

Evaluating the success of coral reef restoration programmes requires consideration of ecosystem functioning

Running head: *Considering ecosystem functioning in reef restoration*

Authors: Zach Boakes^{1*}, Sri Y. Cahyarini¹, Albert Sulaiman¹, Richard Stafford², Tries B. Razak^{3,4,5}, Simon J. Brandl⁶

Affiliations:

¹ National Research and Innovation Agency (BRIN), Research Center for Climate and Atmosphere, Bandung, Indonesia.

² Bournemouth University, Department of Life and Environmental Sciences, Poole, UK.

³ Department of Marine Science and Technology, Faculty of Fisheries and Marine Science, IPB University, Bogor, Indonesia

⁴ School of Coral Reef Restoration (SCORES), Faculty of Fisheries and Marine Science, IPB University, Bogor, Indonesia

⁵ General Organization for Conservation of Coral Reefs and Sea Turtles in the Red Sea, Jeddah, Saudi Arabia School of Coral Reef Restoration (SCORES), Faculty of Fisheries and Marine Science, IPB University, Bogor, Indonesia

⁶ Department of Marine Science, The University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, US.

Corresponding author: Zach Boakes (boakeszach@gmail.com / zach001@brin.go.id).

Corresponding author postal address: Research Center for Climate and Atmosphere, Jalan Sangkuriang, Bandung City, West Java, Indonesia, 40135.

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Abstract:

In the past twenty years, there has been a sharp rise in the establishment of coral reef restoration programmes, which generally aim to restore key services provided by healthy, natural reefs. However, the effect of restoration on arguably more important metrics related to ecosystem functioning is rarely monitored, with most programmes focusing their monitoring on static variables (e.g. coral cover) only. With crucial metrics related to ecosystem functioning left largely unmonitored, it is difficult to assess the true outcomes of reef restoration through an ecological lens. We therefore propose that ecosystem functioning should be placed at the forefront of reef restoration, and suggest the following focus points for improvements in the field: 1) Implement a set of standardized methods to monitor key functional processes on restored reefs (and neighboring natural reefs), 2) Better understand how reef restoration will support ecosystem functioning in a changing ocean, and the identity of organisms that carry most of the 'functionality load' on reefs, and 3) Adopt a function-centric approach that implements techniques specifically targeted at protecting the respective species and processes of interest.

Conceptual implications:

Coral reef restoration practice should shift from monitoring only static variables, to also quantifying key ecosystem functions, and comparing these to natural reefs. Restoration practice should also aim to identify and protect biota which provide important contributions to coral reef functioning. Prioritising ecosystem functioning in reef restoration approaches will contribute towards enhancing resilience, supporting the provisioning of ecosystem services, and enable restoration programmes to maximise their ecological outcomes.

Introduction:

The physicochemical and biological processes that govern fluxes of energy and nutrients through ecosystems (often collectively termed 'ecosystem functioning') not only maintain life, but also underpin ecosystem services (Duarte, 2000). In recent decades, the rapid degradation of ecosystems globally has forged intersections between their functioning and the field of restoration ecology, as the preservation of functionality has become an increasingly urgent priority (Isbell et al. 2017). In response to global declines in coral reef health, the past twenty years have seen a sharp rise in coral reef restoration initiatives, aiming to capture some of the key services previously provided by healthy natural reefs (Hein et al. 2021).

Coral reef ecosystem functioning may be defined as fluxes and storage of energy, nutrients, or inorganic materials that are mediated by living organisms (Brandl et al. 2019). More specifically, Brandl et al (2019) propose a definition of coral reef functioning, which is centred on eight complementary, reciprocal ecological processes: (1) calcium carbonate production and (2) bioerosion, (3) primary production and (4) herbivory, (5) secondary production and (6) predation, and (7) nutrient uptake and (8) release (illustrated through Figure 1A). While exact definitions of coral reef functioning remains debatable and can vary between studies, the eight aforementioned processes provide a practical and applicable framework for understanding and actively bolstering coral reef ecosystems.

Challenge: reef restoration efforts often lack consideration of functioning

Coral reef restoration has attracted criticism because of the lack of sustained monitoring using standardised metrics to define success (Vardi et al., 2021). Long-term monitoring is rarely integrated into

reef restoration projects, with over 60 % of programmes reporting fewer than 18 months of monitoring data (Suggett et al. 2024). As a consequence, coral restoration has, at times, been cast as distracting attention from the primary cause of reef decline (i.e. climate change-induced bleaching; Streit et al., 2024). In the supplementary text (ST1), we discuss the topical and relevant issues in the field of coral reef restoration in the context of ecosystem functioning.

Many reef restoration programmes, and the media attention surrounding them, tend to focus on the short term ‘successes’ that “save reefs” (Suggett et al. 2024), which are usually defined by basic static metrics such as coral cover and/or growth. This has led to the prioritisation of restoration approaches that produce near-immediate, short-term results, such as the transplantation of fast-growing branching corals. A restoration site consisting of transplanted branching corals only, may lack long-term stability and other forms of habitat complexity, as well as support limited assemblages of functionally important fish which drive processes like predation and herbivory. Furthermore, these approaches lack consideration of other important benthos, including sponges and crustose coralline algae (Boakes et al. 2023), which provide important contributions to nutrient uptake and release, as well as calcification (De Goeij et al. 2017). Figure 1B highlights that with these restoration approaches, it is likely that none of the eight ecosystem function processes disappear completely - but many will be severely compromised or in rudimentary form, as we explain in the supporting text of the figure. The criticisms that these well-intentioned approaches receive may be considered akin to those of a monoculture palm oil plantation, which are known to support a reduced level of ecosystem functioning compared to the natural forests which they often replace (Dislich et al., 2017). Importantly, the ability of reef restoration initiatives to successfully support similar levels of ecosystem functioning as natural reefs has remained largely untested. If we are to better understand the ability of coral reef restoration programmes to tangibly regenerate previously degraded reef ecosystems, or tailor future restoration initiatives to achieve this goal, a rigorous and clear assessment of reef ecosystem functioning on restored reefs will be indispensable.

Reef restoration efforts that do not consider functioning in their approaches, strategies and monitoring, will likely create a restoration site which lacks the ability to determine which ecosystem functions and services—if any—are being influenced by the intervention. Furthermore, the absence of suitable indicators and sustained long-term monitoring, makes assessing whether the initiative is producing any significant ecological or functional outcomes particularly challenging. In fact, the vast majority of coral reef management programmes (including those which focus on reef restoration) monitor reefs by using metrics based on species diversity and the number of coral individuals planted. Only a small minority focusing on monitoring the functional processes (Lam et al. 2017), with one example including the Coral Restoration Foundation in Florida, which actively monitors processes like calcium carbonate production and bioerosion (Monitoring Guidelines available here: <https://coralrestoration.org/restoration/#monitoring>). Effective reef restoration is a long game (Suggett et al. 2024), and we argue it needs to be centered around long-term impacts rather than short-term metrics of success, including metrics of ecosystem functioning, as well as coral survival over ecologically relevant timescales.

Solution: Prioritising ecosystem functioning in coral reef restoration

As increasing amounts of funding are poured into reef restoration, we propose that practitioners, stakeholders, funders, and scientists consider the following focus points:

Focus point 1: *Implement a set of standardized methods to monitor ecosystem functioning on restored reefs (and neighboring natural reef sites).*

Currently, most studies on coral reef functioning use descriptors collected from secondary literature (e.g. FishBase [www.fishbase.org], such as Mouillot et al. (2014)) because it is simpler to obtain details on functional traits this way, than by collecting direct empirical measurements (Brandl et al., 2019). Given the current lack of in-depth monitoring by most of the world's restoration programmes (Eger et al., 2022), we first propose that long-term monitoring (5+ years, as suggested by Goergen et al. (2020)) is built into every restoration project, following that of the Mars Inc. monitoring program. We then propose that, within their monitoring, restoration programmes should include ecosystem functioning parameters as metrics to assess their success, beyond the most commonly used standard biodiversity metrics. Based on the eight key processes of reef functioning, we provide suggestions on the practical methods which can be used by coral reef scientists and restoration practitioners for reef monitoring that includes the consideration of functionality:

1. **Calcium carbonate production:** Measure crustose coralline algae using settlement tiles for 12 months (Johnson et al. (2022)).
2. **Calcium carbonate bioerosion:** Monitor bioerosion of dead branching corals through measuring weight before and after deployment for 12 months [Click or tap here to enter text.](#) (Londoño-Cruz et al. (2003)).
3. **Primary production:** Harvest macroalgae on a caged (closed-off) plate which cannot be grazed by fish. Then, after 12 months measure the growth of algal filaments growing on the plates over time McClanahan et al. (2002)).
4. **Herbivory:** Remove the cages of the above and monitor the consumption rate of the algae which has grown on the tiles over a two week period (Paddack et al. (2006)).
5. **Predation:** Monitor consumption of 'squid-pops' to determine relative consumption by predatory fish over a 24 hour period (following Rodemann and Brandl (2017)).
6. **Secondary production:** Use a simple demographic models that predict secondary production based on easily obtainable fish surveys and broadly inferable rates of growth and mortality creation of a demographic model (following Morais and Bellwood (2020)).
7. **Nutrient uptake** and 8. **Release:** Collect data of fish assemblages (using Remote Underwater Video (following (Boakes et al. 2023)) and then model fluxes of carbon, nitrogen and phosphorous using the '[Fish Flux' model](#) (following Schiettekatte et al. (2020)). This extensive resource is readily available to use and is accessible to relatively inexperienced researchers.

Each method has been specifically chosen as an already-established, relatively simple and affordable option to quantify each functional process, with the hope that this will make including functioning more accessible for reef restoration monitoring programmes with limited budgets. Goergen et al. (2020) discuss how the success of ecological restoration should be measured by how much ecological function is created or achieved after restoration efforts, compared to a nearby reference ecosystem. We propose that the eight suggested parameters are also measured on a nearby natural reef, to allow practitioners to understand the extent to which their restoration programmes can support key functional processes, relative to nearby natural reefs. This should be used as one defining factor for success for reef restoration. In the supplementary text (ST2), we also discuss how and why monitoring programs should also try to identify taxa which provide locally-important contributions to functioning.

In addition to the above metrics used to quantify reef ecosystem functioning, it is also important to consider coral demographics, which are also critical for evaluating how restoration influences coral

ecosystem functions and services. In the supplementary material (ST3), we propose that the monitoring of key parameters of coral demographics are also important to include in reef restoration monitoring programs, and suggest five key methods to do this.

Focus point 2: Address the current literature gaps in the field

Examining how restoration programmes will perform in a changing ocean:

Almost all the threats which natural reefs face (e.g. bleaching) also threaten restoration sites. Most of the key research highlighting successful reef restoration does so on sites which have adjacent natural reefs, which are considered healthy (e.g. Vida et al. (2024)). We do not know how restoration sites will perform in the absence of nearby natural reefs, because as nearby reefs degrade due to climate change, this will likely impact larval supply, and influence the recruitment organisms which have a potentially important functional role. Furthermore, to date, restoration initiatives have not explicitly accounted for future disturbances in their planning, relying instead on reactive responses to past stress events, as discussed by (Mulà et al. (2025)). Moreover, the coral genera most commonly used in reef restoration—such as species of Acroporidae, are among the most vulnerable to bleaching events (Hoogenboom et al., 2017), making these restoration programs particularly susceptible to large-scale mortalities in the face of climate change (Shaver et al., 2022). Consequently, there is a high risk that restoration gains could be entirely lost, irrespective of potential larval input from adjacent reefs post-disturbance.

Identifying organisms which are particularly important for supporting and undertaking functional processes on coral reefs:

In order to prioritise management actions to preserve coral reefs, research is needed to clarify the species and functional groups which are most important to protect, in order to preserve key ecosystem functions and promote reef recovery (Madin et al. 2023). Reef restoration programmes vary in their techniques, and more research is also needed to assess which methods work best for enhancing functionality by targeting these key organisms.

Focus point 3: Adopt a function-centric restoration approach

Reef restoration and management programmes should implement changes to adopt a function-centric approach that introduces techniques specifically targeted at respective species and processes of interest. Locally, often a single or handful of species disproportionately dominate a given function (Topor et al. 2019). We propose that efforts should focus on identifying key genera which provide important contributions to the processes supporting functioning (Madin et al. 2023) through ensuring that a broad range of ‘functionally important’ organisms are protected. However, the specific functional role of a given organism (and its relative importance) varies between regions, and thus, it is difficult to pinpoint widespread key species that dominate functioning over large spatial scales (Schiettekatte et al. 2022). We propose that restoration monitoring programmes aim to identify and protect specific taxa which are important for reef functioning. This approach should also be introduced alongside management measures aiming to protect reef biodiversity more generally, given the role of biodiversity in supporting ecosystem functions (Lefcheck et al. 2019).

Conclusion

Coral restoration is a burgeoning field that continues to attract substantial interest and funding. This article is not intended to discourage these efforts, but to recenter the attention of restoration efforts

towards the ultimate goal of aiming to create ecologically functional reefs. If these efforts are to eventually produce structures that resemble natural coral reef ecosystems and can provide similar services, then ecological functioning –as encapsulated by the core processes that operate on coral reefs– need to be at the forefront of ecological monitoring and restoration design. Doing so, will contribute towards the increased resilience and provisioning of associated ecosystem services, and will allow for reef restoration programmes to maximise their potential.

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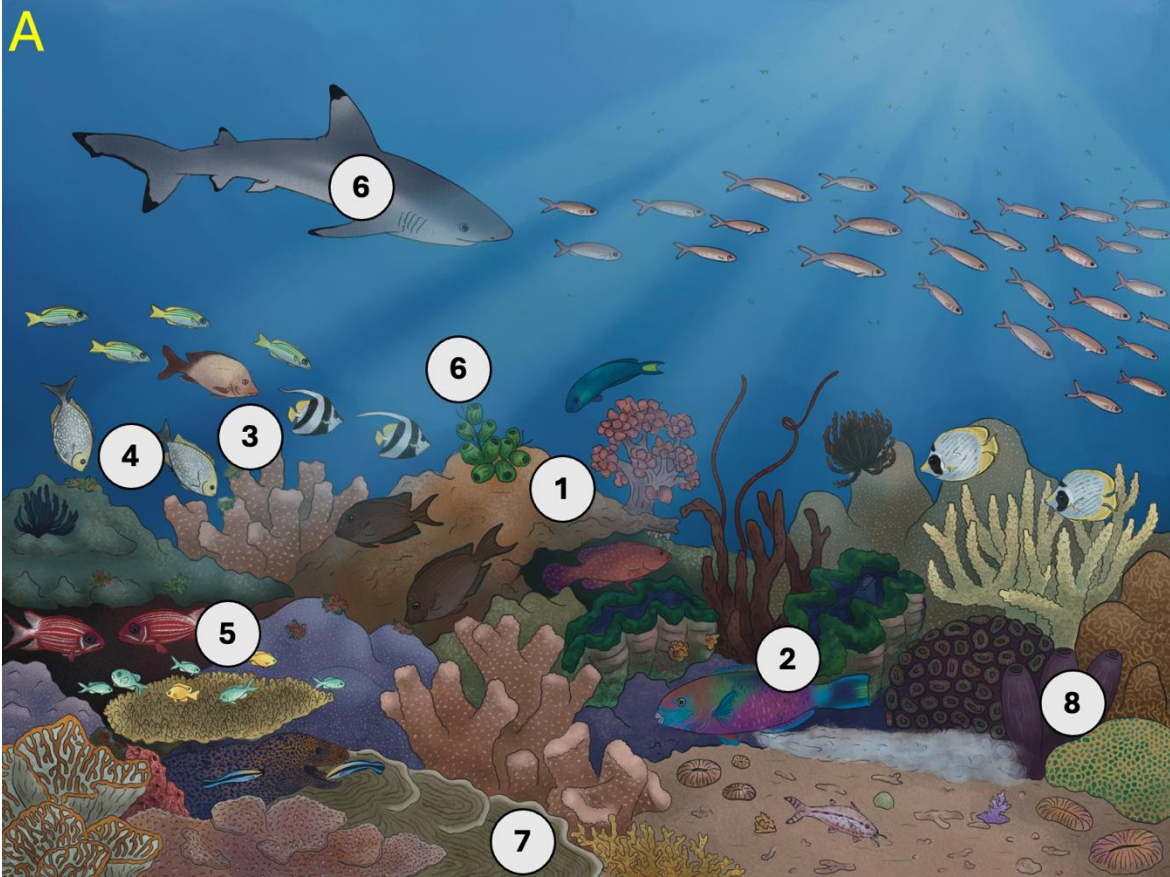
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1 Figures



Functional processes occurring on natural coral reefs:

- 1) **CaCO₃ production** by hard corals to build their skeletons, as well as calcifying algae, especially crustose coralline algae and Halimeda.
- 2) **CaCO₃ bioerosion** by bioeroding fish such as parrotfish
- 3) **Primary production** by benthic algae and corals
- 4) **Herbivory** - grazing of algae by herbivores like rabbitfish and surgeonfish
- 5) **Secondary production** by secondary consumers like damselfish which produce the bulk of "consumable" secondary production.
- 6) **Predation** by large predatory fish
- 7) **Nutrient uptake** by corals which absorb nitrogen and phosphorus
- 8) **Nutrient release** by benthos and fish which release organic matter

2
3



Attenuation of core processes at restoration sites:

1) CaCO_3 production: Loss of calcification from diverse benthic organisms, including slow-growing corals unsuitable for fragmentation, as well as benthic algae (crustose coralline algae and Halimeda; Castro-Sanguino et al. 2020; Kench et al. 2022).

2) Bioerosion: Limited availability of abiotic substrate with nutritious endolithic communities (Clements et al. 2017; Clements and Choat 2018).

3) Primary production: Limited primary production by filamentous turf algae and macroalgae, due to reduced habitat availability (Hatcher 1990).

4) Herbivory: Limited resources available for herbivorous fishes, leading to low abundances (Russ et al. 2015; Tootell and Steele 2016).

5) Secondary production: Pruned suite of trophic pathways and microhabitats for small consumers resulting in limited productivity (Brandl et al. 2019; Robinson et al. 2023).

8) Nutrient release: compromised retention and release of nutrients by consumers due to lack of structural complexity and strong trophic cycling (Kerry and Bellwood 2016; Schiethkatte et al. 2023).

7) Nutrient uptake: Nutrient uptake: limited uptake by crucial nutrients from diverse benthic organisms (e.g. algae, sponges, bryozoan; (Den Haan et al. 2016; De Goeij et al. 2017).

6. Predation: Limited availability of large predators due to insufficient supply of prey (Bax 1998)

Figure 1: (A) an example highlighting a natural reef that would be considered to have high functionality due to the flora and fauna undertaking key functional processes, and (B) an example highlighting how a specific reef restoration approach may not fully support functioning due to the absence of organisms able to undertake key functional processes.