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Isolation predicts compositional change after discrete disturbances in a global meta-study

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Abstract

Globally, anthropogenic disturbances are occurring at unprecedented rates and over extensive spatial and temporal scales. Human activities also affect natural disturbances, prompting shifts in their timing and intensities. Thus, there is an urgent need to understand and predict the response of ecosystems to disturbance. In this study, we investigated whether there are general determinants of community response to disturbance across different community types, locations, and disturbance events. We compiled 14 case studies of community response to disturbance from four continents, twelve aquatic and terrestrial ecosystem types, and eight different types of disturbance. We used community compositional differences and species richness to indicate community response. We used mixed-effects modeling to test the relationship between each of these response metrics and four potential explanatory factors: regional species pool size, isolation, number of generations passed, and relative disturbance intensity. We found that compositional similarity was higher between pre- and post-disturbance communities when the disturbed community was connected to adjacent undisturbed habitat. The number of generations that had passed since the disturbance event was a significant, but weak, predictor of community compositional change; two communities were responsible for the observed relationship. We found no significant relationships between the factors we tested and changes in species richness. To our knowledge, this is the first attempt to search for general drivers of community resilience from a diverse set of case studies. The strength of the relationship between compositional change and isolation suggests that it may be informative in resilience research and biodiversity management.

Keywords: *meta-analysis, resilience, resistance, richness, compositional dissimilarity, disturbance, recovery, community diversity, connectivity*

Introduction

Pervasive human modification of ecosystems is causing shifts in the type, frequency, extent, and intensity of disturbance at a global scale (Ellis and Ramankutty 2007). As disturbance regimes change, understanding how ecosystems, communities, and populations change as a result of discrete disturbances has become an imperative for ecological research. Several ecological concepts have arisen to quantify aspects of community response to disturbance (see Pimm 1984; Grimm and Wissel 1997; Brand and Jax 2007). Three of the most commonly applied concepts are resistance, defined as the degree to which a variable (e.g. species composition) is changed following a disturbance (Pimm 1984); engineering resilience, defined as the time taken for an ecosystem to return to its pre-disturbance state following a disturbance (Pimm 1984) and widely interpreted as ‘recovery’ (Standish *et al.* 2014); and ecological resilience, defined as the ability of an ecosystem to absorb changes in state or controlling variables and to persist after disturbance (Holling 1973). Ultimately, these concepts aim to address a single broader question around community response to disturbance—how changed will a community be after a disturbance compared with its pre-disturbance state?

How a community changes after a disturbance is determined by multiple factors encompassing the attributes of both the community and the disturbance itself. Community attributes influence the trajectory of the community after disturbance. For instance, high species diversity is expected to increase post-disturbance community similarity to pre-disturbance states through increased response diversity (Elmqvist *et al.* 2003) and functional redundancy (Peterson *et al.* 1998). Regional diversity, on the other hand, may increase the importance of priority effects (Fukami 2015), leading to alternative recovery trajectories based on arrival order or survival status. At a landscape scale, connectivity with undisturbed communities can provide propagule sources necessary for recolonization post-disturbance (Cramer *et al.* 2008; Standish *et al.* 2014). Mechanisms like these potentially increase the resistance of the community (i.e., dampen the initial community change post-disturbance), hasten recovery after the disturbance, or both (**Figure 1**).

Additionally, the attributes of the disturbance can impact community change. A disturbance is defined by a few key characteristics: temporal scale (duration), spatial scale (extent), frequency, intensity (Pickett and White 1985), and timing (Lytle 2001). Each attribute can influence community changes post-disturbance, with longer, larger and more intense disturbances causing greater changes in community composition that persist for longer (Turner *et al.* 1998; Hobbs *et al.* 2006). Alternatively, the effects of the disturbance may fade rapidly, resulting in a strong difference initially, but a short recovery to the pre-disturbance state. Additionally, the most intense disturbances may fundamentally alter abiotic or biotic resources; for example higher intensity flooding may scour substrates from freshwater communities (Bornette and Puijalon 2011), or longer grazing regimes may deplete seed banks (Hobbs *et al.* 2006). These chronic shifts may lead to permanent changes in the community (**Figure 1**).

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Finally, time plays an important role in the change between pre- and post-disturbance communities. Equilibrium-based theories of community dynamics hypothesize that communities return to a pre-disturbance state predictably through time (Pimm 1984) if prevailing abiotic conditions and available species pools remain constant. Succession theory hypothesizes similar dynamics, with the added complexity of an initial flush of fast-colonizing species that are succeeded through time by more competitive species that characterized the pre-disturbance community (Connell 1978; Huston and Smith 1987). However, there is a lack of evidence supporting single equilibrium-based successional dynamics (Wu and Loucks 1995). Community assembly theory has driven some of these developments, by providing evidence of a more complex relationship with time, in which species establishment depends on chance, historical patterns, dispersal, abiotic factors, and biotic interactions (Gleason 1926; Götzenberger *et al.* 2012). Trajectories of community development are modified by each of these factors, and many opportunities exist for a community to develop towards a new state rather than return to the pre-disturbance state, often confounding estimates of recovery. Taken together, the set of theoretical frameworks suggest an uncertain relationship between community change post-disturbance and the amount of time that has passed since the disturbance (**Figure 1**).

Studies of community response to disturbance tend to focus on a subset of the different attributes of community change post-disturbance. For example, studies on fire ecology tend to focus on detailed attributes of the disturbance and either post-disturbance development through time (e.g. Abella and Fornwalt 2015) or initial response based on functional group distributions (e.g. Lamont *et al.* 1999). In this study, we quantify the relative importance of a broad spectrum of potential factors by including time, disturbance- and community-based attributes on community recovery using data from multiple datasets. We do so over a range of communities and disturbance types. We focus on four variables refined from a wide range of possible collinear covariates: disturbance intensity, time since disturbance, connectivity, and species richness. We hypothesized that general relationships between community recovery and one or more predictors could be found in the case studies considered, including plant, animal, terrestrial, and marine communities over a global geographic extent and following a variety of disturbance types. Specifically, we hypothesized that community differences post-disturbance would be greatest following higher intensity disturbances and would decrease with time and higher species richness, and increase with isolation from the surrounding landscape.

Methods

Data compilation

Data sets were compiled across a variety of ecosystem and disturbance types. Requirements for inclusion were: community composition data for a control (i.e., data describing the pre-disturbance state) and the same data for at least one time point post-disturbance. The control could either be a temporal control – data from the sampling area before the disturbance – or a spatial control – an undisturbed sampling area deemed appropriate to use as a reference location. The disturbance had to be temporally discrete, to enable an

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assessment of community change post-disturbance. Because of the need for raw composition data and detailed involvement of study authors, a comprehensive meta-analysis was not conducted. Rather, a generalized meta-study over globally distributed data was performed. Fourteen authors with their existing datasets were recruited to the project (**Table 1**) based on publications of the appropriate study type. When split by site, this resulted in 27 points of post-disturbance data. For individual sites, we used one post-disturbance time point. The studies spanned a wide range of organisms from plant to animal communities and covered eleven regions around the globe. Some studies included presence-absence data only, while others also included cover or the number of individuals. Studies ranged in time from one reproductive event for annual plants to more than a dozen reproductive events encompassing several full generations of snail communities. Details of each study are provided in **Appendix S1** in Supporting Information.

Response variables

The data were used to calculate two response variables: the difference in species composition (as measured by compositional dissimilarity) between pre- and post-disturbance communities and the difference in species richness. Distance metrics such as the one we calculated compress multivariate community data into a univariate metric commonly used by ecologists to capture how similar or different communities are to each other (Clarke 1993). We acknowledge that community composition may not necessarily return to its pre-disturbance state, even in very resilient communities, and particularly in situations where the sequence in which species (re)colonise strongly affects the trajectory of community assembly (Chase 2003). In cases where priority effects have been observed, the functional (i.e. based on species characteristics rather than species identity) and structural composition of a community are less sensitive to community assembly dynamics compared with species composition (Fukami *et al.* 2005). However, despite some empirical evidence for priority effects, such effects are not universal and appear to occur most strongly between phylogenetically related species (Peay *et al.* 2011) or between species that have adapted to similar functional roles (Urban and Meester 2009). Additionally, priority effects are strongest when a community is 'wiped clean' by a disturbance (Fukami 2015). The disturbances considered here left survivors and *in situ* propagules, likely influencing the community to return to a similar compositional state. Although it would have been ideal to evaluate functional change to compare with compositional change, a lack of trait data prevented that method.

Species richness, on the other hand, provides one of the simplest univariate measures of community diversity (Magurran 1988). There are drawbacks to considering richness alone: species identity and abundance are ignored, even in the cases where communities may change dramatically with species changes. A simple example is biological invasions, where the introduction of a single species such as *Myrica faya* in Hawaiian volcanic communities leads to completely different community trajectories than one in which it is absent (Vitousek and Walker 1989). Despite these issues, species richness is commonly used to prioritize

conservation areas (Myers *et al.* 2000) and has been tied to important ecological processes such as productivity (Mittelbach *et al.* 2001). Because of its simplicity and ecological importance, we investigated species richness changes post-disturbance. We aimed to compare results for richness with those of dissimilarity metric, a metric that does not share many of the same issues as richness on its own.

Raw data were provided by each author, and the response variables were calculated for each plot (controls and post-disturbance). Dissimilarity was calculated as the Bray-Curtis dissimilarity of each plot to the compositional centroid of the control communities, which was calculated through a modification of betadisper in vegan in R (Oksanen *et al.* 2013). Species richness was the number of species present in each study. Both response variables were then transformed for meta-analysis using the Hedges g variable (Hedges and Olkin 1985). The Hedges g calculation allows multiple data points to be condensed into a single continuous value for each study while taking into consideration the differing variances among datasets. It is calculated as the difference between control and post-disturbance means divided by the pooled standard deviation, with a correction for small sample bias:

$$s_{pooled} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}$$
$$g = \frac{\bar{x}_1 - \bar{x}_2}{s_{pooled}}$$
$$J(n) = \frac{\Gamma(n/2)}{\sqrt{n/2} \Gamma((n-1)/2)}$$
$$g_{corrected} = g \times J(n_1 + n_2 - 2)$$

where n is the total number of samples in the study; n_1 , s_1 , and \bar{x}_1 are the number of samples, standard deviation, and mean of the response in treatment 1; n_2 , s_2 , \bar{x}_2 are the number of samples, standard deviation, and mean of the response in treatment 2; s_{pooled} is the pooled standard deviation; g is the Hedges g statistics; $J(n)$ is the correction factor where Γ is the Gamma function; and $g_{corrected}$ is the Hedges g weighted by the correction factor. The $g_{corrected}$ value is the final variable used as a response in the meta-analysis.

Explanatory variables

Available data contributors convened in December 2013 to discuss and agree on a set of generalizable explanatory variables. A wide range of variables were initially considered based on knowledge of their data and the literature specific to their ecosystem (see **Appendix S2** in Supporting Information for full details). The number of variables was then refined by grouping those with common attributes and removing collinearity. In all of the ecosystems considered, four variables captured the key attributes underlying community change post-disturbance (i.e., community attributes, disturbance attributes and time). The four variables included size of the regional species pool, connectivity of the landscape, disturbance intensity, and time since disturbance. Size of the species pool and connectivity of the landscape were selected to capture the

community attributes. Both variables have been explored extensively for their relationships with community stability (e.g. McCann 2000 for richness; e.g. Starzomski and Srivastava 2007 for connectivity) and offer inherent attributes of communities that are relatively easy to measure. Disturbance intensity was selected to capture the disturbance. Our dataset captured a broad range of data in which other attributes of disturbance such as duration or timing were only sporadically relevant. Intensity, however, was a characteristic relevant to all our studies of community response to disturbance. Finally, to capture potential for recovery we included time since disturbance.

The taxonomic pool (usually species) was estimated by summing the number of unique species found in all of the study plots, both control and disturbed. For coral communities, species-level data was not available, so these calculations were made at the genus level. Connectivity was captured in a simplified manner measuring whether the disturbed community was isolated from other undisturbed communities. In landscape ecology, connectivity is split into structural connectivity, or the physical characteristics of a landscape that allow for movement, and functional connectivity, or how well genes, individuals, or population move through the landscape (Rudnick *et al.* 2012). Both forms of connectivity depend on the species of interest as well as the landscape under consideration and are impossible to generalize between communities, much less between communities of entirely different taxa. Isolation as we defined it is thus a simplified metric of structural connectivity that ignores species-specific requirements. However, it is easily compared among studies while still capturing an ecologically meaningful trait, that is, whether propagule sources were confined solely to the disturbed area. This was particularly relevant for the datasets we considered, as no large-scale or highly mobile animals were included outside of fish, with a clear connection to propagule sources, and coral, with a measured isolation from propagule sources. Isolation was measured as a binary variable: if 100% of the community extent was covered by the disturbance, the community was considered isolated. If only a portion of the intact community was affected by the disturbance, the community was considered connected.

Disturbance intensity was quantified relative to previous disturbances of the same type. For example, the strength of a hurricane was expressed as the maximum wind speed of the hurricane compared with the average wind speed of hurricanes in the region for the past century. Time since disturbance could not be captured in a single generalizable unit and was standardised according to community life histories. For example, three months in a microarthropod community is very different than three months in a coral reef community. Thus, time since disturbance was divided by the weighted average generation time of the organisms in each community to derive a standard measure. This measure was derived from an estimate of generation time for each species in each study. Plant species estimates were based on life form. Trees were assigned 100 years per generation, shrubs 30 years, perennial herbs 5 years, and annuals or biennials 1 or 2 years respectively. For other organisms, we used maximum lifespan where the data was available in the literature. We tallied the number of plots in which each species was recorded, then calculated a weighted

average based on their frequency. For microarthropods, there is too little information on individual species life histories, though they are known to range from weeks to years (Krantz *et al.* 2009). A general estimate of four months was used. Additionally, distinguishing coral species is difficult (Gilmour, *et al.* 2016; Richards, *et al.* 2016; Wallace 1999) and the turnover times for populations vary widely according to their diverse life histories (Darling, *et al.* 2012; Madin, *et al.* 2016). For the most abundant populations, turnover times are likely in the order of 20 years and so we used that value as our estimated generation time. Finally, the three continuous variables – disturbance intensity, species pool, and time since disturbance (*i.e.* the average number of generations passed since the disturbance) – were standardized by subtracting their respective means and dividing by their respective standard deviations. Standardisation allowed direct comparison of coefficient estimates.

Statistical analysis

Explanatory variables were checked for collinearity and were found to be adequately orthogonal (variance inflation factors all less than 1.4) . We ran separate linear mixed-effects models for the two response variables. Because a few studies had multiple points, or authors had provided multiple sites within a similar region, we included the location of the study as a random effect. Additionally, we tested models based on a quasi-Gaussian distribution (Wedderburn 1974) for a potentially better fit to the response data. There was no significant improvement using this approach and so we returned to the linear methods. Given the potential non-linear relationships between recovery and time (**Figure 1**), we also tested a nonlinear model. We ran a Generalized Additive Mixed-effects Model using the *mgcv* package in R (Wood, 2007), with a smoother included around the time-since-disturbance variable. The result was a linear relationship; the smoother returned only one degree of freedom and was subsequently removed. Final models were validated by checking the residuals against the fitted values and each of the explanatory variables (Zuur *et al.* 2009) as well as checking residuals for normality using a Shapiro-Wilks test and diagnostics plots. Additionally, we removed single studies and reran the models to assess the sensitivity of model results to each dataset and to investigate the influence of outliers. We used the package *lme4* (Bates *et al.* 2014) in the statistical program R (R Core Team 2014) for the analysis.

Results

Compositional dissimilarity results ranged over the studies from almost no similarity to the controls (dissimilarity = 0.65) in wetlands seven years after Hurricane Katrina to almost complete similarity to the controls (dissimilarity = 0.05) in forest two years after Hurricane Gilbert (**Table 1**). There were changes in species richness in all but four of the 27 studies. Of those, 12 had more species in communities post-disturbance than in undisturbed communities, and 11 had fewer species in communities post-disturbance (**Table 1**). The highest number of species gained was in rangeland after an intense grazing event, where undisturbed controls averaged eight species and post-disturbance communities averaged 20 species. The

largest loss of species occurred in disturbed moss systems, where undisturbed microarthropod communities averaged 38 species, while post-disturbance communities averaged 17.

We found that connected communities were significantly more similar to control communities post-disturbance than isolated communities (**Table 2**). The coefficient estimate for the isolation variable was around three times larger (in absolute terms) than the next largest coefficient (**Table 2**). Time since disturbance was also significantly correlated with similarity – the more generations that passed, the more similar the controls to the disturbed communities (**Figure 2**). However, the coefficient estimate of this variable was small and the sensitivity test showed that the significance was driven by two outliers: the study with the highest number of generations (snail community response after clearcutting), and the study with the highest Hedges *g* value for compositional dissimilarity (rangeland after summer grazing). Disturbance intensity and species pool size were not significantly related to compositional similarity.

Changes in richness after disturbance were not significantly correlated with any of the four explanatory variables: size of the species pool, isolation, number of generations passed, or relative disturbance intensity. Sensitivity tests did not alter the results for the richness model, though the coefficient estimate of the species pool variable changed when the study with the largest species pool was removed (**Figure 3**), becoming large and negative.

Discussion

From this diverse dataset came one strong signal – isolation from surrounding landscapes/seascapes was significantly correlated with compositional dissimilarity between pre-disturbance and post-disturbance communities. Isolated communities within the dataset ranged from overgrazed rangelands to experimentally disturbed moss-microarthropod communities to wetlands impacted by Hurricane Katrina. The variety of communities and disturbance types within these studies supports the generality of our findings. Research on corridors and landscape configuration has long shown ecological benefits of connectivity. Species populations are maintained through time by connectivity with dispersing populations (Damschen *et al.* 2006; Valanko *et al.* 2015). When species are lost or densities critically lowered post-disturbance, inputs from connected landscapes can prevent species losses (Heller and Zavaleta 2009). Additionally, abiotic and biotic flows can support community function in disturbed communities (Standish *et al.* 2014) such as increased rainfall near intact vegetation stands (Lyons 2002) or influxes of dispersers and pollinators from adjacent communities (Lundberg and Moberg 2003).

In parallel, isolation has been linked with degradation from edge effects, species loss, and shifts in historical disturbance regimes (Turner 1989, Debinski and Holt 2000). Each of these factors may independently alter the response of a community to disturbance events. For example, the increased prevalence of non-native

species in edges may lead to rapid changes in a post-disturbance community as the non-natives increase opportunistically (Didham *et al.* 2007); species losses may restrict the role of compensatory dynamics (Loreau *et al.* 2001); and loss of disturbances such as fire may lead to the loss of reproductive cues (*e.g.* Yates and Ladd 2002) and local heterogeneity (Turner 2010). Thus, disturbed communities in connected landscapes are more likely to experience species inputs and pre-disturbance conditions that speed recovery, whereas isolated communities are more likely to experience novel species dynamics and additional stressors that inhibit resistance and recovery (**Figure 1, Panel B**). Human land use is increasingly fragmenting landscapes globally, leading to higher levels of isolated and shrinking habitat patches (Fahrig 2003). Given our results and the many studies on direct and indirect impacts of fragmentation (*e.g.* Andren 1994, Honnay *et al.* 2005, Levey *et al.* 2016), it is clear that landscape context is a major factor in community response to disturbance that should be explicitly considered across scales of management.

One major exception to the importance of isolation stood out in our dataset. Coral communities showed high similarity to pre-disturbance communities after bleaching despite isolation from any external propagule source (Gilmour *et al.* 2013). The particular example in Scott Reef emphasises the importance of biotic legacies in a community such as remnant corals or propagule banks. Seed banks and surviving individuals in plant communities or surviving individuals in animal communities play a similar role on land (Tanner and Bellingham 2006), again with biotic legacies likely acting to increase the speed of community recovery (**Figure 1, Panel B**). Isolation in the case of Scott Reef also meant reduced exposure to the many anthropogenic disturbances that add significantly to the disturbance regime of reef communities closer to shore. However, the recovery of coral assemblages at Scott Reef still clearly relied on the patterns of local connectivity, which had profound implications for the recovery of coral assemblages with contrasting dispersal potential (Done *et al.* 2015). So while connected communities may generally show less change post-disturbance than isolated ones, there must still be some contextualization for individual communities.

We found no significant relationship between the explanatory variables and changes in species richness. Conservation work is commonly aimed at preserving biodiversity levels, often through a simple measure of the species richness in a community (Fleishman *et al.* 2006). For such conservation approaches to be effective in the long term, we require a better understanding of how species richness reflects community responses to disturbance. Many studies report a disconnect between metrics that ignore species identity and other indicators of the community dynamics (*e.g.* Magurran and Henderson 2010) as well as pitfalls in the measurement and quantification of metrics like species richness (Gotelli and Colwell 2001, Fleishman *et al.* 2006). Our results agree with these findings. We found no general response of species richness to disturbance; almost an equal number of communities exhibited increases in species richness as decreases post-disturbance. Additionally, we found no significant relationship between species richness and the

explanatory variables. If species identity is more important than species richness for determining community-level response, then the impact of potential drivers as outlined in **Figure 1** may not apply to how species richness will change post-disturbance. Rather, the mechanisms behind richness patterns may be more complex than other measures of response to disturbance, and important community-specific interactions between drivers of richness (*e.g.* the interaction between disturbance and connectivity; Alstad and Damschen 2016) may need more detailed data than those available for this study. The known importance of species identity in other community patterns, coupled with the complexity of species richness patterns (Cardinale *et al.* 2006) suggests that the use of species richness as a response metric is potentially meaningless in some instances and should be complemented by additional metrics.

Species pool size and relative disturbance intensity with compositional change were also weak or absent in our results. Contrary to our hypothesis, relative disturbance intensity showed no relationship with community changes post-disturbance. Higher intensity disturbances may have implications for both the initial change post-disturbance as well as the long-term recovery (Turner *et al.* 1998). The intensities considered here, however, may not have captured enough variation, or the scale used may not have been appropriate for elucidating these dynamics. Additionally, the size of the species pool had no relationship with community change post-disturbance. Species diversity is generally hypothesized to aid community recovery through response diversity and functional redundancy (Elmqvist *et al.* 2003). These two traits both focus on how local diversity influences the return of community function, not community composition. The role of diversity in compositional return has been discussed in community assembly theory, where increased regional richness may increase the importance of species arrival order (Chase 2003). We defined local species richness as any species surveyed in a single study. At times, this included sites that were separated by distance and/or physical barriers, which may more accurately capture regional species richness (see Pärtel *et al.* 1996 for definitions of regional vs local species pools). Most communities in this study were also influenced by survivors and *in situ* propagules, offsetting assembly rule dynamics. The combination of all these factors, and of the limited manner in which we could define richness, could potentially mask any clear role that richness may play in compositional return. For future studies, it is important to determine the scale at which ‘local richness’ is assessed relative to the regional species pool (Fukami 2015), as is the consistent measurement of both among study units; this may be the only way to distinguish the unique roles that different types of richness play in local dynamics.

Time had a weak relationship with community change. Given that there are many hypotheses about how recovery processes play out in a community after a disturbance (**Figure 1**), it is unsurprising that no strong signal emerged from our data. Overall, composition was more similar to the pre-disturbance state as more generations passed. This relationship, however, was driven by two studies. The first spanned the most generations. Snail communities, with an average estimated generation time of less than three years, were

studied 40 years after a logging event (Ström *et al.* 2009) and were compositionally similar to pre-disturbance communities (this study). The second study had the largest Hedges g value of compositional dissimilarity and occurred in seasonally grazed rangelands. Recovery post-disturbance can be altered by the timing of the disturbance (*e.g.* Pakeman and Small 2005). Bestelmeyer *et al.* (2013) tested both winter and summer grazing impacts in the same rangeland system, datapoints from both of which have been included in this study. The point with the large Hedges g value is the winter-grazed treatment. The authors found that winter grazing elevated post-disturbance exposure to harsh environmental conditions, leading to higher mortality and slower recovery of the dominant grass species. Thus, the large compositional distance may be attributed to the disturbance season and its impact on dominants rather than the short time since disturbance. Though we did not have enough data to test the relative role of timing in driving community response to disturbance, it is an important factor to understand as global change continues to shift the timing of extreme events (IPCC 2007, Rahmstorf and Coumou 2011). Additionally, the importance of two outlier points in shaping the relationship between time and community change call for further research to determine the nature of that relationship.

One complexity of time as an explanatory variable is that life history traits may slow community response to scales not captured in this study. For example, the Jamaican forest grew increasingly dissimilar over 15 years post-Hurricane Gilbert as the damaged trees experienced delayed mortality and as newly recruited stems grew into the minimum size class for measurement (Tanner and Bellingham 2006). Though we considered generation time in our estimate of time since disturbance, data for a full generational turnover was unavailable in some datasets and could be important to capture predicted dynamics (Connell and Sousa 1983). The availability of this kind of data is limited for long-lived communities and management concerns are likely to be shorter than the centuries required by some communities. However, consideration of short-term community change through time must be informed by an understanding of longer-term processes.

Larger datasets on effects of disturbance on species composition are slowly becoming available (*e.g.* the PREDICTS database: Hudson *et al.* 2014) and may capture the long term dynamics needed to study broad relationships between community change post-disturbance and time. Larger dataset collections would also allow repetition of disturbance types and taxa, consideration of further important covariates like sampling scale, and the inclusion of interactions between explanatory variables. However, such data have to be paired with generalized explanatory variables to make sense of community responses to disturbance. A single measurement of disturbance intensity between grazing, hurricanes, or logging, for instance, is necessary for the development of broad, testable theory around resistance and recovery (Marquet *et al.* 2014). Our solution to this problem was to estimate relative disturbance intensity, and we acknowledge that it is imperfect because disturbances that had never previously occurred in a community had to be assigned a high intensity dummy value. Similarly, connectivity was simplified to a binary isolation variable. This leaves out all complex issues of functional connectivity versus structural connectivity that vary across taxa (Rudnick *et al.* 2012), making it

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applicable to all datasets but particularly blunt in the ecological effects it captures. Whether ecological variables and relationships are truly generalizable to such an extent in this context is largely unknown, though the strong, predicted relationship with isolation shows promise in this regard.

Our data spans four continents, half a dozen aquatic and terrestrial ecosystem types, and a dozen different types of disturbance to assess community response to disturbance as measured by the amount of change between pre- and post-disturbance communities. This metric bundles the initial response of the community, i.e. the community resistance (Pimm 1984), with the longer-term response that can encompass community recovery and resilience (i.e., engineering resilience and ecological resilience), in addition to other measures of stability (e.g. see Pimm 1984; Grimm and Wissel 1997). The search for influences on broad community response to disturbance is of theoretical and practical interest. Our conclusions support the broad, generalizable role that connectivity has in community response to disturbance. This was not a comprehensive meta-analysis due to limitations in available data, and the dataset size makes drawing strong conclusions from complex analyses difficult. The results emphasize the potential for testing over a broad extent, and call for the standardised measure of generalizable variables such as those we have identified here, to create the large, cross-system datasets that are considered useful for progressing ecological theory (Marquet *et al.* 2014).

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Table 1: List of studies used in meta-analysis. The reference (where data published) is given in the first column; the author's name is listed if the study is unpublished. The organism, location, data type (where PA = presence-absence; AC = abundance measured as cover; AF = abundance measured as frequency), disturbance type, maximum time since disturbance, type of control, and number of datapoints from the study are also listed. Only one time point post-disturbance was taken for each study. However, some studies had separated sites with differing abiotic conditions that allowed the use of multiple data points. The last two columns list response results for each of the studies, dissimilarity and the change in species richness. Studies with more than one data point have been listed as individual datapoints with a brief description of treatment identifier. For full details of the treatments, please see individual references. The Hedges g response values were calculated from these values and the corresponding control values for each dataset.

Study	Organism	Location	Data type	Disturbance	Max Time	Control	Data Points	Compositional Dissimilarity	Change in Species Richness
Dwyer <i>et al.</i> 2010	Plant (forest)	Queensland, Australia	AF	Ringbarking	40 years	Spatial	1	0.46	-3.5
Bestelmeyer <i>et al.</i> 2013	Plant (perennial)	New Mexico, United States	AC	Grazing	9 years	Spatial	2	0.65 (winter grazing) 0.47 (summer grazing)	13.3 (winter grazing) 4.6 (summer grazing)
Åström <i>et al.</i> 2007	Plant (bryophyte)	Sweden	AF	Clear cut	22 years (south facing) 5 years (north facing)	Spatial	2	0.29 (south facing) 0.19 (north facing)	-0.5 (south facing) 4.5 (north facing)
Dynesius <i>et al.</i> 2009	Plant (bryophyte)	Sweden	PA	Clear cut	35 years (streamside) 50 years (upland)	Spatial	2	0.42 (streamside) 0.33 (upland)	-5.5 (streamside) -8.2 (upland)
Ström <i>et al.</i> 2009	Animal (snails)	Sweden	AF	Clear cut	40 years	Spatial	1	0.57	1
Starzomski and Srivastava 2007	Animal (microarthropods)	British Columbia, Canada	AF	Drought/h eat	4 months	Spatial	4 (by spatial extent of disturbance)	0.33 (sm) 0.3 (med) 0.28 (lg) 0.64 (total)	-7.2 (sm) -6.4 (med) -9.4 (lg) -20.6 (total)
Battaglia,	Plant	Florida,	AC	Saline	3 years	Tempor	5 (by	0.44 (dist 1)	0.67 (dist

Loretta L. (unpublished)	(perennial)	United States		flood		al	distance from sea, close to far)	0.38 (dist 2) 0.42 (dist 3) 0.53 (dist 4) 0.37 (dist 5)	1) 4 (dist 2) 1 (dist 3) 3.4 (dist 4) -0.1 (dist 5)
Foster, Marc A. and Battaglia, Loretta L. (unpublished)	Plant (perennial)	Mississippi, United States	PA	Hurricane	7 years	Temporal	2	0.22 (windthrow) 0.65 (windthrow + flood)	-0.67 (windthrow) -4.57 (windthrow + flood)
Becker <i>et al.</i> 2009	Animal (fish)	Victoria, Australia	AF	Anoxia	9 months	Temporal	1	0.67	0.33
Tanner and Bellingham 2006	Plant (forest)	Jamaica	AF	Hurricane	2 years (site 1) 15 years (site 2)	Temporal	2 (by location on island)	0.05 (site 1) 0.2 (site 2)	-0.57 (site 1) -1.1 (site 2)
Gilmour <i>et al.</i> 2013	Animal (coral)	Western Australia, Australia	AC	Bleaching	12 years	Temporal	1	0.34	1.33
Hobbs and Mooney 1991; plus additional datapoints to 2010	Plant (annual-perennial)	California, United States	AC	Gopher digging	3 years	Temporal	1	0.64	0.69
Price <i>et al.</i> 2011	Plant (annual-perennial)	New South Wales, Australia	AC	Flood	2 months	Temporal	1	0.21	-0.52
Sasaki <i>et al.</i> 2013	Plant (perennial)	Dundgobi and Southgobi province, Mongolia	AC	Grazing	9 years	Spatial	2 (by disturbance intensity)	0.81 (high) 0.82 (low)	2.7 (high) -6.8 (low)

Table 2: Model results for mixed effects modeling of compositional dissimilarity between post-disturbance communities and controls (top row) and differences in species richness (bottom row). Each standardized explanatory variable effect size \pm SE and p-value are listed. Because they are standardized, effect sizes are comparable between variables. Number of generations is an estimate of the potential for species turnover given elapsed time since disturbance. The last two columns show marginal and conditional r^2 calculations for the full models.

Model	Isolation: coefficient estimate	Isolation: p-value	Species pool: coefficient estimate	Species pool: p-value	Relative intensity: coefficient estimate	Relative intensity: p-value	Number of generations: coefficient estimate	Number of generations: p-value	Marginal r^2	Conditional r^2
Dissimilarity (Hedges g)	2.19 \pm 1.51	0.02	-0.46 \pm 0.51	0.11	0.78 \pm 1.18	0.22	-0.55 \pm 0.43	0.03	0.30	0.85
Richness difference (Hedges g)	0.001 \pm 1.59	0.99	-0.28 \pm 0.71	0.46	0.13 \pm 1.00	0.80	0.09 \pm 0.59	0.78	0.03	0.43

Figure 1: Conceptual models of the factors in community composition in response to disturbance, where compositional dissimilarity from the pre-disturbance reference composition is represented on the y-axis. In panel A, three hypothesized relationships of community composition with time are shown: linear recovery (top) of post-disturbance community (D) to pre-disturbance community, initial increase in the compositional difference with a subsequent decrease (middle) as fast colonizing species are replaced by slower growing better competitors that characterize the pre-disturbance community, and no recovery (bottom) but rather a different trajectory of community assemblage through time. Panel B and C use the linear recovery as a baseline (dotted lines) to illustrate the relationship of community change with stronger resilience facilitating mechanisms (B) and increased severity of disturbance (C). Increasing the intensity of community mechanisms beneficial for resilience may lead to reduced initial compositional difference but equal recovery speeds (top where D_2 represents the community trajectory with increased intensity of community mechanisms), similar initial compositional difference but faster recovery (middle), or both reduced initial compositional difference and faster recovery (bottom). Finally, severity of disturbance may impact community response. Increased intensity, duration, etc. may lead to higher initial compositional difference but with a faster recovery in response, resulting in a similar time to total recovery (top where D_2 represents the community trajectory with increased severity of disturbance), higher initial compositional difference, similar recovery speed and later full recovery (middle), or if abiotic or biotic factors are permanently shifted after disturbance, community recovery may be incomplete (bottom).

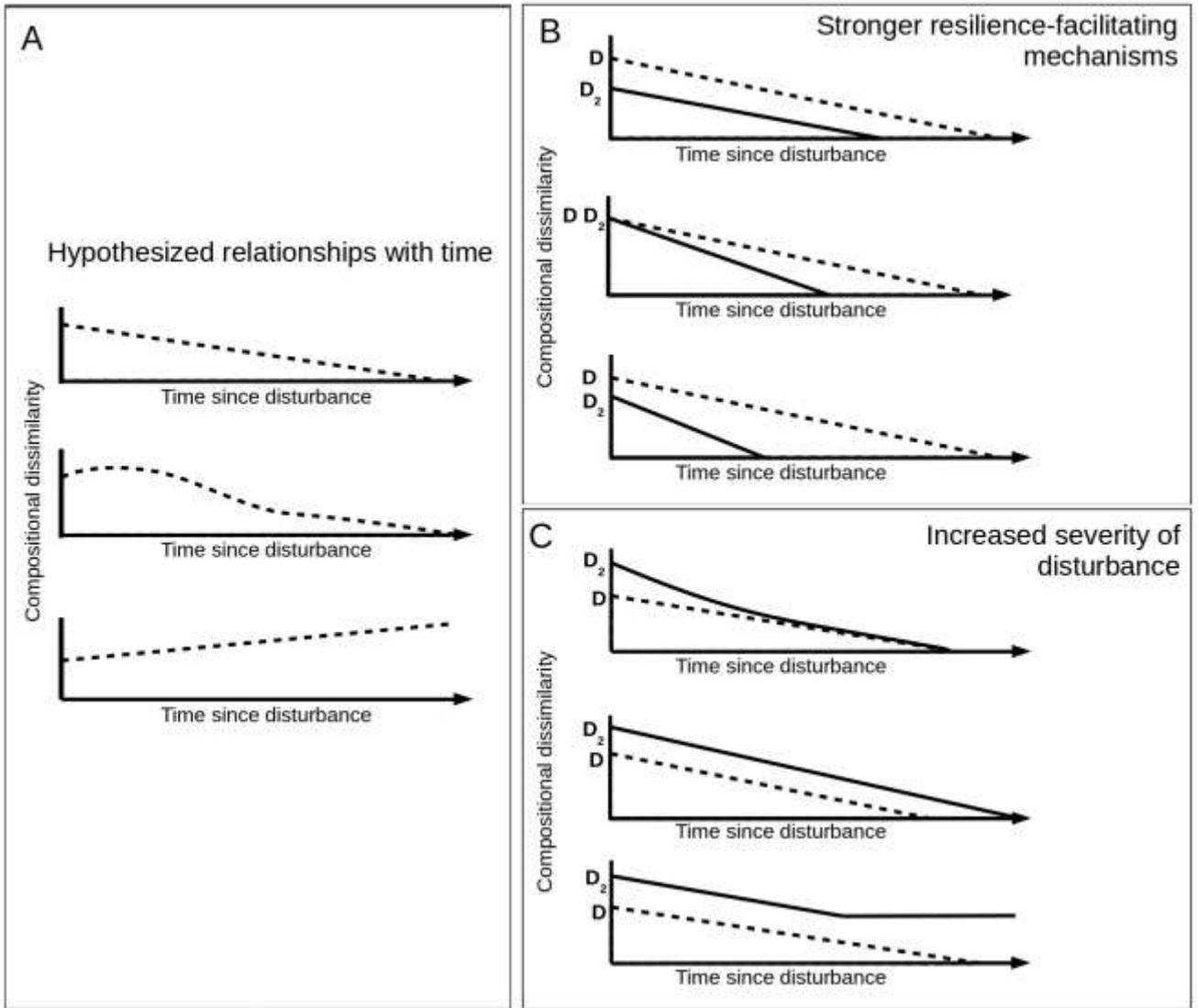


Figure 2: Compositional distance post-disturbance plotted against isolation (left; coefficient estimate \pm standard error = 2.19 ± 1.51 ; $p = 0.02$) and number of generations passed since the disturbance (right; coefficient estimate \pm standard error = -0.55 ± 0.43 ; $p = 0.03$). Outliers were dropped in sensitivity runs and model impacts assessed.

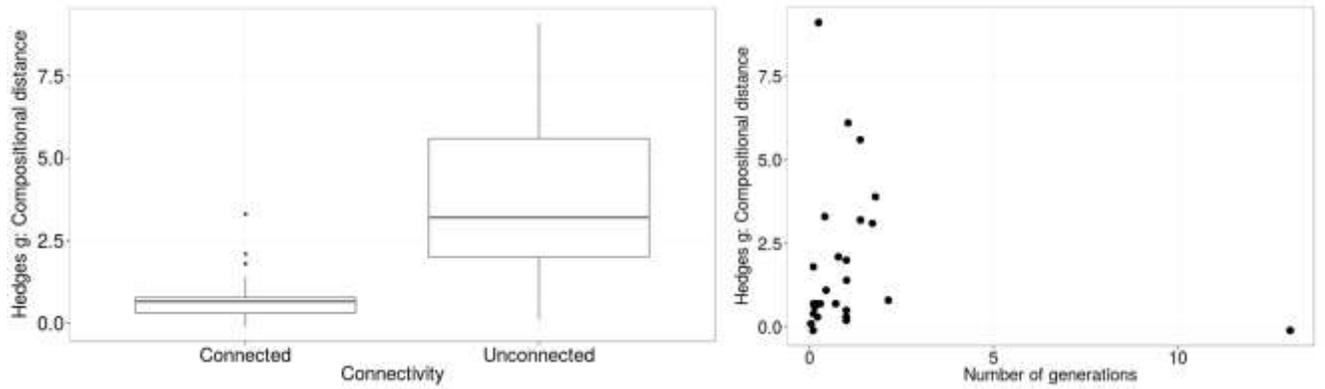


Figure 3: Richness differences between controls and disturbed sites plotted against the estimated size of the species pool (coefficient estimate \pm standard error = -0.28 ± 0.71 ; $p = 0.46$). Outliers were dropped in sensitivity runs and model impacts assessed.

