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Marine protected areas maintain pyramid-like structures of coral-reef fish communities

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Abstract

Maintaining the species composition of marine communities is critical for supporting many bio-physical processes including human well-being. Marine Protected Areas (MPAs) can successfully help to protect the abundance of target marine species, however, we know little about their ability to protect the composition of entire communities. This is a challenging task given that the effects of MPAs on community structure can be intertwined with numerous internal (e.g., species interactions) and external factors (e.g., thermal stress). Here, we show that on average MPAs increase by 23 % the chance that a community displays a stronger pyramid-like structure: energetically efficient systems with small basal species as the most abundant and large apex predators as the least abundant. We show that this effect is done indirectly by regulating the interaction constraints within a community, which in turn regulate the community structure. To test these effects, we follow a nonparametric causal-inference approach using observational data from 286 geographical sites and a total of 1,548 fish species together with

spatial, temporal, and climatic factors. We estimate the interaction constraints by inferring the effect of species interactions on the tolerance of a community to structural perturbations following theoretical population dynamics. Our findings provide a quantitative platform to differentiate the role of internal and external factors affecting the composition of marine communities, and provide additional evidence of the importance of MPAs.

Relationship between community structure and marine protection

Sampling effort and the distribution of the estimated variables









(A) Global distribution of sampling sites and their attributes. The color of the circles corresponds to the number of species observed at a given site. The background color corresponds to the sum of thermal stress anomalies (sumTSA). The black lines show the Marine Protected Areas (MPAs). (B) We quantify the community structure [-1,1] as the Spearman's rank correlation between average body size and species abundances, where the perfect pyramid structure corresponds to rho=-1 and the perfect inverted pyramid structure is rho=1. Here we hypothesize that MPAs maintain the pyramid-like community structure as opposed to perturbed non-MPA areas, where inverted pyramid-like structures dominate.

(A) The grey circles represent communities aggregated in a given location across a year. The majority of communities were sampled once per year, only a small fraction of the aggregated communities were sampled more than once in a year (sampling effort > 1). For communities sampled more than once in a given year, we conducted a rarefaction analysis to estimate the effect of sampling effort on species richness by resampling communities and then plotting the number of species in each constructed community against sampling effort (an example shown in the top right panel). (B-E) shows the distributions of community structure, interaction constraints, relative herbivory and the sum of thermal stress anomalies (sumTSA) for each communities.

Estimating interactions constraints

The average causal effect (ACE) of MPAs on community structure







The figure shows a simple illustration of a 3-species community. The interaction coefficients of the interaction matrix (A) represent the overall effect of species *i* on the growth rate of species *j*, which can be positive (red colors) or negative (blue colors). The interaction constraints are quantified as the size of the feasibility domain (omega) defined by the column vectors (v) of the interaction matrix. Note that this feasibility domain corresponds to the combination of values of intrinsic growth rates (sphere) that species can take leading to a positive equilibrium following Lotka-Volterra dynamics. High interaction constraints lead to small feasibility domains, i.e., lower tolerance to changes in intrinsic growth rates. Instead, low interaction constraints correspond to larger feasibility domains, i.e., higher tolerance.

The figure shows the directed acyclic causal graph that depicts the causal relationships of the studied variables. The arrows (edges) represent a direct causal effect between two variables (nodes). Dashed lines represent the spurious association between two variables confounded by an unknown factor. Following the rules of do-calculus, we show the direct average causal effect (ACE) between Herbivory and Interaction Constraints, the direct ACE between Interaction Constraints and Community Structure, the direct ACE between MPAs and Interaction Constraints, and the total ACE between MPAs and Community Structure. Note that all variables have been transformed to binary values, where a value of 1 is a data point above the median and 0 otherwise. Recall that high (resp. low) values of Community Structure represent inverted-pyramid (resp. pyramid) like structures. The ACE then corresponds to the probability difference in observing a value of 1 in the target effect when the cause takes a value of 1 compared to when it takes a value of 0. Note that the total effect of MPAs on community structure manifests indirectly through interaction constraints.

Conclusions

- Using a global dataset of coral reef fish species, we show that MPAs lead fish communities towards pyramid-like structures (larger fishes are less abundant compared to smaller fishes) by regulating species interactions
- That is, since MPAs ensure lower human disturbances, more energetically efficient structures can emerge that require lower tolerance to changing conditions compared to communities within non-MPAs
- These findings shed new light on and quantify one of the potentially many conservation benefits of MPAs





