Is coral richness related to community resistance to and recovery from disturbance?

More diverse communities are thought to be more stable – the diversity-stability hypothesis – due to increased resistance to and recovery from disturbances. For example, high diversity can make the presence of resilient or fast growing species and key facilitations among species more likely. How natural geographic biodiversity patterns and changes in biodiversity due to human activities mediate community-level disturbance dynamics is largely unknown, especially in diverse systems. For example, few studies have explored the role of diversity in tropical marine communities, especially at large scales. We tested the diversity-stability hypothesis by asking whether coral richness is related to resistance to and recovery from disturbances including storms, predator outbreaks, and coral bleaching on tropical coral reefs. We synthesized the results of 41 field studies conducted on 82 reefs, documenting changes in coral cover due to disturbance, across a global gradient of coral richness. Our results indicate that coral reefs in more species rich regions were marginally less resistant to disturbance and did not recover more quickly. Coral community resistance was also highly dependent on pre-disturbance coral cover, probably due in part to the sensitivity of fast-growing and often dominant plating acroporid corals to disturbance. Our results suggest that coral communities in biodiverse regions such as the western Pacific may not be more resistant to natural and anthropogenic disturbances. Further analyses controlling for disturbance intensity and other drivers of coral loss and recovery could improve our understanding of the influence of diversity on community stability in coral reef ecosystems.

2   Stacy Y. Zhang[1], Speare, Kelly E.[1]; Long, Zachary T.[2]; McKeever, Kimberly A.[1]; Gyoerkoe,

3   Megan[1]; Ramus, Aaron P.[1,2,]; Mohorn, Zach[1;] Akins, Kelsey L.[1]; Hambridge, Sarah M.[1]; Graham,

4   Nicholas A. J.[3]; Nash, Kirsty L.[3]; Selig, Elizabeth, R.[4], Bruno, John F.[1*]

5   [1] Department of Biology, The University of North Carolina at Chapel Hill, Chapel Hill, NC

6   27599-3300 USA

7   [2]Department of Biology and Marine Biology, University of North Carolina at Wilmington,

8   Wilmington, NC 28403 USA

9   [3]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook

10   University, Townsville, QLD 4811, Australia

11   [4]The Betty and Gordon Moore Center for Ecosystem Science and Economics, Conservation

12   International, 2011 Crystal Drive, Suite 500, Arlington, VA 22202

13   [*] Corresponding author: jbruno@unc.edu

Introduction

15 A large body of recent and classical ecological research has focused on how biodiversity

16 influences the stability of communities (May 1973; McCann 2000; Pimm 1984; Hughes and

17 Stachowicz 2004; Steiner et al. 2006; Cardinale et al. 2012). Despite this interest, there is still no

18 consensus on whether or why diversity influences stability. This may be due in part to the

19 multitude of ways stability has been defined (Grimm & Wissel 1997; McCann 2000; Pimm

20 1984). Here, we define community stability as the ability to maintain a given state regardless of

21 perturbation, invasion, or extinction (McCann 2000). Mechanistically, stability is made up of two

22 components: resistance – the degree to which a community changes in response to a disturbance,

23 and recovery or "resilience" – the rate of return to pre-disturbance conditions (Grimm & Wissel

24 1997; Ives & Carpenter 2007; May 1973; McCann 2000).

25 Species richness (the number of species within an area) is thought to influence community

26 stability via several mechanisms (Ives et al. 2005). For example, species rich communities are

27 more likely, due to chance alone, to include greater functional diversity, and redundancy of

28 function within functional groups – the insurance hypothesis (McNaughton 1977; Tilman &

29 Downing 1994). The inclusion of species that can tolerate or benefit from disturbance could

30 increase community resistance (McCann 2000; Tilman & Downing 1994; Yachi & Loreau 1999).

31 Additionally, positive feedbacks among species via facilitation may be more common in diverse

32 communities, which may enhance post-disturbance recovery (Naeem 1998; Naeem & Li 1997;

33 Yachi & Loreau 1999).

34 Understanding the role of species richness in community stability has been a focus of a

35 number of field studies and meta-analyses (Duffy et al. 2001; Ives & Carpenter 2007; Stachowicz

36 et al. 2007; Stachowicz et al. 2008; Cardinale et al. 2012). Some experimental studies in

37 terrestrial plant communities have found a positive relationship between species richness and

38 stability (Ives & Carpenter 2007; Tilman & Downing 1994). For example, more diverse plant

39 communities appear to be more resistant to disturbances including drought (Tilman & Downing

40 1994). Manipulations of marine plant and invertebrate community richness have found that

41 diversity is positively related to resistance and recovery (Stachowicz et al. 2007). Likewise,

42 Boyer et al. (2009) experimentally demonstrated that species-rich algal communities were more

43 resistant to disturbances than species-poor communities in estuarine ecosystems of eastern North

44 Carolina. One of the few large scale tests of the diversity-stability concept was a study of boreal

45 forest communities in north-western Quebec (Grandpre et al. 1997), which found that greater

46 species-richness conferred more resistance to changes in community composition and abundance

47 following a disturbance.

48   We tested the hypothesis that species richness is related to community stability

49 (resistance and recovery) in coral reef ecosystems. Coral communities are affected by a large

50 range of natural and anthropogenic disturbances including storms, disease outbreaks, coral

51 bleaching due to ocean warming, dynamite fishing, and predator outbreaks (e.g., *Acanthaster*

52 *planci* or Crown-of-Thorns Starfish (COTS)). A recent study of coral-community recovery found

53 that disturbance type, e.g., "physical" vs. "biological" disturbances, and other reef characteristics

54 had little effect on recovery rate; although, recovery was influenced by post-disturbance coral

55 cover, geographic region, and reef management (Graham et al. 2011). We expanded on this work

56 by asking whether coral richness is related to resistance to and or recovery from disturbances at a

57 large spatio-temporal scale using coral cover as a metric of reef state. We hypothesized that coral

58 communities in species rich regions would exhibit greater resistance and recovery in response to

59 disturbances. We synthesized the results of 41 field studies documenting post-disturbance

60 changes in coral cover across a natural gradient of coral richness.

61 **Methods**

62 *Data Sources and Study Selection*

63   Our analyses were based on an expanded version of the coral cover change database

64   compiled by Graham et al. (2011). We added 18 new studies (35 additional reefs), resulting in a

65   total of 82 reefs (Text S1). Twenty-eight studies were used in the decline analyses, and 30 were

66   included in the recovery analyses, with many studies providing both resistance and recovery data.

67   We identified and added studies that quantitatively documented community responses following

68   disturbances, both losses and recoveries, in percentage of benthos covered by living coral species

69   on subtidal reefs (0.5 – 40 m depth, median survey depth = 10 m). If component values were in a

70   graphical format, ImageJ software was used to extract values for analysis. Survey locations were

71   categorized into four regions: Eastern Pacific, Western Pacific, Indian Ocean, and Caribbean (Fig.

72   S1). In addition to browsing relevant coral reef and ecology journals, we also used online

73   academic search tools (e.g., Google Scholar, ISI Web of Science) to search for published peer-

74   reviewed sources of coral-cover change data using the search terms: "disturbance," "coral cover,"

75   "*Acanthaster planci,*" "bleaching," "storm," "cyclone," "hurricane," "resistance," "resilience,"

76   "recovery," and "richness."

77   Studies had to meet four criteria to be included in the present analysis (Graham et al.

78   2011). 1) A clear description of sampling methods. Most surveys were performed using a

79   variation of the line transect method where a 10–30 m transect is placed on the reef and coral

80   cover is estimated either *in situ* or from digital images or videos. Although manta tow data can be

81   unbiased if extensive training is involved (Miller & Müller 1999), all manta tow data was

82   excluded because we were unable to verify the accuracy of the majority of manta tow surveys

83   performed. 2) Documented changes in coral cover due to one of three types of disturbance:

84   *Acanthaster planci* outbreaks, coral bleaching, and storm (hurricanes and cyclones) impacts.

85   Other disturbances such as dynamite fishing and ship groundings were not included due to a lack

86   of studies and the small scale of disturbance. 3) Changes in hard coral cover were documented for

87   resistance: pre-disturbance (initial cover) and immediately after disturbance (remnant cover); or

88 recovery: remnant cover and peak recorded cover post-disturbance (peak recovery). Where peak

89 recovery was assessed, post-disturbance cover was monitored for at least 3 years following

90 disturbance. 4) Coral cover decreased at least 10% relative to pre-disturbance cover due to

91 disturbance (Eqn. 1).

92
$$\text{Initial cover} - \text{Post disturbance cover} \geq 0.1\left(\text{Initial cover}\right) \quad \text{(Eqn. 1)}$$

93 We excluded studies in which the change in coral cover was < 10% relative to initial coral cover

94 because such relatively small year to year changes cannot be reliably distinguished from random

95 noise, e.g., stochastic variation and sampling error. Benthic survey methodologies rarely are able

96 to detect changes in cover < 5–10%. Graham 2011 et al. used a similar justification for excluding

97 such studies: "the initial drop in coral cover as a result of the disturbance exceeded 10%. Studies

98 recording lower initial mortality were excluded as small disturbances may have negligible impact

99 on hard coral cover (e.g., Edmunds 2002). Furthermore, inter-annual variation in coral cover can

100 be ~5% prior to a disturbance (e.g., Halford et al. 2004). A 10% relative decline reflects a sudden

101 change in benthic cover in response to a pulse disturbance." However, in contrast to Graham et

102 al. 2011, we chose a 10% relative decline as a cutoff to account for disturbances that cause little

103 absolute change but may in fact have a proportionally significant impact to reefs, particularly

104 those with low levels of initial coral cover.

105 Predicted coral richness values in our analyses are geographic estimates based on coral

106 species range distributions (Veron 2000; Veron et al. 2011) and have been used by previous

107 studies (e.g., Roberts et al. (2002); Veron et al. (2009)). Maps were originally vector data, but we

108 gridded them to a resolution of 50 km. The coral richness predictions that result from this

109 database are relatively coarse-grained, however, given the strong association between local and

110 regional coral richness (Karlson et al. 2004), our richness values likely correspond in a relative

111 sense to local richness at a site.

112   *Statistical Analysis*

113   We used the R programming environment ([R Core Team 2012](#)) to perform two separate sets of

114   regression analyses to test whether predicted coral richness was related to coral community

115   resistance to and recovery from disturbance. Variance inflation factors (VIFs) were calculated for

116   each pair of predictors to test for collinearity in both sets of analyses. The initial model for

117   decline included predicted coral richness, initial (pre-disturbance) coral cover, maximum survey

118   depth, region, and disturbance type as predictors. Initial predictors for recovery rate included

119   predicted coral richness, post-disturbance coral cover, maximum survey depth, region, and

120   disturbance type. We incrementally and individually removed non-significant predictors from the

121   models using backwards stepwise elimination. Akaike Information Criteria (AIC) was used in

122   model selection to assess which model provided the best fit. Decline (resistance) analyses were

123   performed using square root transformed net absolute coral loss, and in the recovery analysis, we

124   used log transformed recovery rate, calculated as the change in coral cover, generally an increase,

125   divided by the number of years until peak coral cover was observed (Eqn 2).

$$\log\left(\frac{\text{peak recorded recovery } - \text{ post-disturbance cover}}{\text{peak recovery year } - \text{ post-disturbanc year}} \div \right) \text{Eqn. 2}$$

126

127   In cases where recovery was not observed and reefs continued to decline i.e. negative recovery,

128   recovery rate was equated to zero. Transformations were based on the distribution of the raw

129   data. All models were also performed on raw data, the results of which did not different

130   qualitatively from those based on transformed data. The core database (including all response and

131   predictor variables), the R code, and model outputs were made available for editors and reviewers

132   upon manuscript resubmission and will remain available for future readers. We did this to enable

133   our analysis to be reproduced, to be as open as possible about our procedures, and to facilitate

134   future analysis based on our database.

135 **Results**

136 There was substantial variation among sites in predicted coral richness (24-552 species, Fig. 1),

137 coral cover loss (Fig. 1), and recovery rate (Fig. 2). The full linear regression model testing the

138 null hypothesis that coral species richness was not related to (sqrt transformed) post-disturbance

139 coral cover loss (decline) found that all covariates (including richness; p=0.79) except pre-

140 disturbance coral cover (blcc, p<0.0001) were unrelated to decline (Fig. S2, Table 1, Model 1,

141 Adj. R^2= 0.63, see all model results and R code in the Statistical Supplement). A simpler model

142 (Model 2, Adj. R^2= 0.60) that included three covariates (depth, richness, and blcc) with a similar

143 fit indicated that the richness effect was marginally significant (p=0.03). There was no

144 relationship (Adj. R^2= 0.01, p = 0.50) between predicted coral richness and initial cover, thus it is

145 unlikely that collinearity between these two covariates led to the putative effects of richness on

146 resistance. When we removed sites (two potential outliers) with extreme decline and high

147 diversity, the relationship between relative decline and predicted species richness was still

148 significant (in the reduced model with three covariates).

149   The full recovery model (Table 1, Model 4 in the Statistical Supplement, Adj. R^2= 0.26)

150 was the best fit and indicated that none of the covariates were related to recovery rate. Predicted

151 coral richness in particular appeared a very poor predictor of coral recovery rate (p=0.56).

152 **Discussion**

153 We did not detect an effect of region, disturbance type or depth on absolute loss in coral cover

154 due to disturbance (Table 1, Statistical Supplement). There was a weak positive relationship

155 between predicted species richness and coral loss (Fig. 1). However, a richness effect (p=0.03)

156 was only detected in the reduced model (Model 2), from which maximum depth, region, and

157 disturbance type were removed (Statistical Supplement). In the full model with all five covariates

158 (Model 1), the richness effect was not significant (p=0.79).

159   Concordant with several previous studies (Graham et al. 2008; Selig & Bruno 2010; Selig

160 et al. 2012), reefs with greater initial cover lost the most coral following disturbance (Fig. 1,

161 Statistical Supplement). This could be due in part to the dominance of high cover reefs in the

162 western Pacific and Indian ocean by plating acroporid corals, that are especially sensitive to both

163 physical and biological disturbances (Darling et al. 2012), i.e., not due to a cover effect *per se*,

164 but instead to the relationship, both among reefs and regions, between coral cover and species

165 composition. Acroporids are among the most sensitive coral species to most of the disturbances

166 known to cause declines in coral cover, e.g., thermal stress, disease, predation, and physical

167 disturbance (Bruno et al. 2001; Darling et al. 2012; Willis et al. 2004). Therefore reefs dominated

168 by plating and branching acroporids – the highest cover reefs – are likely to be especially

169 susceptible to disturbance. Although high taxonomic richness may confer greater functional

170 diversity and redundancy, this also implies a greater number of specialists that may not be well

171 adapted to disturbance or stressful conditions (Dobzhansky 1950; Schluter 2000) and may

172 partially explain our results. In fact, Côté and Darling (2010) argued that managing for coral

173 cover could counter-intuitively make reefs more susceptible to disturbances including climate

174 change.

175   Unlike several previous experimental studies in marine systems (Allison 2004; Reusch et

176 al. 2005; Williams 2001), our mensurative study found that the rate of post-disturbance recovery

177 was not significantly related to taxonomic richness (Table 1, Fig. 2). The large observed variance

178 in recovery rate among sites and studies (up to 12.5 % per year) appears to be due to factors not

179 included in our model and unrelated to estimated species richness.

180   Graham et al. (2011) reported that coral recovery varied somewhat among regions, with

181 the highest observed recovery rates in the western Pacific, the most species rich region, (Roberts

182 et al. 2002). Despite that finding, in our analysis coral richness was a poor predictor of recovery

183 rate (Fig. 2); although, the low richness reefs of the eastern Pacific recovered slowly, recovery of

184 Caribbean reefs with similar richness was greater and similar to that seen in the more diverse

185 western Pacific and Indian ocean (Fig. 2). This finding could be due in part to a publication

186 biases towards studies that document recovery and the fact that we searched for studies

187 documenting acute disturbances, whereas chronic perturbations are also responsible for

188 Caribbean coral losses. Furthermore, studies conducted in the eastern Pacific and included in our

189 analysis were mostly conducted on reefs dominated by slow-growing, massive *Porites*. Given the

190 current state of the Caribbean (Bruno et al. 2009) there is no doubt that coral cover on most

191 Caribbean reefs has not recovered from various natural and anthropogenic disturbances over the

192 last several decades (Roff and Mumby 2012). Hence, our results suggest that low diversity

193 Caribbean reefs have the potential to recover (in terms of coral cover) quite rapidly (e.g., Idjadi et

194 al. 2006), but for a variety of reasons they rarely do (Roff and Mumby 2012).

195   The majority of reefs in our study were monitored for less than eight years and few were

196 monitored long enough to recover fully (Fig. S3), given observed rates in recovery. Of the 23

197 reefs for which we had both initial post-disturbance and peak-year coral cover, only five (all

198 monitored for at least 11 years after disturbance) recovered to pre-disturbance levels of cover. If

199 recovery (coral cover increase) is indeed non-linear over time, we could have seen different

200 results, e.g., a significant richness effect if the component studies were conducted longer. To a

201 degree, our results could also be an artifact of the loss of Acroporid corals from Caribbean reefs

202 in the 1980s, due primarily to disease but in some locations to storms and predation (Aronson &

203 Precht 2006). Our earliest Caribbean recovery study began in 1987 (Edmunds 2002), after

204 Acroporid populations had crashed regionally (Aronson & Precht 2006). Had *Acropora*

205 *cervicornis* and *A. palmata* been present on Caribbean reefs when the datasets used in our

206 analyses were collected, we might have seen more rapid recovery on low diversity reefs because

207   these corals were amongst the fastest growing corals in the Caribbean region. However, we may

208   also have seen even less resistance to disturbance due to their high coral cover and vulnerability

209   to various stressors.

210   It is possible that systematic variation in disturbance intensity could obscure a richness

211   effect on coral community resistance. For example, disturbance intensity may have co-varied

212   with coral richness or peak coral cover. Although quantification of the intensity of disturbance is

213   beyond the scope of this study, it would, at least in theory, be possible. Our study also addresses a

214   very large scale richness gradient but ignores smaller scale variation, e.g., among reefs or zones

215   (Huston 1985). Furthermore, we used predicted richness values from known biogeographic

216   ranges (Veron 2000, Veron et al. 2011), which should reflect patterns of richness at this scale, but

217   can make richness and region hard to tease apart and cannot account for local site level

218   differences due to factors such as reef zone, disturbance history, micro-climates. Diversity of fish

219   assemblages may also be critical for coral recovery dynamics (Bellwood et al. 2004), which was

220   not considered in this study. Future analyses with empirical diversity data of corals and fish,

221   controlling for disturbance intensity and other drivers of coral loss and recovery, could improve

222   our understanding of the influence of diversity on community stability in coral reef ecosystems.

223   **Literature Cited**

224   Allison G. 2004. The influence of species diversity and stress intensity on community resistance

225   and resilience. *Ecological Monographs* 74:117-134.

226   Aronson RB, and Precht WF. 2001. White-band disease and the changing face of Caribbean coral

227   reefs. *Hydrobiologia* 460:25-38.

228   Aronson RB, and Precht WF. 2006. Conservation, precaution, and Caribbean reefs. *Coral Reefs*

229   25:441-450.

230   Bellwood, DR, TP Hughes, C. Folke, M. Nyström. 2004. Confronting the coral reef crisis. Nature

231   429: 827-833

232   Boyer KE, Kertesz JS, and Bruno JF. 2009. Environmental context influences the effects of

233   species richness on productivity but not stability of marine macroalgal communities.

234   *Oikos* 118:1062-1072.

235   Bruno JF, Siddon CE, Witman JD, Colin PL, and Toscano MA. 2001. El Niño related coral

236   bleaching in Palau, Western Caroline Islands. *Coral Reefs* 20:127-136.

237   Bruno, J. F., and E. R. Selig. 2007. Regional decline of coral cover in the Indo-Pacific: timing,

238   extent, and subregional comparisons. PLoS One:e711.

239   Bruno JF, Sweatman H, Precht WF, Selig ER, and Schutte VGW. 2009. Assessing evidence of

240   phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.

241   Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM,

242   Tilman D et al. 2012. Biodiversity loss and its imp[act on humanity. *Nature* 486: 59-67.

243   Côté IM, and Darling ES. 2010. Rethinking ecosystem resilience in the face of climate

244   change. *PLoS Biol* 8:e1000438.

245   Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, and Côté IM. 2012. Evaluating life-

246   history strategies of reef corals from species traits. *Ecology Letters* 15:1378-1386.

247   Dobzhansky T. 1950. Evolution in the tropics. *American Scientist* 38:209-221.

248 Duffy JE, Macdonald KS, Rhode JM, and Parker JD. 2001. Grazer diversity, functional

249   redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82:2417-

250   2434.

251 Edmunds PJ. 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands. *Coral*

252   *Reefs* 21:357-367.

253 Graham N, Nash K, and Kool J. 2011. Coral reef recovery dynamics in a changing world. *Coral*

254   *Reefs* 30:283-294.

255 Graham NAJ, McClanahan TR, MacNeil MA, Wilson SK, Polunin NVC, Jennings S, Chabanet P,

256   Clark S, Spalding MD, Letourneur Y et al. . 2008. Climate Warming, Marine Protected

257   Areas and the Ocean-Scale Integrity of Coral Reef Ecosystems. *PLoS ONE* 3:e3039.

258 Grandpre D, L., Bergeron, and Y. 1997. *Diversity and stability of understorey communities*

259   *following disturbance in the southern boreal forest*. Oxford, Royaume-Uni: Blackwell.

260 Grimm V, and Wissel C. 1997. Babel, or the Ecological Stability Discussions: An Inventory and

261   Analysis of Terminology and a Guide for Avoiding Confusion. *Oecologia* 109:323-334.

262 Halford A, Cheal AJ, Ryan D, Williams DMcB. 2004. Resilience to large-scale disturbance in

263   coral and fish assemblages on the Great Barrier Reef. Ecology 85:1892–1905.

264 Hughes, A. R., and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass

265 ecosystem to disturbance. Proceedings of the National Academy of Sciences 101:8998–9002.

266 Huston MA. 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and*

267   *Systematics* 16:149-177.

268 Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem

269   function of biodiversity. *Oecologia* 110:449-460.

270 Idjadi, JA, SC Lee, JF Bruno, WF Precht, L Allen-Requa, and PJ Edmunds. 2006. Rapid phase-

271   shift reversal on a Jamaican coral reef. Coral Reefs 25:209-211

272   Ives AR, Cardinale BJ, and Snyder WE. 2005. A synthesis of subdisciplines: predator-prey

273   interactions, and biodiversity and ecosystem functioning. *Ecology Letters* 8:102-116.

274   Ives AR, and Carpenter SR. 2007. Stability and Diversity of Ecosystems. *Science* 317:58-62.

275   Karlson, RH, HV Cornell, TP Hughes. 2004. Coral communities are regionally enriched along an

276   oceanic biodiversity gradient. Nature 429, 867.

277   May RM. 1973. *Stability and complexity in model ecosystems*. Princeton: Princeton University

278   Press.

279   McCann KS. 2000. The diversity-stability debate. *Nature* 405:228-233.

280   McNaughton SJ. 1977. Diversity and Stability of Ecological Communities: A Comment on the

281   Role of Empiricism in Ecology. *The American Naturalist* 111:515-525.

282   Miller I, and Müller R. 1999. Validity and reproducibility of benthic cover estimates made during

283   broadscale surveys of coral reefs by manta tow. *Coral Reefs* 18:353-356.

284   Naeem S. 1998. Species Redundancy and Ecosystem Reliability. *Conservation Biology* 12:39-45.

285   Naeem S, and Li S. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507-509.

286   Pimm SL. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.

287   R Core Team. 2012. R: A Language and Environment for Statistical Computing. Vienna, Austria:

288   R Foundation for Statistical Computing.

289   Reusch TBH, Ehlers A, Hammerli A, and Worm B. 2005. Ecosystem recovery after climatic

290   extremes enhanced by genotypic diversity. *PNAS %R 101073/pnas0500008102* 102:2826-

291   2831.

292   Roberts CM, McClean CJ, Veron JEN, Hawkins JP, Allen GR, McAllister DE, Mittermeier CG,

293   Schueler FW, Spalding M, Wells F et al. . 2002. Marine biodiversity hotspots and

294   conservation priorities for tropical reefs. *Science* 295:1280-1284.

295   Roff G, and Mumby PJ. 2012. Global disparity in the resilience of coral reefs. *Trends Ecol Evol*

296   27:404-413.

297   Schluter D. 2000. *The ecology of adaptive radiation*: OUP Oxford.

298   Selig ER, and Bruno JF. 2010. A global analysis of the effectiveness of marine protected areas in

299   preventing coral loss. *PLoS ONE* 5:e9278.

300   Selig ER, Casey KS, and Bruno JF. 2012. Temperature-driven coral decline: the role of marine

301   protected areas. *Global Change Biology* 18:1561-1570.

302   Stachowicz JJ, Bruno JF, and Duffy JE. 2007. Understanding the effects of marine biodiversity

303   on communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*

304   38:739-766.

305   Stachowicz JJ, Graham M, Bracken MES, and Szoboszlai AI. 2008. Diversity Enhances Cover

306   and Stability of Seaweed Assemblages: The Role of Heterogeneity and Time. *Ecology*

307   89:3008-3019.

308   Steiner CF, Long ZT, Krumins JA, and Morin PJ. 2006. Population and community resilience in

309   multitrophic communities. *Ecology* 87:996-1007.

310   Tilman D, and Downing JA. 1994. Biodiversity and stability in grasslands. *Nature* 367:363-365.

311   Veron J. 2000. Corals of the world. *Australian Institute of Marine Science Townsville, Australia*.

312   Veron J, Devantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, and Peterson N.

313   2009. Delineating the coral triangle. *Galaxea, Journal of Coral Reef Studies* 11:91-100.

314   Veron JEN. 1986. *Corals of Australia and the Indo-Pacific*. Sydney: Angus and Robertson.

315   Veron JT, E; DeVantier, LM; Stafford-Smith, MG; Kininmonth, S 2011. Coral Geographic.

316   Version 1.1. ed: Aust. Inst. Mar. Sci.

317   Williams SL. 2001. Reduced genetic diversity in eelgrass transplantations affects both population

318   growth and individual fitness. *Ecological Applications* 11:1472-1488.

319   Willis BL, Page CA, and Dinsdale EA. 2004. Coral disease on the Great Barrier Reef. In:

320   Rosenberg E, and Loya Y, eds. *Coral Health and Disease*. Berlin: Springer-Verlag, 69-

321   104.

322   Yachi S, and Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating

323   environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*

324   96:1463-1468.

Table 1

Linear models performed in analyses.

Linear model description -Decline

Raw data	AIC	R²	p-value
Richness + maxdepth + disturbance + region + blcc	351.94	0.71	4.04e-07
Richness + maxdepth + blcc	349.46	0.65	5.56e-09
Richness + blcc	414.92	0.60	2.73e-10
Richness + maxdepth + disturbance + region + blcc + maxdepth:disturbance interaction	354.75	0.71	2.85e-06

Square root transformed

	AIC	R²	p-value
Richness + maxdepth + disturbance + region + blcc[†]	148.77	0.70	5.62e-07
• Intercept			0.05
• Richness			0.78
• Max depth			0.95
• Disturbance – COTS			0.69
• Disturbance – Storms			0.51
• Region – E. Pacific			0.17
• Region – Indian Ocean			0.67
• Region – W. Pacific			0.98
• BLCC			3.72e-8
Richness + maxdepth + blcc *[†]	147.60	0.63	1.50e-08
• Intercept			0.15
• Richness			0.03
• Max depth			0.61
• BLCC			1.02e-08
Richness + blcc	174.83	0.59	6.82e-10
Richness + maxdepth + disturbance + region + blcc + maxdepth:disturbance interaction	150.30	0.72	2.49e-06

Linear model description - Recovery

Raw data	AIC	R²	p-value
Richness + maxdepth + disturbance + region + pdcc	264.05	0.27	0.03
Richness + maxdepth	264.11	0.12	0.04
Richness	274.63	0.062	0.07

Log transformed

	AIC	R²	p-value
Richness + maxdepth + disturbance + region + pdcc*	104.77	0.38	0.04e-1
• Intercept			3.95e-06
• Richness			0.56
• Max depth			0.10
• Disturbance – COTS			0.35
• Disturbance – Storms			0.21
• Region – E. Pacific			0.25

• Region – Indian Ocean			0.46
• Region – W. Pacific			0.46
• PDCC			0.13
Richness + maxdepth	109.21	0.15	0.01
Richness	115.60	0.11	0.01

Table 1. Linear models performed in analyses.

* indicates best fit model for coral cover decline and recovery based upon lowest AIC. p-values for best fit model factors listed below model description.

† indicates best fit decline models which did not differ significantly based upon AIC.

Figure 1

Coral community richness and resistance to disturbance.

3-D scatter plot of the relationship between coral community richness, coral loss (net change in absolute percent cover in response to disturbance) and initial coral cover. See Table 1 for results of statistical analysis. Dashed lines represent the regression plane, and point coloration represents region. Refer to the Statistical Supplement for a version of this figure plotted with the response variable square root transformed.
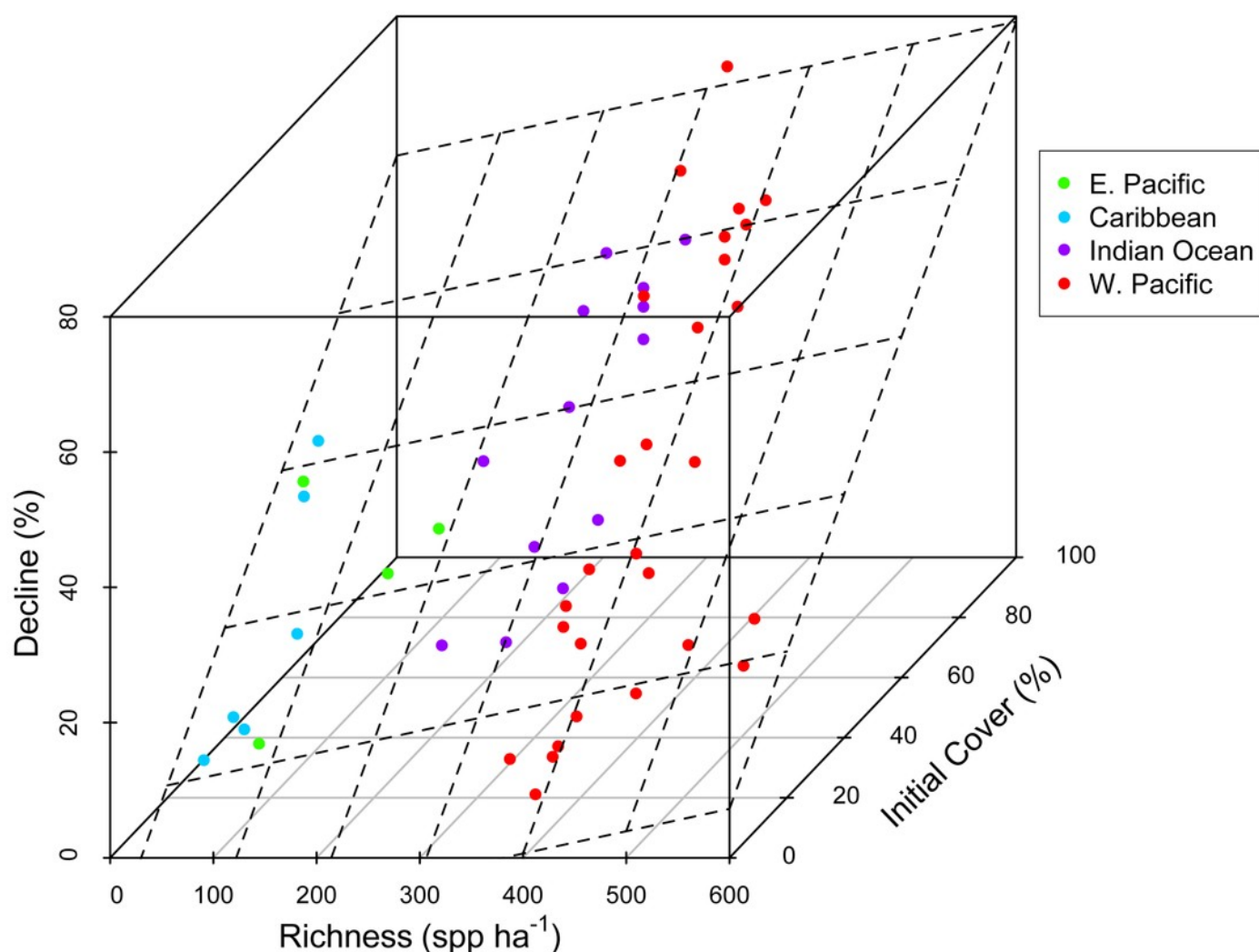
Figure 2

Coral community richness and recovery from disturbance.

Scatter plot of the relationship between the post-disturbance recovery of absolute coral cover and estimated coral species richness. Refer to the Statistical Supplement for a version of this figure plotted with the response variable log transformed.