmental change could be compared *within* time series between different time points, and that the variability of the microbiomes at each time point could be measured. We defined a pulse disturbance as a “discrete, short-term event” (Shade *et al.* 2012a). We excluded datasets for which raw sequencing data was not publicly available, and stopped data collection in (Ho *et al.* 2017) October 2020. In all, 29 datasets matched our criteria (David *et al.* 2015; Seekatz *et al.* 2015; Datta *et al.* 2016; Džunková *et al.* 2016; Fuentes *et al.* 2016; Vaquer-Sunyer *et al.* 2016; Venkataraman *et al.* 2016; Wu *et al.* 2016; Dong *et al.* 2017; Jurburg *et al.* 2017, 2018, 2019; Qian *et al.* 2017; de Vries *et al.* 2018; Flancman *et al.* 2018; Frenk *et al.* 2018; Kennedy *et al.* 2018; Li *et al.* 2018, 2019; Mateos *et al.* 2018; van Kruistum *et al.* 2018; Lavelle *et al.* 2019; Lu *et al.* 2019; Santi *et al.* 2019; Ward *et al.* 2019; Yan *et al.* 2020) Table S1). We grouped these time series into three environmental categories: aquatic, mammal-associated, and soil microbiomes (including rhizosphere microbiomes).

Sequence reprocessing

We obtained raw 16S rRNA gene amplicon data and metadata from the NCBI Sequence Read Archive with the exception of two datasets, one of which came from another database, and the other was obtained directly from the authors (see Table S1 for accession numbers). We processed sequences in R 3.4.3 (Team 2017) using the *dada2* package (Callahan *et al.* 2016a). Prior to processing, we visually inspected two sequences per study with the *plotQualityProfile* to determine whether the reads had been merged prior to archiving and to confirm that primers were not present. We only used forward reads because reverse reads were not available for all studies. Following inspection, we trimmed and truncated sequences on a study-by-study basis (see Table S1 for trimming and truncation lengths) to preserve a 90 bp segment, the minimum recommended in the Earth Microbiome Project protocols (Thompson *et al.* 2017). We filtered, dereplicated, and chimera-checked each read using standard workflow parameters (Callahan *et al.* 2016b), and assigned reads to exact sequence variants (ASVs, 100% sequence identity in the 90 bp segment) with the SILVA v.132 training set (Quast *et al.* 2013). We removed reads not assigned to the domain Bacteria. Details about the percentage of reads lost at each step of sequence processing, per study, are included in Figure S1. Due to the wide range of sequencing depths across samples, we standardized samples to 1,500 reads per sample. To ensure that our findings were not affected by observation depth, we ran all analyses in parallel using the deepest possible observation depth (with a lower bound of 1,500 reads per sample) for each study (Table S1). As our findings were consistent regardless of standardization (Figure S2), and we present only the results from the global standardization. To examine the completeness of each sample relative to the total richness in a community, we calculated coverage (Chao and Jost 2012) using the BetaC package (Engel *et al.* 2020). On average, our samples represented 0.96 ± 0.05 (mean \pm sd) of the community. We removed any time points that had less than three experimental replicates for each time series. We coded time series so that time (days) [?] 0 occurred after disturbance, and time < 0 denoted the pre-disturbance community. In line

with our conservative approach to sequence processing, our analyses focused on the dominant portion of the community.

Calculation of richness and turnover metrics

We calculated richness and turnover metrics using the *phyloseq* package's data structure (McMurdie & Holmes 2013). We calculated species richness as the number of unique ASVs per sample.

We used Bray-Curtis distances to quantify two aspects of compositional variation. First, for each time series and for each time point, we calculated dispersion as the pairwise Bray-Curtis distances between all combinations of experimental replicates. For studies that resampled the same experimental unit (e.g., host organism or microcosm) over time, we excluded pairwise comparisons between samples from the same experimental units. Second, to quantify turnover, we calculated pairwise distances between all control samples (i.e., pre-disturbance) and all subsequent replicate samples at each time point following disturbance. Communities that largely recover to their pre-disturbance conformation will have a negative slope through time, while communities that become increasingly different from the pre-disturbance community over time will have a positive slope estimate (Figure 1).

To disentangle compositional changes from changes in richness, we randomly permuted abundance values within each sample 1000 times, preserving the number of taxa and observations for each sample, and recalculated turnover and dispersion metrics for each matrix to derive a null expectation for each. For both metrics, Z-scores were calculated as $\frac{\text{observed} - \mu^{\text{expected}}}{\sigma^{\text{expected}}}$. We present analyses of the Z-scores in the main text, and analyses of the raw compositional metrics (i.e., Bray-Curtis) in the Supplementary Methods. All code for bioinformatics processing and null models is available at <https://github.com/drcarrot/DisturbanceSynthesis>.

Statistical analyses

We fit statistical models to assess how 1) richness, 2) dispersion, and 3) turnover change in response to the disturbance relative to undisturbed control samples immediately after disturbance (i.e., before-after analyses), and through time. Unless otherwise specified, we performed all analyses at the ASV level. Before-after analyses compared data from prior to the disturbance to samples taken < 4 days post disturbance, and models included before-after and environment (i.e. aquatic, mammal, soil) as categorical covariates that were allowed to interact. A list of the studies excluded from before-after analyses due to lack of samples is included in Table S1. We assessed diversity change through time with models fit to data from the first 50 days post-disturbance only (i.e., pre-disturbance samples were not included, with the exception of the turnover analysis that quantified the compositional change between pre-disturbance and post-disturbance assemblages). We fit time series models with time (in days) as a continuous covariate; time was centered by subtracting the mean duration from all observations prior to modelling and allowed to interact with the environment. We fit all models with the same, hierarchical grouping (or random-effects) structure. To account for methodological variation between studies, we included varying intercepts in all models; and, because many studies included more than one disturbance type (e.g., (Džunková *et al.* 2016), we included varying slopes and intercepts for time series within studies (i.e., one time series per disturbance type).

We assumed a negative-binomial error distribution and a log-link function for models fit to species richness calculations (i.e., the before-after and time series models). In addition to the parameters and the grouping structure described above, the shape parameter of the negative-binomial distribution (that estimates aggregation) was also allowed to vary among studies. Models fit to the z-transformed compositional change metrics (i.e., Bray-Curtis) assumed Gaussian error distributions and identity-link functions. In addition to the parameters and grouping structure described above, we also modelled residual variation as a function of environment to account for heteroscedasticity, with additional random variation among studies also modelled.

For Bayesian inference and estimates of uncertainty, we fit models using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017), which were coded using the 'brms' package (Bürkner 2017). We used weakly regularising priors, and visual inspection of the HMC chains showed excellent convergence. All code

for statistical analyses is available at <https://github.com/sablowes/microbiome-disturbance>.

RESULTS

Our dataset included 2588 samples in 86 time series from 29 studies (Table S1) belonging to soil micro- and mesocosms (n=49), seawater mesocosms (n=16), and mammalian microbiomes (n=21) that were sampled multiple times within 50 days after disturbance (Figure 2a). Across all samples, we detected 56,480 ASVs. Of the 824 families in our dataset, 85.6% were detected in seawater, mammalian, and soil microbiomes (Figure S3). Coverage was highest in mammalian microbiomes (0.98 ± 0.02 ; mean \pm sd), lowest and most variable in soil microbiomes (0.93 ± 0.06), and was significantly different between environments (ANOVA, $F=475.1$, $p < 0.001$, Figure 2b).

Richness in disturbed and recovering microbiomes

Prior to disturbance, mean richness was highest in soil microbiomes with 327 ASVs [95% CI: 196 - 506], followed by aquatic 184 [111- 281], and mammalian 86 [51 - 133] microbiomes (Figure 3a). While all environments exhibited slight decreases in microbiome richness following disturbance, only the decrease in the mammalian microbiomes differed from zero. On average, the post-disturbance richness in mammalian microbiomes was approximately 43% of that found pre-disturbance (Figure 3a), and over time, richness increased approximately 2% (1-3%) per day (Figure 3b). In general, the mammalian microbiomes that lost the most richness after disturbance also recovered this richness most rapidly over the following 50 days (Figure S4).

Dispersion and turnover

All microbial communities were underdispersed relative to the null expectation, and 97% of Z-scores were negative. On average, dispersion did not change in response to disturbance for any environment, either immediately or over time (Figure 4, Table S2). We found a decrease in the Bray-Curtis dispersion values for mammalian microbiomes (Figure S5), however this pattern was not present in the Z-scores, indicating that this decrease was due to losses in richness rather than compositional change .

Following disturbance, aquatic microbiomes exhibited positive turnover, tending away from their pre-disturbance controls over time (slope estimate: 0.06 [0.04-0.08]). No temporal patterns were observed in mammalian (slope estimate: -0.02 [-0.04- -0.01]; Figure 5, 6) or soil (slope estimate: 0 [-0.01- 0.02]) microbiomes. We found that mammalian microbiomes exhibited negative turnover when assessed with the raw Bray-Curtis values, tending to recover to their pre-disturbance composition. However, once again, our null model confirmed that this pattern was due to an increase in richness, not due to compositional recovery (Figure S6). Immediate richness loss was not directly related to turnover responses over time, however both parameters were environment-dependent (Figure 6).

DISCUSSION

By investigating patterns of microbial community reassembly at time scales that are relevant to microbiome turnover rates and bacterial life histories (Shade *et al.* 2018; Kenney *et al.* 2020), our study takes advantage of relatively standardized and available microbiome data (i.e., the V3-V4 region of the 16S rRNA marker gene, (Jurburget *et al.* 2020)). We found that in general, microbiomes experienced modest richness losses and no change in dispersion following disturbance. We also found environment-specific responses: aquatic microbiomes tended away from their pre-disturbance composition following disturbance, while mammalian and soil microbiomes exhibited no clear patterns. These findings can help reconcile disparate observations previously noted in the literature.

Contrary to our expectation, we only found modest losses in richness following disturbance. On average, only mammalian microbiomes experienced significant richness loss. This loss likely underscores the efficacy of antibiotics and other targeted treatments, which were the disturbance most frequently used to induce disturbances in mammalian microbiomes (Seekatz *et al.* 2015; Džunková *et al.* 2016); disturbances in the other environments in our study tended to be untargeted (e.g., inorganic nitrogen and phosphorus inputs

in aquatic microbiomes, (Santiet al. 2019); or humic acid amendments in soil, (Liet al. 2019). The host's response may have also played a role in both the immediate response and the long-term recovery of richness following disturbance. Host responses depend on the degree of richness loss, the identity of the lost taxa (Yaoet al. 2016), and the intensity of disturbance (Van de Guchte et al. 2020), and can exacerbate the effect of disturbance on the microbiome (e.g., through inflammation (Van de Guchte et al. 2020)). We found that more strongly disturbed mammalian microbiomes tended to recover their richness more rapidly, and here, too, host behaviors such as eating (Guptaet al. 2017) and socializing (Rauloet al. 2021) may have functioned as mechanisms of active dispersal. The mild decline in richness following disturbance in aquatic and soil microbiomes contrasts the stronger responses found in eukaryotic communities to disturbance (Murphy & Romanuk 2012, 2014). This may be because the disturbances applied in these communities only mildly affected them, or because rare taxa were disproportionately affected and we were unable to detect their decrease due to the conservative approaches selected for sequence processing.

Our work further highlights the need to reframe the consequences of disturbances in the microbiome (Buma 2021). We included a wide range of disturbances that are not usually considered in the eukaryotic literature. For example, when sterilized, organic amendments represent a novel source of resources, but when applied unsterilized, they also include a potentially invasive community, a scenario that deviates from the classic invasion literature (Rilliget al. 2015). Furthermore, the duration of disturbances varied, especially relative to bacterial life histories and ecologies (Kenneyet al. 2020). Pulse disturbances which last multiple days may encompass multiple life cycles for many microbial taxa. Similarly, disturbances which may be considered long-term changes for macroorganisms (i.e., oil pollution), may represent short-term resource pulses for oil-degrading bacteria. In a world in which microbiomes are exposed to increasing disturbance pressures, developing a set of descriptors for disturbances based on their effect on the microbiome's niche space and competitive landscape is urgently needed.

We found no patterns in dispersion, either immediately after or over time following disturbance, in any environment. While changes in dispersion are often reported in the microbial literature (Ferrenbergeret al. 2013; Lavrinienko et al. 2020; Neely et al.2021), dispersion is generally measured as pairwise Bray-Curtis distances among experimental or field replicates, and thus confound changes in richness with compositional changes (Chaseet al. 2011; Stegen et al. 2013). Our null modelling approach allowed us to partition these two sources of change, revealing that in general, compositional dispersion does not consistently increase or decrease following disturbance, even when richness changes (i.e., in mammalian microbiomes). In particular, despite recovering their richness, mammalian microbiomes did not recover their composition, in line with findings across a wide range of ecosystems (Hillebrand & Kunze 2020). Whether these altered microbial community compositions are important for the maintenance of community functions (Nemergut et al. 2014) and resilience (Paineet al. 1998) is an open, but pressing issue.

Surprisingly, aquatic microbiomes tended to become more dissimilar from their pre-disturbance compositions over time. Due to the different temporal sampling schemes included in this synthesis, it is not possible to determine whether the communities were generally drifting towards a specific composition. The observed pattern may be due to the high connectivity of aquatic microbiomes (Mestreet al. 2018), where dispersal limitation is greatly reduced relative to other microbiomes and nutrients are constantly mixed, facilitating the random recolonization of taxa following disturbance. Indeed, in the highly heterogeneous soil environment, microbiomes exhibited little consistent responses to disturbance, likely due to the extreme diversity and heterogeneity found in this system (Rilliget al. 2017), or due to technical limitations of this study. The conservative approaches we employed for the selection, processing and analysis of the data aimed to facilitate cross-study comparisons, but limited the contribution of rare or lowly abundant taxa to our analysis. This effect was likely stronger for soil, which has the highest overall richness (Thompsonet al. 2017), where our sample completeness estimates (i.e., coverage) were lowest. Rare taxa are important sources of variation in soil microbiomes (Joussetet al. 2017; Jiao et al. 2019), and are key drivers of community assembly (Shadeet al. 2014).

Our synthesis is intended to explicitly compare microbial community reassembly patterns in response to

disturbance across realms that are highly segmented by researcher identity. Our study reconciles several hypotheses that have been proposed for microbiomes in the different realms. First, we find support for the tendency to drift away from the pre-disturbance condition in aquatic systems. Second, we find that mammalian microbiomes often recover their richness, but not their composition following disturbance (e.g., they maintain the same number of taxa but have different memberships with different relative contributions). Third, we find little general evidence for changes in compositional dispersion (after accounting for changes in richness) following disturbance. Finally, our study reframes microbial community reassembly from a community ecology perspective. Future work should focus on distinguishing targeted from untargeted disturbances, to determine what constitutes a disturbance for a microbiome given its ecosystem context, and to perform research at temporal scales which match microbial life histories and turnover /growth in microbiomes. Overall, this work provides a new perspective on the dynamics and generalities of microbiome disturbance responses that is supported by directly comparable metrics, equivalent temporal scales among datasets, and a consistent modeling approach. It suggests that, after standardizing and focusing on macroecological patterns, the environment matters for microbiome assembly.

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FIGURES

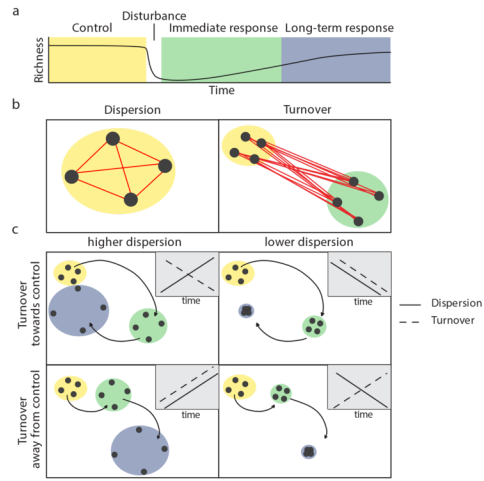


Figure 1. Measuring microbial recovery after disturbance.

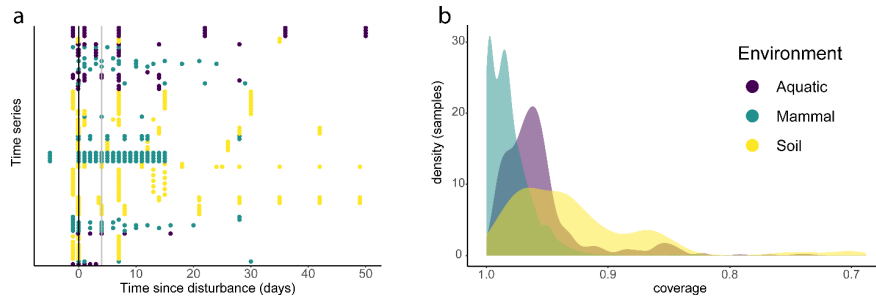


Figure 2. Samples used in this synthesis.

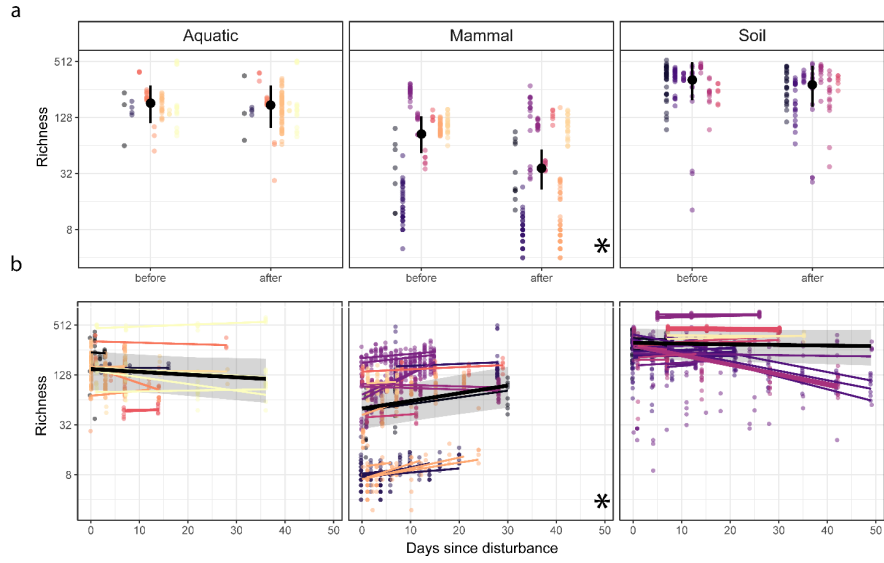


Figure 3. The effect of disturbance on microbiome richness, immediately (<4 days) after disturbance (a), and over 50 days of recovery (b).

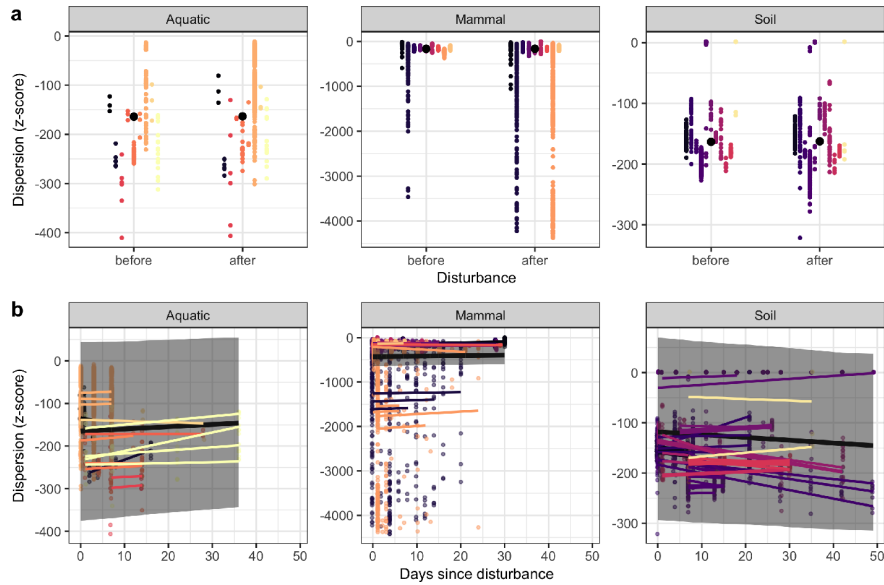


Figure 4. Consistent effect of disturbance on microbiome dispersion are not detected, immediately (<4 days) after disturbance (a), or over 50 days of recovery (b).

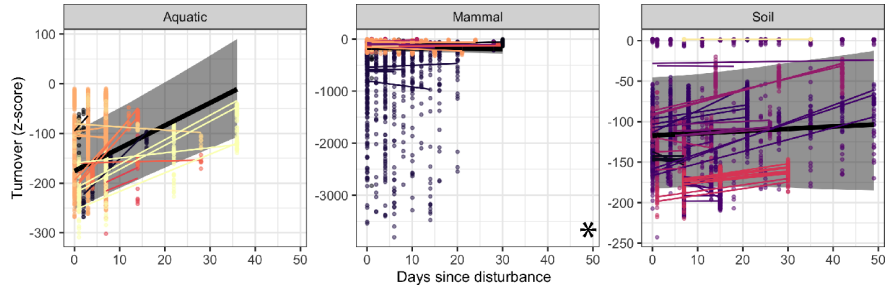


Figure 5. The effect of disturbance on community recovery is environment-dependent.

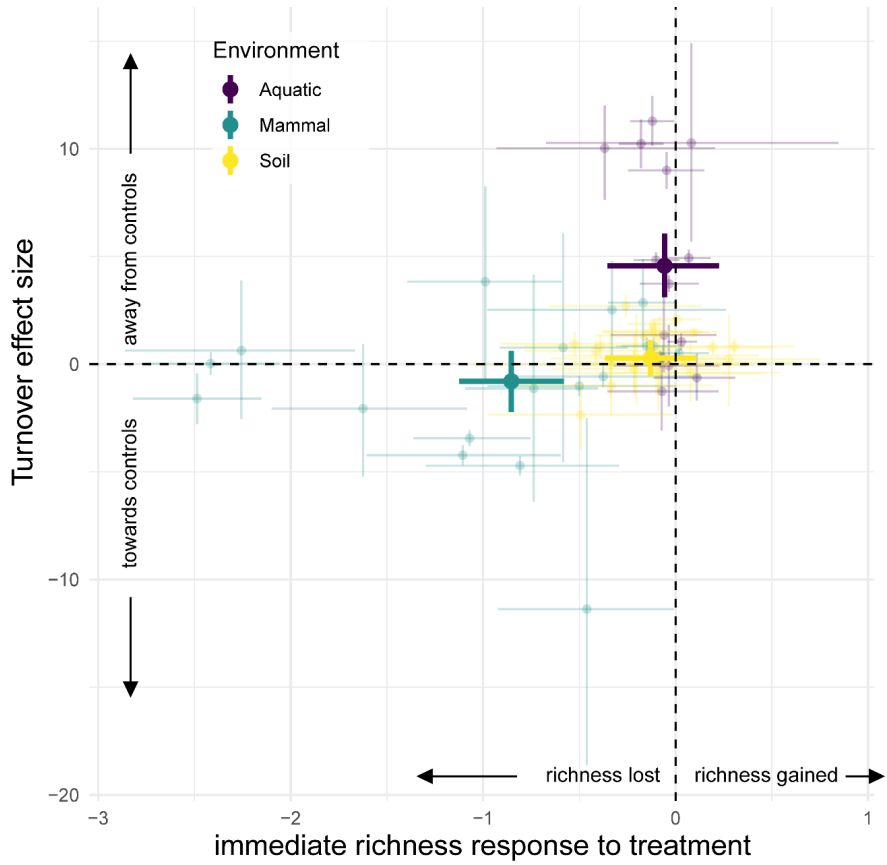


Figure 6. The immediate effect of a disturbance is not related to the microbiome’s long-term compositional recovery.

LEGENDS

Figure 1. Measuring microbial recovery after disturbance. Community richness can be measured before disturbance (yellow), immediately after disturbance (green), and over longer time periods (blue, a). Compositional dynamics can be assessed using compositional dissimilarity metrics (i.e., Bray-Curtis, b). Dispersion can be measured as the pairwise dissimilarity between experimental replicates, and turnover can be measured as the pairwise dissimilarity between pre-disturbance and disturbed communities (red). Following disturbance, communities dispersion can increase or decrease over time if communities become more or less dissimilar, respectively (c). They may also return to their pre-disturbance composition (negative turnover

trend) or become increasingly dissimilar from the pre-disturbance community (positive turnover trend) Insets are the relationship between time (x-axis) and turnover (dashed line, y-axis) or dispersion (solid line, y-axis).

Figure 2. Samples used in this synthesis. We selected time series that had control samples and multiple samples after disturbance (a). A vertical black line denotes a disturbance event in all cases; samples taken on the day of disturbance (before or after) are shown along this line. A vertical grey line indicates the fourth day after disturbance. Studies which had not sampled the recovering microbiome within <4 days after disturbance were excluded from assessments of the immediate impacts of disturbance on richness and dispersion. All samples were standardized to 1,500 observations per sample, and had an average coverage >0.9 (b).

Figure 3. The effect of disturbance on microbiome richness, immediately (<4 days) after disturbance (a), and over 50 days of recovery (b). Richness was calculated as the number of observed taxa in each sample, and is presented with a \log_2 -transformed y-axis. Circles represent samples, and are colored by study. In *a*, solid black circles indicate the mean across time series per environment with a 95% CI indicated by error bars. In *b*, regression lines for each time series are colored by study, and the solid black line shows the mean response across time series per environment. The 95% CI is displayed as a grey shaded area, and environments for which overall trends deviate from zero are indicated with an asterisk (*) on the bottom right corner.

Figure 4. Consistent effect of disturbance on microbiome dispersion are not detected, immediately (<4 days) after disturbance (a), or over 50 days of recovery (b). Dispersion was calculated as the pairwise Bray-Curtis distance between replicates for each time point within each time series, and each circle is a pairwise comparison, colored by study. In *a*, solid black circles indicate the mean across time series per environment with a 95% CI. In *b*, regression lines for each time series are colored by study, and a solid black line indicates the mean response across time series per environment. The 95% CI of the overall response in each environment is displayed as a grey shaded area. y-axis scales differ per environment, and the overall trends from each environment did not deviate from zero.

Figure 5. The effect of disturbance on community recovery is environment-dependent. For each time series, recovery was calculated as the pairwise distance between post-disturbance samples and pre-disturbance controls. Each point is a pairwise comparison, colored by study. recover to increasingly different conformations Regression lines for each time series are colored by study, and a solid black line indicates the mean response across time series per environment. The 95% CI is displayed as a grey shaded area, and environments for which overall trends deviate from zero are indicated with an asterisk (*) on the bottom right corner.

Figure 6. The immediate effect of a disturbance is not related to the microbiome's long-term compositional recovery. Each point is a time series, colored by its environment. Immediate richness responses were calculated as the effect of disturbance on community richness (Figure 3a), and log-transformed. Turnover rates were calculated as the slope estimate for turnover over time. Error bars show the 95% CI for both metrics. Large circles indicate the mean response per environment.