1   **Title:** *Isolation predicts compositional change after discrete disturbances in a global meta-study*

2

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48   **Running title:** *Isolation predicts compositional change*

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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.

71 **Introduction**

72 Pervasive human modification of ecosystems is causing shifts in the type, frequency, extent, and

73 intensity of disturbance at a global scale (Ellis and Ramankutty 2007). As disturbance regimes change,

74 understanding how ecosystems, communities, and populations change as a result of discrete

75 disturbances has become an imperative for ecological research. Several ecological concepts have arisen

76 to quantify aspects of community response to disturbance (see Pimm 1984; Grimm and Wissel 1997;

77 Brand and Jax 2007). Three of the most commonly applied concepts are resistance, defined as the

78 degree to which a variable (e.g. species composition) is changed following a disturbance (Pimm 1984);

79 engineering resilience, defined as the time taken for an ecosystem to return to its pre-disturbance state

80 following a disturbance (Pimm 1984) and widely interpreted as 'recovery' (Standish *et al.* 2014); and

81 ecological resilience, defined as the ability of an ecosystem to absorb changes in state or controlling

82 variables and to persist after disturbance (Holling 1973). Ultimately, these concepts aim to address a

83 single broader question around community response to disturbance—how changed will a community

84 be after a disturbance compared with its pre-disturbance state?

85

86 How a community changes after a disturbance is determined by multiple factors encompassing the

87 attributes of both the community and the disturbance itself. Community attributes influence the

88 trajectory of the community after disturbance. For instance, high species diversity is expected to

89 increase post-disturbance community similarity to pre-disturbance states through increased response

90 diversity (Elmqvist *et al.* 2003) and functional redundancy (Peterson *et al.* 1998). Regional diversity,

91 on the other hand, may increase the importance of priority effects (Fukami 2015), leading to alternative

92 recovery trajectories based on arrival order or survival status. At a landscape scale, connectivity with

93 undisturbed communities can provide propagule sources necessary for recolonization post-disturbance

94 (Cramer *et al.* 2008; Standish *et al.* 2014). Mechanisms like these potentially increase the resistance of

95 the community (i.e., dampen the initial community change post-disturbance), hasten recovery after the

96 disturbance, or both (**Figure 1**).

97

98 Additionally, the attributes of the disturbance can impact community change. A disturbance is defined

99 by a few key characteristics: temporal scale (duration), spatial scale (extent), frequency, intensity

100 (Pickett and White 1985), and timing (Lytle 2001). Each attribute can influence community changes

101   post-disturbance, with longer, larger and more intense disturbances causing greater changes in

102   community composition that persist for longer (Turner *et al.* 1998; Hobbs *et al.* 2006). Alternatively,

103   the effects of the disturbance may fade rapidly, resulting in a strong difference initially, but a short

104   recovery to the pre-disturbance state. Additionally, the most intense disturbances may fundamentally

105   alter abiotic or biotic resources; for example higher intensity flooding may scour substrates from

106   freshwater communities (Bornette and Puijalon 2011), or longer grazing regimes may deplete seed

107   banks (Hobbs *et al.* 2006). These chronic shifts may lead to permanent changes in the community

108   (**Figure 1**).

109

110   Finally, time plays an important role in the change between pre- and post-disturbance communities.

111   Equilibrium-based theories of community dynamics hypothesize that communities return to a pre-

112   disturbance state predictably through time (Pimm 1984) if prevailing abiotic conditions and available

113   species pools remain constant. Succession theory hypothesizes similar dynamics, with the added

114   complexity of an initial flush of fast-colonizing species that are succeeded through time by more

115   competitive species that characterized the pre-disturbance community (Connell 1978; Huston and

116   Smith 1987). However, there is a lack of evidence supporting single equilibrium-based successional

117   dynamics (Wu and Loucks 1995). Community assembly theory has driven some of these developments,

118   by providing evidence of a more complex relationship with time, in which species establishment

119   depends on chance, historical patterns, dispersal, abiotic factors, and biotic interactions (Gleason 1926;

120   Götzenberger *et al.* 2012). Trajectories of community development are modified by each of these

121   factors, and many opportunities exist for a community to develop towards a new state rather than return

122   to the pre-disturbance state, often confounding estimates of recovery. Taken together, the set of

123   theoretical frameworks suggest an uncertain relationship between community change post-disturbance

124   and the amount of time that has passed since the disturbance (**Figure 1**).

125

126   Studies of community response to disturbance tend to focus on a subset of the different attributes of

127   community change post-disturbance. For example, studies on fire ecology tend to focus on detailed

128   attributes of the disturbance and either post-disturbance development through time (e.g. Abella and

129   Fornwalt 2015) or initial response based on functional group distributions (e.g. Lamont *et al.* 1999). In

130   this study, we quantify the relative importance of a broad spectrum of potential factors by including

131 time, disturbance- and community-based attributes on community recovery using data from multiple

132 datasets. We do so over a range of communities and disturbance types. We focus on four variables

133 refined from a wide range of possible collinear covariates: disturbance intensity, time since disturbance,

134 connectivity, and species richness. We hypothesized that general relationships between community

135 recovery and one or more predictors could be found in the case studies considered, including plant,

136 animal, terrestrial, and marine communities over a global geographic extent and following a variety of

137 disturbance types. Specifically, we hypothesized that community differences post-disturbance would be

138 greatest following higher intensity disturbances and would decrease with time and higher species

139 richness, and increase with isolation from the surrounding landscape.

140

141 **Methods**

142 *Data compilation*

143 Data sets were compiled across a variety of ecosystem and disturbance types. Requirements for

144 inclusion were: community composition data for a control (i.e., data describing the pre-disturbance

145 state) and the same data for at least one time point post-disturbance. The control could either be a

146 temporal control – data from the sampling area before the disturbance – or a spatial control – an

147 undisturbed sampling area deemed appropriate to use as a reference location. The disturbance had to be

148 temporally discrete, to enable an assessment of community change post-disturbance. Because of the

149 need for raw composition data and detailed involvement of study authors, a comprehensive meta-

150 analysis was not conducted. Rather, a generalized meta-study over globally distributed data was

151 performed. Fourteen authors with their existing datasets were recruited to the project (**Table 1**) based

152 on publications of the appropriate study type. When split by site, this resulted in 27 points of post-

153 disturbance data. For individual sites, we used one post-disturbance time point. The studies spanned a

154 wide range of organisms from plant to animal communities and covered eleven regions around the

155 globe. Some studies included presence-absence data only, while others also included cover or the

156 number of individuals. Studies ranged in time from one reproductive event for annual plants to more

157 than a dozen reproductive events encompassing several full generations of snail communities. Details

158 of each study are provided in **Appendix S1** in Supporting Information.

159

160 *Response variables*

161   The data were used to calculate two response variables: the difference in species composition (as

162   measured by compositional dissimilarity) between pre- and post-disturbance communities and the

163   difference in species richness. Distance metrics such as the one we calculated compress multivariate

164   community data into a univariate metric commonly used by ecologists to capture how similar or

165   different communities are to each other (Clarke 1993). We acknowledge that community composition

166   may not necessarily return to its pre-disturbance state, even in very resilient communities, and

167   particularly in situations where the sequence in which species (re)colonise strongly affects the

168   trajectory of community assembly (Chase 2003). In cases where priority effects have been observed,

169   the functional (i.e. based on species characteristics rather than species identity) and structural

170   composition of a community are less sensitive to community assembly dynamics compared with

171   species composition (Fukami *et al.* 2005). However, despite some empirical evidence for priority

172   effects, such effects are not universal and appear to occur most strongly between phylogenetically

173   related species (Peay *et al.* 2011) or between species that have adapted to similar functional roles

174   (Urban and Meester 2009). Additionally, priority effects are strongest when a community is 'wiped

175   clean' by a disturbance (Fukami 2015). The disturbances considered here left survivors and *in situ*

176   propagules, likely influencing the community to return to a similar compositional state. Although it

177   would have been ideal to evaluate functional change to compare with compositional change, a lack of

178   trait data prevented that method.

179

180   Species richness, on the other hand, provides one of the simplest univariate measures of community

181   diversity (Magurran 1988). There are drawbacks to considering richness alone: species identity and

182   abundance are ignored, even in the cases where communities may change dramatically with species

183   changes. A simple example is biological invasions, where the introduction of a single species such as

184   *Myrica faya* in Hawaiian volcanic communities leads to completely different community trajectories

185   than one in which it is absent (Vitousek and Walker 1989). Despite these issues, species richness is

186   commonly used to prioritize conservation areas (Myers *et al.* 2000) and has been tied to important

187   ecological processes such as productivity (Mittelbach *et al.* 2001). Because of its simplicity and

188   ecological importance, we investigated species richness changes post-disturbance. We aimed to

189   compare results for richness with those of dissimilarity metric, a metric that does not share many of the

190   same issues as richness on its own.

7

191

192   Raw data were provided by each author, and the response variables were calculated for each plot

193   (controls and post-disturbance). Dissimilarity was calculated as the Bray-Curtis dissimilarity of each

194   plot to the compositional centroid of the control communities, which was calculated through a

195   modification of betadisper in vegan in R (Oksanen *et al.* 2013). Species richness was the number of

196   species present in each study. Both response variables were then transformed for meta-analysis using

197   the Hedges *g* variable (Hedges and Olkin 1985). The Hedges *g* calculation allows multiple data points

198   to be condensed into a single continuous value for each study while taking into consideration the

199   differing variances among datasets. It is calculated as the difference between control and post-

200   disturbance means divided by the pooled standard deviation, with a correction for small sample bias:

201
$$s_{pooled} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}$$
$$g = \frac{\overline{x_1} - \overline{x_2}}{s_{pooled}}$$
$$J(n) = \frac{\Gamma(n/2)}{\sqrt{n/2}\,\Gamma((n-1)/2)}$$
$$g_{corrected} = g \times J(n_1 + n_2 - 2)$$

202   where *n* is the total number of samples in the study; n_1, s_1, and $\overline{x_1}$ are the number of samples,

203   standard deviation, and mean of the response in treatment 1; n_2, s_2, $\overline{x_2}$ are the number of samples,

204   standard deviation, and mean of the response in treatment 2; s_{pooled} is the pooled standard deviation; g is

205   the Hedges *g* statistics; J(n) is the correction factor where Γ is the Gamma function; and $g_{corrected}$ is the

206   Hedges *g* weighted by the correction factor. The $g_{corrected}$ value is the final variable used as a response in

207   the meta-analysis.

208

209   *Explanatory variables*

210   Available data contributors convened in December 2013 to discuss and agree on a set of generalizable

211   explanatory variables. A wide range of variables were initially considered based on knowledge of their

212   data and the literature specific to their ecosystem (see **Appendix S2** in Supporting Information for full

213   details). The number of variables was then refined by grouping those with common attributes and

214   removing collinearity. In all of the ecosystems considered, four variables captured the key attributes

215   underlying community change post-disturbance (i.e., community attributes, disturbance attributes and

216   time). The four variables included size of the regional species pool, connectivity of the landscape,

217   disturbance intensity, and time since disturbance. Size of the species pool and connectivity of the

218   landscape were selected to capture the community attributes. Both variables have been explored

219   extensively for their relationships with community stability (e.g. McCann 2000 for richness; e.g.

220   Starzomski and Srivastava 2007 for connectivity) and offer inherent attributes of communities that are

221   relatively easy to measure. Disturbance intensity was selected to capture the disturbance. Our dataset

222   captured a broad range of data in which other attributes of disturbance such as duration or timing were

223   only sporadically relevant. Intensity, however, was a characteristic relevant to all our studies of

224   community response to disturbance. Finally, to capture potential for recovery we included time since

225   disturbance.

226

227   The taxonomic pool (usually species) was estimated by summing the number of unique species found

228   in all of the study plots, both control and disturbed. For coral communities, species-level data was not

229   available, so these calculations were made at the genus level. Connectivity was captured in a simplified

230   manner measuring whether the disturbed community was isolated from other undisturbed communities.

231   In landscape ecology, connectivity is split into structural connectivity, or the physical characteristics of

232   a landscape that allow for movement, and functional connectivity, or how well genes, individuals, or

233   population move through the landscape (Rudnick *et al.* 2012). Both forms of connectivity depend on

234   the species of interest as well as the landscape under consideration and are impossible to generalize

235   between communities, much less between communities of entirely different taxa. Isolation as we

236   defined it is thus a simplified metric of structural connectivity that ignores species-specific

237   requirements. However, it is easily compared among studies while still capturing an ecologically

238   meaningful trait, that is, whether propagule sources were confined solely to the disturbed area. This

239   was particularly relevant for the datasets we considered, as no large-scale or highly mobile animals

240   were included outside of fish, with a clear connection to propagule sources, and coral, with a measured

241   isolation from propagule sources. Isolation was measured as a binary variable: if 100% of the

242   community extent was covered by the disturbance, the community was considered isolated. If only a

243   portion of the intact community was affected by the disturbance, the community was considered

244   connected.

245

246   Disturbance intensity was quantified relative to previous disturbances of the same type. For example,

247   the strength of a hurricane was expressed as the maximum wind speed of the hurricane compared with

248   the average wind speed of hurricanes in the region for the past century. Time since disturbance could

249   not be captured in a single generalizable unit and was standardised according to community life

250   histories. For example, three months in a microarthropod community is very different than three

251   months in a coral reef community. Thus, time since disturbance was divided by the weighted average

252   generation time of the organisms in each community to derive a standard measure. This measure was

253   derived from an estimate of generation time for each species in each study. Plant species estimates were

254   based on life form. Trees were assigned 100 years per generation, shrubs 30 years, perennial herbs 5

255   years, and annuals or biennials 1 or 2 years respectively. For other organisms, we used maximum

256   lifespan where the data was available in the literature. We tallied the number of plots in which each

257   species was recorded, then calculated a weighted average based on their frequency. For

258   microarthropods, there is too little information on individual species life histories, though they are

259   known to range from weeks to years (Krantz *et al.* 2009). A general estimate of four months was used.

260   Additionally, distinguishing coral species is difficult (Gilmour, et al. 2016; Richards, et al. 2016;

261   Wallace 1999) and the turnover times for populations vary widely according to their diverse life

262   histories (Darling, et al. 2012; Madin, et al. 2016). For the most abundant populations, turnover times

263   are likely in the order of 20 years and so we used that value as our estimated generation time. Finally,

264   the three continuous variables – disturbance intensity, species pool, and time since disturbance (*i.e.* the

265   average number of generations passed since the disturbance) – were standardized by subtracting their

266   respective means and dividing by their respective standard deviations. Standardisation allowed direct

267   comparison of coefficient estimates.

268

269   *Statistical analysis*

270   Explanatory variables were checked for collinearity and were found to be adequately orthogonal

271   (variance inflation factors all less than 1.4) . We ran separate linear mixed-effects models for the two

272   response variables. Because a few studies had multiple points, or authors had provided multiple sites

273   within a similar region, we included the location of the study as a random effect. Additionally, we

274   tested models based on a quasi-Gaussian distribution (Wedderburn 1974) for a potentially better fit to

275   the response data. There was no significant improvement using this approach and so we returned to the

276 linear methods. Given the potential non-linear relationships between recovery and time (**Figure 1**), we
277 also tested a nonlinear model. We ran a Generalized Additive Mixed-effects Model using the *mgcv*
278 package in R (Wood, 2007), with a smoother included around the time-since-disturbance variable. The
279 result was a linear relationship; the smoother returned only one degree of freedom and was
280 subsequently removed. Final models were validated by checking the residuals against the fitted values
281 and each of the explanatory variables (Zuur *et al.* 2009) as well as checking residuals for normality
282 using a Shapiro-Wilks test and diagnostics plots. Additionally, we removed single studies and reran the
283 models to assess the sensitivity of model results to each dataset and to investigate the influence of
284 outliers. We used the package lme4 (Bates *et al.* 2014) in the statistical program R (R Core Team 2014)
285 for the analysis.

286

287 **Results**
288 Compositional dissimilarity results ranged over the studies from almost no similarity to the controls
289 (dissimilarity = 0.65) in wetlands seven years after Hurricane Katrina to almost complete similarity to
290 the controls (dissimilarity = 0.05) in forest two years after Hurricane Gilbert (**Table 1**). There were
291 changes in species richness in all but four of the 27 studies. Of those, 12 had more species in
292 communities post-disturbance than in undisturbed communities, and 11 had fewer species in
293 communities post-disturbance (**Table 1**). The highest number of species gained was in rangeland after
294 an intense grazing event, where undisturbed controls averaged eight species and post-disturbance
295 communities averaged 20 species. The largest loss of species occurred in disturbed moss systems,
296 where undisturbed microarthropod communities averaged 38 species, while post-disturbance
297 communities averaged 17.

298

299 We found that connected communities were significantly more similar to control communities post-
300 disturbance than isolated communities (**Table 2**). The coefficient estimate for the isolation variable was
301 around three times larger (in absolute terms) than the next largest coefficient (**Table 2**). Time since
302 disturbance was also significantly correlated with similarity – the more generations that passed, the
303 more similar the controls to the disturbed communities (**Figure 2**). However, the coefficient estimate of
304 this variable was small and the sensitivity test showed that the significance was driven by two outliers:
305 the study with the highest number of generations (snail community response after clearcutting), and the

306   study with the highest Hedges *g* value for compositional dissimilarity (rangeland after summer

307   grazing). Disturbance intensity and species pool size were not significantly related to compositional

308   similarity.

309

310   Changes in richness after disturbance were not significantly correlated with any of the four explanatory

311   variables: size of the species pool, isolation, number of generations passed, or relative disturbance

312   intensity. Sensitivity tests did not alter the results for the richness model, though the coefficient

313   estimate of the species pool variable changed when the study with the largest species pool was removed

314   (**Figure 3**), becoming large and negative.

315

316   **Discussion**

317   From this diverse dataset came one strong signal – isolation from surrounding landscapes/seascapes

318   was significantly correlated with compositional dissimilarity between pre-disturbance and post-

319   disturbance communities. Isolated communities within the dataset ranged from overgrazed rangelands

320   to experimentally disturbed moss-microarthopod communities to wetlands impacted by Hurricane

321   Katrina. The variety of communities and disturbance types within these studies supports the generality

322   of our findings. Research on corridors and landscape configuration has long shown ecological benefits

323   of connectivity. Species populations are maintained through time by connectivity with dispersing

324   populations (Damschen *et al.* 2006; Valanko *et al.* 2015). When species are lost or densities critically

325   lowered post-disturbance, inputs from connected landscapes can prevent species losses (Heller and

326   Zavaleta 2009). Additionally, abiotic and biotic flows can support community function in disturbed

327   communities (Standish *et al.* 2014) such as increased rainfall near intact vegetation stands (Lyons

328   2002) or influxes of dispersers and pollinators from adjacent communities (Lundberg and Moberg

329   2003).

330

331   In parallel, isolation has been linked with degradation from edge effects, species loss, and shifts in

332   historical disturbance regimes (Turner 1989, Debinski and Holt 2000). Each of these factors may

333   independently alter the response of a community to disturbance events. For example, the increased

334   prevalence of non-native species in edges may lead to rapid changes in a post-disturbance community

335   as the non-natives increase opportunistically (Didham *et al.* 2007); species losses may restrict the role

336   of compensatory dynamics (Loreau *et al.* 2001); and loss of disturbances such as fire may lead to the
337   loss of reproductive cues (*e.g.* Yates and Ladd 2002) and local heterogeneity (Turner 2010). Thus,
338   disturbed communities in connected landscapes are more likely to experience species inputs and pre-
339   disturbance conditions that speed recovery, whereas isolated communities are more likely to experience
340   novel species dynamics and additional stressors that inhibit resistance and recovery (**Figure 1, Panel**
341   **B**). Human land use is increasingly fragmenting landscapes globally, leading to higher levels of isolated
342   and shrinking habitat patches (Fahrig 2003). Given our results and the many studies on direct and
343   indirect impacts of fragmentation (*e.g.* Andren 1994, Honnay *et al.* 2005, Levey *et al.* 2016), it is clear
344   that landscape context is a major factor in community response to disturbance that should be explicitly
345   considered across scales of management.
346
347   One major exception to the importance of isolation stood out in our dataset. Coral communities showed
348   high similarity to pre-disturbance communities after bleaching despite isolation from any external
349   propagule source (Gilmour *et al.* 2013). The particular example in Scott Reef emphasises the
350   importance of biotic legacies in a community such as remnant corals or propagule banks. Seed banks
351   and surviving individuals in plant communities or surviving individuals in animal communities play a
352   similar role on land (Tanner and Bellingham 2006), again with biotic legacies likely acting to increase
353   the speed of community recovery (**Figure 1, Panel B**). Isolation in the case of Scott Reef also meant
354   reduced exposure to the many anthropogenic disturbances that add significantly to the disturbance
355   regime of reef communities closer to shore. However, the recovery of coral assemblages at Scott Reef
356   still clearly relied on the patterns of local connectivity, which had profound implications for the
357   recovery of coral assemblages with contrasting dispersal potential (Done *et al.* 2015). So while
358   connected communities may generally show less change post-disturbance than isolated ones, there
359   must still be some contextualization for individual communities.
360
361   We found no significant relationship between the explanatory variables and changes in species
362   richness. Conservation work is commonly aimed at preserving biodiversity levels, often through a
363   simple measure of the species richness in a community (Fleishman *et al.* 2006). For such conservation
364   approaches to be effective in the long term, we require a better understanding of how species richness
365   reflects community responses to disturbance. Many studies report a disconnect between metrics that

366   ignore species identity and other indicators of the community dynamics (*e.g.* Magurran and Henderson

367   2010) as well as pitfalls in the measurement and quantification of metrics like species richness (Gotelli

368   and Colwell 2001, Fleishman *et al.* 2006). Our results agree with these findings. We found no general

369   response of species richness to disturbance; almost an equal number of communities exhibited

370   increases in species richness as decreases post-disturbance. Additionally, we found no significant

371   relationship between species richness and the explanatory variables. If species identity is more

372   important than species richness for determining community-level response, then the impact of potential

373   drivers as outlined in **Figure 1** may not apply to how species richness will change post-disturbance.

374   Rather, the mechanisms behind richness patterns may be more complex than other measures of

375   response to disturbance, and important community-specific interactions between drivers of richness

376   (*e.g.* the interaction between disturbance and connectivity; Alstad and Damschen 2016) may need more

377   detailed data than those available for this study. The known importance of species identity in other

378   community patterns, coupled with the complexity of species richness patterns (Cardinale *et al.* 2006)

379   suggests that the use of species richness as a response metric is potentially meaningless in some

380   instances and should be complemented by additional metrics.

381

382   Species pool size and relative disturbance intensity with compositional change were also weak or

383   absent in our results. Contrary to our hypothesis, relative disturbance intensity showed no relationship

384   with community changes post-disturbance. Higher intensity disturbances may have implications for

385   both the initial change post-disturbance as well as the long-term recovery (Turner *et al.* 1998). The

386   intensities considered here, however, may not have captured enough variation, or the scale used may

387   not have been appropriate for elucidating these dynamics. Additionally, the size of the species pool had

388   no relationship with community change post-disturbance. Species diversity is generally hypothesized to

389   aid community recovery through response diversity and functional redundancy (Elmqvist *et al.* 2003).

390   These two traits both focus on how local diversity influences the return of community function, not

391   community composition. The role of diversity in compositional return has been discussed in

392   community assembly theory, where increased regional richness may increase the importance of species

393   arrival order (Chase 2003). We defined local species richness as any species surveyed in a single study.

394   At times, this included sites that were separated by distance and/or physical barriers, which may more

395   accurately capture regional species richness (see Pärtel *et al.* 1996 for definitions of regional vs local

396   species pools). Most communities in this study were also influenced by survivors and *in situ*

397   propagules, offsetting assembly rule dynamics. The combination of all these factors, and of the limited

398   manner in which we could define richness, could potentially mask any clear role that richness may play

399   in compositional return. For future studies, it is important to determine the scale at which 'local

400   richness' is assessed relative to the regional species pool (Fukami 20015), as is the consistent

401   measurement of both among study units; this may be the only way to distinguish the unique roles that

402   different types of richness play in local dynamics.

403

404   Time had a weak relationship with community change. Given that there are many hypotheses about

405   how recovery processes play out in a community after a disturbance (**Figure 1**), it is unsurprising that

406   no strong signal emerged from our data. Overall, composition was more similar to the pre-disturbance

407   state as more generations passed. This relationship, however, was driven by two studies. The first

408   spanned the most generations. Snail communities, with an average estimated generation time of less

409   than three years, were studied 40 years after a logging event (Ström *et al.* 2009) and were

410   compositionally similar to pre-disturbance communities (this study). The second study had the largest

411   Hedges *g* value of compositional dissimilarity and occurred in seasonally grazed rangelands. Recovery

412   post-disturbance can be altered by the timing of the disturbance (*e.g.* Pakeman and Small 2005).

413   Bestelmeyer *et al* (2013) tested both winter and summer grazing impacts in the same rangeland system

414   we studied here. The authors found that winter grazing elevated plant community exposure to harsh

415   environmental conditions. Thus, the difference found here may be attributed to the disturbance season

416   rather than the short time since disturbance. Though we did not have enough data to test the relative

417   role of timing in driving community response to disturbance, it is an important factor to understand as

418   global change continues to shift the timing of extreme events (IPCC 2007, Rahmstorf and Coumou

419   2011). Additionally, the importance of two outlier points in shaping the relationship between time and

420   community change call for further research to determine the nature of that relationship.

421

422   One complexity of time as an explanatory variable is that life history traits may slow community

423   response to scales not captured in this study. For example, the Jamaican forest grew increasingly

424   dissimilar over 15 years post-Hurricane Gilbert as the damaged trees experienced delayed mortality and

425   as newly recruited stems grew into the minimum size class for measurement (Tanner and Bellingham

426 2006). Though we considered generation time in our estimate of time since disturbance, data for a full

427 generational turnover was unavailable in some datasets and could be important to capture predicted

428 dynamics (Connell and Sousa 1983). The availability of this kind of data is limited for long-lived

429 communities and management concerns are likely to be shorter than the centuries required by some

430 communities. However, consideration of short-term community change through time must be informed

431 by an understanding of longer-term processes.

432

433 Larger datasets on effects of disturbance on species composition are slowly becoming available (e.g.

434 the PREDICTS database: Hudson *et al.* 2014) and may capture the long term dynamics needed to study

435 broad relationships between community change post-disturbance and time. Larger dataset collections

436 would also allow repetition of disturbance types and taxa, consideration of further important covariates

437 like sampling scale, and the inclusion of interactions between explanatory variables. However, such

438 data have to be paired with generalized explanatory variables to make sense of community responses to

439 disturbance. A single measurement of disturbance intensity between grazing, hurricanes, or logging, for

440 instance, is necessary for the development of broad, testable theory around resistance and recovery

441 (Marquet *et al.* 2014). Our solution to this problem was to estimate relative disturbance intensity, and

442 we acknowledge that it is imperfect because disturbances that had never previously occurred in a

443 community had to be assigned a high intensity dummy value. Similarly, connectivity was simplified to

444 a binary isolation variable. This leaves out all complex issues of functional connectivity versus

445 structural connectivity that vary across taxa (Rudnick *et al.* 2012), making it applicable to all datasets

446 but particularly blunt in the ecological effects it captures. Whether ecological variables and

447 relationships are truly generalizable to such an extent in this context is largely unknown, though the

448 strong, predicted relationship with isolation shows promise in this regard.

449

450 Our data spans four continents, half a dozen aquatic and terrestrial ecosystem types, and a dozen

451 different types of disturbance to assess community response to disturbance as measured by the amount

452 of change between pre- and post-disturbance communities. This metric bundles the initial response of

453 the community, i.e. the community resistance (Pimm 1984), with the longer-term response that can

454 encompass community recovery and resilience (i.e., engineering resilience and ecological resilience),

455 in addition to other measures of stability (e.g. see Pimm 1984; Grimm and Wissel 1997). The search for

456   influences on broad community response to disturbance is of theoretical and practical interest. Our

457   conclusions support the broad, generalizable role that connectivity has in community response to

458   disturbance. This was not a comprehensive meta-analysis due to limitations in available data, and the

459   dataset size makes drawing strong conclusions from complex analyses difficult. The results emphasize

460   the potential for testing over a broad extent, and call for the standardised measure of generalizable

461   variables such as those we have identified here, to create the large, cross-system datasets that are

462   considered useful for progressing ecological theory (Marquet *et al.* 2014).

463

474

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671 **Table 1:** *List of studies used in meta-analysis. The reference (where data published) is given in the first*

672 *column; the author's name is listed if the study is unpublished. The organism, location, data type*

673 *(where PA = presence-absence; AC = abundance measured as cover; AF = abundance measured as*

674 *frequency), disturbance type, maximum time since disturbance, type of control, and number of*

675 *datapoints from the study are also listed. Only one time point post-disturbance was taken for each*

676 *study. However, some studies had separated sites with differing abiotic conditions that allowed the use*

677 *of multiple data points. The last two columns list response results for each of the studies, dissimilarity*

678 *and the change in species richness. Studies with more than one data point have been listed as*

679 *individual datapoints with a brief description of treatment identifier. For full details of the treatments,*

680 *please see individual references. The Hedges* g *response values were calculated from these values and*

681 *the corresponding control values for each dataset.*

682

Study	Organism	Location	Data type	Disturbance	Max Time	Control	Data Points	Compositional Dissimilarity	Change in Species Richness
Dwyer *et al.* 2010	Plant (forest)	Queensland, Australia	AF	Ringbarking	40 years	Spatial	1	0.46	-3.5
Bestelmeyer *et al.* 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 *et al.* 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 *et al.* 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 *et al.* 2009	Animal (snails)	Sweden	AF	Clear cut	40 years	Spatial	1	0.57	1
Starzomski and Srivastava	Animal (microarthropods)	British Columbia, Canada	AF	Drought/heat	4 months	Spatial	4 (by spatial extent of	0.33 (sm) 0.3 (med) 0.28 (lg)	-7.2 (sm) -6.4 (med) -9.4 (lg)

25

2007							disturbanc e)	0.64 (total)	-20.6 (total)
Battaglia, Loretta L. (unpublishe d)	Plant (perennial)	Florida, United States	AC	Saline flood	3 years	Tempor al	5 (by distance from sea, close to far)	0.44 (dist 1) 0.38 (dist 2) 0.42 (dist 3) 0.53 (dist 4) 0.37 (dist 5)	0.67 (dist 1) 4 (dist 2) 1 (dist 3) 3.4 (dist 4) -0.1 (dist 5)
Foster, Marc A. and Battaglia, Loretta L. (unpublishe d)	Plant (perennial)	Mississipp i, United States	PA	Hurricane	7 years	Tempor al	2	0.22 (windthrow) 0.65 (windthrow + flood)	-0.67 (windthro w) -4.57 (windthro w + flood)
Becker *et al.* 2009	Animal (fish)	Victoria, Australia	AF	Anoxia	9 months	Tempor al	1	0.67	0.33
Tanner and Bellingham 2006	Plant (forest)	Jamaica	AF	Hurricane	2 years (site 1) 15 years (site 2)	Tempor al	2 (by location on island)	0.05 (site 1) 0.2 (site 2)	-0.57 (site 1) -1.1 (site 2)
Gilmour *et al.* 2013	Animal (coral)	Western Australia, Australia	AC	Bleaching	12 years	Tempor al	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	Tempor al	1	0.64	0.69
Price *et al.* 2011	Plant (annual-perennial)	New South Wales, Australia	AC	Flood	2 months	Tempor al	1	0.21	-0.52
Sasaki *et al.* 2013	Plant (perennial)	Dundgobi and Southgobi province, Mongolia	AC	Grazing	9 years	Spatial	2 (by disturbanc e intensity)	0.81 (high) 0.82 (low)	2.7 (high) -6.8 (low)

683

684 ***Table 2:*** *Model results for mixed effects modeling of compositional dissimilarity between post-*

685 *disturbance communities and controls (top row) and differences in species richness (bottom row). Each*

686 *standardized explanatory variable effect size ± SE and p-value are listed. Because they are*

687 *standardized, effect sizes are comparable between variables. Number of generations is an estimate of*

688 *the potential for species turnover given elapsed time since disturbance. The last two columns show*

689 *marginal and conditional r^2 calculations for the full models.*

690

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 ± 1.51	0.02	-0.46 ± 0.51	0.11	0.78 ± 1.18	0.22	-0.55 ± 0.43	0.03	0.30	0.85
Richness difference (Hedges g)	0.001 ± 1.59	0.99	-0.28 ± 0.71	0.46	0.13 ± 1.00	0.80	0.09 ± 0.59	0.78	0.03	0.43

691

692

693   **Figure 1:** Conceptual models of the factors in community composition in response to disturbance,
694   where compositional dissimilarity from the pre-disturbance reference composition is represented on the
695   y-axis. In panel A, three hypothesized relationships of community composition with time are shown:
696   linear recovery (top) of post-disturbance community (D) to pre-disturbance community, initial increase
697   in the compositional difference with a subsequent decrease (middle) as fast colonizing species are
698   replaced by slower growing better competitors that characterize the pre-disturbance community, and no
699   recovery (bottom) but rather a different trajectory of community assemblage through time. Panel B and
700   C use the linear recovery as a baseline (dotted lines) to illustrate the relationship of community change
701   with stronger resilience facilitating mechanisms (B) and increased severity of disturbance (C).
702   Increasing the intensity of community mechanisms beneficial for resilience may lead to reduced initial
703   compositional difference but equal recovery speeds (top where D_2 represents the community trajectory
704   with increased intensity of community mechanisms), similar initial compositional difference but faster
705   recovery (middle), or both reduced initial compositional difference and faster recovery (bottom).
706   Finally, severity of disturbance may impact community response. Increased intensity, duration, etc. may
707   lead to higher initial compositional difference but with a faster recovery in response, resulting in a
708   similar time to total recovery (top where D_2 represents the community trajectory with increased severity
709   of disturbance), higher initial compositional difference, similar recovery speed and later full recovery
710   (middle), or if abiotic or biotic factors are permanently shifted after disturbance, community recovery
711   may be incomplete (bottom).
712
713   **Figure 2:** Compositional distance post-disturbance plotted against isolation (left; coefficient estimate $\pm$
714   standard error $= 2.19 \pm 1.51$; $p = 0.02$) and number of generations passed since the disturbance (right;
715   coefficient estimate $\pm$ standard error $= -0.55 \pm 0.43$; $p = 0.03$). Outliers were dropped in sensitivity runs
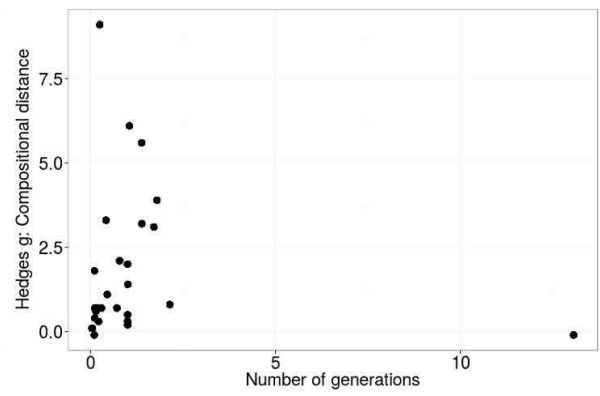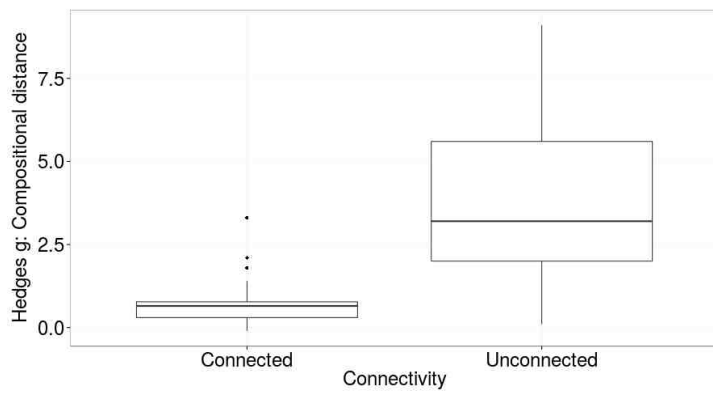716   and model impacts assessed.
717
718   **Figure 3:** Richness differences between controls and disturbed sites plotted against the estimated size
719   of the species pool (coefficient estimate $\pm$ standard error $= -0.28 \pm 0.71$; $p = 0.46$). Outliers were
720   dropped in sensitivity runs and model impacts assessed.
721
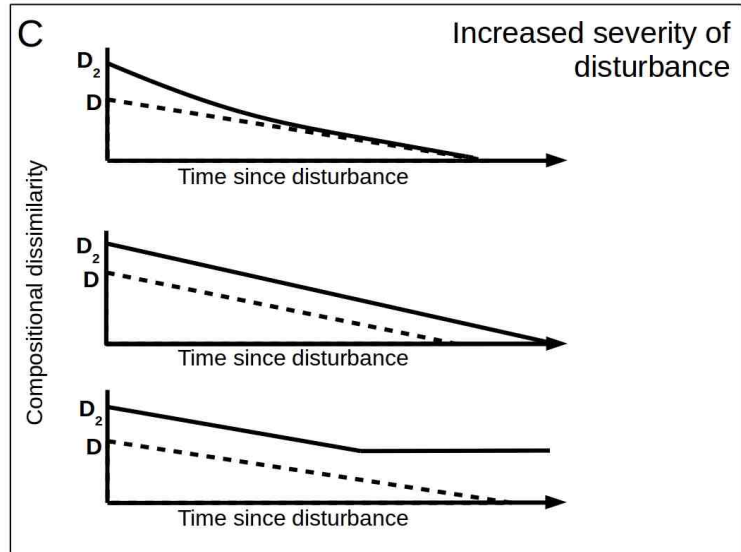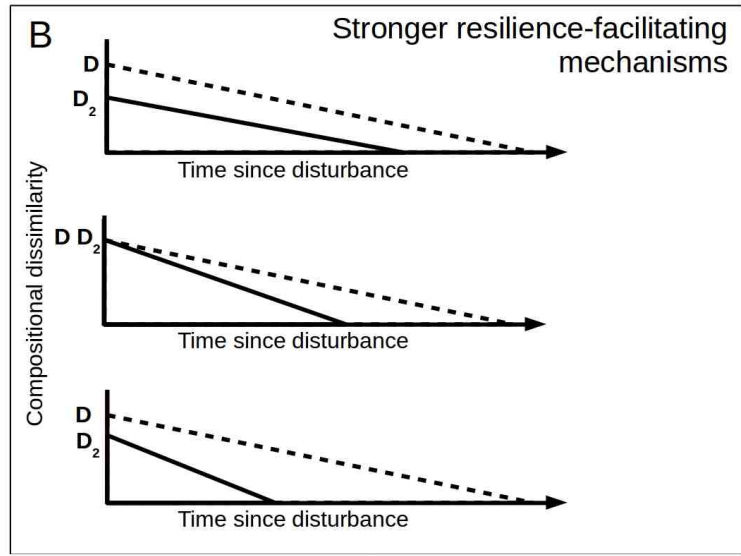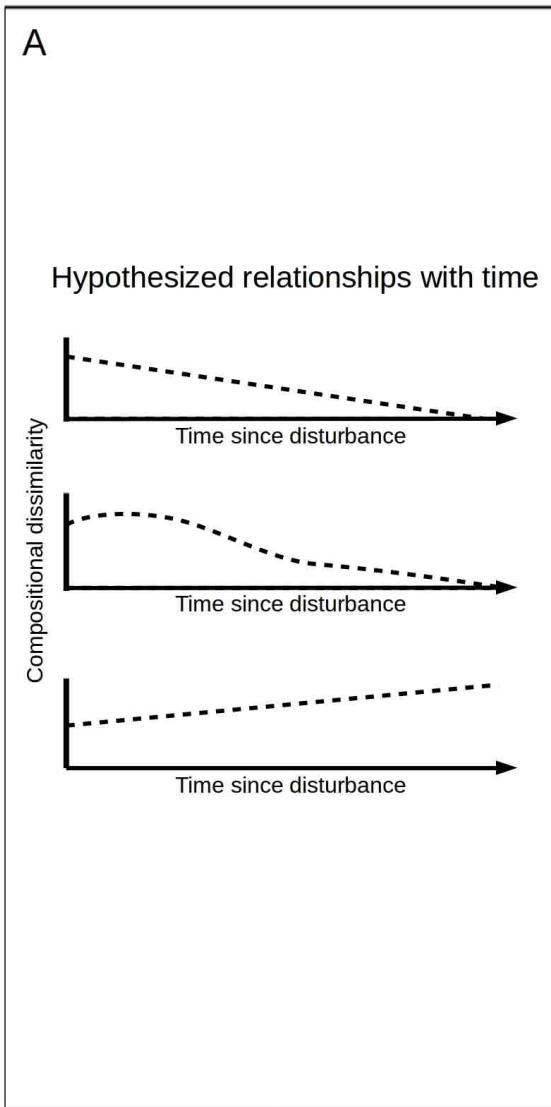
Isolation predicts compositional change

Isolation predicts compositional change