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Species-level and community-level responses to disturbance: a cross-community analysis

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Abstract. Communities are comprised of individual species that respond to changes in their environment depending in part on their niche requirements. These species comprise the biodiversity of any given community. Common biodiversity metrics such as richness, evenness, and the species abundance distribution are frequently used to describe biodiversity across ecosystems and taxonomic groups. While it is increasingly clear that researchers will need to forecast changes in biodiversity, ecology currently lacks a framework for understanding the natural background variability in biodiversity or how biodiversity patterns will respond to environmental change. We predict that while species populations depend on local ecological mechanisms (e.g., niche processes) and should respond strongly to disturbance, community-level properties that emerge from these species should generally be less sensitive to disturbance because they depend on regional mechanisms (e.g., compensatory dynamics). Using published data from terrestrial animal communities, we show that community-level properties were generally resilient under a suite of artificial and natural manipulations. In contrast, species responded readily to manipulation. Our results suggest that community-level measures are poor indicators of change, perhaps because many systems display strong compensatory dynamics maintaining community-level properties. We suggest that ecologists consider using multiple metrics that measure composition and structure in biodiversity response studies.

Key words: abundance; biodiversity; community properties; compensatory dynamics; disturbance; resilience; richness; species populations.

INTRODUCTION

In an era of rapid natural and anthropogenic change, it is increasingly clear that ecology needs to do more than quantify biodiversity for a snapshot in time. Ecology must also be able to forecast changes in biodiversity for systems in flux (Thomas et al. 2004, Araujo and Rahbek 2006, Dawson et al. 2011). Predicting biodiversity in disturbed systems has several challenges, including the need to understand the network of processes driving biodiversity and the ability to predict changes of multiple components of biodiversity under global environmental change scenarios (Fisher et al. 2010, White et al. 2010). Since disturbance frequency and intensity (e.g., fire, flood, fragmentation) may be altered under global change scenarios, a general framework for understanding biodiversity response to disturbances is critical.

The taxonomic diversity of communities is one of the most commonly studied aspects of diversity (Magurran 2004). The diversity of any community emerges from the populations of species that inhabit it. Many of the commonly used diversity metrics can be derived from the identities of those species and their abundances. For example, species richness is simply the count of species living in a community. Both evenness and the rank species-abundance distribution quantify how similar species are in their population abundances. Total abundance, a measure of the productivity of a community, is simply the sum of abundances across all the species living there. Because community-level diversity metrics are derived from the presence and abundance of individual species, it is not unreasonable to assume that changes at the species level generate changes at the community level. Clearly, changes in the list of species present and how abundance is divided among those species could impact any metrics using this information.

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However, experimental and observational studies suggest that changes in composition may not always scale up to impact community-level properties (e.g., Harte 2011, Supp et al. 2012). This creates the possibility that disturbances that influence species may not influence higher levels of biological organization.

Species populations and community-level diversity metrics could show different responses to disturbance if they are at least partially influenced by different processes. Within a community, the presence and abundance of species is often thought to reflect niche-based processes operating primarily at the local scale (Chase and Leibold 2003, Tilman 2004, Martorell and Freckleton 2014). As such, the identity and abundance of individual species often exhibit high spatial and temporal sensitivity to environmental change (Cottenie 2005, Ernest et al. 2008, Donohue et al. 2013), as fit between the environment and the specific niche parameters of individual species change. However, community-level properties may still be maintained by mechanisms that compensate for population declines or local extinction of species (Ernest and Brown 2001, Goheen et al. 2005, Vasseur and Gaedke 2007, Dornelas et al. 2011). Compensatory colonization events can maintain species richness when local extinctions occur (Brown et al. 2001, Dornelas et al. 2011) by providing new species with niches better suited to the new environmental conditions. Compensatory dynamics in populations can potentially allow distributions of abundance to be maintained, as declines in abundance by some species are compensated for by increases in others (Ernest and Brown 2001). These compensatory mechanisms can potentially result in disturbances having little influence on community-level properties despite large changes at the species level.

We currently lack an understanding of how the impacts of disturbance at the species level relate to widely studied community-level properties. Are strong responses at the species level closely coupled with strong changes at the community level or are the species- and community-level responses to disturbance decoupled? To address this question, we collected terrestrial animal community data from the published literature to assess whether species populations and community-level properties exhibited different sensitivities to disturbance events (Appendix A: Table A1). We evaluated the response of species-level population abundances, total abundance (N; total number of individuals in the community), species richness (S; number of species in the community), Simpson's evenness, and the rank species-abundance distribution (RAD; relative abundance of each species ranked from most to least abundant) to environmental changes. We used these species- and community-level measures to broadly test whether general patterns exist across communities in species-level and community-level responses to disturbance.

Methods

Database compilation

We conducted a literature search using Google Scholar in October 2011–February 2012 (for details see Appendix A). We accessed peer-reviewed articles, government publications, and theses that were freely available with the Utah State University library subscription and were published in English. We extracted data from articles that reported species-level abundance for a control community and at least one manipulated community. Published data were often summed or averaged over replicates, rather than reporting abundance separately for each replicate. For this reason, in our analyses, we used summarized data representing a single data point each for the control treatment and the manipulated treatment(s). Data came from a wide variety of sites including artificial experiments (i.e., caged exclosures, habitat modules, nutrient addition) and human-mediated "natural" experiments (e.g., wildfire or controlled burn, logging, grazed plots, pollution; Appendix A). Sites represent all continents except Antarctica, and widely varying terrestrial animal groups (arachnid, insect, herpetofauna [reptiles and amphibians], mammal, and bird; Fig. 1; Appendix A).

Data selection

We originally recorded data from 562 terrestrial animal communities representing 91 references. For this analysis, we eliminated communities where >10% of individuals were not identified to the species level or where the total area sampled for paired control–experiment communities was unequal. We used data where raw abundance was reported as a summed total for each species or where mean abundance was reported across the replicates, excluding percent cover, biomass, and presence-only data. When mean abundance was reported using inequality symbols (e.g., <0.01) we assumed the value was at the top of that range of potential values. Rank-abundance distributions are difficult to characterize when the number of species or total abundance is very low (McGill et al. 2007), so we included only communities with $S \geq 5$ and $N \geq 30$. We compared pairs of communities from sites that were sampled at the same spatial scales and at similar temporal scales (e.g., we did not compare data from different seasons or across a time series) to avoid complications due to differences in sampling intensity or timing (Gotelli and Colwell 2001, Magurran 2004). After filtering the data, there were 114 paired control–experiment comparisons from 41 published papers that met our criteria (59 controls, 112 experiments). Across studies, S ranged from 5 to 189 and N ranged from 30 to 6483.

Characterizing and comparing paired communities

The magnitude of change between a control and its experiment was calculated using the absolute value of the log ratio
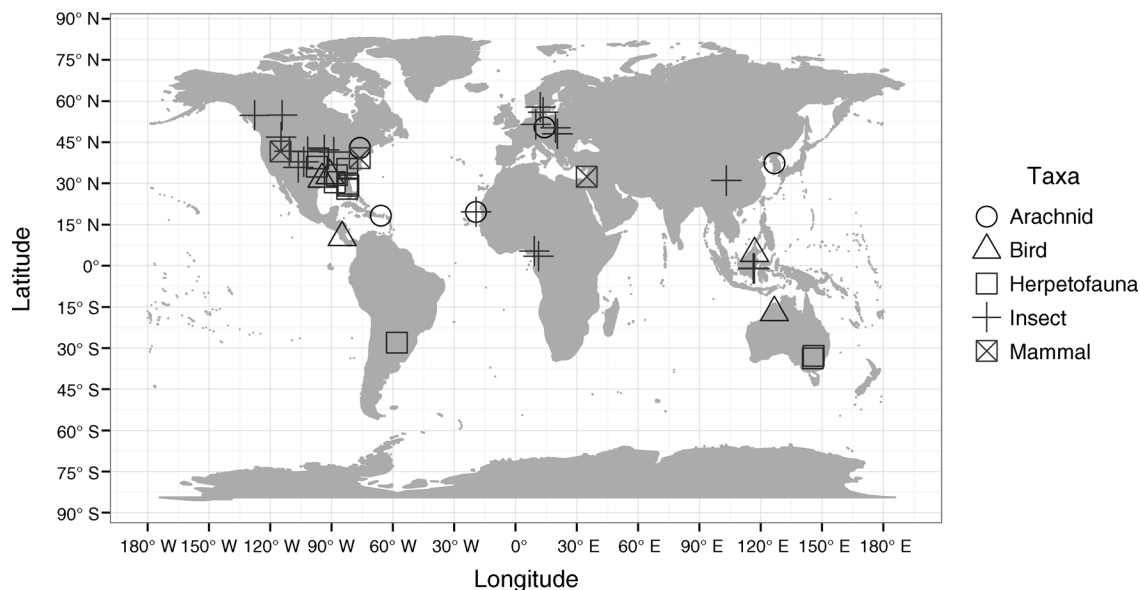
FIG. 1. Global map showing the locations and taxonomic group for each of the sites included in the study.

$$\text{absolute log ratio} = \left| \ln\left(\frac{x_{\text{experiment}}}{x_{\text{control}}} \right) \right|.$$

The log ratio measures the magnitude of difference between two values, often referred to as an effect size. For each control–experiment pair, we calculated an absolute log ratio for species richness, total abundance, and Simpson's evenness. The species-level response was calculated for each individual species by adding a constant to all raw abundances before calculating the relative abundance to account for zeroes in the data. We assessed two different constants: a small value (0.01), which reflected the minimum abundance level used in our data set, and a larger value (1.0). The small value emphasized species dynamics as a result of colonization or extinction events and the larger value effectively assumed species maintain at least one individual on a plot. For each constant, we took the median of the species-level absolute log ratios for a site to represent the average magnitude of response. To characterize the change in the rank-abundance distribution, which consists of the relative abundance of each species ranked from most to least abundant, we used the same approach that we used for the species-level response. We calculated the absolute value of the log ratio at each individual rank. We then calculated the median across the log ratios for that control–experiment pair to represent the average change across ranks. We focused primarily on the small constant value results for species level and rank abundance, but large value results can be found in Appendix C, along with additional metrics that were also assessed (i.e.,Bray-Curtis dissimilarity and percentage of change), which all exhibited similar qualitative results.

We could not employ a formal meta-analysis to test the significance of our responses, because we did not have data on the variance across replicates within a given treatment. However, the log ratio still provides a standardized metric for examining the magnitude and consistency of responses of species- and community-level properties to disturbance. We used the absolute value of the log ratio because our question focused on the magnitudes of responses at the species and community levels, not the directions. The lack of replicates prevented us from excluding spatial variability as a factor influencing differences between controls and manipulations. If our results reflect spatial variability across the landscape and not responses to disturbances such as clear-cutting and fire, it still supports the general framework that community-level properties are less sensitive than species abundances to environmental changes.

Statistical analysis

We compared the mean, median, and standard deviation of the log-ratio values to assess the magnitude in response observed across the species- and community-level metrics. We calculated Pearson's correlation coefficient to evaluate if responses across the five metrics were related to one another. Statistical analyses were conducted in R (R Development Core Team 2011). Data and all necessary code for replicating the results are available in the Supplement.

RESULTS

All of the 114 paired communities demonstrated strong responses in species-level population abundances to disturbance (Fig. 2a; median absolute log-ratio values ranged from 0.476 to 5.892). All but three communities
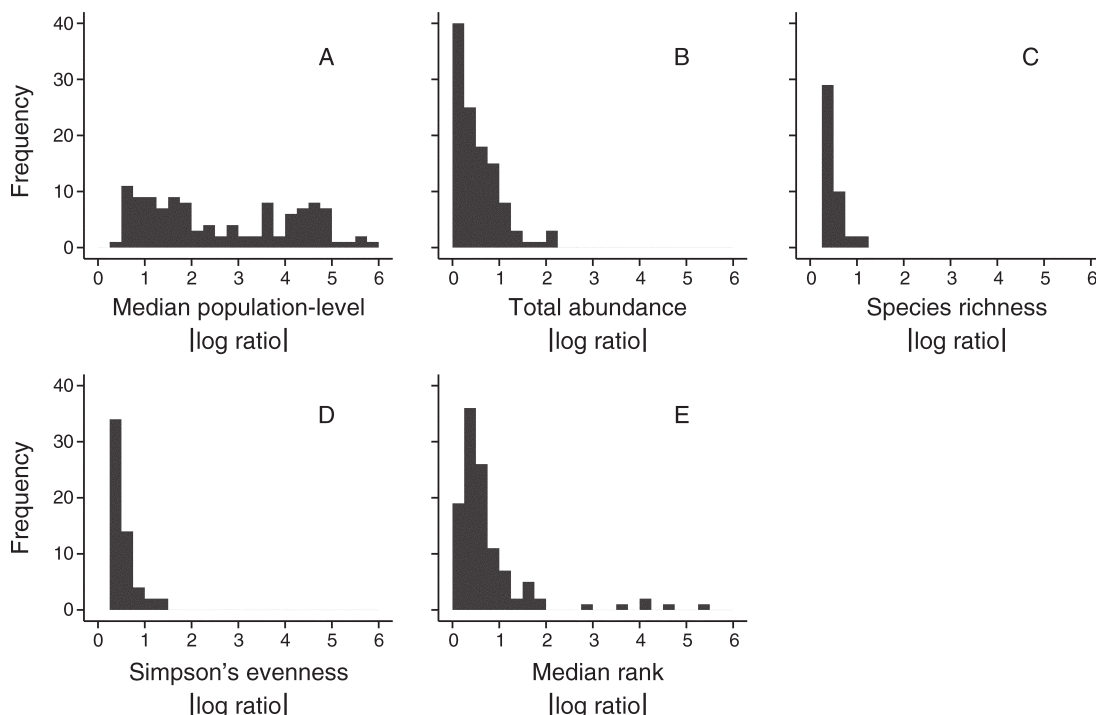
FIG. 2. Response of the biodiversity metrics among the paired control–experiment sites as absolute log-ratio values: (A) median species composition, (B) total abundance, (C) species richness, (D) Simpson's evenness, and (E) median relative abundance at each rank for compared rank-abundance distributions.

also experienced a change in total abundance (Fig. 2b; absolute log-ratio values ranged from 0 to 2.169), and almost 33% of all communities (37 paired communities) at least doubled or halved their total number of individuals in response to manipulation (absolute log ratio ≥0.693). Most communities experienced smaller magnitude change in species richness than in total abundance (Fig. 2c; absolute log-ratio values ranged from 0 to 1.056). Eleven sites demonstrated no change in species richness, and only 4% of sites (five paired communities) demonstrated at least a doubling or halving in the number of species. Changes were also generally smaller in magnitude for the abundance at each rank (Fig. 2e; absolute log-ratio values ranged from 0.018 to 5.311) in comparison with composition and for evenness of paired RADs (Fig. 2d; absolute log-ratio values ranged 0.006–1.491), in comparison with total abundance. All Simpson's evenness values differed among control–treatment pairs, and 11 sites demonstrated at least a doubling or halving in Simpson's evenness. Pearson's correlation coefficients were generally weak, suggesting a weak correlation between species-level and community-level responses (Fig. 3). Taxonomic group did not have a significant impact on the log-ratio response for any of the biodiversity metrics in our results (linear model, $P > 0.05$). Using the median and standard deviation of the log-ratio response (Appendix C: Table C1), we would rank response to disturbance, from greatest to least, as species popula-

tions (2.288, [1.577]; presented as median [SD]), relative rank abundance (0.508, [1.073]), total abundance (0.432, [0.476]), Simpson's evenness (0.247, [0.279]), and species richness (0.177, [0.220]). Using the larger constant value to adjust for zeroes in species-level and rank-abundance data generated similar qualitative results: species-level responses exceeded community-level responses. Adding the larger value reduced median effect size of species and ranks to disturbance, but resulted in a similar ordering: species populations (0.728, [0.346]), total abundance (0.432, [0.476]), relative rank abundance (0.421, [0.397]), Simpson's evenness (0.247, [0.279]), and species richness (0.177, [0.220]; Appendix C: Table C1).

DISCUSSION

Our results suggest that, in general, the largest magnitude responses to disturbance are observed at the species level (Fig. 2; Appendix C: Figs. C1 and C2). On average, a species was likely to exhibit an approximately ninefold change in its population size in response to a disturbance event (median log-ratio value = 2.288). Colonization and extinction events in response to the disturbance accounted for much of this variability. When we restricted the analysis to only species present in both the experiment and control plots (i.e., ignoring species that colonize or go extinct due to the disturbance), the median log-ratio values dropped to 0.715. (Appendix C: Fig. C5). Therefore, species that persist in the altered environmental conditions exhibited
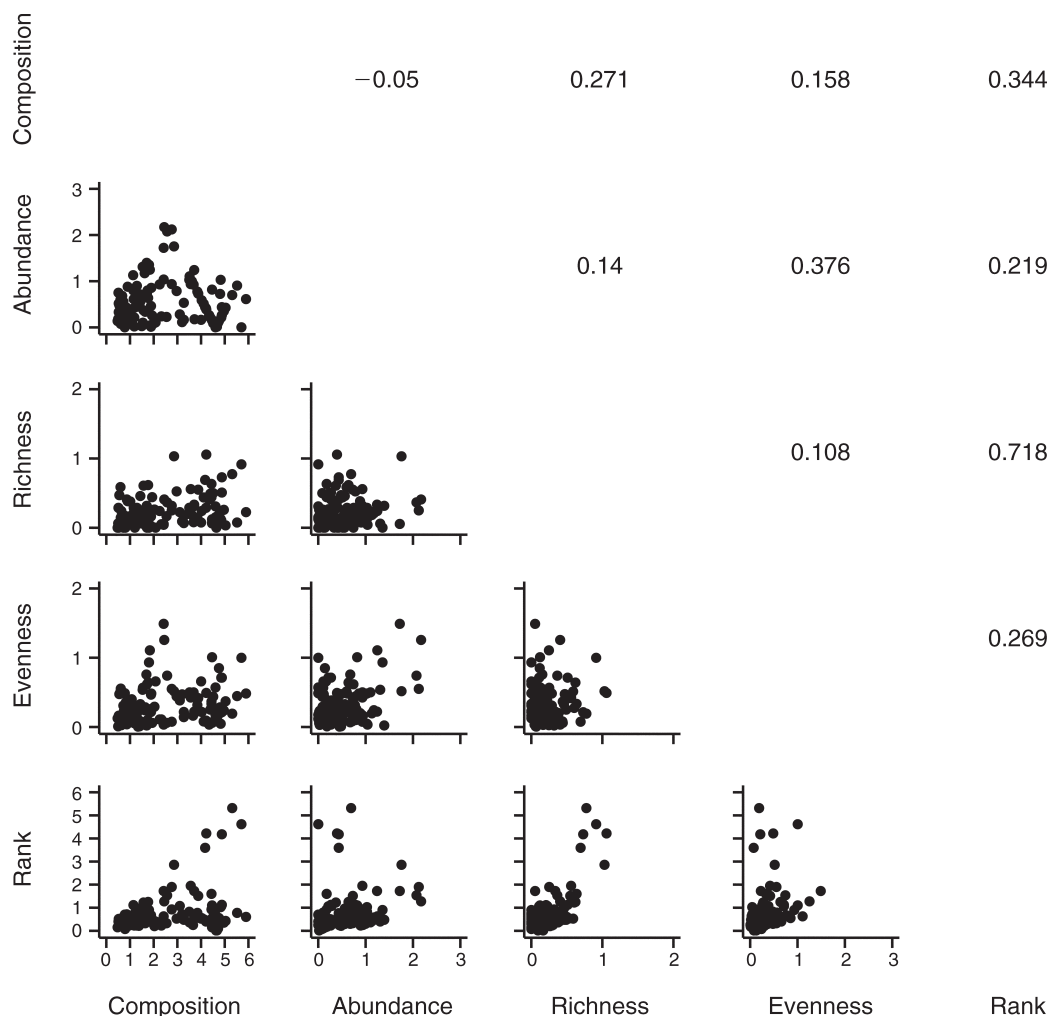
Fig. 3. Paired comparisons of the absolute log-ratio values for the species- and community-level properties. Pearson's correlation coefficient is shown in line with the paired variables (e.g., composition, abundance, richness).

an approximately twofold change in their population abundances. Clearly, changes in populations due to extinctions and colonizations are a major component of the species-level response to disturbance.

Reorganization at the level of individual species' populations did not result in equivalently large-magnitude changes in community-level properties. Only weak correlations generally existed among the species- and community-level measures (Fig. 3; Appendix C: Fig. C7). Community-level properties also exhibited smaller magnitude changes on average (Fig. 2): ~1.5-fold change in total abundance, ~1.2-fold change in species richness, ~1.3-fold change in species evenness, and ~1.6-fold change in the relative abundance at any given rank in the rank-abundance distribution. Large changes in the rank-abundance distribution appear to be driven primarily by changes in species richness (Fig. 3). As species richness increases or decreases, the community gains or loses ranks, and these lost or gained ranks drive much of the response we observed. When we examine

communities that have exhibited no change in species richness, the median log-ratio value drops to 0.402 (~1.5-fold change; Appendix C: Fig. C6). Taken together, our results suggest that changes in population sizes, and colonizations and extinctions will cause large species-level responses to the altered environment. However, changes in community-level properties are only weakly correlated with species-level dynamics. Therefore, it is reasonable to conclude that some process is mitigating the community-level impacts of species-level dynamics.

Compensatory dynamics occur when changes in the population of one species are offset by changes in the populations of other species. These compensatory dynamics can result from a balance between colonization–extinction dynamics or via adjustments in the populations of resident species. Compensatory dynamics have been implicated in other studies assessing stability of community-level properties and may be an important mechanism mitigating the effects of species-level dy-

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namics (Brown et al. 2001, Ernest and Brown 2001, Vasseur and Gaedke 2007, Gonzalez and Loreau 2009, but see Elmendorf and Harrison [2011]). If sites maintain adequate connectivity with regional species pools or if the species pool is relatively large, compensatory colonization–extinction dynamics may be possible through immigration (Chao and Jost 2012). If extinctions can be offset by colonizations, then relatively high-magnitude changes in species richness and the rank-abundance distribution may be rare (e.g., Ernest and Brown 2001, Gonzalez and Loreau 2009, Dornelas 2010). Similarly, diverse species traits within a community may allow population-level compensatory dynamics to maintain abundance-related community-level properties under changing environmental conditions (Ernest and Brown 2001).

While compensation-based explanations for the stability of community-level properties focus on niche-based mechanisms, alternative processes unrelated to the niche are possible. Stochastic colonization–extinction events (Elmendorf and Harrison 2011) and statistical averaging across independent populations (i.e., portfolio effect; Doak et al. 1998) have both been shown to be able to regulate community-level properties within relatively narrow bounds. Unfortunately, the nature of our data prevents us from distinguishing between niche-based and other mechanisms. However, understanding the mechanisms linking species- and community-level responses to disturbances is clearly an important next step.

The low-magnitude responses of species richness to disturbance are particularly intriguing, given conservation concerns about biodiversity. Decades of diversity experiments have manipulated species richness to study the impacts of species gain or loss on ecosystems (e.g., Naeem et al. 1995, Hector et al. 1999, Reich et al. 2012). However, we still generally lack an understanding of the magnitude of changes that occur in response to disturbance, or what magnitude of change in richness is biologically significant (Vellend et al. 2013). In our analysis, only one site experienced a doubling in species richness, (Lemieux and Lindgen 2004 [carabids in undisturbed forest vs. clear-cut forest]), and only four sites experienced a halving in species richness (Cleary et al. 2004 [lepidopterans in a large unburned forest vs. a slash and burn agricultural area], Bobo et al. 2006 [lepidopterans in primary forest vs. agriculture with few trees], Skalski et al. 2010 [carabids far from vs. near to mining pollution], and Styring et al. 2011 [birds in logged native forest vs. exotic tree plantations]). This result raises the important question of what diversity experiments actually reveal about ecological response to disturbance if the magnitude of species richness change studied experimentally is often much larger than what is observed in nature. Instead, our results suggest that perhaps future research should focus on how ecosystem function responds to changes in individual species (Srivastava and Vellend 2005, Cardinale et al. 2006,

Pereira et al. 2012) and on which processes allow species richness to be maintained when disturbances cause species-level reorganization.

A major challenge facing biodiversity research is to understand how changes at the species level scale up to impact community and ecosystem properties. Our results suggest that to some degree, species-level responses to disturbance may offset each other; colonization offsets extinction and population increases offset population decreases. This results in surprising constancy in community-level properties. Our results suggest two important paths forward for biodiversity research linking species dynamics with community-level properties. First, we need a better understanding of the mechanistic or stochastic processes behind the maintenance of community-level properties. Second, we need a better understanding of what magnitude of change in community-level properties reflects fundamental shifts in the operation of a community. Because our results suggest that species richness, evenness, and the form of the RAD are relatively resilient to disturbance, we suggest that even potentially low-magnitude shifts may indicate fundamental species-level changes that warrant further study and attention.

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SUPPLEMENTAL MATERIAL

Appendix A

Metadata and data for the communities included in the analysis (*Ecological Archives* E095-151-A1).

Appendix B

Figures for the paired community data represented as rank-abundance distributions (*Ecological Archives* E095-151-A2).

Appendix C

Supplementary figures and tables for species- and community-level diversity (*Ecological Archives* E095-151-A3).

Supplement

Details on the computational analyses needed to replicate the results (*Ecological Archives* E095-151-S1).