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## Historical analysis of the recovery of physical functionality in a coral reef community following the implementation of active restoration practices

Adahara Muñoz-Alfaro<sup>1,2</sup>;  <https://orcid.org/0009-0006-1736-4670>

Alma Paola Rodríguez-Troncoso<sup>3</sup>;  <https://orcid.org/0000-0001-6243-7679>

Amílcar Levi Cupul-Magaña<sup>3</sup>;  <https://orcid.org/0000-0002-6455-1253>

José de Jesús Adolfo Tortolero-Langarica<sup>4</sup>;  <https://orcid.org/0000-0001-8857-5789>

Rafael Andrés Cabral-Tena<sup>5\*</sup>;  <https://orcid.org/0000-0002-2836-2834>

1. Posgrado en Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California. Carretera Ensenada – Tijuana, No. 3918, Zona Playitas, 22860, Ensenada, B.C., México; adaharam\_24@alu.uabcs.mx
2. Doctorado en Ciencias Marinas y Costeras, Universidad Autónoma de Baja California Sur. Boulevard Forjadores S/N, Col. Universitario, La Paz, Baja California Sur, México.
3. Laboratorio de Ecología Marina, Centro Universitario de la Costa, Universidad de Guadalajara. Avenida Universidad 203, Delegación Ixtapa, Puerto Vallarta, Jalisco, 48280. México; alma.rtroncoso@academicos.udg.mx, levi.cupul@academicos.udg.mx
4. Tecnológico Nacional de México, Instituto Tecnológico de Bahía de Banderas, Nayarit, México. Crucero a Punta de Mita S/N, col. La Cruz de Huanacastle, Nayarit, 63734. México; adolfo.tl@bahia.tecnm.mx
5. Laboratorio de Arrecifes y Biodiversidad/Departamento de Ecología Marina, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California. Carretera Ensenada – Tijuana, No. 3918, Zona Playitas, 22860, Ensenada, B.C. México; rcabral@cicese.mx (\*Correspondence)

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### ABSTRACT

**Introduction:** The Reef Functional Index (RFI) is a tool used to analyze the physical functionality of coral assemblages based on morpho-functional traits that support their geo-ecological roles. This tool has been applied to assess the effects of active restoration on coral reefs under varying levels of stress. However, to date, it has not been used to analyze long-term assisted recovery through restoration activities.

**Objective:** This study evaluated the historical trajectory of physical functionality over the long term (2012–2023) in six coral reef communities within the Islas Marietas National Park (PNIM), considering that active restoration efforts have been in place since 2014, using the RFI as a metric.

**Methods:** The RFI was used as an indicator of physical functionality to assess temporal changes in reef condition throughout the analysis period. The percentage of natural change and change subsidized by restoration was calculated for both RFI and live coral cover (LCC).

**Results:** RFI values revealed that although coral communities in the PNIM had, by 2023, regained LCC levels exceeding those recorded in 1997, physical functionality had not yet been fully restored. Restoration activities have contributed to approaching historical functional values, even under the impact of various natural stressors; however, spatial analysis at the island and site level indicated that recovery has not been uniform.

**Conclusions:** The findings highlight the need to review and adapt restoration strategies, emphasizing greater efforts in sites where coral functionality remains below pre-disturbance levels. Additionally, the results demonstrate that the RFI is a valuable tool for evaluating the long-term success of coral restoration and identifying potential areas of opportunity in degraded reef sites.



**Key words:** physical functionality; Reef Functional Index (RFI); coral reef restoration, long-term recovery; Marietas Islands National Park reefs.

## RESUMEN

### Análisis histórico de la recuperación de la funcionalidad física en una comunidad coralina tras la implementación de prácticas de restauración activa

**Introducción:** El Índice de Función Arrecifal (RFI) es una herramienta que sirve para analizar la funcionalidad física de los ensamblajes coralinos con base en rasgos morfofuncionales que sustentan sus roles geo-ecológicos. Esta herramienta se ha aplicado para evaluar los efectos de la restauración activa en arrecifes coralinos bajo diferentes niveles de estrés. Sin embargo, hasta la fecha, no se ha utilizado para analizar la recuperación asistida a largo plazo mediante actividades de restauración.

**Objetivo:** Este estudio evaluó la trayectoria histórica de la funcionalidad física a largo plazo (2012-2023) en seis comunidades arrecifales dentro del Parque Nacional Islas Marietas (PNIM), considerando que se han realizado esfuerzos de restauración activa desde 2014, utilizando el RFI como métrica.

**Métodos:** El RFI se utilizó como un indicador de la funcionalidad física para evaluar cambios temporales en la condición del arrecife a lo largo del período de análisis. El porcentaje de cambio natural y cambio subsidiado por la restauración se calculó tanto para el RFI como para la cobertura de coral vivo (LCC).

**Resultados:** Los valores del RFI revelaron que, si bien las comunidades coralinas del PNIM habían recuperado, para 2023, niveles de LCC superiores a los registrados en 1997, la funcionalidad física aún no se había restaurado por completo. Las actividades de restauración han contribuido a aproximarse a los valores funcionales históricos, incluso bajo el impacto de diversos estresores naturales; sin embargo, el análisis espacial a nivel de isla y de sitio indicó que la recuperación no ha sido uniforme.

**Conclusiones:** Los hallazgos resaltan la necesidad de revisar y adaptar las estrategias de restauración, enfatizando mayores esfuerzos en sitios donde la funcionalidad coralina se mantiene por debajo de los niveles previos a la perturbación. Adicionalmente, los resultados demuestran que el RFI es una herramienta valiosa para evaluar el éxito a largo plazo de la restauración coralina e identificar áreas de oportunidad potenciales en sitios arrecifales degradados.

**Palabras clave:** funcionalidad física; Índice de Función Arrecifal (RFI); restauración de arrecifes de coral, recuperación a largo plazo; arrecifes del Parque Nacional Islas Marietas.

## INTRODUCTION

Coral reefs are highly productive and bio-diverse ecosystems (Burke et al., 2011), with an estimated value of USD \$352 000 ha<sup>-1</sup> yr<sup>-1</sup>, stemming from the social, economic, and ecological functions they provide (Allemand & Osborn, 2019; Woodhead et al., 2019). They also fulfill essential geo-ecological functions such as reef structure formation, the generation of microhabitats, and sediment production (de Groot et al., 2012; Perry & Álvarez-Filip, 2018).

Currently, coral reefs face both local and global threats that are driving their degradation (Souter et al., 2021), leading to declines in the abundance of reef-building corals and causing

shifts in the composition and structure of associated communities (Norström et al., 2009). To mitigate reef degradation, restoration strategies have been implemented over the past three decades, aiming to support the recovery of both foundational species and the ecosystem's functional capacity (Hein et al., 2021). However, most interventions have focused on short-term recovery (1–2 years), prioritizing indicators such as coral survival and growth (Vaughan, 2021). As a result, it is now recommended to implement long-term interventions (>5 years) that allow for the evaluation of restoration outcomes from both functional and geological perspectives in a synergistic manner (Goergen et al., 2020; Rinkevich, 2019).

One approach to functionally assess coral reefs is the Reef Functional Index (RFI), which evaluates the status of physical functionality in coral communities based on morpho-functional traits that underpin their geo-ecological roles (González-Barrios & Álvarez-Filip, 2018). In the Eastern Tropical Pacific (ETP), the RFI has been applied to understand the role of coral species in reef functioning, particularly in the Mexican Pacific, and to assess the effects of active restoration from a functional perspective across areas with varying anthropogenic impacts (Cabral-Tena et al., 2020; Muñoz-Alfaro et al., 2023; Navarrete-Torices et al., 2023). It also enables the characterization of natural reef recovery following exposure to both natural and anthropogenic stressors (González-Barrios et al., 2021; McWilliam et al., 2018), showing that the physical functionality of coral reefs is not restored solely by increasing live coral cover (LCC). However, to date, no long-term (>1 year) analysis of assisted recovery through restoration activities has been conducted using the physical functionality approach.

Coral reefs in the Mexican Pacific (MP) are characterized by patchy distributions and are composed of assemblages dominated by the genera *Pocillopora*, *Porites*, *Psammocora*, and *Pavona* (Reyes-Bonilla et al., 2005). In this region, average RFI values vary among localities, with the southern MP showing the highest values ( $0.71 \pm 0.1$ ; Cabral-Tena et al., 2020), followed by northern communities ( $0.65 \pm 0.15$ ; Navarrete-Torices et al., 2023), while the Central Mexican Pacific (CMP) exhibits the lowest values, ranging from 0.28 to 0.71 (Muñoz-Alfaro et al., 2023). However, these values do not reflect the current condition, as the recent 2023–2024 El Niño event (López-Pérez et al., 2024) resulted in accumulated coral losses of over 70 % in several MP localities. Furthermore, the CMP region is particularly affected by local stressors such as coastal development and increased tourism (Burroughs & Rodríguez-Troncoso, 2024). In response to these adverse conditions, passive restoration strategies—such as the implementation of tourist load regulations (Cupul-Magaña & Rodríguez-Troncoso,

2017)—and active coral reef restoration programs have been promoted. One such program has been ongoing in the Islas Marietas National Park (IMNP) since 2014 (Tortolero-Langarica et al., 2014) and continues to this day. Within this context, the present study assessed the historical trajectory of physical functionality over the long term (2012–2023) in the coral communities of PNIM, under the influence of active restoration, using the RFI as a tool for functional analysis.

## MATERIALS AND METHODS

**Study area.** The evaluation of physical functionality was carried out at six sites within Islas Marietas National Park (IMNP) ( $20^{\circ}40'35''$ – $20^{\circ}41'45''$  N,  $105^{\circ}33'30''$ – $105^{\circ}38'10''$  W). IMNP comprises two volcanic islands, Isla Larga and Isla Redonda, located approximately 7 km off the coast of the Central Mexican Pacific (CMP). Coral communities in this area are mainly distributed between 1 and 15 m in depth, with Isla Larga harboring the highest coral species richness (Hernández-Zulueta et al., 2017) (Fig. 1).

This region is an oceanographic convergence zone influenced by three major currents: the California Current, which brings cold, nutrient-rich waters; the Mexican Coastal Current, which carries warm, nutrient-poor waters; and the Gulf of California Current, characterized by warm, high-salinity waters. Sea surface temperature in the region shows interannual variation ranging from 23.3 to 30 °C (Kessler, 2006; Palacios-Hernández et al., 2010). The area is also subject to decadal and interannual thermal anomalies, including El Niño–Southern Oscillation (ENSO) events, with positive phases reaching anomalies  $\geq 3$  °C and negative phases (La Niña)  $\leq -4$  °C (Palacios-Hernández et al., 2010).

**Fieldwork.** Six study sites were selected, and starting in 2012, annual monitoring of live coral cover (LCC, %) was conducted. At each site, five semi-permanent 25 m transects were laid parallel to the shoreline. LCC was assessed using six 1 m<sup>2</sup> quadrats per transect, spaced



**Fig. 1.** Map of the study area and sampling sites: Isla Larga (IL); Zona de Restauración (ZR); Zona de restauración Sur (ZRS); Cueva del Muerto (CM); Isla Redonda (IR); Playa del Amor (PA); Pavonas Platform (PP); and Túnel Amarradero (TA).

approximately 4 m apart. Historical data from 1996–1997 were also incorporated, based on previous monitoring by Rodríguez-Zaragoza (2001), which used three 10 m permanent transects parallel to the shore. The transect average was used as the experimental unit in this study. Coral species at each site were identified based on morphological traits following taxonomic descriptions (Veron et al., 2016). Between 2014 and 2023, active restoration activities were implemented, involving direct transplantation of opportunity fragments from the genus *Pocillopora*, as described by Tortolero-Langarica et al. (2019).

To calculate the RFI, in addition to LCC data (%), 15 coral colonies per species (7 spp.) were randomly selected along the transects at each site. For each colony, the maximum and minimum diameters, height, and linear length along the colony's major axis were measured. The perimeter was also measured using a No. 9 bead chain (2–3 mm) from one end of the colony to the other.

**Data analysis.** The Reef Functional Index (RFI) was calculated based on LCC. To estimate the calcification rate ( $\text{kg m}^{-2} \text{yr}^{-1}$ ), the

morphology of each coral species was considered, following the method proposed by González-Barrios & Álvarez-Filip (2018). Extension rate ( $\text{cm yr}^{-1}$ ) and skeletal density ( $\text{g cm}^{-3}$ ) were based on local values reported by Tortolero-Langarica et al. (2016) and Tortolero-Langarica et al. (2017). Structural complexity was estimated using the rugosity index (RI) at the colony level, calculated as the ratio between the perimeter, linear length of the major axis, and the maximum colony height (Álvarez-Filip et al., 2009).

Calcification rate, rugosity, and colony height were standardized to values ranging from 0 to 1 using the following formula (González-Barrios & Álvarez-Filip, 2018):

$$y = \frac{(x - \text{minimum value})}{\text{maximum value} - \text{minimum value}}$$

where  $x$  is the observed value of each growth parameter.

To compute the RFI (González-Barrios & Álvarez-Filip, 2018), the Functional Coefficient (FC) was first calculated for each species by averaging the standardized values of calcification, rugosity, and height. Then, the RFI for each site and year was calculated by summing

the product of the LCC of each species present at the site (expressed as a percentage), by its respective CF value for each site and year.

$$RFI = \sum_i \left( \frac{LCC_i}{100} \right) FC_i$$

To aid interpretation, a fourth root transformation was applied to the RFI values, resulting in scores between 0 and 1, where values closer to 0 represent low reef functionality and values near 1 indicate high functionality (González-Barríos & Álvarez-Filip, 2018) (Table 1).

LCC and RFI were evaluated for each transect. Both datasets were averaged annually at three spatial scales: park-wide (IMNP), island-level (Isla Larga and Isla Redonda), and site-level (Zona de Restauración: ZR, Zona de Restauración Sur: ZRS, Cueva del Muerto: CM, Playa del Amor: PA, Plataforma Pavonas: PP, and Túnel Amarradero: TA). The percentage of natural change and change supported by restoration were calculated for both RFI and LCC.

**Statistical analysis.** To evaluate temporal (2012-2023) and spatial patterns in coral cover (LCC) and Reef Functional Index (RFI) across the PNIM, Generalized Linear Mixed Models (GLMM) were fitted. LCC was modeled using beta-binomial distributions with a logit link. This family was used because LCC data corresponded to proportions derived from counts and exhibited over-dispersion. RFI was modeled using beta-regression with a logit link. This was selected because RFI is a continuous

variable bounded between 0 and 1. For each metric, we first fitted a global model including centered year as a fixed effect, followed by models incorporating site or island as fixed factors, and full interaction structures (Year  $\times$  Site, Year  $\times$  Island) to test for spatial differences in temporal trends. Additionally, we fitted independent models for each site and each island to assess localized trajectories. Model fit was evaluated using AIC and likelihood-based diagnostics, and significance of fixed effects was assessed using Type III Wald  $\chi^2$  tests. All analyses were performed in R 4.2.2 using the *glmmTMB* function of the *glmmTMB* package for model fitting and *Anova* function from the *car* package for inference. The model's assumptions were validated through the generation of residual plots using the *simulateResiduals* function in the *DHARMA* package.

## RESULTS

The historical analysis of live coral cover (LCC) in the Islas Marietas National Park (IMNP) began with a baseline established in 1997, showing a park-wide LCC of 19.85 %, with 18.1 % at Isla Larga and 21.6 % at Isla Redonda (Fig. 2A, Fig. 2B, Fig. 2C). The average baseline for the Reef Functional Index (RFI) at the PNIM scale was 0.6, with values of 0.59 for Isla Larga and 0.61 for Isla Redonda (Fig. 2D, Fig. 2E, Fig. 2F).

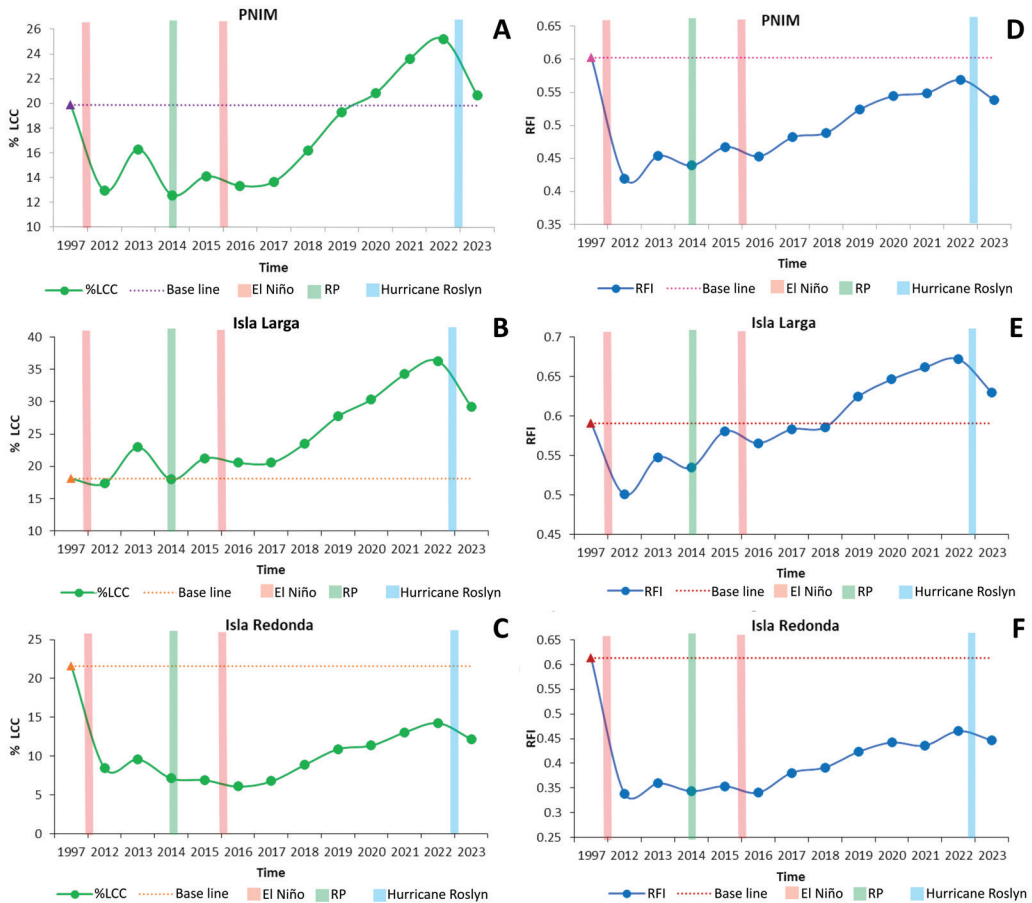
In 2012, at the start of the current monitoring effort, the data showed a park-level LCC decrease of -34.87 % (LCC =  $12.93 \pm 12.50$  %),

**Table 1**

Calcification rate, rugosity index, mean colony height, and functional coefficient for each coral species recorded in PNIM.

| Species                       | Calcification Rate (kg CaCO <sub>3</sub> m <sup>-2</sup> yr <sup>-1</sup> ) | Rugosity Index | SD   | Height (cm) | SD | FC   |
|-------------------------------|---|----------------|------|-------------|----|------|
| <i>Porites panamensis</i>     | 3.66  | 1.59           | 0.29 | 9           | 5  | 0.01 |
| <i>Pocillopora damicornis</i> | 24.97   | 3.43           | 0.24 | 23          | 0  | 0.57 |
| <i>Pocillopora verrucosa</i>  | 25.70   | 5.13           | 2.00 | 17          | 9  | 0.67 |
| <i>Pocillopora capitata</i>   | 23.28   | 5.41           | 0.93 | 21          | 7  | 0.68 |
| <i>Pocillopora grandis</i>    | 25.44   | 5.75           | 0.95 | 21          | 7  | 0.74 |
| <i>Pavona clavus</i>          | 12.79   | 1.88           | 0.47 | 25          | 10 | 0.28 |

SD = Standard deviation; FC = Functional coefficient.



**Fig. 2.** Historical trends in live coral cover (LCC; A, B, C) and reef function index (RFI; D, E, F) across different spatial scales (a and d: PNIM; b, c, e, f: Islands). RP = start of the restoration program.

with a reduction of -3.87 % at Isla Larga (LCC =  $17.40 \pm 14.57$  %) and -60.85 % at Isla Redonda (LCC =  $8.46 \pm 8.28$  %) (Appendix 1). This trend was also reflected in the RFI, which showed a park-level decline of -30.37 % (RFI =  $0.42 \pm 0.19$ ), with decreases of -15.27 % at Isla Larga (RFI =  $0.50 \pm 0.17$ ) and -44.90 % at Isla Redonda (RFI =  $0.34 \pm 0.18$ ) (Fig. 2; Appendix 1).

At the site level, the highest LCC values in 2012 were recorded at all three sites on Isla Larga, with the highest in Zona de Restauración ( $32.40 \pm 14.10$  %), while the lowest values were recorded at Isla Redonda, particularly at Túnel Amarradero ( $7.00 \pm 7.39$ %) (Table 2). For RFI, no clear spatial pattern was observed, with the highest value at Cueva del Muerto ( $0.48 \pm 0.09$ )

and the lowest at Playa del Amor ( $0.30 \pm 0.22$ ) (Table 2).

In 2014, the year restoration activities began, LCC at the park scale was  $12.57 \pm 11.51$  %, with an average of  $18 \pm 13.29$  % at Isla Larga and  $7.14 \pm 5.86$  % at Isla Redonda (Fig. 2c). These patterns were also reflected in RFI, with a park-wide value of  $0.44 \pm 0.17$ , and values of  $0.53 \pm 0.13$  at Isla Larga and  $0.34 \pm 0.14$  at Isla Redonda (Fig. 2d, Fig. 2e, Fig. 2f). In general, sites located on Isla Larga exhibited higher average LCC and RFI values compared to those on Isla Redonda (Table 2).

Temporal analysis showed an increase in both LCC and RFI from 2014 to 2015, followed by a decline associated with the 2016 El Niño

**Table 2**

Average live coral cover (LCC) and Reef Functional Index (RFI) values at the site level for the years 2012 (start of monitoring), 2014 (beginning of active restoration activities), and 2023 (end of the present study's analysis).

| Site | 2012          |             | 2014          |             | 2023          |             |
|------|---------------|-------------|---------------|-------------|---------------|-------------|
|      | LCC (%)       | RFI         | LCC (%)       | RFI         | LCC (%)       | RFI         |
| ZR   | 32.40 ± 14.10 | 0.65 ± 0.10 | 27.70 ± 17.14 | 0.61 ± 0.11 | 36.30 ± 11.90 | 0.68 ± 0.07 |
| ZRS  | 8.67 ± 8.31   | 0.38 ± 0.19 | 12.93 ± 7.63  | 0.50 ± 0.13 | 24.37 ± 13.20 | 0.59 ± 0.15 |
| CM   | 11.13 ± 7.03  | 0.48 ± 0.09 | 13.37 ± 9.49  | 0.50 ± 0.13 | 26.93 ± 15.66 | 0.62 ± 0.12 |
| PP   | 10.37 ± 8.37  | 0.41 ± 0.13 | 8.40 ± 5.57   | 0.37 ± 0.15 | 16.07 ± 4.67  | 0.52 ± 0.04 |
| TA   | 7.00 ± 7.39   | 0.31 ± 0.20 | 6.20 ± 4.94   | 0.34 ± 0.14 | 7.20 ± 4.33   | 0.35 ± 0.18 |
| PA   | 8.00 ± 10.39  | 0.30 ± 0.22 | 6.83 ± 7.85   | 0.32 ± 0.17 | 13.27 ± 13.26 | 0.47 ± 0.17 |

ZR = Zona de Restauración, ZRS = Zona de Restauración Sur, CM = Cueva del Muerto, PP = Plataforma Pavonas, TA = Túnel Amarradero, PA = Playa del Amor.

event and Hurricane Roslyn in 2022 (Fig. 2, Appendix 2, 3). In 2023, LCC increased to 20.69 ± 14.24 % across PNIM, with 29.2 ± 13.73 % at Isla Larga and 12.18 ± 8.75 % at Isla Redonda. The site with the greatest increase was Cueva del Muerto, while the lowest was Túnel Amarradero (Table 2; Appendix 1).

RFI also increased in 2023 compared to values at the start of the restoration program, reaching 0.54 ± 0.15 at the park scale (+22.59 %), 0.63 ± 0.12 at Isla Larga (+17.82 %), and 0.44 ± 0.13 at Isla Redonda (+30 %). At the site level, the highest RFI increase was recorded at Playa del Amor (+43.78 %), and the lowest at Túnel Amarradero (RFI = 0.35) (Fig. 2, Table 2; Appendix 1).

Over a period of more than 20 years, LCC and RFI values surpassed the 1997 baseline in 67 % and 44.44 % of the cases, respectively. Zona de Restauración showed the highest increase in both metrics (LCC +100.55 %, RFI +15.40 %), followed by Isla Larga (LCC +61.36 %, RFI +6.64 %). The lowest increases were observed at the park scale for LCC (+4.23 %) and at Zona de Restauración Sur for RFI (+0.12 %). Notably, the sites located on Isla Redonda did not surpass the historical LCC baseline from 1997 (Table 2), a pattern that was also evident for RFI. On the island scale, Isla Redonda showed a -27.24 % decrease in LCC relative to the baseline, while IMNP showed a -10.62 % decrease (Appendix 2–3).

When analyzing the GLMM models, we found that the LCC showed a pattern of sustained recovery in the PNIM between 2012 and 2023. The model (Appendix 4–5) indicated a significant increase over time ( $\beta = 0.061$ ,  $p < 0.001$ ;  $\chi^2 = 20.29$ ,  $df = 1$ ,  $p < 0.001$ ), equivalent to an average positive trend of approximately 6% per year. This result suggests that, on a regional scale, the coral communities of the PNIM have experienced continuous recovery during the analyzed period. At the island scale, the model (Appendix 6–7) showed a significant increase over time ( $\beta = 0.084$ ,  $p < 0.001$ ,  $\chi^2 = 30.39$ ,  $df = 1$ ,  $p < 0.001$ ) and differences between Isla Larga and Isla Redonda ( $\chi^2 = 146.14$ ,  $df = 1$ ,  $p < 0.001$ ). Isla Larga exhibited a significant positive slope ( $\beta = 0.084$ ,  $p < 0.001$ ), while Isla Redonda maintained significantly lower initial LCC values ( $\beta = -1.03$ ,  $p < 0.001$ ) and a weaker trend that did not differ statistically from that observed on Isla Larga (Year × Island interaction:  $p = 0.171$ ). Overall, both islands show signs of recovery, but Isla Larga has higher values and greater rates of increase. When analyzing site-level patterns, the models (Appendix 8–10) revealed marked heterogeneity in recovery, showing differences between sites ( $\chi^2 = 243.82$ ,  $df = 5$ ,  $p < 0.001$ ) and years ( $\chi^2 = 12.70$ ,  $df = 1$ ,  $p < 0.001$ ). Four sites showed positive and statistically significant trends: Zona de Restauración ( $\beta = 0.104$ ,  $p < 0.001$ ), Cueva del Muerto ( $\beta = 0.090$ ,  $p < 0.001$ ),



Plataforma Pavonas ( $\beta = 0.092$ ,  $p < 0.001$ ), and Zona de Restauración Sur ( $\beta = 0.059$ ,  $p = 0.042$ ). These sites represent the areas with the clearest recovery, with annual increases ranging from 6% to 10% of the LCC. In contrast, Playa del Amor showed a positive but not statistically significant trend ( $p = 0.109$ ), while Túnel Amarradero showed no evidence of recovery ( $p = 0.625$ ) during the analyzed period. The year  $\times$  site interaction model confirmed this spatial pattern. Most sites presented significantly different intercepts (Appendix 8), reflecting the contrast in initial conditions.

On the other hand, the GLMM models performed with the RFI as the response variable indicate that there is a general pattern of significant increase in functionality in the PNIM between 2012 and 2023. The global model (Appendix 11–12) indicated a positive and significant effect of the year on the change in RFI ( $\beta = 0.058$ ,  $p = 0.005$ ;  $\chi^2 = 7.89$ ,  $df = 1$ ,  $p < 0.01$ ), revealing a sustained improvement in reef functioning at a regional scale during the study period. At the island scale, as with the LCC case, the model (Appendix 13–14) showed a significant temporal increase ( $\beta = 0.0548$ ,  $p < 0.001$ ,  $\chi^2 = 18.09$ ,  $df = 1$ ,  $p < 0.01$ ) and differences between Isla Larga and Isla Redonda ( $\chi^2 = 176.29$ ,  $df = 1$ ,  $p < 0.01$ ). Isla Redonda ( $\beta = -0.839$ ,  $p < 0.001$ ) presented significantly lower initial values than Isla Larga ( $\beta = 0.055$ ,  $p < 0.001$ ), reflecting more degraded baseline conditions. However, both islands showed positive trends that did not differ statistically between islands (Year  $\times$  Island interaction:  $p = 0.841$ ), indicating that, despite differences in initial state, the rate of reef function recovery is similar between the two islands. Site-specific models (Appendix 11–12) revealed marked spatial heterogeneity ( $\chi^2 = 251.37$ ,  $df = 5$ ,  $p < 0.001$ ) in the RFI trajectory. Five of the six monitored sites showed significant increases over time (Appendix 15): Zona de Restauración ( $\beta = 0.062$ ,  $p < 0.001$ ), Cueva del Muerto ( $\beta = 0.060$ ,  $p < 0.001$ ), Plataforma Pavonas ( $\beta = 0.075$ ,  $p < 0.001$ ), Playa del Amor ( $\beta = 0.085$ ,  $p = 0.004$ ), and Zona de Restauración Sur ( $\beta = 0.050$ ,  $p = 0.016$ ). In contrast, Túnel Amarradero did not show a significant temporal

effect ( $p = 0.577$ ), suggesting the absence of a clear recovery trajectory at this site during the study period. The year  $\times$  site interaction model (Appendix 12) confirmed spatial differences in initial RFI values but did not detect significant differences in the rates of change between sites (Year  $\times$  Site:  $p = 0.166$ ). Thus, although the sites differ in their starting state (Appendix 15), most follow parallel recovery trajectories, with Túnel Amarradero being the only exception.

Overall, the LCC and RFI trajectory results indicate that, from 2012 to 2023, the coral communities in the PNIM were steadily recovering their ecological functionality, although with significant spatial variation. Zona de Restauración, Zona de Restauración Sur and several sites on Isla Larga show the clearest signs of improvement, while the trend is lagging in Túnel Amarradero. This suggests that local factors—including restoration efforts, specific environmental conditions, and historical disturbances—play a decisive role in the dynamics of reef function recovery within the PNIM.

## DISCUSSION

Data showed that over a decade (2012–2023), both live coral cover (LCC) and the Reef Functional Index (RFI) increased in most years and sites, indicating a trend of coral community recovery in the IMNP. Previous studies have documented that coral communities in the Eastern Tropical Pacific (ETP) exhibit high resistance and recovery capacity in response to positive thermal anomalies caused by El Niño events, which can reach up to  $+3.5 \text{ }^\circ\text{C mo}^{-1}$ , as well as to other natural and anthropogenic stressors (Martínez-Castillo et al., 2022; Romero-Torres et al., 2020). Therefore, the observed increases in both indices reflect not only the efforts of the restoration program (Hein et al., 2019) but also the natural recovery capacity developed by corals in the region (Martínez-Castillo et al., 2022; Romero-Torres et al., 2020).

Considering historical data, the highest LCC and RFI values were recorded in 1997, prior to the 1997–98 El Niño event (Rodríguez-Zaragoza, 2001), which caused one of

the greatest coral mortalities reported in the last four decades, resulting in a 96 % loss of coral cover in the Central Mexican Pacific (Carriquiry et al., 2001). From that point until 2012, values continued to decline, driven by the synergistic effects of subsequent thermal anomalies such as the 2011 La Niña event (Cruz-García et al., 2020) and the impacts of coastal urbanization (Martínez-Castillo et al., 2022). Notably, while the coral community has recovered, its composition has changed. Earlier studies reported that Redonda Island harbored the highest live coral cover, primarily dominated by *Porites panamensis* (Rodríguez-Zaragoza, 2001). However, currently the highest coral abundance is recorded at Larga Island, and as in the rest of the ETP region, is dominated by *Pocillopora* (Hernández-Zulueta et al., 2017; Sotelo-Casas et al., 2016; Tortolero-Langarica et al., 2014; Tortolero-Langarica et al., 2019). In the Eastern Pacific, *Pocillopora* is the genus with the lowest thermal stress resistance but shows higher recovery capacity compared to massive and sub-massive morphologies such as *Porites* and *Pavona* (Cruz-García et al., 2020). As a result, recovery has largely been driven by the proliferation of *Pocillopora*, leading to monospecific communities, similar to those in the rest of the ETP (Romero-Torres et al., 2018; Romero-Torres et al., 2020), with slower recovery at Redonda Island and greater heterogeneity in the system (Hernández-Zulueta et al., 2017; Sotelo-Casas et al., 2016; Tortolero-Langarica et al., 2014; Tortolero-Langarica et al., 2019).

Given that the restoration program began in 2014, the declines observed at Redonda Island and some sites at Larga Island from 2012 to 2014 reflect the natural dynamics of the area and may be linked to increasing tourism pressure. Since 2010, IMNP has grown in popularity, with tourist influx increasing from ~50 000 individuals in 2013 to 322 535 in 2015 (Burroughs & Rodríguez-Troncoso, 2024). This led to the implementation of regulations and passive restoration actions such as carrying capacity limits (Cupul-Magaña & Rodríguez-Troncoso, 2017) to mitigate coral cover loss. The negative impact of uncontrolled

tourism on coral cover and biodiversity loss has been extensively documented (Cupul-Magaña & Rodríguez-Troncoso, 2017; Harriott, 2004). In contrast, data indicate that in sites classified as restricted use areas, particularly in Zona de Restauración Sur (Comisión Nacional de Áreas Naturales Protegidas [CONANP], 2007), live coral cover was maintained or even increased.

In our study, active restoration actions generated a gradual positive effect on the trajectory of both LCC and RFI. Following implementation and over a decade, a sustained increase was observed, though it was negatively affected by the 2015–2016 El Niño event, considered the first extreme ENSO of the 21st century (Santoso et al., 2017). This event negatively impacted both LCC and RFI not only at restoration sites but throughout the entire Central Mexican Pacific (Rodríguez-Troncoso et al., 2023a). However, given that restoration efforts continued, both indicators recovered on both islands, demonstrating that restoration interventions can contribute to coral reef resilience in the face of extreme climatic disturbances. This pattern suggests that active restoration favors the long-term recovery of physical functionality, thereby reinstating key processes such as habitat provision for multiple species.

Meteorological events such as hurricanes have also been described as negative stressors for coral reefs due to the mechanical damage they can cause (Heron et al., 2008). Nonetheless, in the study area, *Pocillopora* spp. uses asexual reproduction via fragmentation as a primary strategy. Therefore, hurricane-induced fragmentation may benefit coral communities (Chávez-Romo et al., 2007; Rodríguez-Troncoso et al., 2023b). Nonetheless, considering that after the impact of Hurricane Roslyn in IMNP, a sharper decrease in LCC and RFI was observed compared to the 2015–2016 El Niño event, continued monitoring is essential to identify recovery trajectories following such meteorological events.

Although restoration consistently promoted an increase in both LCC and RFI across all cases, the magnitude of this increase was not spatially homogeneous. Unlike the 2012–2014



period, when LCC and RFI were unaffected by restoration efforts, a greater increase was recorded at Redonda Island compared to Larga Island. The larger increase at Redonda Island is noteworthy, as Larga Island is generally considered more suitable for reef development due to its broader continental shelf, greater distance from the coast, and shallower depth (CONANP, 2007; Hernández-Zulueta et al., 2017; Sotelo-Casas et al., 2016). In fact, the Túnel Amarradero site showed the lowest increase in both LCC and RFI regardless of restoration efforts. This underscores the importance of considering site-specific characteristics when implementing restoration programs. Túnel Amarradero has limited available substrate compared to other sites, which not only restricts active restoration actions but also natural processes such as coral recruitment (Hernández-Zulueta et al., 2017), thereby limiting restoration success (Burroughs & Rodríguez-Troncoso, 2024).

In 2023, RFI values in IMNP indicated that the average physical functionality remains lower than that of other Mexican Pacific reefs. Moreover, reef sites to the north and south of the study area, dominated mainly by *Pocillopora*, show nearly twice the live coral cover (Cabral-Tena et al., 2020; Navarrete-Torices et al., 2023), suggesting that they likely have higher RFI values, given the strong contribution of branching species to reef physical functionality.

The observed increases in LCC and RFI from 1997 to 2023 support the notion of a recovery trend for coral communities within the park, partially driven by active restoration efforts. The greater increase at Redonda Island, despite Larga Island previously showing greater natural gains without intervention, suggests that restoration actions are supporting the recovery of both coral cover and physical functionality.

Overall, RFI analysis in this study followed a similar trend to LCC across spatial scales. However, the main difference between LCC and RFI emerged when comparing baseline data with values observed after nine years of active restoration. Starting from the concept that restoration is an intervention that seeks to recover a degraded, damaged or destroyed

ecosystem (Bayraktarov et al., 2020; Boström-Einarsson et al., 2020), this distinction is relevant because, based solely on LCC, one might conclude that by 2023, restoration had fully recovered the ecosystem to pre-disturbance levels. However, physical functionality had not been fully restored. Similar patterns have been observed in the Mexican Caribbean, where functional recovery progresses more slowly than LCC due to continuous exposure to natural and anthropogenic stressors (González-Barrios et al., 2021).

Based on the results of this study, it can be inferred that a historical analysis of coral reef recovery using functional metrics like RFI provides a more comprehensive and accurate perspective. This approach allows us to track LCC trends and the recovery of key reef functions, such as habitat provision, and assess the effectiveness and long-term sustainability of restoration interventions. However, it is important to note that RFI focuses solely on physical functionality, and future studies should explore complementary ecosystem-level functional indices. Historical analysis further revealed that restoration efforts in PNIM have aided in restoring coral reef physical functionality to levels approaching pre-disturbance conditions. Nevertheless, as recovery has not been spatially uniform, we recommend reviewing and adjusting strategies for sites that have not yet regained their physical functionality.

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