

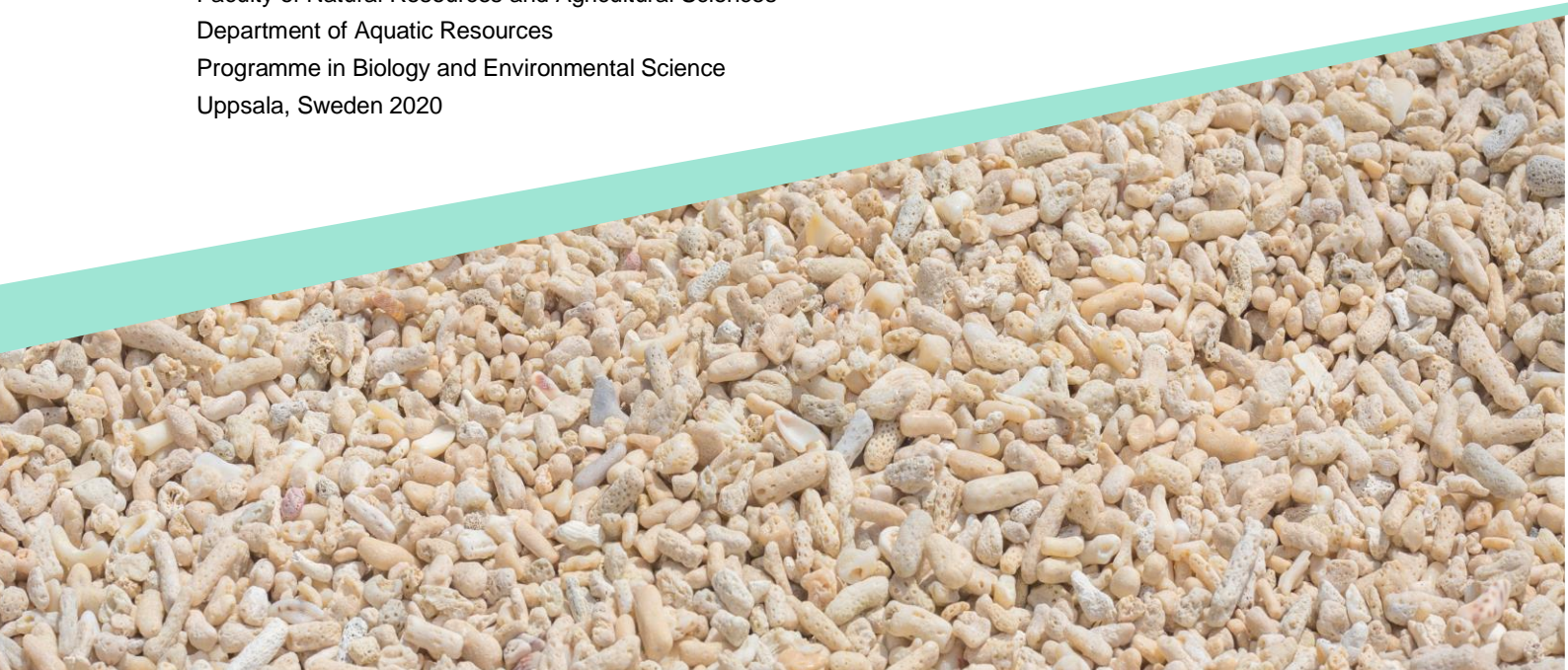


Approaches to Coral Reef Restoration in a Changing Climate

– identifying objectives behind a sea of options

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Independent project in Biology • (15 hp)
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Abstract

Traditionally, researchers have strived to intervene as little as possible when restoring coral reefs, to avoid risks and let the ecosystem recover naturally. But at present time, those restoration options are often insufficient due to the increasing impacts of climate change. Some researchers have therefore turned to intensive options that risk changing the natural ecosystem. It is, however, not clear if the paradigm is shifting and if restorations are commonly tailored to tolerate the predicted future climate changes. Terrestrial systems are facing the same issues and a typology has recently been created to organize terrestrial restoration options and to put them into a climate change context. The aim of this thesis is to identify objectives and motivations behind restoration options for coral reefs, by using this typology.

A broad literature search was done to include various types of active restoration options. Manual selection generated 55 unique studies from the last 10 years. Among these, 26 restoration options were identified and 25 of them were organized using the typology. Low intensity options, assisting the ecosystem to recover naturally without much intervention were more commonly used than highly intensive, more intrusive options, suggesting that a paradigm shift has not yet occurred in practice. High costs and other logistical factors might explain these results where researchers may be forced to use low intensity options, even if they believe highly intensive options are needed.

Keywords: coral reef, climate change, restoration, concept, typology

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Glossary

Adaptability	The ecosystems capacity to adapt to changing environments
Asexual propagation	Fragments are broken off the donor coral and can grow to a new colony with the same genotype
Attachment	Corals' abilities to fixate themselves on surfaces
Bleaching	A harmful and potentially deadly process that cause corals to lose their symbionts
Donor	Parental colony of the coral fragment/gametes
Ex situ	Off-site, here it refers to laboratories and outdoor tanks
In situ	On-site, here it refers to the ocean
Nursery	Artificial structure to keep coral fragments in better conditions where they are kept until they are big enough to be transplanted onto the reef
Options	Here it refers to practical active restoration methods
Recruitment	When coral larvae settle, attach and establish
Settlement	When free-floating coral larvae land on a surface where they can attach
Sexual propagation	Gametes are collected manually and placed together to produce coral larvae with new genotypes
Symbiont	Algae living inside of corals, providing them with energy through photosynthesis

1. Introduction

Tropical coral reefs only cover a small fraction of the oceanic surface, yet they provide crucial functions for both humans and wildlife (Moberg & Folke, 1999; Spalding & Grenfell, 1997). They provide local inhabitants in tropical coastal areas with fish, building material, a source of income and protection from erosion of shorelines (Moberg & Folke, 1999). Poor people in developing countries are therefore affected the most when coral reefs decline (Barbier, 2008).

Other functions provided by coral reefs include CO₂ and Ca budget control, promoting growth of seagrass beds and mangroves and creating a habitat for fish and invertebrates (Moberg & Folke, 1999). Dead corals can to some degree still serve as a habitat for many of the reef organisms by remaining as skeletons, but will eventually be broken down into rubble and lose its function as important habitat (Wilson *et al.*, 2006).

The diversity and spatial extent of coral reefs have steadily declined throughout the history of mankind, but this has gone unnoticed until recent decades' catastrophic mass mortality events (Pandolfi *et al.*, 2003). Some severely degraded coral reefs have been overgrown with macroalgae and turned into a completely different ecosystem that is unlikely to reverse (Scheffer *et al.*, 2001). The causes to coral degradation are largely anthropogenic and involve interactions between local and global threats (Ateweberhan *et al.*, 2013).

Significant local threats include over-fishing, which can cause the ecosystem to collapse and sediment loading, which can smother the corals (Fourney & Figueiredo, 2017; Jackson *et al.*, 2001). Sediment loading can also cause higher turbidity levels in the water, which inhibits the photosynthesis of the corals' symbionts (Fourney & Figueiredo, 2017). These symbionts are algae that live inside the corals and provide much of the corals' energy. Although the threat is mainly local, these problems are common and significantly reduces the resilience to climate change (Ateweberhan *et al.*, 2013).

The global threats are mainly caused by climate change, which has led to increasing temperatures and decreasing pH in the oceans at an unnatural rate (Hughes *et al.*, 2018; Hoegh-Guldberg *et al.*, 2007). During periods of high temperature, the sensitive symbionts are rejected, which leaves the corals pale in a process called bleaching (Chakravarti & van Oppen, 2018). If they cannot find another symbiont in time they eventually starve to death. Historically, coral reefs

have been able to recover naturally after acute disturbances that cause bleaching events, but chances of recovery are reduced as these events increase in severity and occur with shorter intervals, as seen during the past couple of decades (Hughes *et al.*, 2018; Connell *et al.*, 1997).

This is especially worrying due to the future predictions of climate change. Even if emissions were to stop, the water temperature is still likely to keep rising, while dissolved oxygen and pH are likely to keep decreasing (IPCC, 2014). Therefore, researchers and practitioners have for the past couple of decades worked on various conservation and restoration projects, to secure a future that includes coral reefs and their functions (Bostrom-Einarsson *et al.*, 2020).

1.1. Background of conservation efforts

The field of nature conservation has strong bonds with the traditional values of ecology (Prober *et al.*, 2019). These include that nature should be kept wild and natural recovery is preferred with as little human assistance as possible. The objectives of conservation and restoration options are therefore to restore ecosystems to their previous undisturbed state. This point of view has been prominent during the short history of coral reef conservation.

The primary way to protect coral reefs has been to create marine protected areas (MPAs) and to regulate legislations (Sale, 2008). The idea is to alleviate from anthropogenic local disturbances without active interference and is therefore considered as passive conservation (Rinkevich, 2008). These efforts have, however, not sufficiently slowed down degradation of the protected reefs (Sale, 2008). This is partially due to flaws in management, but the growing consensus is that recovery of degraded coral reefs needs active restoration, by actively interfering in the ecosystem (Rinkevich, 2008). Active restoration has been focused on different ways to transplant corals in order to restore degraded reefs to what they previously looked like.

At first, transplantation was done by relocating whole coral colonies to the degraded area to restore the three-dimensional structure that provides the basis of the reef ecosystem (Lirman & Schopmeyer, 2016). These projects did not only harm the reefs where corals were taken, the “donor” reefs, but were also time-consuming and expensive, which only lead to small-scale restorations that were completed long after bleaching occurred.

Later, the gardening approach was created by implementing a two-step reforestation method to coral reefs (Epstein *et al.*, 2003). This approach usually uses asexual propagation by only taking small fragments of the coral colony and places them in a “nursery”, where the fragments are temporarily kept in better conditions and allowed to grow until they are large enough to be transplanted onto the reef. The nursery usually consists of a mid-water structure in situ, on-site in the

ocean, but can also be held *ex situ*, off-site in an indoor facility or outdoor tanks. The nursery phase has been proven important for the survival of the transplanted coral and only taking small fragments is less harmful than moving a whole colony. However, these restoration efforts are still unlikely to help coral reefs endure future climate change and researchers are turning to more intensive engineering options, even if they contradict the traditional values (Rinkevich, 2019). This is also happening in terrestrial and freshwater systems as some researchers call for a paradigm shift (Prober *et al.*, 2019).

Prober *et al.* (2019) thereby created a typology to categorize active restoration options and how they relate to climate change. But marine ecosystems were not included in their study. The field of marine ecology is usually separated from terrestrial and freshwater ecology, which causes bad exchange of knowledge and delays before established research is implemented in marine conservation (Webb, 2012; Elliott *et al.*, 2007). The emergence of every new option in coral reef restoration, from protected areas to transplantation, has been a delayed response to already established terrestrial methods (Bostrom-Einarsson *et al.*, 2020; Carr *et al.*, 2003).

Although there are some practical and ecological differences, many still suggest that terrestrial approaches can be a useful tool in coral reef restoration (Bostrom-Einarsson *et al.*, 2020; Epstein *et al.*, 2003).

1.2. A new typology

Prober *et al.* (2019) noticed an array of new active restoration ideas and the lack of organization and typology to guide management planning. Therefore, they sampled a wide range of restoration options for terrestrial and freshwater ecosystems that are affected by climate change and examined the objectives behind each option. They then defined two axes that divide the options into four quadrants (Figure 1).

The vertical axis describes the main motivation of the option, how it intends to help the ecosystem deal with climate change. The two upper quadrants (A and B) reflect options that focus on affecting the conditions that have worsened due to climate change in order to spare specific species or functions (Prober *et al.*, 2019). This type of objective seeks to directly address specific problems and tends to give short-term solutions. As an example from reforestation, seedlings can be planted instead of seeds to avoid vulnerability to dryness during the germination period. Mulch as a top layer can then be used to create a moist microhabitat until the tree is established and more tolerant to the dryness caused by climate change.

The two lower quadrants (C and D) refer to options with the objective to enhance the biodiversity and resilience (Prober *et al.*, 2019). Biodiversity on all levels is important, as it creates a buffer that helps the ecosystem tolerate more disturbance as well as enhances the adaptability, in other words the capacity to adapt to

changing conditions (Folke *et al.*, 2004). This type of objective has a large-scale point of view and strives for long-term solutions (Prober *et al.*, 2019). For example, reforestation might be done by using many different species and genotypes and when adaptation is too slow, it can be accelerated by human-assisted evolution.

The horizontal axis describes the physical intensity to the ecosystem, i.e. how much the options interferes with nature (Prober *et al.*, 2019). The two quadrants to the left (A and C) refer to low intensity options that strive to assist the ecosystem to recover naturally without much intervention. They more often follow the traditional principles of ecology. These options can be beneficial for the ecosystem with or without the threat of climate change, due to the low risk of severe consequences. For example, replanting native species that have been recently lost might benefit the ecosystem even without any threat from climate change.

But since climate change has made self-recovery less likely, sometimes more intrusive options are needed to meet conservation goals (Prober *et al.*, 2019). The two quadrants to the right (B and D) represent options that contradict traditional ecological views. They are associated with higher risks, a higher level of intervening and often higher costs. For example, if the native species in an area could no longer survive due to increased temperatures, then certain tolerant species could be introduced to provide similar functions and contribute to the persistence of the ecosystem. This could of course lead to many expected and unexpected consequences. Engineered structures are also placed here, as certain conditions can be affected artificially, for example shade structures for amphibians.

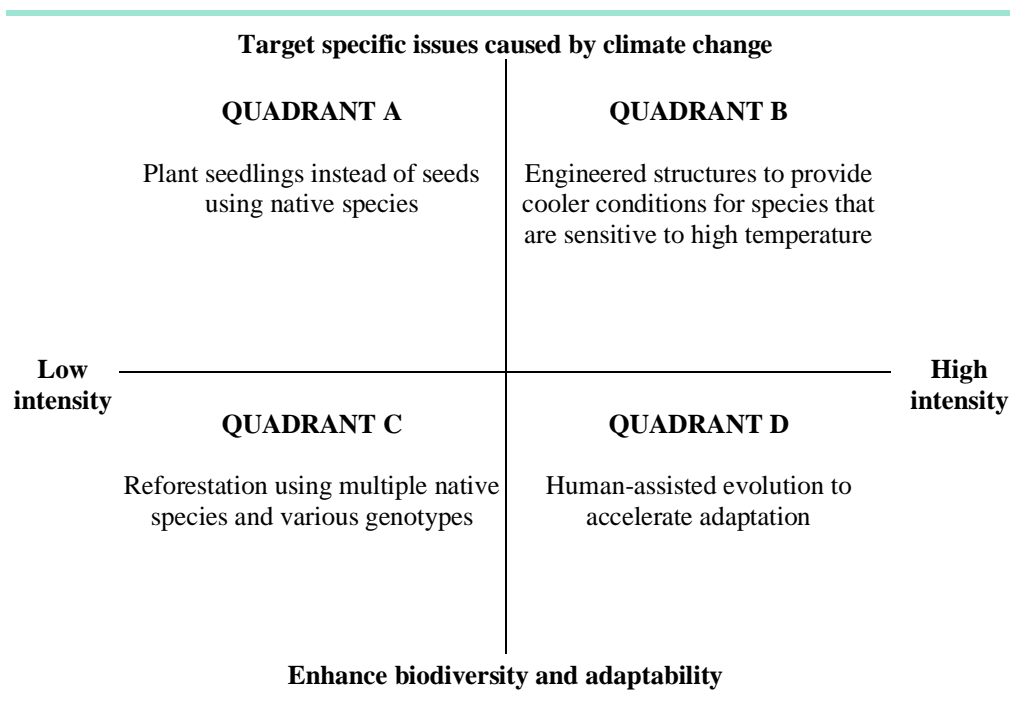


Figure 1. A modified version of the typology by Prober *et al.* (2019), created to organize restoration options and present objectives behind each choice.

1.3. Aim

The aim of this thesis is to identify motivations and objectives behind active restoration options for coral reefs, by using the typology by Prober *et al.* (2019), in an attempt to organize restoration options and see how researchers tailor the restoration to combat climate change. Specifically, I wish to answer the following questions:

- Does restoration mainly target specific problems, tending towards short-term solutions or do they address biodiversity with hopes of long-term outcomes?
- Is restoration either low in intensity to the natural ecosystem, striving to assist natural recovery without much intervention or high in intensity, being more intrusive and deviating from traditional ecological views?
- Is it applicable and relevant for coral reef restoration to use this typology that was created to organize restoration options in terrestrial and freshwater ecosystems?
- Are objectives behind restoration in coral reefs similar to those in terrestrial systems?

2. Method

2.1. Literature search

A literature search for this thesis was done on Web of Science and included all their databases. To make the results comparable with those of Prober *et al.* (2019), the search string and selection methods were created to match theirs. Some adaptations were made due to time limitations or irrelevance to coral reef ecosystems.

The search string used by Prober *et al.* (2019) included 3 groups where at least one term must be used from each. Their first group covered different terrestrial ecosystems and was here replaced by terms related to coral reefs (see table 1).

The second group consisted of active management phrases such as “restoration” (Prober *et al.*, 2019), where all but “revegetation” were considered applicable and included in my search string.

The third group was assumed to target cases where the ecosystem is affected by climate change, in order to exclude those that were degraded for other reasons and that can recover naturally. However, since all coral reefs are known to be affected by climate change, this group seemed redundant and was excluded completely.

I limited the search with a time span of 10 years, refined by English only and excluded all document types but peer-reviewed articles before the manual selection. This generated 6198 articles (2020-04-20). Further changes in the search string were tested which reduced the number of articles generated but was avoided since they also limited the type of content that got included.

2.2. Manual selection

The search results were sorted by relevance and a manual selection was done from most relevant towards least relevant for the first 300 articles. This was due to time limitations and the data used was regarded as a representative sample. Prober *et al.* (2019) of course viewed all their search results.

In their manual selection for relevant studies, Prober *et al.* (2019) included studies that both suggested, applied or tested options for restoration of ecosystems

that are affected by climate change. They focused on articles that emphasised the ecological point-of-view instead of the socio-economic perspective. Although they focused on active restoration, articles about managing marine protected areas were still included. I, however, excluded all reviews, model-based and articles that proposed options that they did not test themselves. This was mainly to focus on what was being done, since hypothetical suggestions might differ from practice. Articles about marine protected areas were excluded here, but socio-economic views were included since they were hard to separate from coral reef ecosystems.

I also excluded studies about non-tropical or deep-sea coral reefs, to focus on tropical shallow-water coral reefs. Lastly, I excluded articles without access through SLU and cases that have been surveyed in previous articles, to avoid replication.

A total of 55 articles, each one a unique study, were selected for further analysis.

Table 1. Differences in search methods between Prober *et al.* (2019) and the present study

	Article by Prober <i>et al.</i> (2019)	This thesis
Search string group 1	ecolog*, ecosystem, biodiversity, forest, woodland, rangeland, grassland, shrubland, heathland, rainforest, wetland, mangrove, saltmarsh, shore, tidal, dune, river, stream, freshwater, riparian, desert, dryland, species, nature	coral*, coral reef*
Search string group 2	adapt*, interven*, restor*, engineer*, revegetation, conserve*	adapt*, interven*, restor*, engineer*, conserve*
Search string group 3	climate change, warming, CO2, aridif*, changing climate	-
Timespan	-	2010-2020
Emphasis	Ecological	Ecological, socio-economic
Active restoration	Yes, but including management of protected areas	Yes, excluding management of protected areas
Other exclusions	-	Reviews Model studies Studies without access Previously studied cases Deep-sea reefs Non-tropical

2.3. Analysis

The method section of each study was examined and various options that might affect the conservation result were identified and compiled (see appendix 1). These options were compared to the options and descriptions by Prober *et al.* (2019) and placed in the quadrant where they seemed to fit in the typology from fig. 1. For example, Prober *et al.* (2019) put enhancing establishment conditions as a category in quadrant A, so controlling the density of transplanted corals to improve survival and decrease competition was considered a match. Whenever the appropriate quadrant was unclear, reasoning found in the studies and sometimes other literature was used to explain certain choices; e.g. researchers said they controlled density of corals for the survival and not that it somehow relates to biodiversity. Sometimes the process of elimination was part of the decision.

If one option still seemed to fit in more than one quadrant, the classification of that option was deemed inappropriate and was split into more specific options. For example, transplantation can be done by using asexual propagation with multiple species. Since multiple species enhances biodiversity and asexual propagation does not, it was split into two separate options: “asexual propagation” and “multiple species used”.

One study could use several options that belonged to different quadrants. To rank the popularity of the quadrants, all studies that used at least one option from quadrant A were counted, and for quadrant B etc. To rank the popularity of the options, the number of studies that used each of the options were counted.

3. Results

From the 55 studies that were analysed, 26 options were identified and placed in the quadrants A-D (Figure 2). Most studies (n=49) dealt with some form of coral transplantation, as did most of the options (n=20). Many of these options can, however, in theory be used outside of transplantation, e.g. feeding wild corals.

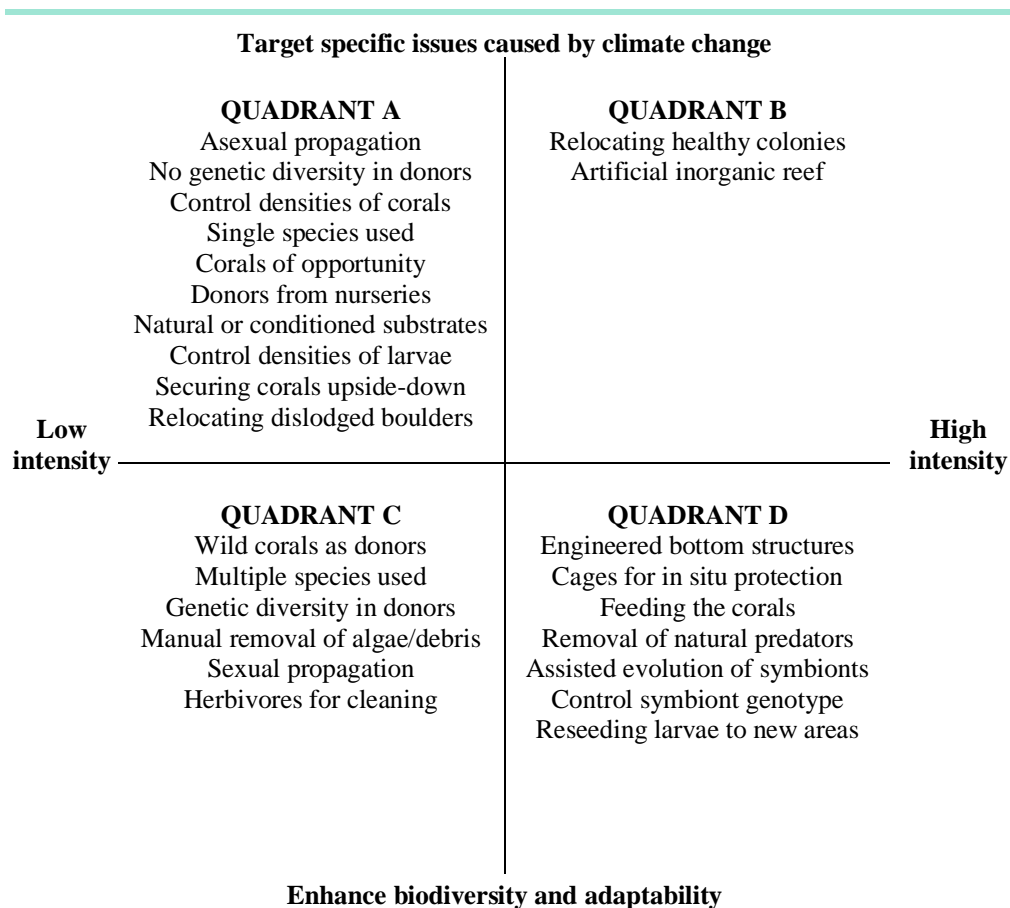


Figure 2. Restoration options found in the literature search (nursery excluded) on coral restoration during the last 10 years. Options are placed in the typology by Prober et al. (2019) to identify objectives behind choices. Low intensity options strive to assist natural recovery without much intervention, while high intensity options are more intrusive and may modify the natural environment.

The only option that was not placed in the typology was *nurseries*, since they can be used for several reasons and in different ways that ranges in intensity

(Rinkevich, 2015). Here, nurseries included arrangements both in situ and ex situ (in oceans and research facilities). This option was not further modified, but instead considered as a broad option that can fit into any quadrant.

3.1. Quadrant A – target specific issues, low intensity

Quadrant A consists of options that are low risk and low in intensity to the natural ecosystem, as well as working towards fixing a specific issue caused by climate change. This quadrant had the highest number of identified options (n=10) and 96% of the studies included at least one of these options.

3.1.1. Overlooking biodiversity

Asexual propagation is a quick and easy way to produce more corals for transplantation, by cutting small fragments off a bigger coral colony, hereafter called “donor” (Adolfo Tortolero-Langarica *et al.*, 2019). This has low impact on the donor corals, while the fragments can then grow into big colonies themselves and eventually reproduce both sexually and asexually (Omori, 2019). Since every study used native species that can be found or have been lost in that area, this is considered a low intensity option. However, since fragments share the same genotype as the donor, this limits the biodiversity in the transplanted corals (Omori, 2019). Instead, the goal of asexual propagation is often to quickly counter species loss and to restore the 3D structure of the reef, so that fish will have a habitat and coral larvae can attach to the surface and establish themselves (e.g. Williams *et al.*, 2019; Nithyanandan *et al.*, 2018; Nava & Figueroa-Camacho, 2017). These are all examples of specific issues that can be directly targeted.

Single species used for transplantation also fits in this quadrant because while several species could have increased the biodiversity, ignoring this and using only one species implies that resolving another issue was the main objective.

No genetic diversity in donors refers to studies which did not specify if they took extra measures to make sure that their donors were diverse within the species. E.g. they did not state that they took fragments or gametes from donors that were far away from each other, they did not look for different morphologies nor test genotype. This could be the case for both asexual and sexual propagation.

Using **donors from nurseries** refers to propagation of corals that already were growing in nurseries, which reduces the need to harm the wild donor reefs. However, using the same genotype limits the genetic diversity and might contribute to a founder effect and other problems later (Baums, 2008).

Corals of opportunity refers to collection of coral fragments that have naturally been fragmented during storms to be used for transplantation (Flores *et al.*, 2017). This way, there is no additional harm to the donor reef and the genetic diversity

might in theory be higher than for other asexual propagation options. However, in the present study it is considered as a direct way of affecting specific issues, because their choice was an explicitly asexual and simple way to quickly restore specific functions, while the potentially enhanced diversity is seen as a side effect.

3.1.2. Improving growth and survival

Controlling densities of corals as well as **controlling densities of larvae** was done to improve survival and to accelerate growth during the sensitive phases (e.g. Pollock *et al.*, 2017; Ladd *et al.*, 2016). The same reasoning was behind **securing corals upside-down** or tilted to accelerate corals' attachment to surfaces (e.g. Rachmilovitz & Rinkevich, 2017); **relocating dislodged boulders** to accelerate their healing (e.g. Konh & Parry, 2019) and using **natural or conditioned substrates** to signal larvae that they should settle on the surface where they can attach (e.g. Ligson *et al.*, 2020). These options fit in quadrant A since growing faster will alleviate impacts from climate change by shortening the time period when organisms are extra sensitive to them (Prober *et al.*, 2019).

3.2. Quadrant B – target specific issues, high intensity

Only 2 options were placed in quadrant B and a mere 4% of the studies used one of these options. These are engineering options that severely modify the nature of the reef and strive to affect specific issues caused by climate change.

One study involved building an **artificial reef out of inorganic matter** (Reguero *et al.*, 2018). This was done to improve wave control in order to protect the shoreline in an area with severely degraded reefs. Large steel frames were filled with concrete blocks and rocks to create an underwater wall-like structure. This had no resemblance to a coral reef, but it did serve its' purpose as a fish habitat and as wave control, making it a prime example of a quadrant B option.

Relocation of healthy colonies are placed in this quadrant because it involves whole colonies, not just fragments. Since they are healthy, they normally would not be moved unless there are considerable reasons to do so. This was done in two of the studies. The first one only did it to clear the area before building the artificial reef mentioned above (Reguero *et al.*, 2018). The relocated corals were later placed on the artificial reef. The other study that relocated healthy corals had a large-scale plan as a compromise to meet both socio-economic and coral needs (Kotb, 2016). The plan was to move all port services to a new area, so the anthropogenic stressors would not be so wide-spread and give relief to a marine protected area. However, the new port area was the host of a diverse and significant reef that now risked being harmed by the port development. Therefore, thousands of healthy corals were moved from the new port to degraded parts of

the marine protected area. Manipulations like this might have consequences for the large-scale metapopulation connectivity and biodiversity (Doropoulos & Babcock, 2018).

If asexual propagation would have been done using non-native tolerant species, it would be placed here, but no study seems to have done that even outside of the scanned literature.

3.3. Quadrant C – enhance adaptability, low intensity

Quadrant C covers the low intensity options that strive to enhance the adaptability of the ecosystem, often by focusing on biodiversity. 6 of the options are found in this quadrant and 93% of the studies used at least one of these options.

3.3.1. Enhancing biodiversity

Here we find *sexual propagation* which is performed by collecting gametes or gravid colonies to an ex situ facility where they can fertilize in controlled conditions and be reared for transplantation (e.g. Villanueva *et al.*, 2012). This contributes to a higher genetic diversity compared to asexual propagation (Omori, 2019). *Using multiple species* for transplantation, *donors with genetic diversity* within the species and *donors that are collected from wild reefs* also contribute to biodiversity (e.g. Cabaitan *et al.*, 2015; Villanueva *et al.*, 2012).

3.3.2. Improving survival to non-climatic stressors

Manual removal of algae from transplanted corals can be done to improve survival during sensitive phases when there is a lack of cleaner fishes to do the work (e.g. Nithyanandan *et al.*, 2018). *Herbivores are also used for cleaning* for the same reason and was usually done by placing snails in the tanks during an ex situ phase (e.g. Ligson *et al.*, 2020). The other way to do it was to purposely place the nursery in an area with plenty of cleaner fish (Frias-Torres *et al.*, 2015; Frias-Torres & van de Geer, 2015). This dramatically decreases the diver time needed as well as the detachment of newly transplanted corals (Frias-Torres & van de Geer, 2015). This differs from the similar intention of alleviating from climatic stressors in quadrant A, since these options alleviates from anthropogenic *non-climatic* stressors, which might increase the resilience to climate change (Prober *et al.*, 2019).

3.4. Quadrant D – enhance adaptability, high intensity

Quadrant D represents the engineering, high intensity options that strive to enhance biodiversity. 49% of the studies used at least one of the 7 options in this quadrant.

The most distinct examples are *assisted evolution* and *controlling the genotype of the symbionts*. Assisted evolution attempts to accelerate the symbionts adaptation to increased temperatures, which would make the corals more tolerant to bleaching (Chakravarti & van Oppen, 2018). Knowing which genotype has the highest adaptability can then be useful when controlling the genotype and symbiosis. Symbionts with a specific genotype can be cultured or harvested and released in the coral tanks for uptake in optimal conditions (Pollock *et al.*, 2017). These are highly intervening options with the goal to enhance the adaptability for a long-term persistence of the species.

Engineered bottom structures and *reseeding larvae to new areas* can both contribute to expanding the potential coral habitat (Golomb *et al.*, 2020; Doropoulos *et al.*, 2019). The targeted areas are usually highly unlikely to recover naturally, since coral larvae must settle on a hard surface and have trouble establishing on rubble that moves around (Fox *et al.*, 2003). Engineered structures can therefore be placed on degraded soft bottom or rubble and host transplanted corals as well as potential recruited larvae, that can attach and establish themselves. Reseeding of coral larvae was done in one study that tested equipment for pumping up large quantities of larvae into a tank, to then be released on a reef that was too far away for them to reach naturally (Doropoulos *et al.*, 2019).

Feeding corals, putting *corals in cages* and *removing predators* are all done to increase survival during the sensitive phases of the transplanted corals life. The difference from quadrant A and C is that the stressors that are removed here are natural (Prober *et al.*, 2019). Alleviating natural stressors might in turn increase the resilience to climatic changes.

If sexual propagation with introduced species had been done by any study it would be placed here, because it would increase the biodiversity while being intensive and possibly risky.

3.5. Tailoring the method with mixed options

Almost every study (n=54) included options from more than one quadrant. The popularity of each option varied, with some options only occurring in one study and others occurring in up to 40 out of the 55 studies (see figure 3). All the top 7 most used options are low intensity options that belong to quadrants A and C (not counting nurseries), while the 6 least used options are all high intensity options that belong to quadrant B and D.

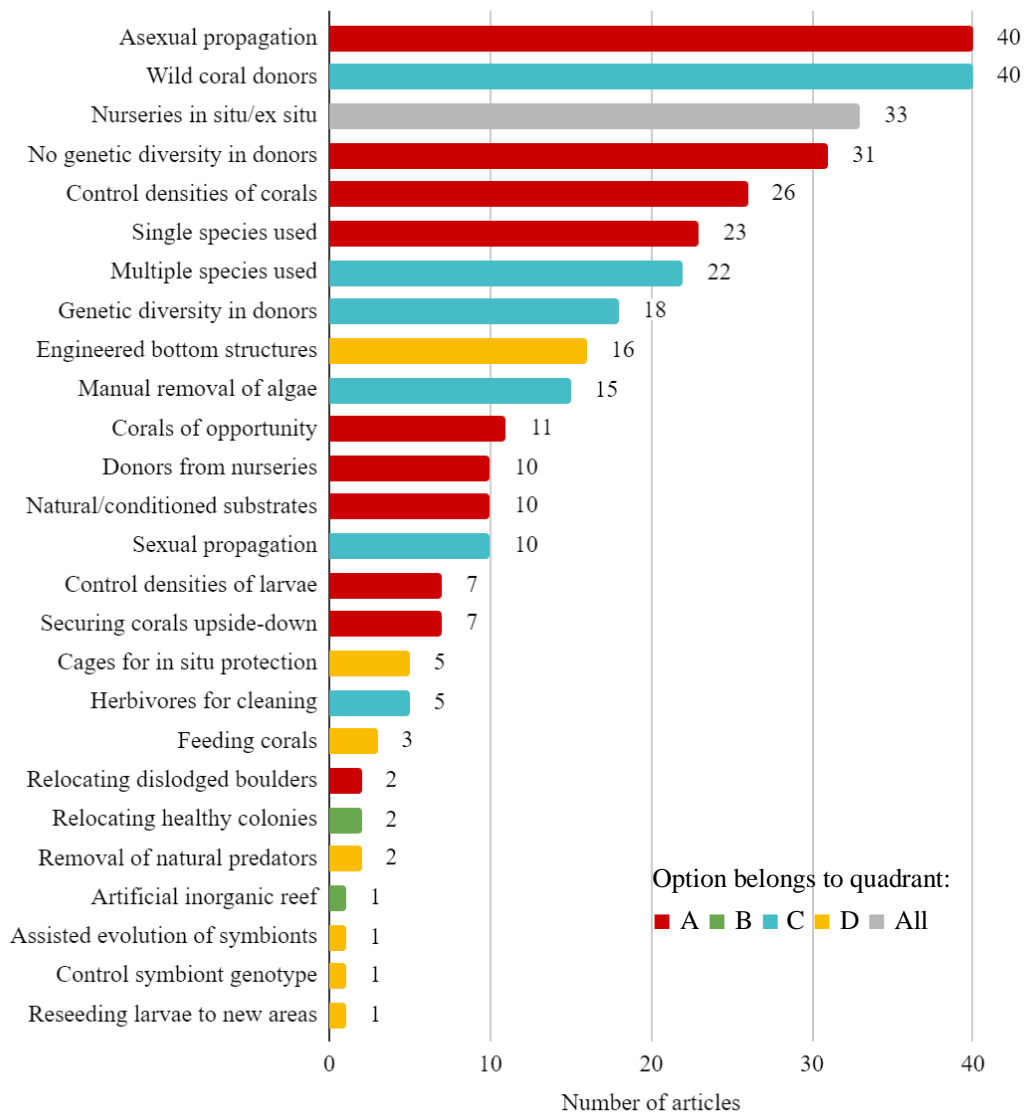


Figure 3. The variety of coral restoration options and their popularity; i.e. number of studies using each option.

One group of options stood out for being explicitly connected to transplantations and the chance of enhancing biodiversity. They could be paired up as opposing options to which *type of propagation* was used, *how many species* was used, if *genetic diversity* were pursued and *where the donors were found*. The options either belong to quadrant A or C (see figure 4). Although these opposing options seem to contradict each other, only 2 studies used all 4 of the options belonging to the same quadrant (A). The remaining studies that included transplantation mixed options from both quadrant A and C, both attempting to enhance the diversity as well as neglecting it. They would for example use sexual propagation that enhances biodiversity, but at the same time only use one species.

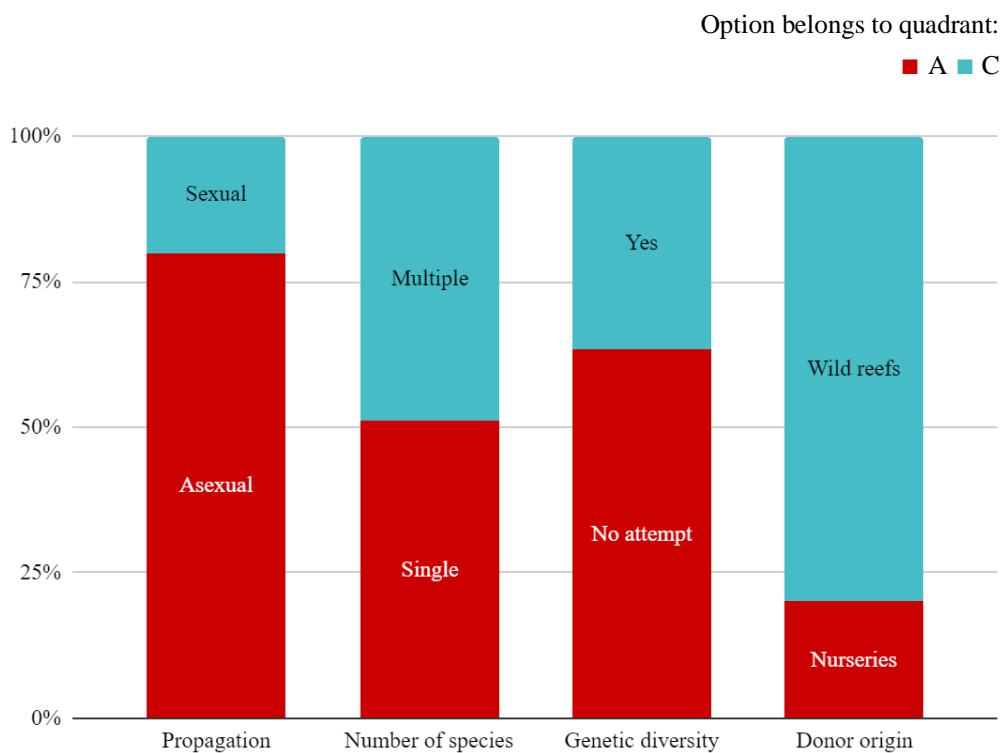


Figure 4. Pairs of opposing coral restoration options related to diversity enhancement and how often they were used. These options are all low in intensity and belong to quadrant A or C. Quadrant A referring to options not enhancing biodiversity, while quadrant C referring to options enhancing biodiversity.

4. Discussion

The aim of this thesis was to get an insight in researchers' choice-making in coral restoration and how choices were tailored to mitigate climate change impacts. The results show that it was both common to target specific issues like restoring lost fish habitats by using asexual propagation, as well as to enhance biodiversity by using multiple species. Meanwhile, there was a clear preference for low intensity options that generally require less risk, effort and time compared to high intensity options. The results also showed a very low number of studies that did something completely different than coral transplantation, which means it's the go-to method, even if specific details differ.

The motivations and objectives presented here have some similarities and some differences to those found in terrestrial systems by Prober *et al.* (2019). However, various reasons make this typology unfit for identifying objectives behind restoration options for coral reefs but might assist in other ways.

The different quadrants contained different numbers of restoration options, ranging from 2 to 10 options per quadrant. However, this should not be used to judge the popularity of each quadrant, since the options could easily be combined and hence create fewer options or be split and create more options. The fact that the most used options were low intensity and the least used options were high intensity is an interesting result but does not necessarily represent the true picture. Instead focus should be on how many studies that used options from each quadrant.

4.1. Targeting specific issues or biodiversity

Almost every study used at least one option from quadrant A (96%) and C (93%), meaning that both aiming towards resolving specific issues as well as enhancing biodiversity were popular objectives. This was different for Prober *et al.* (2019) where quadrant C (enhancing adaptability, low intensity) was three times more popular than any other quadrant. Their second most used quadrant was B (targeting specific issues, high intensity), closely followed by A (targeting specific issues, low intensity) and then D (enhancing adaptability, high intensity). Their results suggest that researchers within terrestrial systems were more interested in enhancing the adaptability. Coral reefs might differ from several of the terrestrial ecosystems by

being social ecological systems. This could mean that researchers are more prone to target specific issues for the sake of directly helping poor local inhabitants by increasing ecosystem goods and services provided by coral reefs.

One important difficulty in categorizing the options was that many of the options can have several objectives. This was also experienced by Prober *et al.* (2019). The clearest example is the use of nurseries, which can be considered as both targeting specific issues as well as biodiversity (Rinkevich, 2015). Since many of the studies lacked clear explanations to their choice of restoration options, it is hard to know what the most important objective was for researchers.

Another example is asexual propagation, which is clearly worse for the diversity compared to sexual propagation (Omori, 2019). Asexual propagation was often used to quickly and cheaply restore the 3D structure (e.g. Williams *et al.*, 2019), which was here interpreted as targeting specific issues. However, creating a larger scale 3D structure can provide many functions that in turn lead to better adaptability and higher biodiversity. For example, coral recruitment, connectivity and the occurrence of fish are all enhanced by large-scale restorations and are also related to the reefs resilience to be overgrown by macroalgae (Hughes *et al.*, 2010).

4.2. Low intensity or high intensity options

There was a preference for low intensity options, as fewer researchers used at least one option from quadrant B (4%) and C (49%). This preference to low intensity options was also seen by Prober *et al.* (2019), although the popularity of quadrants differed. This suggests that the paradigm has not yet shifted and that it is easy to fall back to the safe and established traditional views. This can also be supported by the shortage of studies that studied something other than transplantation.

It is, however, important to note that some things simply cannot be properly categorized and ends up in grey zones. Feeding corals can probably be considered low intensity, especially when compared to other high intensity options like artificial reefs. This might explain the low popularity of quadrant B options. Those options might have been avoided simply because they are considered as too intensive, even compared to those in quadrant D. The intensity to the ecosystem might be more appropriately distributed on a scale instead of these two categories.

Another example of restoration options in grey zones is of course the use of nurseries. If complex engineered structures that are expensive and time-consuming are considered high in intensity; should simple nurseries consisting of a hanging rope be considered low in intensity and regarded as a separate option? Where should the line be drawn to divide these two categories – low versus high? Even if I placed the options correctly according to the descriptions by Prober *et al.* (2019), every placement can still be debated, since the consequences and effects on the ecosystem are not fully known.

4.3. Applicability and relevance of the typology

This climate change-oriented typology was chosen as it was assumed that researchers would do their utmost to choose options that they believed were best from an ecological perspective. I thereby expected to see that each study only consisted of options from one quadrant, e.g. researchers who wanted to enhance adaptability while keeping the ecosystem natural would only use options from quadrant C. The results, however, show that most researchers use a mix of options from different quadrants, which was not addressed by Prober *et al.* (2019). Many of the mixed options had contradicting objectives, e.g. sexual propagation but with only one species. This makes it hard to interpret what the researcher actually aimed for, enhanced diversity or targeting specific issues. Therefore, mixing restoration options suggests that researchers are influenced by motivations that are not considered in the typology.

Many of the researchers seemed concerned with cost and convenience (e.g. Golomb *et al.*, 2020; Williams *et al.*, 2019). This can be related to the need for large-scale restoration projects to be able to compensate for the speed of degradation (Bayraktarov *et al.*, 2016). Coral restoration has incredibly high costs compared to terrestrial restoration and are commonly criticized for being too small in scale.

Working in water also seems to add some logistical difficulties. The simple task of removing algae from corals growing in nurseries requires many hours of diver time and quickly becomes costly (Frias-Torres *et al.*, 2015).

Options that are more intensive and those that lead to better biodiversity often cost more and are more time-consuming (Omori, 2019). Sexual propagation is an example of this and might explain why most researchers chose to use asexual propagation. Researchers may have wanted to enhance biodiversity but were forced to use asexual propagation due to limited resources. They then might have tried to compensate by increasing biodiversity with simpler and cheaper options, like using multiple species or genotypes. This would explain the mixing of opposing options.

4.4. Implications

In conclusion, coral reef restorations, similar to terrestrial systems, show a lack of paradigm shift towards highly intensive restoration options. Contrary to terrestrial systems, coral reef restoration has not been as focused towards enhancing biodiversity. These results can be explained by searching for objectives outside the typology. Objectives for choosing certain restoration options are not only based on knowledge about ecology and climate change, but also various factors such as costs, time, practicality and social factors. The typology by Prober *et al.* (2019) only accounts for objectives regarding climate change and cannot be properly applied to

coral reef restoration in practice. However, it might still serve as a tool outside the limitations of this thesis.

Literature analyses could instead focus on conceptual review articles to find out researchers' opinions and objectives when cost is not an issue. The categorization of options could then be backed up by the in-depth reasonings that can be found in review articles. Each unique study should also be viewed in the search results and each author should only appear once, unlike in this thesis.

While this thesis focused on researchers' opinions, the fact that they were researchers also posed a problem. Scientists might have used certain options only for the purpose of whatever test they were doing. Especially the *number of species used* seemed to be for comparisons between multiple species or to focus on learning something new about one single species. It might therefore be useful to do survey studies to find out common objectives.

This thesis can be used as an overview of common options and their relation to climate change, especially by non-researching practitioners and sponsors. Practitioners could use it in the planning stage to choose restoration options that they may never have heard of before, while sponsors need to be educated to fund researchers who want to use intensive options to enhance biodiversity. Even if there are many concerning reasons to avoid those options, researchers must be able to develop them further to lower the costs and risks. Only then can tools such as pumps for large-scale larval reseedling or multi-usage nurseries be invented.

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Appendix 1

Options	Articles	#
No genetic diversity	6, 7, 8, 9, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 29, 31, 33, 36, 37, 42, 43, 44, 45, 46, 50, 51, 52, 53, 54, 56, 57	31
Genetic diversity	11, 12, 14, 15, 17, 27, 28, 30, 34, 35, 38, 39, 40, 41, 49, 55, 58, 59	18
Single species	8, 11, 12, 15, 16, 17, 18, 19, 20, 21, 28, 30, 33, 36, 39, 41, 42, 43, 45, 53, 54, 56, 57	23
Multiple species	6, 9, 14, 23, 25, 26, 27, 29, 31, 34, 37, 38, 40, 44, 46, 49, 50, 51, 52, 55, 58, 59	22
Sexual propagation	16, 18, 19, 20, 30, 33, 39, 43, 54, 57	10
Asexual propagation	6, 7, 8, 9, 11, 12, 14, 15, 17, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 31, 34, 35, 36, 37, 38, 40, 41, 42, 44, 45, 46, 49, 50, 51, 52, 53, 55, 56, 58, 59	40
Wild corals as donors	6, 7, 8, 11, 12, 14, 15, 16, 18, 19, 20, 21, 23, 24, 25, 26, 27, 29, 30, 31, 33, 34, 35, 37, 38, 40, 42, 43, 44, 45, 46, 49, 52, 53, 54, 55, 56, 57, 58, 59	40
Donors from nurseries	9, 12, 17, 20, 22, 28, 36, 39, 41, 51	10
Corals of opportunity	6, 7, 11, 23, 24, 26, 27, 29, 35, 53, 56	11
Relocate dislodged boulder	5, 47	2
Relocate healthy colonies	13, 48	2
Reseeding larvae	4	1
Nurseries in situ & ex situ	5, 6, 11, 14, 15, 16, 17, 18, 19, 20, 22, 24, 26, 28, 29, 30, 33, 34, 36, 38, 40, 41, 44, 45, 46, 48, 49, 51, 54, 55, 57, 58, 59	33
Engineered bottom struct.	5, 6, 13, 31, 34, 36, 37, 38, 40, 44, 45, 46, 48, 49, 54, 58	16
Natural/conditioned subst.	4, 18, 19, 20, 25, 30, 39, 43, 54, 57	10
Artificial inorganic reef	13	1
Control densities of corals	5, 6, 15, 16, 17, 20, 23, 27, 28, 33, 34, 35, 36, 37, 38, 42, 44, 46, 48, 49, 50, 51, 53, 55, 58, 59	26
Control densities of larvae	16, 19, 20, 30, 39, 43, 57	7
Securing upside-down	14, 16, 21, 41, 44, 53, 55	7
Manual removal of algae	11, 16, 18, 22, 24, 34, 39, 41, 43, 48, 49, 50, 53, 57, 59	15
Herbivores for cleaning	18, 33, 39, 50, 54	5
Cages for protection in situ	16, 19, 30, 54, 57	5
Remove natural predators	6, 51	2
Feeding corals	21, 39, 55	3
Control symbiont genotype	43	1
Assisted evolution	10	1

Articles excluded after numbers where given: 1, 2, 3, 32.

- (4) Doropoulos, C., Vons, F., Elzinga, J., ter Hofstede, R., Salee, K., van Koningsveld, M. & Babcock, R.C. (2019). Testing Industrial-Scale Coral Restoration Techniques: Harvesting and Culturing Wild Coral-Spawn Slicks. *Frontiers in Marine Science* 6.
- (5) Konh, B. & Parry, M. (2019). Design, Fabrication, Installation, and Population of a Novel Fiberglass Reinforced Plastic Coral Nursery Structure Off the South Shore of O'ahu, Hawaii. *Frontiers in Marine Science* 6.
- (6) Williams, S.L., Sur, C., Janetski, N., Hollarsmith, J.A., Rapi, S., Barron, L., Heatwole, S.J., Yusuf, A.M., Yusuf, S., Jompa, J. & Mars, F. (2019). Large-scale coral reef rehabilitation after blast fishing in Indonesia. *Restoration Ecology* 27(2), 447-456.
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- (15) Drury, C., Manzello, D. & Lirman, D. (2017). Genotype and local environment dynamically influence growth, disturbance response and survivorship in the threatened coral, *Acropora cervicornis*. *Plos One* 12(3).
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