



Original Articles

Process-based metrics inform sustainable marine management after a catastrophic natural event

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ABSTRACT

Understanding temporal dynamics in ecological communities is key to develop management plans that target sustainability. Process-based metrics quantify dynamic properties of ecological communities, and thereof have been recently advocated as a promising tool to guide management strategies. To date, however, their empirical application has been limited, hindering their utility to inform conservation planning in response to a range of natural and human-driven disturbances. Here, we compare the succession of fish communities after a catastrophic natural event, a volcanic eruption and the formation of nascent reefs, through the lens of complementary static (species richness, abundance, and biomass) and process-based (productivity and turnover) metrics. We found markedly contrasting dynamics between these metrics, particularly when looking at fish biomass and productivity. During incipient stages of community development, fish productivity increased exponentially, whereas the recovery of fish biomass considerably lagged behind, underscoring high rates of biomass replacement (i.e., turnover) in the system. This buffering response (higher production per unit of biomass) was best predicted by average community body size, highlighting the role of compensatory ecological mechanisms during primary ecological succession. Traits related to resource acquisition, particularly the harnessing of planktonic energy subsidies, further enhanced predicted fish biomass and productivity at local scales. This study therefore supports the burgeoning call to inform conservation and management planning through complementary metrics that give a nuanced understanding on ecosystem functioning.

1. Introduction

The increasing demand for ocean resources by a fast-growing human population is causing the demise of marine biodiversity, the very thing that provides essential ecosystem functions and services that support human livelihoods (Lubchenco and Grorud-Colvert, 2015). This ‘grand’ challenge has called for actions to implement policies that halt the degradation of marine biodiversity, whilst fostering sustainable economic growth (UN Sustainable Development Goal 14; United Nations, 2015). Traditionally, frameworks to guide regional conservation and fisheries management have relied on static metrics, i.e., representing an accumulated quantity over time. The use of fish biomass by management agencies, for instance, is a conventional practice to evaluate the performance of area-based conservation measures, such as Marine Protected Areas (MPAs, Edgar et al., 2014, 2018; Goetze et al., 2021). However, the intrinsic relationship between resource biomass and

productivity have recently come under scrutiny (Jenkins, 2015; Morais et al., 2020a), as biomass-depleted reefs can still support fisheries yields that provide essential social, economic and nutritional benefits to human populations (Morais et al., 2023; Robinson et al., 2019; Robinson et al., 2023). This discrepancy arises from the fact that conventional metrics ignore the complex ecological, evolutionary and demographic dynamics that determine the rate at which a biological resource is produced and stored.

Process-based metrics quantify dynamic properties of ecological communities, such as the rate of biomass gain (i.e., productivity) and replacement (i.e., turnover) per unit of time (Morais and Bellwood, 2020). Both metrics are dependent on individual- and community-level processes (Morais and Bellwood, 2018, 2020). At the individual level, biomass production is the result of investment in somatic growth and reproduction during a fish lifespan, which are generally inversely related in reef fishes — i.e., fishes invest more energy in tissue growth at

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the expense of no reproductive output early in their ontogeny, while investment in reproduction greatly exceeds that of somatic growth with increasing age and size (Choat and Robertson, 2002). At the community-level, the production of biomass results from multiple internal and external processes, such as mortality, inflow and outflow of eggs, larvae and recruits from/to distant populations, and adult movements (Morais and Bellwood, 2020). These processes are closely tied to variation in environmental conditions and biotic interactions across scales of time and space, ultimately determining the rate at which energy and materials flow within and across ecological systems (i.e., ecosystem functioning; Bellwood et al., 2019b). Turnover, typically quantified as the ratio of production to biomass (Allen, 1971), represents the rate of energy flow, as either incorporated into the food chain or released from it, which is a key aspect to understand fish trophodynamics (Polunin, 1996). The direct link between process-based metrics and ecosystem functions, therefore, has call for efforts to understand their response to natural and human-driven disturbances (Morais et al., 2020b; Pessarrodona et al., 2022b; Tebbett et al., 2021).

Quantification of process-based metrics in marine systems have traditionally relied on modelling approaches, particularly trophic models (e.g., ECOPATH) (Christensen and Pauly 1992), that require the input of several parameters that are often unknown for highly diverse reef systems. This limitation has been overcome recently by the development of modelling frameworks that allow to estimate fish productivity from survey data, when counts on abundance and size are included, and species traits (Morais and Bellwood, 2020), opening a new window of opportunities to formulate sustainable development goals (Rogers, 2023). Factoring in process-based metrics, in conjunction with static metrics, offers great promise for conservation planning, as recently exemplified in a conceptual framework proposed for the management of tropical reef ecosystems (Seguin et al., 2023). Under this framework, specific management recommendations can be made based on the relationship between fish biomass and turnover: (i) “restore” — when rates of biomass replacement are high despite low standing biomass, (ii) “partially protect” and/or “fish sustainably” — high harvestable fish biomass and high biomass replacement rates, and (iii) “fully protect” — low biomass replacement rates in spite of high standing stock biomass. Whilst this framework can be a useful tool for management, its applicability to a range of complex scenarios, arising from natural and human driven disturbances, outside tropical reef systems with inherently different local socio-ecological contexts, remains to be validated.

Identifying underlying community properties and socio-environmental factors that underpin rates at which biomass is produced and stored is key to inform adaptive management strategies. For fishes, body size and other ecological traits play a crucial role in shaping these dynamics. Changes in the size-frequency distribution of reef fishes in response to human interventions, such as increases in the abundance of large-bodied fishes in response to the implementation of MPAs and/or fisheries management regulations (Bosch et al., 2022b; McClanahan et al., 2007), can modify the relationship between biomass and productivity at local scales (Morais et al., 2020a). This ‘decoupling’ underpins a negative scaling relationship between body mass and turnover that has important implications for the energetic dynamics of reef fish communities (Allen and Gillooly, 2009). Communities dominated by small-bodied individuals and/or species typically sustain higher productivity per unit of biomass (i.e., turnover) (Jennings and Blanchard, 2004; McCann et al., 2016; Morais et al., 2020a), and such compensatory response (i.e., ‘surplus’ production), appears to be a key mechanism through which biomass-depleted reefs continue to support productive fisheries (Morais et al., 2023). Similarly, shifts in the trophic composition can reshape energetic dynamics of reef fish communities (Seguin et al., 2023). For instance, small-bodied reef planktivores contribute very little to community-level biomass, but they support a remarkable proportion of daily fish production (Morais and Bellwood, 2019; Morais et al., 2021). Changes in local habitat composition can drive these energetic shifts by favouring some trophic groups that can exploit

nutritional resources in benthic habitats (Bosch et al., 2022a; Pessarrodona et al., 2022a,b).

Natural disasters, e.g., hurricanes and storms, pose intricate management challenges to governmental agencies (Adger et al., 2005; Game et al., 2008; Cetin et al., 2024). Understanding the successional dynamics of ecological communities after such events is critical to inform management interventions that promote ecosystem recovery, such as the placement of temporary closed areas where human extractive activities are prohibited (Fodrie and Heck, 2011; Smeed et al., 2020). Volcanic eruptions can have devastating consequences for marine communities and the livelihood of human societies that depend upon them (Crisafulli et al., 2015, Global Volcanisms Program, 2023). The formation of new fertile rocky bottoms, on the other hand, provide opportunities for taxa to colonize, providing a natural laboratory to understand successional dynamics in marine communities (Godwin and Kosaki, 1989; Pinault et al., 2013; Sangil et al., 2024). This natural phenomenon represents an ideal model to empirically test the relevance of process-based metrics to guide conservation planning after natural disasters, minimizing social and economic costs of management interventions.

Here, we evaluate the utility of process-based metrics to inform the management of reef fishes, by taking advantage of ecological succession after a volcanic eruption, the Tajogaite volcano on La Palma, an active oceanic island in the subtropical eastern Atlantic (Carracedo et al., 2001). We first compared the succession of static (i.e., species richness, abundance, and biomass) and processes-based (i.e., productivity and turnover) metrics at 3, 6, 9, and 14 months after the formation of the submerged volcanic delta. Then, we investigated which community attributes underpin biomass (kg m^{-2}), productivity ($\text{kg m}^{-2} \text{ day}^{-1}$) and turnover ($\% \text{ day}^{-1}$), playing particular attention to the role of species traits. Finally, we applied the conceptual framework proposed by Seguin et al. (2023) to guide regional agencies on management interventions that balance ecological and socio-economic outcomes. We hypothesized contrasting dynamics of static and process-based metrics over primary ecological succession, influenced by changes in the size structure of fish communities and availability of trophic resources. In brief, our study adds to the burgeoning literature on informed management decisions through the lens of complementary metrics that give a nuanced understanding on ecosystem functioning.

2. Methods

2.1. Study region and experimental design

Our study was conducted at La Palma Island, Canary archipelago, in the subtropical northeastern Atlantic ocean (28.5°N , 17.8°W , Fig. 1a). This oceanic archipelago originated ca. 20.5 Ma through a series of geological events, where hotspots of magma beneath the earth mantle erupted through the oceanic crust (Morgan, 1971). As the hotspot moved as a result of tectonic plate activity, a nearly 500 km island chain was formed, with the older islands located in the eastern and the younger islands in the western side, respectively (Anguita and Hernán, 2000). La Palma Island, originated ca. 2 Ma, has a recent history of intense volcanic activity with seven eruptions registered in the last 500 years (Hernandez-Pacheco and Valls, 1982). We focused on the last event that took place on September 19th, 2021, in the mountain edifice known as Cumbre Vieja, located in the southwestern part of the island. The eruption of the volcano, recently named Tajogaite, lasted for 85 days, producing large amounts of pyroclastic materials (45 MMm^3) and lava flows (200 MMm^3) that reached the sea in at least seven different events (Carracedo et al., 2022). As the lava ($1000\text{--}1200^{\circ}\text{C}$) entered in contact with the seawater ($22\text{--}25^{\circ}\text{C}$), it rapidly lost heat and solidified into quenched lava fragments, resulting in two volcanic deltas, one of 5.9 ha in the north and one of 88 ha in the south. This event caused transient alternations on seawater physicochemical properties (e.g., temperature, salinity, and pH) at the proximities of the lava-seawater

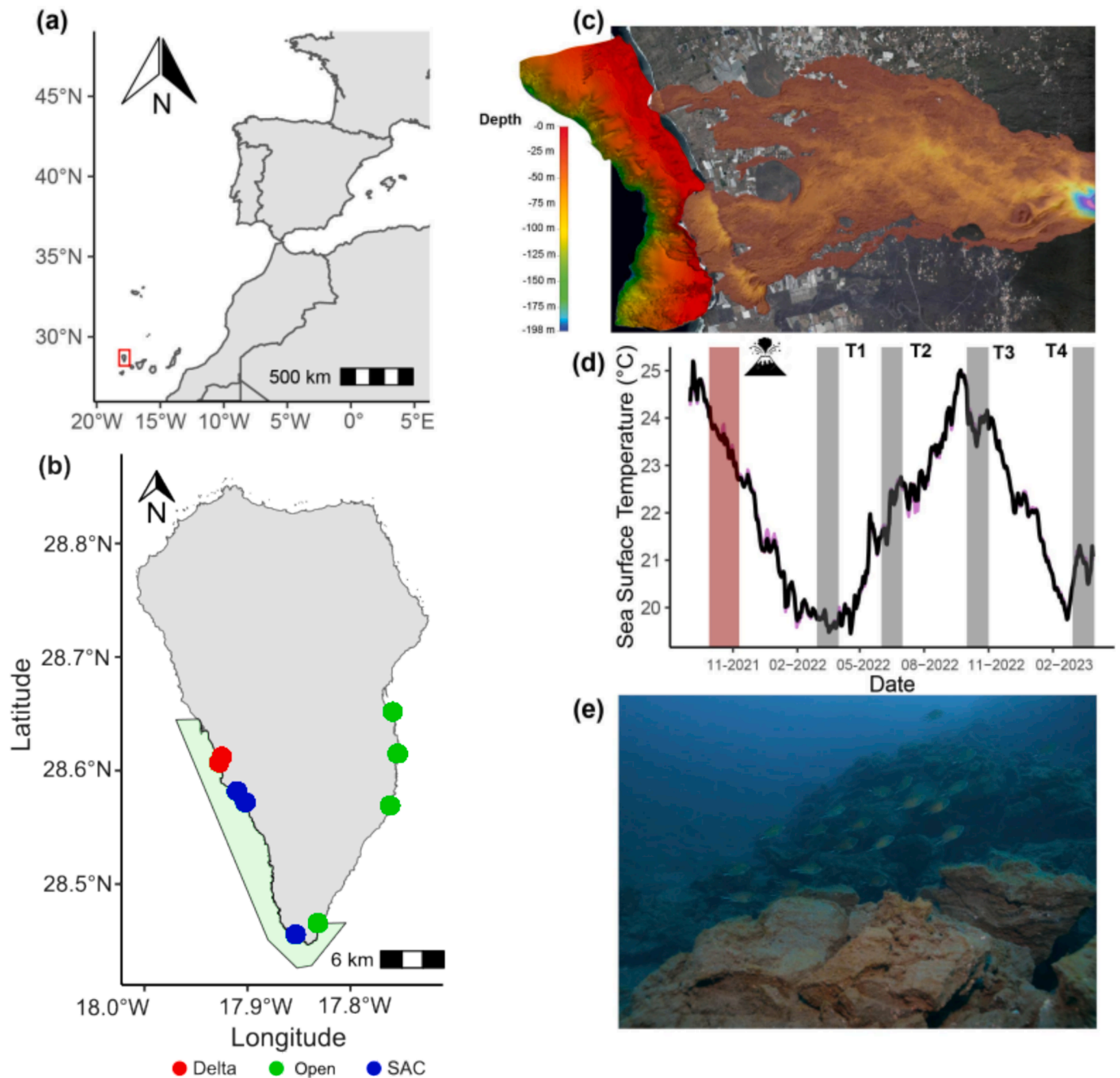


Fig. 1. (a) Map of the geographic context of La Palma Island (red rectangle). (b) Distribution of sites across volcanic delta (red), nearby (green, SAC) and distant (rest, Open) control areas. (c) Topographic and bathymetric profiles of the terrestrial and marine area affected by the eruption of the Tajogaite volcano (<http://www.grafcan.es>). (d) Average trends in daily sea surface temperature (°C, solid black line) at La Palma Island from September 2021 to April 2023. Note, SST trends for individual sites (coloured) are superimposed by island-scale trends. Shaded rectangles indicate the timing of the volcanic eruption (red) and sampling events (gray). (e) Example of early fish colonisers, the Azores damselfish (*Chromis limbata*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interface (Gonzalez-Santana et al., 2022), and created heterogeneous and highly dynamic basaltic rocky bottoms that extend from the intertidal down to 125 m depth (ca. 30 ha area) (Fig. 1c) (Sangil et al., 2024).

Fish and benthic assemblages in the island are strongly shaped by spatial and temporal variability in oceanographic conditions and anthropogenic pressures (Sangil et al., 2013). The east to south-eastern side of the island is predominantly influenced by NNE-NE tradewinds, with moderate wave height (mean 1.4 m) and energy, while the north to south-western side is influenced by energetic winter oceanic swells (sometimes > 3 m wave height) from the NNW-NW (Hernández et al., 2008). These oceanographic features create spatial variability in

temperature and nutrients, with cooler and more nutrient rich waters located in the exposed areas (Martín-García et al., 2011). Benthic assemblages, dominated by macroalgae, are closely linked to variation in these abiotic parameters, with exposed areas more characterised by upright seaweeds (e.g., sheet-shaped brown and red seaweeds), and sheltered areas more dominated by short filamentous and/or corticated algae (i.e., turf and Lobophora beds) (Tuya and Haroun, 2006). Fish consumers vary predictably in response to seaweed cover, particularly herbivores and omnivores, whilst fishing pressure is the main driver of the biomass of large predatory fishes (Tuya et al., 2006). In this regard, hotspots of fish biomass occur in the southern-western side of the island,

where a 3,719 ha marine protected area was established in 2001 (Tuya et al., 2006).

To monitor the colonization dynamics of the volcanic delta, we selected three areas: (i) submerged volcanic delta (i.e., newly formed rocky bottoms where an exclusion area prohibiting any activity, except for scientific purposes, is in place), (ii) a nearby control area, designated as a special area for conservation by the EU HABITAT directive (SAC “*Franja marina de Fuencaliente*”, Council Directive 92/43/EEC of May 21, 1992), and (iii) a distant control area where no specific conservation or fisheries management designation is in place (i.e., only capture and size limits apply) (Fig. 1b). Near and distant control areas were selected to compare the potential convergence of the delta communities to those with relatively similar, vs. distinct, geomorphological and oceanographic conditions, respectively. We note that these distances are somehow confounded by management zones. However, SACs in the island were mainly designated to protect priority species (e.g., marine mammals and sea turtles) and habitats (e.g., sea caves) listed in the EU Habitat Directive, with no explicit regulations on fishing efforts that could entail a confounding effect between “near” and “distant” control areas (Martín-García et al., 2015). Further, although certain fishing modalities, such as spearfishing, are prohibited within the SACs, there is low enforcement and compliance in the island, with a relatively comparable number of spearfishermen in the two management zones (mean 0.05 to 0.30 around our study sites, Sangil et al., 2013). At each zone, we randomly selected two to four sites, separated by at least 1 Km, to minimize spatial dependency, which were surveyed at 3 (T1), 6 (T2), 9 (T3), and 14 months post-eruption (T4). Control areas were only sampled in the first time point, as previous studies have demonstrated high intra-annual stability in fish species richness, abundance, and taxonomic structure (Sangil et al., 2024). Sea surface temperature, downloaded from the NOAA OISST data at 1 Km resolution (Reynolds et al., 2007), ranged between 19.45 °C and 25.21 °C, and was comparable among sampling sites (Fig. 1d, ANOVA, $df = 14$, $F = 0.0083$, $p = 1$).

2.2. Survey methods

Fish assemblages were sampled via underwater visual census techniques, a method that provides information on the identity, abundance, and size of fish. At each site, $n = 4$ replicated belt transects, of 25 m length x 4 m wide (100 m² area), were haphazardly swam by an observer following standard procedures for the study region (Bosch et al., 2017, Bosch et al., 2021). Briefly, one stationary diver held the transect tape, while a second diver swam at a constant speed, identifying all fish entering the sampling area to species-level, excluding individuals entering from behind to minimize double counting. Fish counts were performed up to 20 individuals, while the abundance of fishes forming schools of > 20 individuals was estimated by counting a subset and combining it with an estimate of the proportion of the total school (Edgar and Stuart-Smith, 2014). Fishes were binned into size categories of increasing increments (2.5, 5, 7.5, 10, 12.5, 15, 20, 25, 30, 35, 40, 50, 62.5, 75 cm) to account for greater inaccuracies at estimating the size of larger individuals (Edgar et al., 2004). All transects were separated by at least 10 m, conducted during daylight hours (10 am to 15:30 pm), and along a similar depth contour (range 5.2 m – 13.4 m; $9.34 \text{ m} \pm 1.97 \text{ m}$, mean \pm SD). Visibility ranged between 7 m and 25 m ($16.26 \text{ m} \pm 6.25 \text{ m}$, mean \pm SD). We note that our method largely underestimates the abundances of non-conspicuous species, such as cryptobenthic species that substantially contribute to reef fish productivity (Brandl et al., 2019). However, this bias was systematic across sampling sites and times, and therefore does not affect our comparisons.

The percent cover of sessile benthic organisms was estimated by taking digital photoquadrats (PQs) of the seabed, every 2.5 m along the 25 m transect line ($n = 10$ per transect), which were taken directly downwards from approximately 50 cm above the seabed, encompassing an area of approximately 30 x 30 cm (Edgar et al., 2020). Images were analysed by overlaying a 5 x 4 grid cell of equal area ($n = 20$ per PQ) via

the GIMP software (<https://www.gimp.org/>) and scoring the dominant benthic organisms within each cell. We used broad morpho-functional groups to classify organisms, following a classification scheme that aligns with the ‘Collaborative and Annotation Tools for Analysis of Marine Imagery Video’ (Althaus et al., 2015). Main benthic categories (>5% coverage) included: filamentous red algae (i.e., medium-sized, < 15 cm length, erect algae), foliose brown algae (i.e., medium-sized, < 15 cm length, sheet-shaped algae), crustose coralline algae (i.e., CCA), turf (i.e., low-lying, < 2 cm height, sediment trapping mat formed of single or multi-species aggregations of filamentous algae, detritus and cyanobacteria), and filamentous mats (i.e., dense aggregations of algae, mainly ectocarpaleans, diatoms, and cyanobacteria) (Appendix S1). This approach allowed us to capture variation in architecture of benthic organisms that mediate their role as habitat for epifauna, an important prey group for reef fishes (Bosch et al., 2022c; Fraser et al., 2020a,b; Pessarrodona et al., 2022b). Additionally, within each image, we scored the type of substrate present (i.e. reef platform, pebbles, gravel, and sand) to capture variations in reef geomorphology that can influence fish assemblages (Tuya et al., 2011). We then estimated the percent cover of each benthic morpho-functional group and substrate type, as the proportion of grid cells in which each occurred, excluding cells where the benthos was not clearly visible.

2.3. Static and process-based metrics

We quantified three static (species richness, abundance, and biomass) and two dynamic, process-based (productivity and turnover), univariate metrics. Species richness and abundance were calculated as the number of fish species and individuals per transect, whilst biomass (Kg m⁻²) was calculated as the sum of each fish individual biomass obtained from published length-weight relationships for Atlantic fishes (Quimbayo et al., 2021). We used a recently proposed individual age framework to calculate fish productivity (Kg m⁻² day⁻¹), implemented in the ‘rfishprod’ R package (Morais and Bellwood, 2020). This method employs Gradient Boosted Regression Trees models to predict the rate at which a fish would approach its asymptotic length (K_{max} — a standardized Von Bertalanffy growth coefficient), using empirical information on fish body size, sea surface temperature (SST), ageing method and species-level trait information (Morais and Bellwood, 2018). Fish body size was obtained from survey data, whilst SST was sourced from daily satellite measures obtained from the NOAA OISST data at 1 Km resolution (Reynolds et al., 2007). We used the average annual SST across our study sites in the model, as we were not interested in the potential direct metabolic effects of temperature on productivity (Brown et al., 2004), but rather indirect effects due to shifting species composition. We fixed the ageing factor in the model to the otolith method, as this has demonstrated to have greater performance in predictions of unsampled species (Morais and Bellwood, 2018). Species-level trait information was sourced from a published database of Atlantic reef fish traits (Quimbayo et al., 2021), and included information on the maximum length, diet, and position in the water column.

The individual biomass gain (i.e., somatic growth) per day is then estimated by placing the fish in its growth trajectory and converting the length increment to biomass using published length-weight relationships. To account for biomass losses due to natural mortality, we applied a size- and species-specific mortality risk parameter to simulate fishes that would stochastically perish after a day. This was based on the empirical relationships presented by Pauly (1980) and Gislason et al., (2010), which considers growth parameters, SST, and an exponential negative relationship between body size and mortality risk. An inherent drawback of this method is the impossibility to account for varying levels of fishing mortality across species. The net fish productivity was finally estimated by summing the biomass of fishes surviving after a day of growth, whilst biomass turnover rates (i.e., a measure of the rate of biomass flow in the system, % day⁻¹) was estimated as the quotient of produced to standing biomass (P/B) (Allen, 1971).

2.4. Local-scale drivers of biomass, productivity and turnover

To evaluate how changes in the structure of fish assemblages during the colonization of the volcanic delta influence estimates of biomass, productivity and turnover, we quantified four community descriptors: species richness, size structure, taxonomic structure, and trait structure. We additionally sourced information on the depth and benthic structure of each survey (i.e., transect), to account for known environmental and habitat effects (Bosch et al., 2023; Morais et al., 2023). Size-structure was characterised by two measures of centrality, the mean and median, to account for potential skewness in the size-frequency distribution and the presence of extreme values.

To quantify variation in fish taxonomic, and benthic assemblage structure, we applied a principal coordinate analysis (PCoA) in the 'labdsv' R package (Roberts, 2023). The PCoA was performed on a Bray-Curtis dissimilarity matrix (Clarke et al., 2006), computed in the 'vegan' R package (Oksanen, 2017), relating the abundances of fish species and the percent cover of habitat categories across surveys, respectively. For fish taxonomic structure, species abundances were $\log_{10}(x + 1)$ -transformed to balance the contribution of dominant and rare species. We selected the four first PCoA axes, which together explained 74.3 % of the original variability. For benthic structure, percent cover data was not transformed, and the two first PCoA axes, which together explained 80.55 % of the original variability, were selected. To visualize the species and habitat categories most responsible for community changes in the volcanic delta with time, we calculated their correlation with PCoA axes by fitting a linear trend surface via the 'vegan' R package (Oksanen 2017), and represented them as vectors in the ordination space. We then extracted the scores (i.e., positions) of each transect along these PCoA axes explaining variation in fish and benthic assemblage structure and used them as explanatory variables in models of fish biomass, productivity, and turnover.

We built a multidimensional functional space to quantify variation in the trait structure of reef fishes, by considering 11 functional traits that capture variations in life history parameters (body size, life span, length and age at maturity, and spawning mode), behaviour (home range, gregariousness, level in the water column), trophic ecology (diet and trophic level) and geographic range. Life history traits are key determinants of species demographic dynamics, particularly in the context of environmental changes and disturbances (Pecuchet et al., 2017; Winemiller and Rose, 1992). Behavioural traits can determine the ability of fishes to colonize new suitable substrates through active movement of adult individuals (i.e., home range size) (Nash et al., 2015), avoid predators and compete for ecological space and resources (i.e., sociality or gregariousness) (Stier et al., 2013), and exploit allochthonous nutritional inputs in degraded ecosystem states (e.g., plankton subsidies) (Morais et al., 2021). The trophic ecology of reef fishes can provide valuable insights on species responses to shifts in the availability of nutritional resources during ecological succession (Bosch et al., 2022c; Pessarrodona et al., 2022b), as well as influencing the distribution and abundance of the resource itself (Bennett et al., 2015). Finally, we considered an index of geographic range, as species with larger range sizes are typically characterised by larger dispersal abilities, and hence capacities to colonize new environments (Luiz et al., 2012; Strona et al., 2012). Trait values were sourced from a published database on Atlantic reef fish traits (Quimbayo et al., 2021) and FishBase (Froese and Pauly, 2012), and when missing, they were imputed from sibling species within the same biogeographic extent of occurrence. To avoid including redundant traits, we excluded traits with correlations greater than 0.7 (Appendix S2), which resulted in a final set of 7 traits (Appendix S3, S4).

We then applied a PCoA on a species-by-species Gower distance matrix, capturing dissimilarities among species in the 7 traits selected, a method that is able to accommodate ordinal, nominal, and quantitative traits (Gower, 1971). We chose the first four PCoA axes, which together explained 81.32 % of the variability in species' trait values, as they were the most parsimonious choice that minimized the mean absolute

deviation between the original trait-based distances and the Euclidean distances in the functional space (MAD=0.026, Appendix S5) (Maire et al., 2015). The correlation between individual traits and PCoA axes was calculated using a Kruskal-Wallis test for categorical traits, and an r^2 statistic from simple linear regression for continuous traits via the 'mFD' R package (Magneville et al., 2021). For visualization purposes, correlations between continuous traits, and relative position of level of categorical traits, were represented in the functional space via the 'vegan' R package (Oksanen, 2017). Shifts in the trait composition of reef fish assemblages was then represented by extracting the average position (i.e., centroid or transect-level weighted means) in the functional space via the 'FD' R package (Laliberté et al., 2014).

2.5. Statistical modelling

We used generalised linear mixed effects models (GLMMs) to test for differences in static (species richness, abundance, and biomass), and process-based (productivity and turnover), metrics between the delta and the two control areas (near vs. distant), independently for each sampling event. Models were implemented in the 'glmmTMB' R package (Brooks et al., 2017), with a gaussian error distribution for species richness, a negative binomial error distribution for abundance data, a lognormal distribution for biomass and productivity, and a beta distribution for turnover. In each model, we included a random spatial error term (1|Site) to account for spatial dependency and unmeasured geophysical predictors that are spatially structured. All models were visually inspected for residual patterns using functions in the 'DHARMA' R package (Hartig, 2017).

We implemented a full-subset model selection framework to evaluate the relative influence of local-scale predictors for fish biomass, productivity, and turnover. First, to generate a more manageable set of candidate models, we removed overly correlated predictors (Pearson's $r > 0.7$ and Variance Inflation Factors > 5), which resulted in a final set of 7 predictor variables (Appendix S6). Prior to model implementation, all predictor variables were visually inspected for skewness in the distribution of data points across the predictor space and the presence of potential outliers, and were standardized (mean 0 and SD 1) to avoid numerical estimation problems due to differences in scale. The candidate set of models were created via the 'MuMIn' R package (Kamil, 2018), which included models with combinations of up to four predictor variables to avoid overfitting. Predictor variables with correlations > 0.5 were excluded from the same model to minimize the effect of multicollinearity in parameter estimation (Graham, 2003). A null model containing the intercept and a spatial random effect term (1|Site) was also included in the model set. Models were ranked based on the Akaike Information Criterion for small sample sizes (AICc), with the 'best' candidate set of models considered those within 2 units of the lowest AICc model (Burnham and Anderson, 2003). To account for temporal dependency due to repeated sampling in the volcanic delta, we additionally explored the inclusion of a temporal error structure term (1|Time). However, this generally caused numerical estimation problems and displayed lower support ($\Delta AICc = -2.78$). To draw inferences about the relative influence (i.e., magnitude and direction) of local-scale predictors, we extracted model-averaged coefficients, hence accounting for uncertainty (weight of evidence, ωAIC) in the set of competing models. All models were implemented in the 'glmmTMB' R package (Brooks et al., 2017), with model assumptions visually inspected via plots of residuals vs fitted values and quantile-quantile plots in the 'DHARMA' R package (Hartig, 2017). To decouple the influence of multiple traits that can simultaneously explain variation across a PCoA axis (i.e., synthetic trait), and hence ease model interpretation, we ran an additional model selection framework using community weighted mean trait values (i.e. CWM) as explanatory variables (Lavorel et al., 2008) (Appendix S7). The implementation and validation of these models followed identical procedures as above.

2.6. Reef management classification

We implemented a novel conceptual framework to guide regional agencies on management decisions that foster a balance between conservation and fisheries sustainability targets, in this case around the volcanic delta. We explored the distribution of surveys (i.e., transects) within each zone (i.e., volcanic delta, near and distant control), at each time (i.e., T1, T2, T3, and T4), across three predefined management categories. These management categories were based on the relationship between fish biomass and turnover (Seguin et al., 2023), and included: (i) “restore” — i.e., low biomass but mid to high turnover rates, (ii) “partially protect” and/or “fish sustainably” — i.e., high biomass and mid to high turnover rates, and (iii) “protect” — i.e., high biomass but low turnover. We partitioned surveys based on thresholds defined on the basis of quantiles in the observed distribution of turnover (low = < 25 %, medium = 25–75 %, and high = >75 %) and biomass (low = < 25 %, medium = 25–75 %, and high = >95 %) values. Surveys that fell in the middle of the aforementioned management categories were considered to have no specific management recommendations (“mid-range”).

3. Results

3.1. Spatio-temporal patterns in static vs. process-based metrics

The temporal dynamics of static and process-based metrics following the colonization of the volcanic delta differed markedly (Fig. 2). Species richness responded rapidly to the onset of the colonization process, ranging from an average of 6.25 species per 100 m² at 3 months to 6.88 species per 100 m² at 14 months post-eruption (Fig. 2a). This rapid response, and the high variability found among transects and sites within each zone, resulted in statistically comparable values relative to both distant (average 7.62 species) and near (average 8.08 species) control areas, irrespective of time (Appendix S8). Fish species abundance and productivity steadily increased through time, from an average of 6,000 ind. ha⁻¹, and 0.77 kg ha⁻¹ day⁻¹, at 3 months, to 11,752.6 ind. ha⁻¹, and 1.84 kg ha⁻¹ day⁻¹, at 14 months post-eruption, respectively (Fig. 2b, d). For the former, predicted values were comparable to both distant (average 13,676.28 ind. ha⁻¹) and near (average 15,607.25 ind. ha⁻¹) control areas after 9 months (Appendix S9). In comparison, fish productivity responded more slowly to the colonization process, only displaying statistically comparable values to near control areas (average 2.34 kg ha⁻¹ day⁻¹) after 14 months (Appendix S10). Fish biomass considerably lagged behind in its response to the colonization process,

ranging from an average of 759.10 kg ha⁻¹ at 3 months to 1,204.80 kg ha⁻¹ at 14 months post-eruption (Fig. 2c). This lagged response resulted in consistently lower fish biomass at the volcanic delta compared to near control areas (average 2,364.04 kg ha⁻¹) even at 14 months, whilst predicted values were statistically comparable to distant control areas (1,717.48 kg ha⁻¹) at 9 months post-eruption (Appendix S11). Fish turnover displayed a remarkably contrasting pattern relative to the other metrics (Fig. 2e). At 3 months post-eruption (average 9.90 % day⁻¹), turnover was statistically comparable to both near (average 10.25 % day⁻¹) and distant (average 11.80 % day⁻¹) control areas. However, it later increased and remained considerably higher at 6 (average 25.32 % day⁻¹), 9 (average 16.62 % day⁻¹) and 14 (average 22.06 % day⁻¹) months post-eruption (Appendix S12).

3.2. Influence of local-scale predictors

Fish community body size (both intra- and inter-specific) and ecological traits related to resource acquisition were among the most influential predictors explaining variation in fish biomass, productivity, and turnover (Fig. 3). However, there were fundamental differences both in the relative importance and the direction of the effect. After controlling for the effect of other environmental (habitat composition) and community (species richness) predictors that were supported in the set of competing models (Appendix S13, S14), average community body size had a positive effect on fish biomass (Fig. 3a), whilst turnover scaled negatively (Fig. 3b). This effect reflected the spatio-temporal patterns observed during the colonization of the volcanic delta, where the size structure was skewed towards smaller sizes as a result of the influx of a large number of recruits and juveniles, and then progressively shifted towards larger sizes as a result of individual growth and colonization of adult individuals (Appendix S15b). Despite this progressive increase, average community body size was consistently lower at the volcanic delta compared to both near and distant control areas, which explains the consistently higher turnover levels observed from 6 to 14 months after the eruption. Surprisingly, average community body size had a negligible effect on fish productivity (Fig. 3b), which contrast with the positive effect observed for maximum body size — i.e., a trait that only reflects interspecific size differences. Hence, while size differences within and among species strongly predict fish biomass (Fig. 3a, d), their relative importance varies for predicting production and turnover; i.e., intraspecific variation is additionally important for explaining variation in turnover (Fig. 3c, f), whilst variation in fish productivity is solely explained by interspecific differences (Fig. 3b, e).

The importance of trait composition for predicting fish biomass,

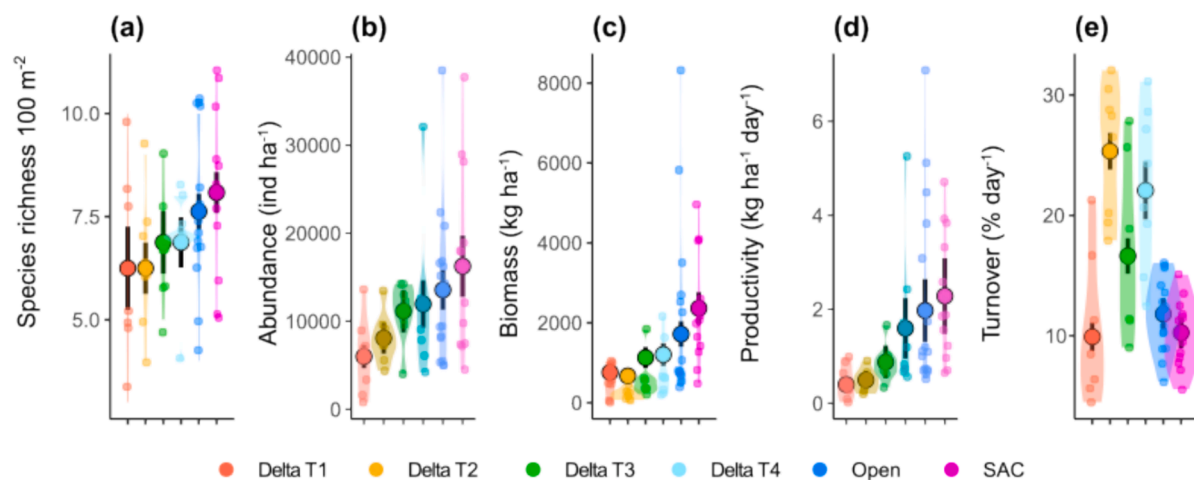


Fig. 2. Fish (a) species richness, (b) abundance, (c) biomass, (d) productivity, and (e) turnover at volcanic delta through time, near (SAC) and distant (Open) control areas in La Palma Island after the eruption of the Tajogaite volcano. Larger dots are model-averaged predictions from GLMMs, and whiskers are SE around the predicted mean. Violin plots and smaller dots are included within each panel to depict the distribution of replicate-level values.

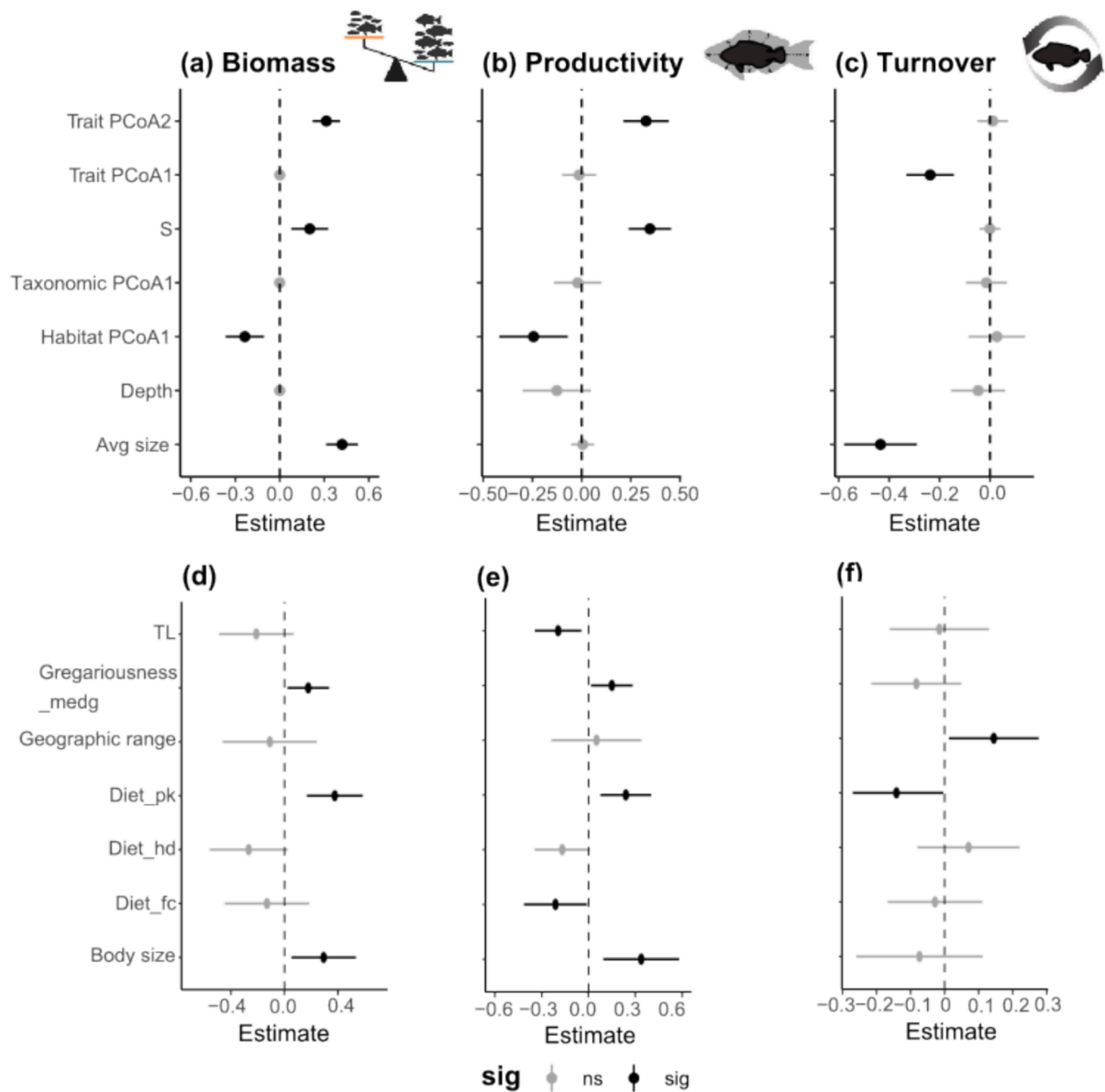


Fig. 3. Relative influence of (a – c) local-scale predictors and (d – f) individual traits (i.e., CWM trait values) for predicting variation in fish biomass (left), productivity (centre), and turnover (right) across volcanic delta and control areas in La Palma Island after the eruption of the Tajogaite volcano. Dots illustrate model-averaged estimates, and whiskers depict 95% confidence intervals. Colour labels indicate significant (dark) vs. non-significant predictors (gray).

productivity, and turnover is noteworthy, given the high overlap and rapid convergence in the functional structure found between the volcanic delta and both near and distant control areas (Appendix S15d, g, S16, S17). This contrasts with the negligible contribution of variation in the taxonomic structure of fish assemblages, that otherwise displayed marked successional dynamics — i.e., dissimilarity was reduced through time and communities only converge with control areas after 14 months (Appendix S15c, f, S18, S19). This suggests that subtle transitions in the trait space from communities initially dominated by small-bodied, low trophic level, species that guard their eggs, towards communities dominated by species that clustered in the centre of the trait space — i.e., medium-sized, mid-trophic level, mobile invertivorous and herbivorous/detritivorous species that form medium-sized schools and have a non-guarding spawning strategy (Appendix S15a, S20, S21, S22) — were more important than changes in the abundance of any particular species. Decoupling the importance of individual traits revealed that this effect was mainly attributed to variation in the trophic composition of fish assemblages, with assemblages with high relative abundance of

planktivorous fishes displaying higher local estimates of fish biomass and productivity, whilst lower estimates of turnover (Fig. 3d – f).

Variation in benthic assemblage structure in the volcanic delta have likely underscore the effect of trophic composition, as this predictor was found to have an important, and independent, effect on both fish biomass and productivity (Fig. 3a, b). Assemblage-level biomass and productivity increased as benthic communities transitioned from a pioneer state, dominated by filamentous mats and algal turf, towards communities characteristic of control areas, dominated by algal turf and higher coverage of architecturally more complex seaweeds (i.e., foliose brown algae and filamentous red algae) (Appendix S15e, h, S23).

3.3. Reef management classification

Exploring the relationship between fish turnover and biomass revealed clear distinctions in the area occupied by the volcanic delta compared to both near and distant control zones (Fig. 4a). The volcanic delta assemblages generally occupied a larger area that overlapped with

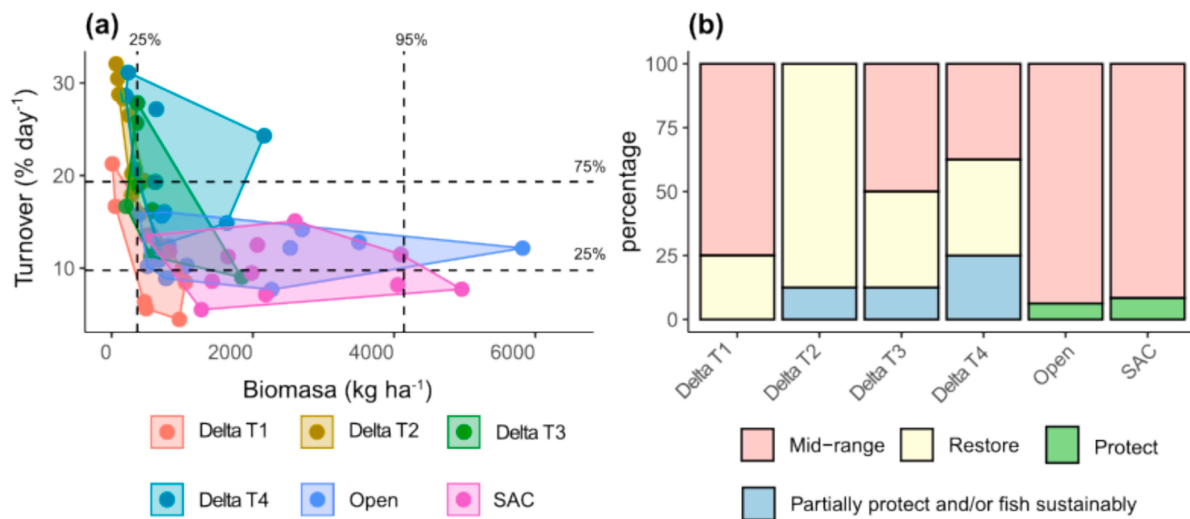


Fig. 4. (a) Position of surveys (i.e., transects) from each zone (coloured dots) across the bivariate space showing the relationship between fish biomass and turnover at La Palma Island after the eruption of the Tajogaite volcano. Convex hulls illustrate the area of the bivariate space occupied by assemblages from each zone, and dashed lines illustrate the thresholds used to classified surveys into the three different management categories: “restore” (i.e., low biomass but mid to high turnover), “protect” and/or “fish sustainable” (i.e., high biomass and mid to high turnover), and “protect” (i.e., high biomass but low turnover). (b) Barplot showing the distribution (%) of surveys (i.e., transects) within each pre-defined management category for each zone.

the thresholds used to classify reefs as “restore”, whereas most of the area occupied by near and distant control sites fell within the thresholds that had no specific management suggestions (i.e., “mid-range”). In fact, the volcanic delta consistently had a relevant proportion of transects that fell within the “restore” management classification, ranging from 25 % at 3 months, to 87 % at 6 months, and 38 % at 9 and 14 months post-eruption (Fig. 4b). In contrast, almost 95 % of the surveys in near and distant control areas fell under the “mid-range” category.

4. Discussion

Our study demonstrated the complementarity between static and process-based metrics, which displayed markedly different spatio-temporal patterns following the formation of the volcanic delta, where nascent reefs triggered a ‘primary ecological succession’ event (Prach and Walker, 2019). Reef fish species richness recovered very rapidly, attaining comparable values to control areas as early as three months post-eruption, while abundance and productivity increased exponentially and converged with control areas only after 14 months. In contrast, fish biomass considerably lagged behind and displayed consistent lower values than control areas. Interestingly, turnover rates were consistently higher in the volcanic delta irrespective of timing, highlighting the incipient state of the system. Our study is the first, to the best of our knowledge, that combine static and process-based metrics to understand the dynamics of ‘primary ecological succession’ in marine systems. We took advantage of a catastrophic natural event, i.e., a volcanic eruption and the formation of nascent reefs, that although rare in ecological timescales, have initial devastating consequences for marine biodiversity and the livelihood of coastal communities (Crisafulli et al., 2015).

The number of fish species settling on the new rocky bottoms increased very rapidly, with no statistically discernible difference to control areas as soon as three months since the onset of the colonization process. Most reef fishes have high dispersal capacities, with a pelagic larval phase that can travel 100 s meters to Kms, settling populations in new suitable environments (Luiz et al., 2012; Siegel et al., 2008). The lack of deep ocean barriers and close proximity of reefs where fish populations were unaffected by the volcanic eruption likely promoted this process, by (i) acting as sources of new recruits and (ii) facilitating the arrival of juveniles and adults (Mora et al., 2012; Nash et al., 2015).

As fish species rapidly arrived at the volcanic delta, they encountered a community within early stages of development, typically characterised by high stochastic dynamics and low biotic interactions (Connell and Slatyer, 1977; Valiela and Valiela, 1995). The limited presence of density-dependent mechanisms, such as competition and predation, likely enhanced the survival and growth of fishes (Almany and Webster, 2006; Hixon and Jones, 2005), driving the observed progressive asymptotic increase in fish abundance, which attained comparable levels to control areas within a year. This rapid colonization and subsequent population growth of reef fish assemblages is well documented in studies of primary ecological succession in volcanic deltas (Godwin and Kosaki, 1989; Pinault et al., 2013; Sangil et al., 2024).

Considering complementary metrics that reflect both accumulated fish biomass over time (i.e., standing stock biomass), and rates of biomass production (i.e., productivity) and replenishment (i.e., turnover), unveiled a profoundly different picture. Fish productivity increased exponentially over time, reaching comparable levels to control areas within 14 months since the formation of the volcanic delta. In contrast, fish biomass considerably lagged behind in its recovery, with consistently lower values than control areas throughout the 14 months studied. The non-proportional gains in fish productivity and biomass in the volcanic delta over time underscores a markedly different spatio-temporal pattern in turnover (i.e., the ratio of production to standing stock biomass), which displayed consistently larger values than control areas, except at the initial stages (3 months) of the colonization process. Recent empirical studies from coral reef ecosystems have demonstrated the role of compensatory ecological mechanisms, where size-selective fisheries exploitation induces shifts towards smaller-bodied individuals and species (Bosch et al., 2021; Robinson et al., 2017) triggering a buffering response where more productivity is generated per unit of biomass (Jenkins, 2015; Morais et al., 2020a). Our study therefore provides evidence to support the role of compensatory ecological mechanisms in triggering ‘surplus production’ during ‘primary ecological succession’, which have strong implications for the management of fisheries resources (Morais et al., 2023).

After an initial rapid colonization by adult fishes from surrounding reefs, fish recruits and juveniles rapidly settled in the new volcanic substrates, shifting the size-structure towards smaller-bodied individuals. The sparse presence of key piscivorous fishes in the region, such as the dusky grouper (*Epinephelus marginatus*) and the Atlantic

cornefish (*Aulostomus strigosus*), likely enhanced their settlement and survival (Almany and Webster, 2006). Demographic explosions of juvenile fishes have been previously observed during early stages of community development from other volcanic systems (Godwin and Kosaki, 1989), including the one studied here (Sangil et al., 2024), and likely explains the high levels of turnover found in our study. In support of this inference, our models revealed that average community body size was the strongest predictor of turnover, with a negative scaling relationship, as predicted by theory and demonstrated empirically in other systems (Allen and Gillooly, 2009; Morais et al., 2020a). We must note that ‘buffering productivity’ can arise from both population- and community-level processes, mechanisms that are unfeasible to disentangle with correlative modelling approaches. The low population biomass of fish species inhabiting the volcanic delta means that they were presumably significantly below their population carrying capacity, which can stimulate ‘surplus production’, a phenomenon widely reported by fisheries scientists for single stocks (Beverton and Holt, 2012; Hilborn and Walters, 2013). At the community-level, ‘buffering productivity’ might be explained by the rapid arrival of pioneering species, characterised by ‘fast’ life-history strategies (e.g., rapid growth, early maturation, and short life spans) (Winemiller and Rose, 1992), which are often the first colonizers during community succession (Connell and Slatyer, 1977). Although community-level effects cannot be discarded with our modelling framework, maximum body size, a trait that only reflect among-species size differences, displayed no overall support in predicting fish turnover. An additional consideration is that fish recruits (<2.5 cm) are underestimated in our surveys, and thus our measure of assemblage-level productivity mainly reflects the somatic (i.e., the gain in biomass after a day of growth) component of productivity (Morais and Bellwood, 2020). Recruitment is hypothesized to make a relatively small contribution to assemblage-level productivity due to strong density-dependent mortality of fish larvae via predation and competition (Almany and Webster, 2006; Caley et al., 1996), even at low to intermediates levels of fish biomass (Beverton and Holt, 2012; Hilborn and Walters, 2013). Yet, we cannot discount the importance of recruitment in buffering productivity in our system due to its incipient state, with low presence of biotic interactions among species.

While variation in fish turnover was mainly attributed to variation in average community body size, we found that both fish biomass and productivity responded strongly to variation in the trophic composition of fish communities. Higher relative abundances of planktivorous fishes were positively associated with local estimates of biomass and productivity, underscoring their importance in the energetic dynamics of reef ecosystems. During initial stages of the colonization process, there was a high influx of fish species exploiting planktonic nutritional pathways, particularly the small-bodied reef planktivore *Chromis limbata*. Reef planktivores typically account for a large proportion of daily fish production in reef systems (Morais and Bellwood, 2019), harvesting allochthonous nutrient subsidies that allow to bypass local energetic constraints imposed by nutrient-poor and/or degraded reef environments (Campbell et al., 2020; Gove et al., 2016; Morais et al., 2021). Although the specific mechanisms require further investigation, reef planktivores might be facilitating the recovery of fish populations on the volcanic delta through (i) fertilizing benthic habitats with highly nutritious detritus via fish faeces (Rempel et al., 2022; Schiettekatte et al., 2023) and (ii) serving as prey for large piscivorous fishes (Skinner et al., 2019).

The fertilization of benthic habitats is likely to be of greater importance in the volcanic delta, exemplified by a progressive increased in the abundance of common fish species in the region that exploit benthic nutritional pathways, particularly omnivores, herbivores/detritivores and invertivores. This rapid population growth was enhanced by a concomitant transition in habitat composition, from a pioneering state dominated by clumped filamentous mats (cyanobacteria, ectocarpaleans, and diatoms) and low-lying turf algae, to a more advanced community stage dominated by turf algae and structurally more complex

seaweeds (i.e., foliose red and brown algae). Turf algae, and the resources bounded within (e.g., detritus and cyanobacteria), is a highly nutritious habitat that is widely exploited by herbivorous/detritivorous fishes (Choat, 1991; Clements et al., 2017; Pessarrodona et al., 2022a). Despite its lower structural complexity, at least at the macro-scale, turf habitats can support high production of mobile invertebrates (Fraser et al., 2021; Kramer et al., 2013). This, coupled with the large availability of microhabitats created by foliose seaweeds (Edgar, 1983; Fraser et al., 2020b), may explain the observed increased in the population abundances of invertivorous fishes. Despite the progressive increase in the abundance of these trophic groups, we found no significant evidence of their contribution to either local estimates of biomass nor productivity, once the relative abundance of planktivorous fishes was accounted for in the models.

The contrasting temporal dynamics of static- and process-based metrics could have important implications for management decisions, particularly when looking at the local relationship between fish biomass and turnover (Rogers, 2023; Seguin et al., 2023). A large proportion of our surveys on the volcanic delta fell under the “restore” category, characterised by low standing stock biomass but high biomass replacement rates. This underscores the incipient state of the system, and appeal to the maintenance of management interventions that promote biomass rebuilding to the point where sustainable fisheries are both ecologically and socially feasible (Duarte et al., 2020; Worm et al., 2009). Critically, this recommendation could have been overlooked if considering static metrics alone. On one hand, the rapid convergence of fish species richness, abundance, and taxonomic composition with reference areas could be interpreted as a sign of recovery (Sangil et al., 2024), prompting management agencies to revoke the current *de facto* restricted area. On the other hand, the recovery of fish biomass to some baseline levels might span years to decades (Babcock et al., 2010; Edgar et al., 2014; McClanahan and Graham, 2015), possibly entailing impractical social and economic costs to local human populations (Cinner et al., 2014; Nowakowski et al., 2023). The limited timescale of our study, however, hindered our ability to detect transitions between ecosystem management states, a crucial research area for advising management agencies on the timing when socio-economic endeavours, like fisheries, have the greatest potential for long-term sustainability. Ultimately, proposal of these management categories would need to be informed by temporal changes in the volcanic delta communities towards a stable climax state. However, predicting the dynamics of this system is complicated in the Anthropocene era, where global and local human stressors are causing the demise of previously vigorous marine forests in the region, with often unknown consequences for associated biota (Valdazo et al., 2024). Theoretical and empirical evidence suggest that the maintenance of strict protection measures, such as the “*de facto*” marine protected area currently in place, could facilitate the recovery of communities towards those characteristic of the relatively undisturbed nearby marine protected area (Sangil et al., 2013).

5. Conclusion

Humanity have entered a new era for the management of reef ecosystems (Bellwood et al., 2019a). Increasing interactions between nature and people hinder complex decisions about which conservation and management actions are most appropriate to simultaneously achieve biodiversity protection and sustainability goals (Cinner et al., 2020; Nowakowski et al., 2023). Process-based metrics, i.e., measures that incorporate dynamic properties of ecological communities, have been advocated as a promising tool to guide regional conservation planning in the face of escalating human pressures and increasingly altered ecosystem states (Rogers, 2023; Seguin et al., 2023). By focusing on a natural catastrophic event in a subtropical oceanic island, we demonstrated the value of locally informed conservation and management decisions through the lens of complementary metrics that give a nuanced understanding on ecosystem functioning.

CRediT authorship contribution statement

Nestor E. Bosch: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sandra Navarro Mayoral:** Writing – review & editing, Data curation. **Fernando Espino:** Writing – review & editing, Data curation. **Francisco Otero-Ferrer:** Writing – review & editing, Data curation. **Ricardo Haroun:** Writing – review & editing, Funding acquisition. **Fernando Tuya:** Writing – review & editing, Data curation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All raw data and R code needed to replicate the analysis can be found in Figshare (DOI: 10.6084/m9.figshare.26947864).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112714>.

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