Time to cash in on positive interactions for coral restoration

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Coral reefs are among the most biodiverse and productive ecosystems on Earth, and provide critical ecosystem services such as protein provisioning, coastal protection, and tourism revenue. Despite these benefits, coral reefs have been declining precipitously across the globe due to human impacts and climate change. Recent efforts to combat these declines are increasingly turning to restoration to help reseed corals and speed-up recovery processes. Coastal restoration theory and practice has historically favored transplanting designs that reduce potentially harmful negative species interactions, such as competition between transplants. However, recent research in salt marsh ecosystems has shown that shifting this theory to strategically incorporate positive interactions significantly enhances restoration yield with little additional cost or investment. Although some coral restoration efforts plant corals in protected areas in order to benefit from the facilitative effects of herbivores that reduce competitive macroalgae, little systematic effort has been made in coral restoration to identify the entire suite of positive interactions that could promote population enhancement efforts. Here, we highlight key positive species interactions that managers and restoration practitioners should utilize to facilitate the restoration of corals, including i) trophic facilitation, ii) mutualisms, iii) long-distance facilitation, iv) positive density-dependence, v) positive legacy effects, and vi) synergisms between biodiversity and ecosystem function. As live coral cover continues to decline and resources are limited to restore coral populations, innovative solutions that increase efficiency of restoration efforts will be critical to conserving and maintaining healthy coral reef ecosystems and the human communities that rely on them.

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24   **Abstract**

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26   critical ecosystem services such as protein provisioning, coastal protection, and tourism revenue.

27   Despite these benefits, coral reefs have been declining precipitously across the globe due to

28   human impacts and climate change. Recent efforts to combat these declines are increasingly

29   turning to restoration to help reseed corals and speed-up recovery processes. Coastal restoration

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31   negative species interactions, such as competition between transplants. However, recent research

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33   interactions significantly enhances restoration yield with little additional cost or investment.

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35   the facilitative effects of herbivores that reduce competitive macroalgae, little systematic effort

36   has been made in coral restoration to identify the entire suite of positive interactions that could

37   promote population enhancement efforts. Here, we highlight key positive species interactions

38   that managers and restoration practitioners should utilize to facilitate the restoration of corals,

39   including i) trophic facilitation, ii) mutualisms, iii) long-distance facilitation, iv) positive density-

40   dependence, v) positive legacy effects, and vi) synergisms between biodiversity and ecosystem

41   function. As live coral cover continues to decline and resources are limited to restore coral

42   populations, innovative solutions that increase efficiency of restoration efforts will be critical to

43   conserving and maintaining healthy coral reef ecosystems and the human communities that rely

44   on them.

45

46

Introduction

47

48   Coral reefs are one of the most biodiverse and productive ecosystems on Earth, and

49 provide critical services to at least 500 million people throughout the world (Wilkinson 2004). In

50 addition to supporting healthy and thriving human communities through food provisioning,

51 coastal protection, and tourism revenue, coral reefs are essential ecosystems within the landscape

52 of coastlines, facilitating seagrass, mangrove, and terrestrial habitats (Dorenbosch et al. 2005,

53 Mumby et al. 2004). Despite the many benefits to both natural and human communities, coral

54 reefs around the world are rapidly degrading due to a combination of human activities and

55 climate change. In response to these losses, conservation efforts are increasingly turning to

56 restoration as a strategy to promote coral reef recovery by transplanting colonies that will

57 hopefully grow, reproduce, and reseed reefs (Johnson et al. 2011, Young et al. 2012). Although

58 active coral transplantation efforts are increasing across the globe (Lirman and Schopmeyer

59 2016), restoration remains costly (median, $162,455 US per ha) and most projects are done on

60 small temporal (1 yr) and spatial smalls (< 1 ha) (Bayraktarov et al. 2016). Transplant

61 survivorship, however, has been high relative to other habitats (64.5% survival) (Bayraktarov et

62 al. 2016); thus, coral restoration shows promise but requires further innovative approaches that

63 improve restoration efficiency. Increased yield for each conservation dollar spent will be critical

64 if we are to reach restoration scales needed to rehabilitate large enough coral populations that

65 restore coral reef processes and services at the ecosystem level.

66   For many decades, the paradigm in coastal conservation has been to minimize negative

67 interactions (e.g., competition) between transplant neighbors (Silliman et al. 2015). This

68 paradigm was transferred directly from forestry science, which developed in the late 1940s

69 (Halpern et al. 2007). However, positive interactions are common in marine systems and often

70 play pivotal roles in ecosystem development and recovery (Bruno and Bertness 2001). For

71 instance, a mutualism between salt marsh grasses and ribbed mussels is key to salt marsh

72 resilience and recovery after severe drought events, as mussel mounds increase nutrients and

73 water retention that reduces marsh grass mortality during drought (Angelini et al. 2016). In kelp

74 forests, predator populations promote ecosystem resistance and recovery by indirectly facilitating

75 kelp populations through a trophic cascade (Estes and Palmisano 1974). Positive species

76 interactions in coral reef ecosystems could likewise be identified and used to assist in the active

77 recovery of coral populations and habitats.

78   With increased consideration of facilitation in ecological theory (Bruno et al. 2003),

79 recent papers have also recently made the case for systematically including positive interactions

80 in aquatic and coastal restoration (Halpern et al. 2007, Gedan and Silliman 2009). Unfortunately,

81 a decade later, a survey of coastal wetland conservation agencies found that reducing negative

82 interactions was still the predominant focus in wetland restoration designs (Silliman et al. 2015).

83 Subsequent experimental studies showed that altering restoration practices to instead harness

84 positive species interactions increased transplant survivorship by ~100% and biomass by ~200%

85 with no additional cost (Silliman et al. 2015). Efforts in coral reef restoration, however, have not

86 been made to systematically use facilitation in restoration designs, even though numerous

87 positive interactions have been identified in ecological studies (e.g., herbivores that facilitate

88 corals by suppressing algae, crustose coralline algae that promotes coral settlement). Indeed, a

89 Web of Science search for coral restoration studies from 1980-2016 (generating 104 studies; see

90 Fig. 1 for search terms) shows very few studies (10 studies, 9.6%) have examined positive

91 interactions in a restoration context, with most of these papers focusing on herbivore-algae

92 interactions (6 studies, Fig. 1). Below, we highlight positive interactions that naturally occur on

93   coral reefs around the world that may be available to use to enhance coral restoration success and

94   thus increase the efficiency and scale of these efforts.

95

96   **Trophic facilitation**

97   Trophic facilitation occurs when one species is positively impacted through the feeding

98   activities of another. One example includes trophic cascades where predators, by suppressing

99   densities of primary consumers, can increase densities of basal prey species such as plants (e.g.,

100   effects of wolves on shrub communities in the Great Lakes: Callan et al. 2013; effects of otters

101   on kelp forests in the Pacific: Estes and Palmisano 1974). Another common example occurs

102   when consumers facilitate species that are competitively inferior. For instance, ungulates in

103   North America (Beschta and Ripple 2009) and elephants in Africa (Sinclair et al. 2010) can

104   facilitate grassland persistence by preferentially feeding on saplings, thereby suppressing the

105   growth of competitively dominant trees.

106   In coral reefs, the facilitation of corals by herbivores (via suppressing the overgrowth of

107   macroalgae) has been studied for decades. Results of comparative and experimental studies have

108   shown that herbivorous fish and urchins are critical for the success of corals, and this positive

109   interaction is general across almost all regions where corals occur (Ogden and Lobel 1978, Hay

110   1984, Mumby et al. 2006, Burkepile and Hay 2008). Because of this research, coral conservation

111   programs often focus on harnessing the positive impacts of herbivores on corals (e.g., NOAA

112   *Acropora* Recovery Plan: NMFS 2015), and many restoration manuals likewise recommend

113   transplanting corals in areas with high herbivore densities, such as in marine protected areas

114   (MPAs; Caribbean *Acropora* Restoration Guide: Johnson et al. 2011) (Fig. 2). Despite the

115   incorporation of these ecological findings into restoration, no studies to date have experimentally

116   evaluated the effects of coral restoration success in areas with high vs. low herbivore abundance.

117   This work is ultimately important as many reef herbivores can negatively affect corals or reef

118   systems by acting as corallivores or bioeroders of reef framework. Recent research suggests that

119   grazing may be more detrimental on degraded reefs with few living corals and reduced reef

120   accretion rates (Rotjan and Lewis 2008, Mumby 2009, Kuffner and Toth 2016). Therefore,

121   taking advantage of ecological interactions that facilitate corals for restoration must also include

122   rigorous evaluation of their effects and can include assessing threshold effects or evaluating how

123   different species vary in their functional roles (as suggested by Rotjan and Lewis 2008). In

124   addition to macroalgae, future restoration designs may also benefit from extending this research

125   to examine how trophic interactions also influence other benthic coral competitors such as

126   sponges, fire corals, and mat-forming zoanthids.

127   In contrast to the indirect effects of herbivores on corals, trophic cascades and direct

128   predation on corals have been considered within the context of restoration and conservation to a

129   far lesser extent. There is experimental and observational evidence, however, to suggest that

130   trophic cascades and food web linkages can positively affect coral populations. For instance,

131   experimental removals of pufferfish in the Caribbean showed that these fish can facilitate soft

132   corals by reducing populations of corallivorous flamingo tongue snails (Burkepile and Hay

133   2007). Similarly, the breakdown of trophic cascades due to overfishing has also been suggested

134   to lead to population outbreaks of corallivores such as nudibranchs in Hawaii (Gochfield and

135   Aeby 1997), *Drupella* snails in the Western Indian Ocean (McClanahan 1997), and crown-of-

136   thorns starfish in Fiji (Dulvy et al. 2004). No research has yet been attempted to evaluate the

137   positive effects of trophic cascades on coral restoration success, even though the potential to

138   enhance restoration efficiency is high given that corallivores are common sources of mortality

139   for new coral transplants (Schopmeyer & Lirman 2015, Lirman and Schopmeyer 2016).

140   Additionally, much time and manpower are currently being invested in the Caribbean to

141   manually remove corallivores from transplants (Williams et al. 2014, NMFS 2015). Like

142   herbivores, one of the best places to examine these effects may be within effectively managed

143   MPAs where predators of corallivores should theoretically be higher (Fig. 2).

144   Beyond tri-trophic facilitation corals through predator control of corallivores, a more

145   general discussion has emerged over whether top predators can create interactions that trickle

146   down to positively affect coral populations. The evidence so far has been equivocal, as recent

147   observational research correlating top predators with coral or algal-dominated systems have

148   found varying results (Sandin et al. 2008, Ruppert et al 2013) potentially caused by the fact that

149   top predators often feed on multiple trophic levels (Valentine and Heck 2005). Despite this, more

150   direct trophic linkages may be found that can be used specifically for restoration when corals are

151   most vulnerable (i.e., when they are first transplanted and small), for instance protecting a

152   predator that strongly controls populations of a particular corallivore population. The ambiguity

153   and paucity of experiments in this research avenue, and therefore its use in informing coral

154   restoration practices, highlights the great need for more research on how complex food web

155   interactions can facilitate coral populations.

156

157   **Mutualisms**

158   Mutualistic interactions, or reciprocal positive interactions between species, are

159   fundamental to the success and persistence of foundation species in many marine and terrestrial

160   ecosystems. For example, mutualisms between plants and mycorrhizal fungi underlie forests

161   (Dighton and Mason 1985) and salt marshes (Daleo et al. 2007) by facilitating plant colonization

162   in otherwise stressful environments. Other reciprocal positive interactions facilitate the

163   persistence of foundation species by protecting them from natural enemies. An example of this is

164   the symbiosis between ants and Acacia trees, where ants protect trees from antagonistic species

165   (stem boring beetles: Palmer et al. 2008) and pathogens (González-Teuber et al. 2014) in

166   exchange for refuge and habitat. Similarly, the formation of coral reefs throughout the tropics

167   would not occur without a mutualism between corals and photosynthetic algae (*Symbiodinium*),

168   which provide substantial nutrition to corals and enhance skeletal deposition (Goreau and Goreau

169   1959). Because of the high biodiversity on coral reefs, there are likely many reciprocal positive

170   interactions that promote coral success and that be identified for use in restoration designs.

171   The relationship between corals and crustose coralline algae (CCA) is one of the most

172   well-known reciprocal positive interactions that can encourage healthy coral reef functioning.

173   While coral reefs provide habitat, CCA is critical for cementing and stabilizing reef structure and

174   facilitating settlement of coral larvae (Heyward and Negri 1999). Reef-dwelling sponges are also

175   important for substrate stabilization as well as food web nutrient cycling through the conversion

176   of detritus into food resources for reef consumers (De Goeij et al. 2013). Other mutualisms can

177   increase restoration efficiency by reducing the harmful effects of natural enemies on corals. In

178   French Polynesia, for example, amphipods that live in corals of the genus *Montipora* protect

179   corals from predatory seastars (Bergsma & Martinez 2011, Bergsma 2012). Similarly,

180   mutualistic crabs in the Pacific increase the survivorship and growth of branching corals by

181   reducing sedimentation (Glynn 1976), predation by crown-of-thorns seastars (Pratchett and

182   Vytopil 2000, Pratchett 2001), and vermetid snail effects (Stier et al. 2010). Many fish species

183   that use coral reefs for habitat can also promote coral growth by enhancing the transfer of

184   nutrients in areas where macroalgae are trophically controlled (Burkepile et al. 2013).

185   Despite these many examples of mutualisms that support coral success, few studies to

186   date have examined or experimented with incorporating species-specific mutualisms into

187   restoration. One recent study that seeded a reef with sponges prior to transplanting corals found

188   significant increases in rubble consolidation that in turn enhanced coral survivorship in that

189   environment (Biggs 2013). Similarly, an experiment that explicitly transplanted corals in areas

190   with high and low abundances of grunts showed that fish significantly increased coral

191   survivorship and growth through nutrient transfer (Shantz et al. 2015). These studies reveal that

192   reciprocal positive relationships can be used in innovative and strategic ways in a restoration

193   context. Thus, future restoration designs across regions should seek to identify local mutualisms

194   that can be harnessed to increase success naturally without additional manpower.

195

196   **Long-distance facilitation**

197   Positive interactions can also occur between species that are not in contact but separated

198   by distances of tens or thousands of meters (van de Koppel et al. 2015). Long-distance, positive

199   impacts can be generated by the amelioration of physical and/or biological stress. For instance, in

200   coastal habitats the structure of intertidal oyster reefs reduces wave energy and erosion allowing

201   mud flats to accrete behind reefs, which then provide a suitable environment for the development

202   of relatively wave-intolerant salt marsh grasses (Meyer, Townsend, and Thayer 1997). Long-

203   distance facilitation can also affect the spatial organization of ecosystems, such as bands of

204   mussel beds that form across large mud flats due to the interaction between local facilitation of

205   mussels but resource competition over larger areas (van de Koppel et al. 2015). As coral reefs are

206   often biologically and physically linked to adjacent tropical habitats, we examine potential long-

207   distance facilitations that may be useful for coral restoration.

208   Decades of research has shown that the health, productivity, and biodiversity of coral

209   reefs is directly related to their proximity to tropical seagrass meadows and mangrove forests.

210   For example, both habitats facilitate corals by reducing stressors such as sedimentation or

211   nutrient pollution from coastal development and runoff that may smother corals or enhance algal

212   overgrowth (Christianen et al. 2013, Storlazzi et al. 2011). Seagrass meadows are also important

213   regulators of water quality, with recent surveys finding 2-fold less coral disease on reefs near

214   seagrasses (Lamb et al. 2017). Coral productivity may be enhanced by naturally-derived

215   nutrients from seagrasses or mangroves through detritus or the excrement of animals that forage

216   in those habitats but live on coral reefs (e.g., grunts: Shantz et al. 2015) (Fig. 2). In addition to

217   trophic linkages, seagrasses and mangroves can enhance the biomass and diversity of many reef-

218   associated species by acting as nursery habitat during critical early life stages (Nagelkerken &

219   van der Velde 2002) (Fig. 3). Rainbow parrotfish, for example, are important large herbivores in

220   the Caribbean that are significantly higher on coral reefs next to healthy mangrove habitats

221   (Mumby et al. 2004), and in general the biomass of herbivorous fish is significantly reduced on

222   reefs without nearby seagrass and mangrove habitats (Dorenbosch et al. 2005, 2007).

223   Major barriers to the long-term survivorship of restored corals include disease and high

224   levels of macroalgae that block coral recruitment (NMFS 2015). However, planting corals

225   specifically near healthy mangrove and seagrass habitats could facilitate increased transplant

226   growth (e.g., increased nutrient transfer) and survivorship (e.g., reduced disease and macroalgae

227   due to herbivore biomass and diversity) (Fig. 3). Within reefs, corals could also benefit from

228   being planted near larger, established corals due to wave protection and/or spillover of facilitated

229   herbivores (i.e., urchins like *Diadema*) that live within the interstitial matrices of larger corals

230   (Fig. 3). Despite the great potential for long distance positive interactions to enhance coral

231   restoration, little consideration has been to scientifically evaluate the effects of restoring corals

232   with and without adjacent and healthy mangroves or seagrasses, or near large corals within reefs.

233   These efforts could be further enhanced with more 'ridge to reef' management or protection

234   (e.g., MPAs) that encompass all coastal habitats from land out to coral reefs.

235

236   **Positive density dependence**

237   Positive density dependence is another mechanism that can enhance population recovery.

238   The role of intraspecific density on a population's growth and success has been examined in a

239   great number of organisms, including insects (e.g., Stiling 1987), plants (e.g., Harms et al. 2000),

240   and marine invertebrates (e.g., Levitan 1991), and can have both negative and positive effects.

241   Positive density dependence, or density-dependent facilitation, occurs when the success of

242   conspecifics increases at higher densities (i.e., the Allee effect: Allee 1931). For example, salt

243   marsh grasses and mangrove trees have higher survivorship and increased rates of recovery in

244   groups vs. in isolation because group benefits emerge from synergistic soil oxygenation and

245   structural protection from wave stress (Gedan and Silliman 2009, Silliman et al. 2015). Animal

246   aggregations, such as mussels and schooling fish, have increased success with higher densities

247   due to reduced predation pressure on individuals (Gascoigne and Lipcius 2004). Recent

248   ecological theory suggests that positive density dependent effects should be more prevalent

249   under stressful physical conditions, while negative density effects like competition will occur

250   more in low stress environments (i.e., the stress-gradient hypothesis, SGH: Bertness & Callaway

251   1994). Because habitats being restored are often degraded areas with high physical stress,

252   positive density effects may emerge and be important for improving restoration success.

253   Recent studies examining the effects of density on the success of conspecific coral

254   transplants have found both negative and positive density dependence. The first study to

255   manipulate density (corals spaced 5-cm apart) and planting configuration of staghorn coral

256   (*Acropora cervicornis*) found increase density significantly reduced coral growth within the first

257   3 months of transplantation, likely due to competition for space (Griffin et al. 2015) (Fig. 4). In

258   the Philippines, Shaish et al. (2010) found no difference in colony survivorship of transplanted

259   *Montipora digitata* in high density (spaced 10-cm apart) and low density (spaced 20-cm apart)

260   plots over 15 months. These studies suggest studies examining the effects of density on coral

261   transplants may have varied results depending on spacing between colonies. For endangered

262   Caribbean acroporid corals, recent experimental research shows a unimodal relationship may

263   exist, with positive density effects occurring at moderate levels (3 corals m^{-2}) but negative

264   density effects occurring at higher densities (Ladd et al. 2016). However, strong positive density

265   effects have been found under natural settings in *A. cervicornis* thickets at high density levels

266   due to a positive feedback loop between these branching corals and the fish that live within their

267   branches and provide nutrients through excrement (Huntington et al. 2017) (Fig. 4).

268   While most of these studies examine colony-specific metrics, such as growth and

269   survivorship of individual corals, the effects of density are likely affected by environmental

270   stressors and temporal scales. Although ecological theory (e.g., the SGH) suggests that positive

271   density dependency may emerge under high stress conditions in coral reefs, no studies to date

272   have examined how the impacts of density vary across a stress gradient. For instance, because of

273   the tendency of branching corals to fuse, higher density plots may enhance structural resistance

274   to wave energy such as intense storms (as suggested in Griffin et al. 2015), yet no study to date

275   has examined this type of positive density effect. Similarly, higher density plots may also

276   enhance structural complexity that attracts more fish (e.g., promoting nutrient transfer) or

277   invertebrates (e.g., that promote corals through mutualisms or trophic facilitation) (Fig. 2).

278   Clearly, further research on the role of density in promoting coral restoration is needed,

279   specifically studies that focus on how density varies along realistic and commonly occurring

280   stress gradients, like wave stress, heat stress, turbidity, and coral predation.

281

282   **Positive legacy effects**

283   Legacy effects, which can be both negative and positive, occur when species interactions

284   have a lasting impact on an ecological community well past the time of the initial interaction.

285   One example is the effect of ditching on salt marshes in the 1930's, where the immediate

286   negative legacy effect of this human-ecosystem interaction included changes to plant

287   distributions, fish and insect abundance, and hydrological patterns that benefited some species

288   but suppressed others (Silliman, Grosholz, and Bertness 2009). Only recently, a positive legacy

289   effect was found that ditched marshes are more susceptible to runaway grazing by crabs and

290   subsequent community die-off because ditched marshes are dominated by plants that are

291   preferred by grazing crabs (Coverdale et al. 2013). A legacy effect evident in the context of

292   restoration includes oyster reefs, which have been decimated by disease and overharvesting over

293   the last century (Beck et al. 2011). Although the individuals that built remnant oyster reefs

294   decades ago are gone, their skeletons remain and are commonly used to facilitate oyster

295   recruitment (i.e., 'spat') (Schrack et al. 2012).

296   Although legacy effects on coral reefs have not been intensely studied, we consider here

297   one strong example that could be used in restoration. Like oyster reefs, coral skeletons remain

298   present on reefs for many years after the veneer of living coral tissue has disappeared. In the

299   same way that oyster spat recruits to old oyster shell, new coral recruits or transplants may also

300   benefit from settling or growing on old skeleton. For instance, corals may be able to grow faster

301   by re-sheeting tissue over the skeleton rather than expending energy on producing new skeleton.

302   Indeed, a reef in Palau was found to recover quickly after a bleaching event because corals

303   regrew tissue over former skeletons rather than laying down new skeleton (Roff et al. 2014).

304   Growing on coral skeletons can also keep smaller, more susceptible coral transplants away from

305   competitors or predators. For instance, coral larvae are known to avoid reefs with high algal

306   cover, but will settle on structures above the substrate to avoid competitive algae (Dixson,

307   Abrego, and Hay 2014). Likewise, corallivores might prefer to feed at low elevations or avoid

308   high elevations to potentially avoid predation (E Shaver *pers. comm.*). The potential to use coral

309   skeletons in a restoration context has recently been realized, for instance using new techniques

310   (i.e., micro-fragging: Forsman et al. 2015) to restore reef-building boulder corals in Florida.

311   Much more research is required, however, to understand and maximize the benefits of coral

312   skeletons in coral restoration efforts and to identify other legacy effects that can be used to

313   increasing the efficiency of coral restoration efforts.

314

315   **Biodiversity and ecosystem function**

316   Biodiversity encompasses the species, genetic, functional, and ecological diversity of

317   living things. Decades of research have shown that for a great variety of marine and terrestrial

318   ecosystems, there is a positive relationship between biodiversity and ecosystem function,

319   (Tilman et al. 1997, Hooper and Vitousek 1997, Kinzig et al. 2002, Hooper et al. 2005, and

320   Srivastava and Vellend 2005). For example, Maester et al. (2012) found that diversity of plant

321   species in semi-arid ecosystems (e.g., drylands) enhanced carbon and nutrient cycling as well as

322   overall ecosystem multifunctionality. In addition to higher ecosystem productivity and

323   functioning, studies have also shown that biodiversity increases ecosystem resilience to

324   disturbance. Proposed mechanisms behind the positive impacts of biodiversity on ecosystem

325   function and resilience include the asynchrony of species responses to environmental changes or

326   disturbances (e.g., the portfolio effect: Tilman 1999, Loreau 2010) and increased functional

327   redundancy, leading to higher resilience and the maintenance of ecological functioning if one or

328   a few species are lost (e.g., the insurance hypothesis: Yachi & Loreau 1999).

329   The most commonly used techniques for coral restoration today (e.g., coral gardening

330   and outplanting: Lirman and Schopmeyer 2016) were designed to restore branching corals in

331   response to severe declines in the populations of two formerly dominant Caribbean acroporid

332   corals after disease and bleaching events (staghorn coral: *A. cervicornis*; elkhorn coral: *A.*

333   *palmata*; Gardner et al. 2003). Coral restoration projects across the globe also largely focus

334   efforts on a few species of branching corals (e.g., *Acropora* spp. and *Pocillopora* spp.), due to a

335   history of restoration methods that take advantage of their high growth rates and ease of

336   propagation through fragmentation (Johnson et al. 2011, Rinkevich 2014). However, coral reefs

337   in both regions have a diversity of coral species and many massive coral species can be

338   important reef-builders (e.g., *Orbicella* spp.). In addition, Caribbean branching corals can be

339   more susceptible to natural enemies such as predators and disease (Bruckner 2002, Baums et al.

340   2003), and due to ecological trade-offs with competitive dominance, tend to be less tolerant of

341   environmental stressors like warm temperatures and bleaching (Loya et al. 2001). Because

342   natural enemies and climate change continue to impede restoration efforts (NMFS 2015) and

343   because coral reefs naturally harbor a greater diversity of corals than just two species,

344   reestablishing a range of coral biodiversity, including species and growth forms, may enhance

345   success and facilitate ecosystem resilience.

346   Several experiments manipulating coral species richness have found improved coral

347   growth and survivorship in mixed versus single species plots. For instance, Dizon & Yap (2005)

348   found that colonies of *Porites cylindrica* had higher growth rates when transplanted in plots with

349   other species (*Porities rus* and *Pavona frondifera*) relative to conspecifics, however this

350   facilitation stopped when nutrient enrichment was introduced to plots. Diverse coral species

351   facilitated *A. cervicornis* growth and survivorship by reducing the number of coral predators

352   (*Coralliophila abbreviata*) that attacked plots of *A. cervicornis* (Johnston and Miller 2014).

353   Similarly, Cabaitan et al. (2015) found that transplants of the coral *Pavona frondifera* had higher

354   success when planted with the coral *Porites cylindrica*, but only in stressful environments with

355   high wave energy. In addition, *P. cylindrica* also appeared to reduced predation on *P. frondifera*

356   by starfish and snails (Cabaitan et al. 2015). Additionally, Montoya-Maya et al. 2016 found

357   successful coral recruitment in areas transplanted mixed coral species, though this study did not

358   manipulate diversity and all species used were acroporid or pocilloporid (e.g., branching) corals.

359   Importantly, restoring diverse functional traits (e.g, growth forms) in addition to species may

360   also increase the resilience of restored sites to climate-change impacts (e.g., bleaching events or

361   intense storms), as boulder corals may be more likely to withstand these stressors (Loya et al.

362   2001). Luckily, new techniques are being designed to improve the propagation of other coral

363   species (Lirman and Schopmeyer 2016). Future research should examine how coral diversity

364   effects transplant success (growth, mortality, recruitment) as well as long-term ecological

365   stability (resistance and recovery processes). These efforts may be especially important in the

366   Caribbean, where it is thought that low diversity relative to the Indo-Pacific has reduced its

367   ability to recover after disturbance.

368

369   **Conclusion and recommendations**

370   Restoration is currently being elevated as a major conservation strategy to help combat

371   coral loss in the Caribbean and across the globe. For this to be realized, the efficacy of

372   restoration efforts must increase long-term coral transplant growth and survivorship while

373   reducing associated costs. It is important to note that like other marine and terrestrial ecosystems,

374   active transplantation efforts are likely to be successful only in sites where environmental or

375   local stressors have been successfully reduced (e.g., effective MPAs) or in areas where stress is

376   not an issue but recruitment limitation is impeding natural recovery (Orth et al. 2012). For new

377   techniques and designs to help increase the scale of coral restoration efforts, these restorative

378   efforts thus must also be tied to successful management strategies.

379   Harnessing naturally-occurring positive interactions in restoration designs has recently

380   been suggested (Halpern et al. 2007, Gedan and Silliman 2009) and demonstrated (Silliman et al.

381   2015) as one primary way scaling up restoration efforts can be accomplished in other aquatic

382   habitats. Coral reef managers have used positive interactions for decades to promote corals with

383   a well-known trophic facilitation by algae-eating herbivores, but have not yet identified other

384   positive species interactions specifically for use in coral restoration designs. In this paper, we

385   highlight several other general facilitative mechanisms that could be used by coral restoration

386   practitioners when designing future projects. Although this paper is focused on facilitations, the

387   relative effects of negative (e.g., competition and predation) and positive interactions (facilitation

388   and mutualism) are likely to vary depending on the species or organisms present and the

389 environment conditions or characteristics of that site (He et al. 2013). Nonetheless, below we

390 recommend general facilitative mechanisms that deserve further testing and consideration in

391 restoration designs including:

392   1) Identifying specific trophic linkages or food webs that promote coral health and

393   transplanting corals in areas with where these food webs are robust and protected.

394   2) Identifying mutualisms between corals and other reef- or coral-associated organisms

395   that promote coral health and enhancing or protecting these mutualistic partners.

396   3) Locating sites for coral restoration close to healthy and well-functioning seagrass and

397   mangrove habitats and protecting these habitats from extractive or destructive uses.

398   4) Identifying species-specific density effects for corals of restoration interest to take

399   advantage of transplant densities that facilitate coral growth or survivorship.

400   5) Exploring the legacy of former reef-builders or occupiers, such as coral skeletons left

401   behind, for use in coral transplantation.

402   6) Determining ways in which increased coral diversity facilitates the success of coral

403   transplants as well as the long-term success of the restored coral reef community to

404   environmental fluctuations and disturbances (e.g., resilience).

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653   **Figures**

654

655   **Figure 1.** Number of coral restoration studies from a Web of Science search for TOPIC: ("Coral

656   Restoration"), OR TOPIC: ("Coral Propagation") OR TOPIC: ("Coral Gardening") OR TOPIC:

657   ("Coral Nurseries") from 1980-2016 that examine negative interactions (i.e., competition,

658   predation) and positive interactions (i.e., facilitation, mutualism, cooperation) or neither.

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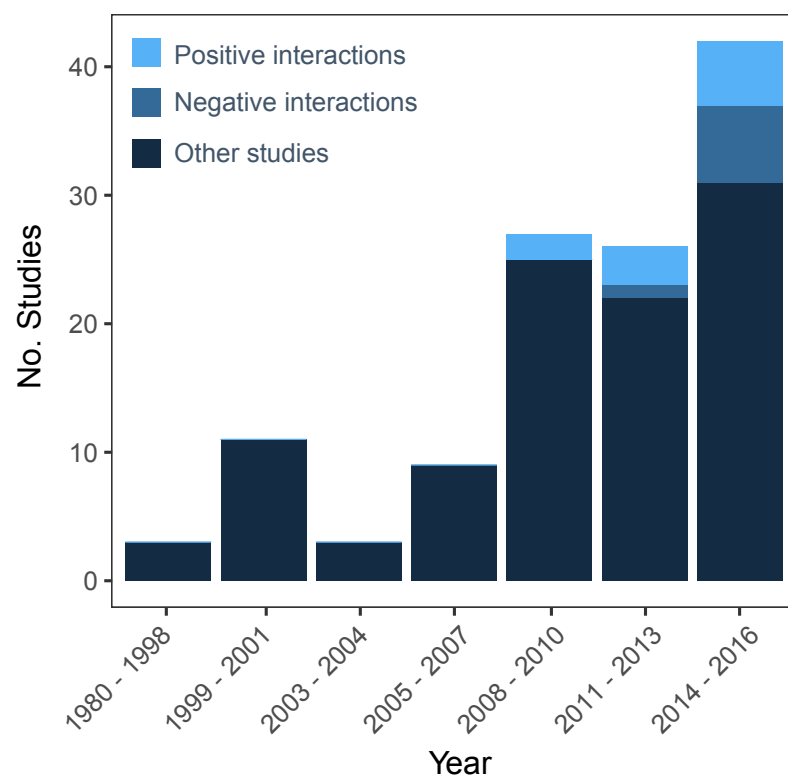
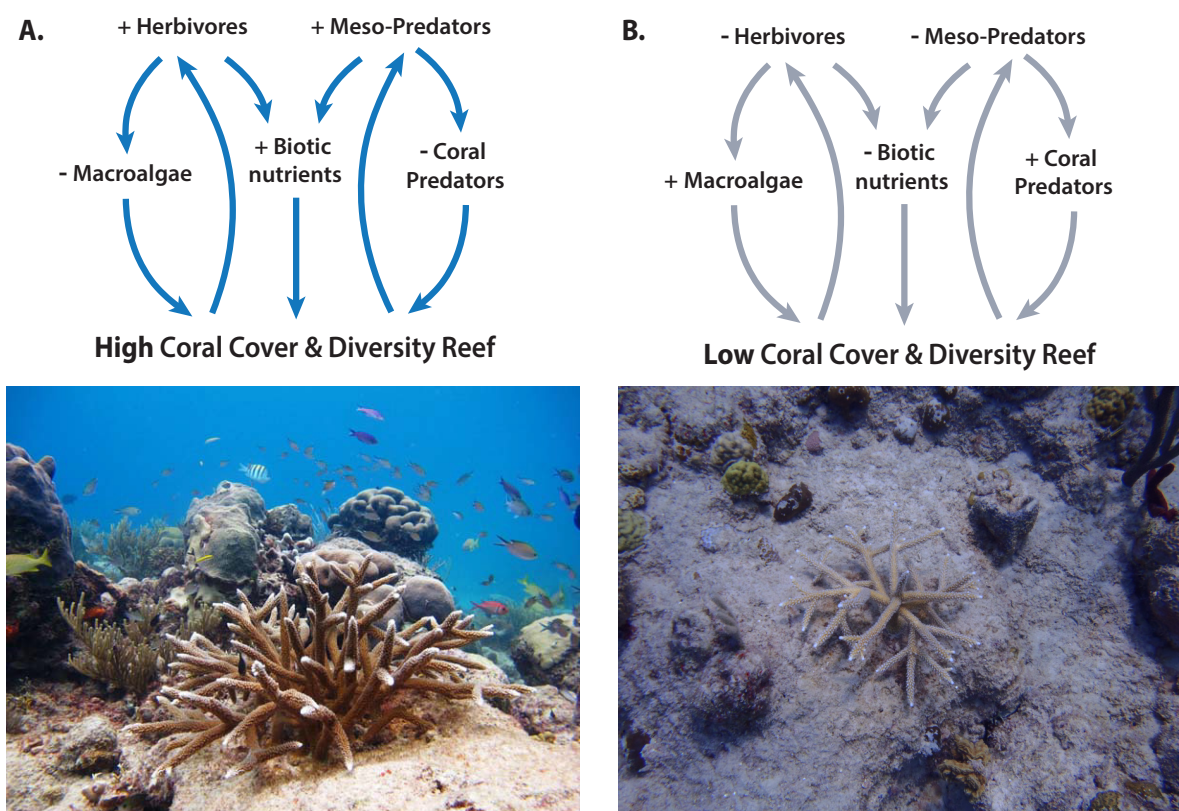


Figure 2. Trophic interactions and feedback loops between corals and reef inhabitants. A) Reefs
with high coral cover and diversity support higher levels of herbivores (e.g., fish and urchins)
that reduce macroalgae and meso-predators. Meso-predators reduce populations of corallivores,
and herbivores reduce macroalgae, which both promote increased coral cover. Additionally,
herbivores and meso-predators produce more biotic-derived nutrients that enhance coral growth.
These effects all facilitate healthy coral communities. B) Reefs with low coral cover and
diversity support fewer herbivores and meso-predators, leading to increased macroalgae and
corallivores but less biotic nutrients. These effects further reduce coral cover. Photo credits: (left)
Kemit Amon-Lewis, The Nature Conservancy; (right) Elizabeth Shaver, Duke University.

677 **Figure 3.** Potential effects of long-distance interactions on coral transplants a) with and b)

678 without adjacent, healthy mangrove and seagrass habitats. Brown lines indicate the movement of

679 coastal or watershed-based run-off (which carry sediments, excess nutrients, and pollutants) from

680 land that gets reduced by mangrove forests and seagrass beds before going on to coral

681 reefs. Purple lines depict microbial cycling by seagrasses that reduces pathogens and coral

682 disease. Thick lines indicate large effects or movements of particles, whereas thin lines indicate a

683 small effects or movements of particles. In Panel A, there is a abundance of herbivores, including

684 greater diversity of parrotfish, due to nearby nursery habitat and food provisioning of mangroves

685 and seagrasses, which leads to reduced macroalgae abundance on reefs. In Panel B, there are

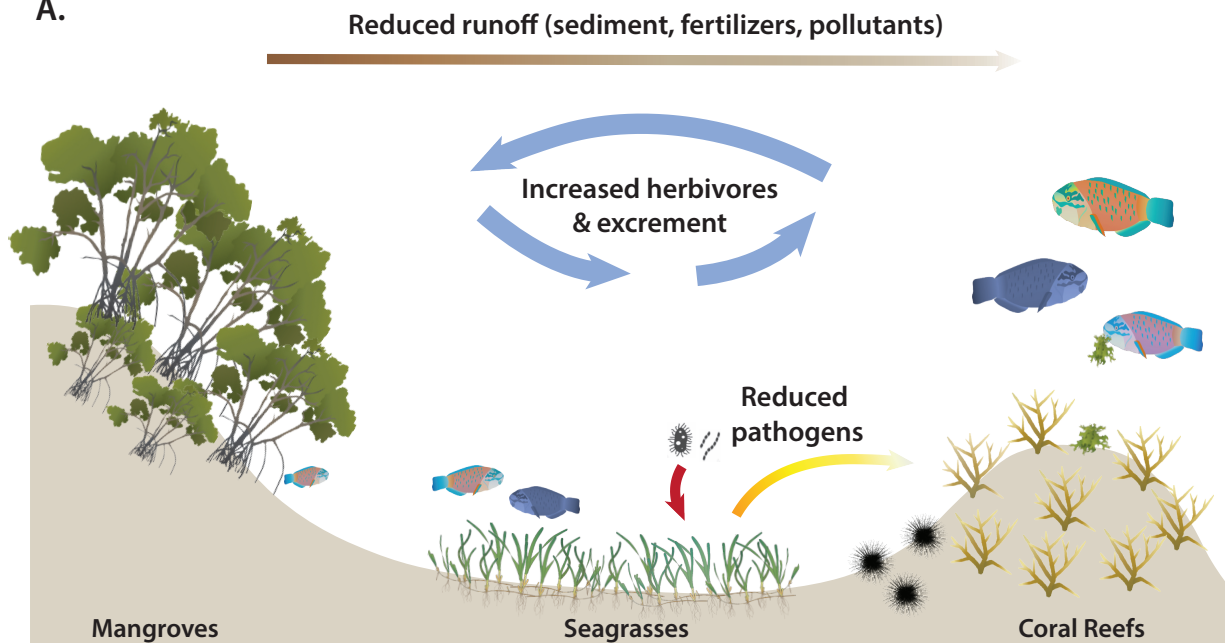
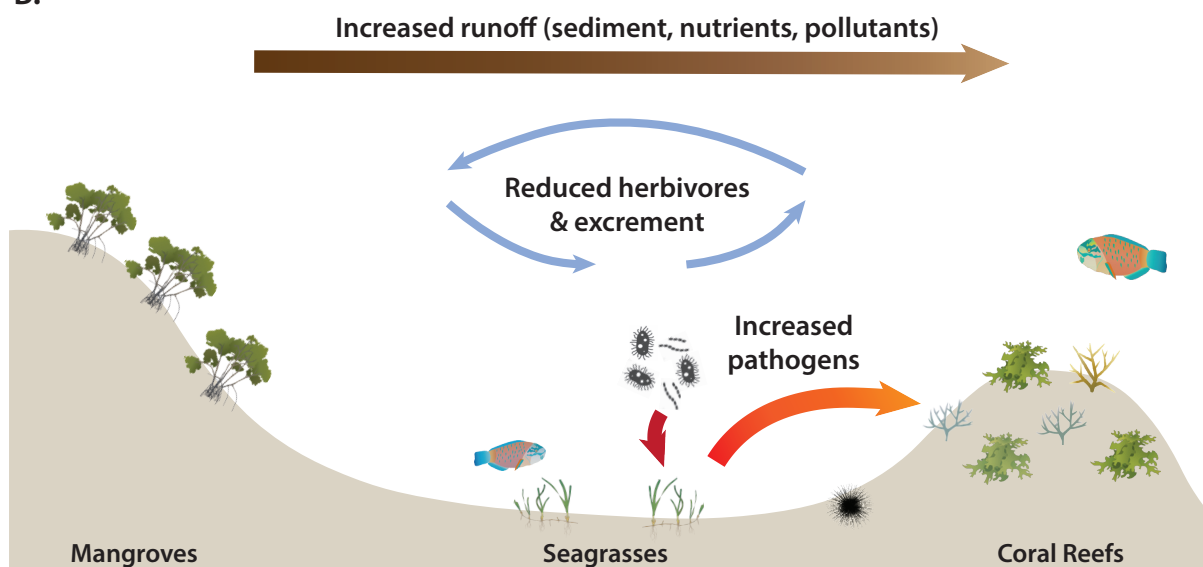
686 fewer herbivores, more algae, disease, and run-off on reefs, leading to reduced success of coral

687 transplants. Image credit (vector graphics): Catherine Collier, Jane Hawkey, Tracey Saxby, and

688 Joanna Woerner, Integration and Application Network, University of Maryland Center for

689 Environmental Science (ian.umces.edu/imagelibrary/)

A.

B.

696   **Figure 4.** Manipulations of coral transplant density and spacing during restoration, including

697   experimental research by Griffin et al. (2015) in which Caribbean staghorn corals (*Acropora*

698   *cervicornis*) were spaced close together (A) and far apart (B) (photograph was taken further

699   away from corals in photo B). Photo credits: John Griffin, Swansea University, United Kingdom.

700   Within a restoration program, restored corals are often planted in varying arrangements, for

701   instance spaced apart in lower densities (C) or closer together to mimic a natural high-density

702   acroporid thicket (D). Photo credits: Kemit Amon-Lewis, The Nature Conservancy. All pictures

703   were taken in the U.S. Virgin Islands.

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