Reduced fish diversity despite increased fish biomass in a Gulf of California marine protected area (#41746)

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Reduced fish diversity despite increased fish biomass in a Gulf of California marine protected area

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Multi-use marine protected areas (MUMPAs) are one of the most common tools used to mitigate fishing pressure in marine ecosystems of developing countries. Nevertheless, their effectiveness varies greatly with much more empirical evaluation required using traditional metrics and functional approaches. We conducted visual censuses of fish at Espíritu Santo Island, México (MUMPA; N= 320; 24°N) from 2005 to 2017 to asses fish richness, size-distribution and density. Three functional indices were calculated using six traits (size, mobility, period of activity, aggregation, position in water column and diet): functional richness (volume occupied by species), dispersion (complementarity between species) and originality (inverse of redundancy). We compared fish diversity among three management zone types (sustainable fishing, traditional fishing and no-take zones), through a 13-year period, assessing which species increased or decreased in occurrence, biomass, and density. We detected a reduction in fish biodiversity in the form of declines in species richness and density that translated to decreases in functional indices (functional richness and dispersion weighted by biomass). Despite a general increase in biomass, Additionally, the enhancement of fish stock was neither achieved, because even the general fish stocks were not enhanced as the biomass of commercial species did not change. The lack of positive response following protection is attributed to lack of regulation in fisheries, small percentage of the MPA designated as no-take zone (1.4%), and different conservation targets of these restricted areas. Nevertheless, fishing pressure and management strategies do not fully explain the observed decrease in fish diversity because non-commercial species also declined, so further studies are needed to clarify the effect of natural disturbances in fish assemblage. Finally, our study demonstrates that, in addition to traditional metrics, functional approaches allow a more complete evaluation of

the effectiveness of MPAs in the maintenance of fish diversity.

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Abstract

Multi-use marine protected areas (MUMPAs) are one of the most common tools used to mitigate fishing pressure in marine ecosystems of developing countries. Nevertheless, their effectiveness varies greatly with much more empirical evaluation required using traditional metrics and functional approaches. We conducted visual censuses of fish at Espíritu Santo Island, México (MUMPA; N= 320; 24°N) from 2005 to 2017 to asses fish richness, size-distribution and density. Three functional indices were calculated using six traits (size, mobility, period of activity, aggregation, position in water column and diet): functional richness (volume occupied by species), dispersion (complementarity between species) and originality (inverse of redundancy). We compared fish diversity among three management zone types (sustainable fishing, traditional fishing and no-take zones), through a 13-year period, assessing which species increased or decreased in occurrence, biomass, and density. We detected a reduction in fish biodiversity in the form of declines in species richness and density that translated to decreases in functional indices (functional richness and dispersion weighted by biomass). Despite a general increase in biomass, Additionally, the enhancement of fish stock was ~~neither~~ not achieved, because even the general fish stocks were not enhanced as the biomass of commercial species did not change. The lack of positive response following protection is attributed to lack of regulation in fisheries, small percentage of the MPA designated as no-take zone (1.4%), and different conservation targets of these restricted areas. Nevertheless, fishing pressure and management strategies do not fully explain the observed decrease in fish diversity because non-commercial species also declined, so further studies are needed to clarify the effect of natural disturbances in fish assemblage. Finally, our study demonstrates that, in addition to traditional metrics, functional approaches allow a more complete evaluation of the effectiveness of MPAs in the maintenance of fish diversity.

Introduction

Marine Protected Areas (MPA) are the most common tool used to mitigate anthropogenic disturbance (mainly fishing pressure) on marine ecosystems (Lester & Halpern, 2008; Lester et al., 2009; Bates et al., 2014). Nevertheless, different MPA schemes exist, from a strict prohibition of any fishing activities (marine reserves), to multi-use marine protected areas (MUMPA) with mixed harvest, restricted harvest, and complete prohibition areas (Agardy et al., 2003). The benefits of marine reserves on fish biomass have been demonstrated in many studies throughout the world, while MUMPAs show more equivocal results (Bates et al., 2014; Coleman et al., 2015; Campbell et al., 2018;).

The Gulf of California (GC) is considered a hotspot of diversity (Roberts et al., 2002) and an important region for fishing industry, providing 70% of the total catch in México (Cisneros-Mata, 2010; Díaz-Uribe et al., 2013). Although human population density is relatively low in the region, it is rapidly increasing, and the GC is not exempt from global coastal and marine degradation trends (Lluch-Cota et al., 2007; Sagarin et al. 2008; Calderon-Aguilera et al., 2012). Since the mid-1980s the Mexican government has established several MPAs to preserve biodiversity and control extraction of natural resources (CONANP, 2007). However, almost all the MPAs in the GC are MUMPAs with small no-take areas surrounded by “buffer” zones where fishing efforts are limited (Rife et al., 2013). In many developing countries, the idea of marine

reserves is not socially and politically feasible (Halpern, 2003), and thus a widespread procedure has been to safeguard the regional biodiversity by establishing MUMPAs, that aid a variety of ecosystem services (including poverty reduction, coastal protection, recreation, tourism, and carbon sequestration) in addition to fish stock enhancement (Spalding et al., 2013; Caveen et al, 2014;).

Few long-term studies have assessed the effects of MPAs in the GC. A two years comparison of Cabo Pulmo National Park between 1999 and 2009 showed a rise in species richness and biomass (Aburto-Oropeza et al., 2011). However, another study in the same MPA comparing two different years (1987 and 2003), revealed a decrease in species richness and fish density (Alvarez-Filip & Reyes-Bonilla, 2006). Cabo Pulmo suffered from habitat deterioration between 1997 and 2003 due to hurricanes and El Niño events, which may have damped the effect of protection. These two studies underpin the limitations of two-year comparisons due to natural environmental oscillation. On the other hand, a single continuous long-term study was carried out in the GC, in Loreto National Park, a MUMPA (Rife et al., 2013). This 13-year long study revealed relatively stable fish biomass (Rife et al., 2013). The authors concluded that, even if the situation does not improve, MUMPAs may at least maintain resource availability. Such longitudinal studies need to be repeated throughout the GC and worldwide, to provide a robust general assessment of the value of MPAs in preserving the living heritage of the GC, and in providing resources to local communities.

A new MUMPA was first implemented in 2007 in the southwest of the GC, a hotspot for reef fishes in the region (Olivier et al., 2018). This MPA called “Parque Nacional Zona Marina del Archipiélago de Espíritu Santo” (PNZMAES), encompasses the entire Espíritu Santo archipelago, located adjacent (less than 30 km) to the city of La Paz, the capital of Baja California Sur state, with over 300,000 inhabitants. PNZMAES is globally significant as it was the first national park of México included in the IUCN Green List of Protected Areas (in 2018). This list includes only 46 areas recognized worldwide for effective management, governance, design and planning in an evaluation conducted during the last five years (2013 to 2018; IUCN, 2018).

Reef ecosystems monitoring at PNZMAES took place before the declaration of the protected area in 2007, providing an important opportunity to assess the effect of a MUMPA on the diversity of multiple reef taxa. We focused on reef fishes because this group play important functions in the ecosystems, and their decline can alter ecosystem processes and services, as availability of reef resources and recreational activities (Miller, Roxburgh, & Shea, 2011; Mouillot et al., 2013).

In the current study we aimed to evaluate how fish assemblages changed through a 13-year study period at PNZMAES. In addition to traditional ecological metrics (species richness, density, and biomass), we evaluated the temporal changes of functional metrics. These have only recently been used to evaluate MPAs (Bates et al., 2014; Coleman et al., 2015), but can sensitively detect early changes in assemblage structure and instability, through redundancy and complementarity processes (Mouillot et al., 2013; Rice et al., 2013; Coleman et al., 2015).

plays

Materials & Methods

Study locations and data sampling

PNZMAES is located at the southwestern GC and encompasses an area of 486 km^2 (24°43'00" to 24°22'44" N, 110°26'58" to 110°17'11"W). This MPA was decreed in 2007 but the management plan was not implemented until 2014 (CONANP-SEMARNAT, 2014). According to the management plan, the park has three levels of use (Figure 1); no-take zones where fishing is strictly prohibited (~1.3% of the MPA); "buffer" zones divided into two categories, traditional use where fishing activities with hook and line, and sport fishing are allowed (~4.4% of the MPA); and sustainable zones where, in addition to the activities in the traditional zones, aquaculture activities are permitted (94% of the MPA). Industrial fisheries (including purse seining, long-lining and trawling) are prohibited in the entire MUMPA (CONANP-SEMARNAT, 2014).

From 2005 to 2017, eleven sites were monitored twice a year, in cold (January to June) and warm (August to November) seasons (Figure 1). In each visited site, ~~from~~ 6 to 8 underwater visual censuses of 50 to 60 m^2 were conducted. Different transect areas were considered in the study period since the methodology were standardized for the GC region in the warm season of 200[illegible]o have a better estimation of the number of replicates, we aggregated the censuses if they were separated by less than 200 m, and were performed the same day and depth range. We obtained a total of 320 transects (average = 333 ± 73 m^2, median = 300 m^2, ESM1). For each transect, data on the number of species (species richness), as well as abundance and individual fish size (to the nearest 5 cm), were collected. The modal size was estimated for fishes in schools. Fish biomass (g/m^2) was estimated using the length-weight relation: $Weight = a*Length^b$, with coefficients a and b obtained from FishBase (Froese & Pauly, 2009).

six to eight

Biological traits of fishes and diversity indices

To estimate the functional diversity of the fish assemblages, each fish species observed was classified according to six categorical traits (nominal or ordinal) that reflect key aspects of fish ecology (Mouillot et al., 2014): 1) maximum body size (ordinal), 2) mobility (ordinal), 3) period of activity (nominal), 4) gregariousness (ordinal), 5) vertical position in the water column (ordinal), and 6) diet (nominal). The same categories have been used in a previous study in the GC (Olivier et al., 2018), and taken together provide "Functional Entities (FEs)" (see ESM1 for further details). FEs were used to build a categorical traits matrix that was transformed into a numeric matrix to calculate the different functional indices. Pairwise distances between species (according to their FE) were computed using a Gower dissimilarity matrix, which allows different types of variables to be mixed while giving them equal weight (Gower, 1971). Then, a principal coordinate analysis (PCoA) was performed using this functional dissimilarity matrix. The first four PCoA axes were then selected according to the method of Maire et al. (2015). These PCoA scores were used to calculate three complementary functional diversity indices: functional richness, functional dispersion, and functional originality (Villéger et al. 2008; Mouillot et al. 2013). The following definitions are aligned with those provided in Mouillot et al., (2013, 2014). Functional richness was defined as the proportional volume of the whole functional space encompassed by the outermost vertices of the assemblage (Figure 2). This

niches

metric represents the range of functional niche found in the assemblage. Functional dispersion was defined as the weighted mean distance between species and the weighted average position of the assemblage in the synthetic niche space (Figure 2). This represents the functional complementarity between species. Functional originality was defined as the weighted mean distance between a species and its nearest-neighbor species in the synthetic niche space (Figure 2), thus, the opposite of functional redundancy. The functional dispersion and functional originality were weighted by the density and the biomass of each species. We used the function "dbFD" and "multidimFD" from the "FD" R packages to calculate the different functional indices (Laliberté, Legendre, & Shipley, 2014).

Statistical analyses

We first ran linear mixed models (LMMs) to compare the eight indices calculated (species richness, density, biomass, functional richness, functional dispersion weighted by density and biomass, and functional originality weighted by density and biomass) among the levels of use of the MPA, i.e. no-take, traditional and sustainable zones. We ran the analyses considering the potential effects of year, season and site by including them as random variables. By considering site as random variable, we could account for spatial and temporal autocorrelation associated with repeated monitoring of the same sites (Zuur et al., 2009). Here, we considered year as a random variable as we first wanted to compare the three levels of use independently of temporal changes. We also considered season as a random variable as it can affect the investigated fish community, which in previous studies of the area has presented the lowest values in cold season (Aburto-Oropeza & Balart, 2001). We then ran additional LMMs to analyze changes in fish diversity through the 13-year period. Finally, we ran a model to evaluate biomass changes amongst commercial species through the 13-year study period (see list of the commercial species in ESM1). Biomass and density variables were log-transformed (base 2) to accomplish normality and homoscedasticity. Visual inspections of the residual values of each model did not reveal any severe violation of parametric assumptions.

Finally, we identified which common species (present in at least 50% of the transects) increased ("winners") or decreased ("losers") in occurrence (presence of species per transect), biomass, and density through the 13-year study period, using generalized linear mixed models (GLMMs) with a binomial distribution for occurrence, and with a negative-binomial distribution for density and biomass, to account for overdispersion in the residuals. Biomass and density values for each common species were rounded to an integer, a prerequisite for use of the negative-binomial distribution. Site and season were also considered as random variables in these evolution analyses. All statistical analyses were performed in R software (R Development Core Team, 2014) with the package *lme4* (Bates et al., 2014).

Results

The LMMs by level of use showed similar values in all the indices except density, which was higher where traditional fishing is allowed (Figure 3; ESM2, Table S1). Temporal LMMs indicated that species richness and density decreased while biomass increased through the 13-year study period (Figure 4; ESM2, Table S2). According to the models, species richness

decreased by 13% (confidence interval (CI): -19% to -5%), density decreased by 65% (CI: -72% to -55%), and biomass increased by 43 % (CI: 2% to 99%). Nevertheless, the biomass of commercial species (28 of the 100 monitored species) did not increase (Estimate: 0.026 ± 0.025 g/m^2, df = 309, t = 1.04, P = 0.30). Functional richness (span of functional niches), decreased through the study period (mean: -24%, CI:-34% to -14%). Functional dispersion (functional complementarity among species), showed contrasting results: increased when weighted by density (mean: 8%, CI: 1.6% to 15%), and decreased if estimated with biomass (mean: -13%, CI: -19% to -8%). Finally no change was observed for functional originality (Figure 4; ESM2, Table S2).

qualitatively similar(??)

Analyzing on the basis of level of use in the park, the trends of temporal LMMs were conserved in the three levels for density, biomass and the functional dispersion. However, the biomass increase was more evident in the traditional use zone, and the increase in functional dispersion weighted by density was higher where in the sustainable use zone (Figure 4). Concerning the species and functional richness, the decrease was only observed in the sustainable use and the no-take zones, while no changes were observed in the traditional use zones (Figure 4).

We identified 26 species present in at least 50% of the 320 transects (Figure 5). Seven decreased significantly in occurrence through time, and several of these "loser" species were located on the outer margins of functional space (Figure 5A). Only two "winner" species were considered, as they increased significantly their occurrence (Figure 5A, ESM2, Table S3). On the other hand, most common species (18 species), decreased significantly in density, while a single "winner" species was identified (Figure 5B; ESM2, Table S4); the "loser" species occupied a large part of the functional space, but many of them were located closed to the patch of functional centroids of the assemblages (Figure 5B). Last, in the case of biomass, the number of fish species that increased or decreased significantly was more balanced, with eight "winners" and six "losers" (Figure 5C; ESM2, Table S5). The former were located near the aggregation of functional centroids, while the latter tended to occupy more outlying positions (Figure 5C

Discussion

The goals of MUMPAs are to: 1) conserve biodiversity, 2) enhance fish stock, and 3) promote the maintenance of other ecosystem services, such as poverty reduction, coastal protection, recreation, tourism, and carbon sequestration (Spalding et al., 2013; Caveen et al., 2014). Our analyses showed that the first two objectives have not been achieved for the reef fishes of PNZMAES through the 13-year study period. Biodiversity of fishes was not maintained because there was a decline in species richness and density that translated into a decrease in some functional indices (functional richness and functional dispersion; Figure 4; ESM2, Table S2). Moreover, enhancement of fish stock was also not achieved, because the biomass of commercial fishes did not change since there was no added value for fisheries (Figure 5C; ESM2, Table S5).

The number of species observed by transects increased and in part this result is linked to the decrease in functional richness since some of the "loser" species in the occurrence evolution analysis, were located at the outer margins which reduced the functional space (Figure 5A; ESM2, Table S3). This reduction could imply a risk on the quality of certain ecosystem

processes, since some species with extreme and unique functions, i.e. the endemic damselfish of the Gulf of California *Chromis limbaughi*, have been gradually less favored as conditions changed in PNZMAES (Mouillot et al., 2013). Additionally, the fact that "loser" species were located in different parts of the functional space, and some of them have quite dissimilar ecological traits, indicated that their decrease in occurrence may be caused by several factors acting synergistically, including natural or human-induced disturbances (Mouillot et al., 2013). In this case, the fact that "loser" species were represented by herbivores, planktivores, invertivores and apex predators (ESM1) indicates that species are losing occurrence all over the trophic net.

One critical observation was the decrease in the density of individuals that went from 55% to 72% of the total population of "loser" species (Figure 5B; ESM2, Table S4). Population decline is a good indicator of local deterioration, and may progress to the point of local extinction (Ceballos, Ehrlich, & Dirzo, 2017). This situation should receive particular attention in future conservation policy of the studied park.

Functional dispersion, which represents the functional complementarity between species, increased when calculated on basis of density of individuals. An increase in this index may be initially perceived as a positive indicator, as it could suggest that species with different (complementary) traits increased in density, which may favor the resilience of the community (Mouillot et al., 2013). However, at Espíritu Santo this increase of functional dispersion is due to "loser" species found near the centroid of the assemblage (Figure 5B), which implies a collapse in the center compared to the border of the functional space, increasing therefore the dispersion (case 2 in Figure 2). In contrast, functional dispersion calculated from species biomass, showed that "winner" species were distributed around the center of the functional space, while the "losers" tended to occupy more extreme positions; this originated a decrease in the index (Figure 5C). Changes in functional dispersion showed that the functional structure of the assemblage is dynamic, reflecting variability in density and biomass among species (Bates et al., 2014). This may in turn influence the ecological resilience of the assemblages, since certain functions are losing importance through time.

Regardless of the total biomass increase, the biomass of commercial fishes did not change (Figure 5C; ESM2, Table S5), which implies that fish stock were not enhanced and possibly the economic gain was not achieved. Furthermore, some target species, such as large predators and large herbivores (i.e. the leopard grouper *Mycteroperca rosacea*, and the common parrotfishes *Scarus ghobban* and *S. rubroviolaceus*), decreased in occurrence, density and biomass (Figure 5). These species play relevant ecological roles in reef ecosystems of the GC as *M. rosacea* is a high level carnivore which may exert top-down control in certain areas such as Cabo Pulmo reef (Reyes-Bonilla & Alvarez-Filip, 2008), and is among the most intensely fished grouper in the region (Sala et al., 2003). Decline in this species commenced over a decade ago (Sala et al., 2004), and, although classified by the International Union for the Conservation of Nature (IUCN) as "Least Concern", shows a decreasing population trend (IUCN, 2019). Parrotfishes are also essential components in eastern Pacific reef environments as their bioerosive activity and later deposition of carbonate sediment helps in the construction of the reef framework, and their role as herbivores influence nutrient cycles and controls algae proliferation (Bellwood, Hoey, & Hughes, 2011). Decline in the populations of large groupers and parrotfishes are indicators of overexploitation in other regions (Bellwood et al., 2004; Bellwood et al., 2011), so our results demonstrate the current lack of success in the maintenance of particular commercial fishes at the park.

According to the IUCN website, "the sites on the Green list are certified as being effectively managed and fairly governed, with a positive impact on people and nature" (IUCN, 2018). This statement appears to be in contrast with the observation of the reduction in commercial fishes biomass, but for a thorough analysis of this controversy, a small digression about the Mexican law needs to be done. In México, national parks can control a number of human activities developing inside the protected polygons, but fisheries are not part of their jurisdiction; instead, the regulations on commercial marine species depend on a second government agency: the National Fishery Commission (CONAPESCA), which regulates extraction volumes, determine seasonal bans, allowed minimal catch sizes, and grants permissions. CONAPESCA inspectors' controls the compliance of the Fishery Law all over the country, and in protected areas they collaborate with ~~elements of~~ a third agency: the Federal Environmental Protection Office (PROFEPA). When a park guardian detects a boat fishing, they have the competence to ask for permissions and examine the catch in order to avoid illegal actions; however if something unusual is detected, they have to ask for personnel of PROFEPA and CONAPESCA, or to the Mexican Navy, to proceed and take legal action, and in many occasions by the time they arrive in the scene, the offender have left. Under these circumstances, the actual control of the condition of the fishing resources inside MPAs is in jeopardy

In addition, not a single commercial species resident at the park has a management plan, and so the fishermen do not have to follow any specific regulation other than to use specific fishing methods such as hook and line (CONANP-SEMARNAT, 2014); consequently the populations can be safe inside the MPA, but as soon as they abandon it, they can be extracted at any size, volume or site. This problem is magnified by the fact that many commercial fishes are large, and because of their good capacity of movement they can travel long distances during his life cycle (TinHan et al., 2014; Munguia-Vega et al., 2018), therefore being exposed to be caught most of their lifetime. The reduction of the biomass of commercial fishes at PNZMAES did not result from inadequate control of the park managers, but instead by the deficient performance of the federal fishery agencies. The analysts of IUCN were aware of this situation and as the fisheries are not under control of the MPA, they granted the Green Card certification

Increased fishing pressure is not the only factor that explains the decrease fish diversity at PNZMAES, because occurrence, density and biomass evolution analyses showed the decline of various non-commercial species, that possess small-size, are highly associated to substratum, and present low mobility (some damselfishes, small wrasses, butterflyfishes hawkfishes, etc; Figure 5). In this case, some other disturbances such as habitat alteration, lowering in larval recruitment or global change, may be part of the explanation for such declines; however, evidence on this particular topic is not available and will require further investigation. Also, large scale phenomenon such as El Niño or the Pacific Decadal Oscillation may affect the GC fish community (Alburto-Oropeza et al., 2007), but the relatively short decadal time frame of our study makes accurate evaluation of such effects difficult, requiring future studies over a longer period and/or larger spatial scale.

Since it is difficult to control external factors, local conservation actions should be taken to try to improve fish assemblages' conditions as the expansion of no-take zones focused on the enhancement of fishing stock. Out of the 6.7 km^2 designated as no-take area in PNZMAES, the largest no-take zone at San Gabriel Bay (3.49 km^2) is devoted to keep the local coral reef in good shape (CONANP-SEMARNAT, 2014), while Los Islotes (0.78 km^2) aim is to protect the breeding colony of the sea lion *Zalophus californiensis* (Hernández-Camacho, Aurioles-Gamboa, & Gerber, 2008). Only Bonanza Bay and Punta Lobos (2.36 km^2) were designed to protect adult

fishes and repopulate areas that were intensively fished. In the GC, two no-take areas showed significant increases in fish biomass: first, a small no-take area (1.27 km^2) in Loreto National Park presented increase in herbivorous and planktivorous non-commercial species after13-years of protection (Rife et al., 2013). Second, the most successful MPA in the region, Cabo Pulmo National Park, presented a dramatic increase of total fish biomass (463%) which included a 30% of increase of predatory fish within its no-take zone (25 km^2; Aburto-Oropeza et al., 2011). Both results support the idea that it is indispensable to increase the no-take area of PNZMAES to promote fish stock enhancement. Besides the relevance of the size of no-take areas, these studies recognized that support of local community in conservation efforts is essential to increase effectiveness of MPAs, so the recent addition of PNZMAES to the IUCN Green List of Protected Areas (2018), represents an opportunity to develop more effective management strategies, in co-responsibility with local stakeholders who can help in reversing the observed decline in fish diversity over the last decade.

In conclusion, this study demonstrates that in addition to changes in traditional metrics (species richness, density and biomass), functional structure of the fish assemblage has changed relative to conditions in 2005 in PNZMAES, so it is necessary to apply the functional approach to provide a better frame of long-term changes of fish diversity in MPAs. The reduced fish diversity despite the increase of fish biomass in PNZMAES could depend on several anthropogenic (lack of regulation in fisheries and small no-take areas) and natural factors (habitat alteration, lowering in larval recruitment and global change), but local conservations strategies should be taken (fishing regulations, expansion of no-take areas and support of local community), to improve the effectiveness of this and other MUMPAs in the GC.

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Figure 1

Figure 1. Location of the surveyed sites in the Parque nacional exclusivamente la zona marina del Archipiélago de Espíritu Santo (PNZMAES).

The levels of use are color-coded. The rectangle-polygons represent the area with traditional use and the no-take zones (in this case, they are also blue-filled).

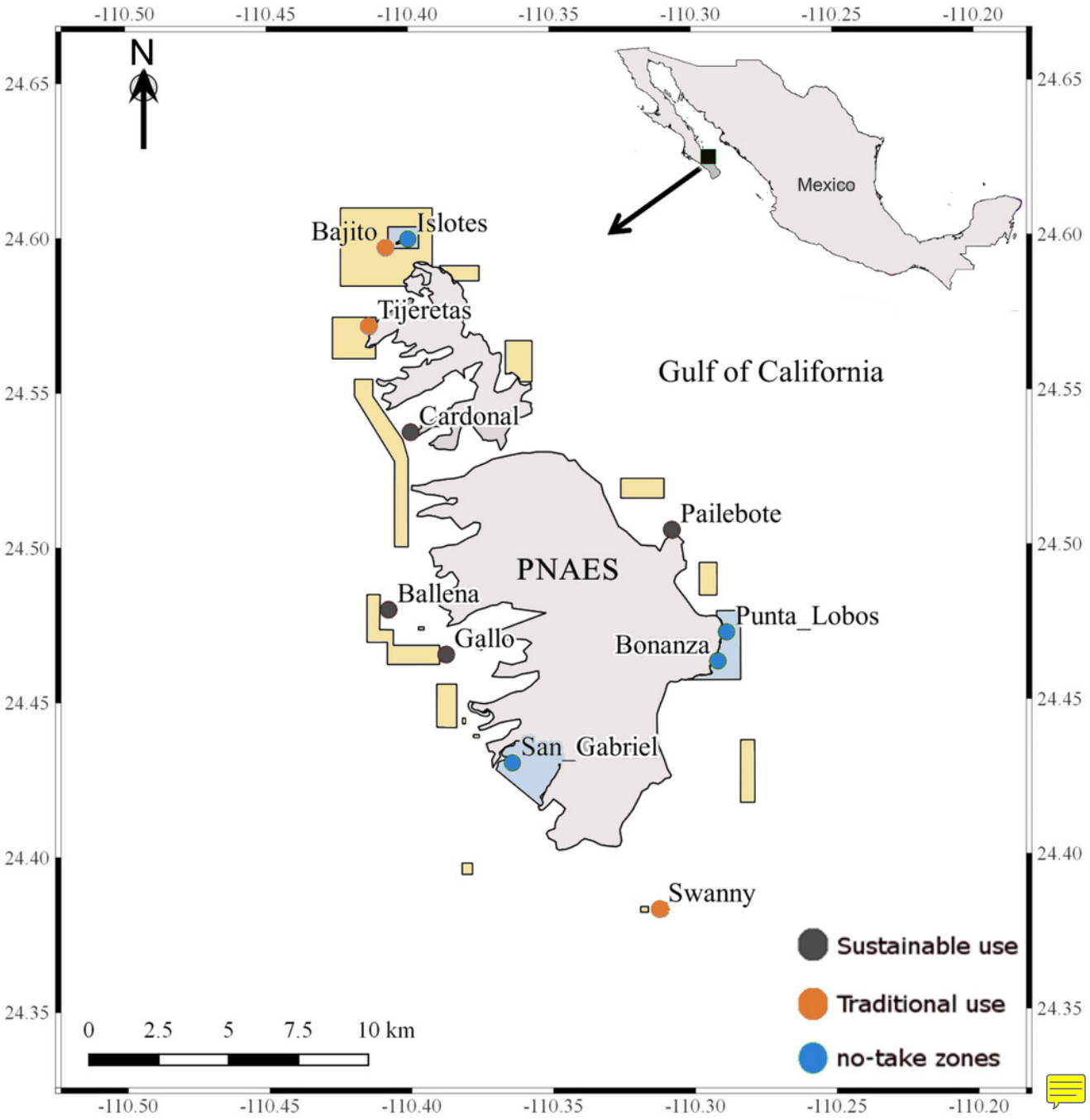

-110.50
-110.45
-110.40
-110.35
-110.30
-110.25
-110.20
24.65
24.60
24.55
24.50
24.45
24.40
24.35
N
Mexico
Bajito
Islotes
Tijeretas
Gulf of California
Cardonal
Pailebote
PNAES
Ballena
Punta_Lobos
Gallo
Bonanza
San_Gabriel
Swanny
Sustainable use
Traditional use
no-take zones
0
2.5
5
7.5
10 km

Figure 2

Figure 2. Functional indices.

A) Illustration of the three functional indices used in this study.The colored-polygons represent the functional space that species present in three distinct transects encompass. The functional richness of a transect is the proportion of the functional space covered by the species present in the survey unit out of all the species pool (all transects). The dashed lines represent the distances between each species of a transect to the weighted centroid of the fish assemblage present in the transect. The weight can be the abundance or biomass of each species. The functional dispersion of a transect is the mean of these distances (weighted by abundance or biomass) divided by the half of the maximum distance among all the species pool. The thick red line represents the distance between a species and its nearest neighbor in one transect. The functional originality is the mean of these distances (weighted by abundance or biomass) divided by the maximum distance to the nearest neighbor found in all the species pool. B) Two hypothetical cases where the functional dispersion increases. In the case 1, the increase in functional dispersion is due the increase in biomass or abundance of certain species (winners) located far from the centroid. In the case 2, the increase in functional dispersion is due to the decrease in biomass or abundance of certain species (losers) located close to the centroid. Functional dispersion can decrease for similar reasons.

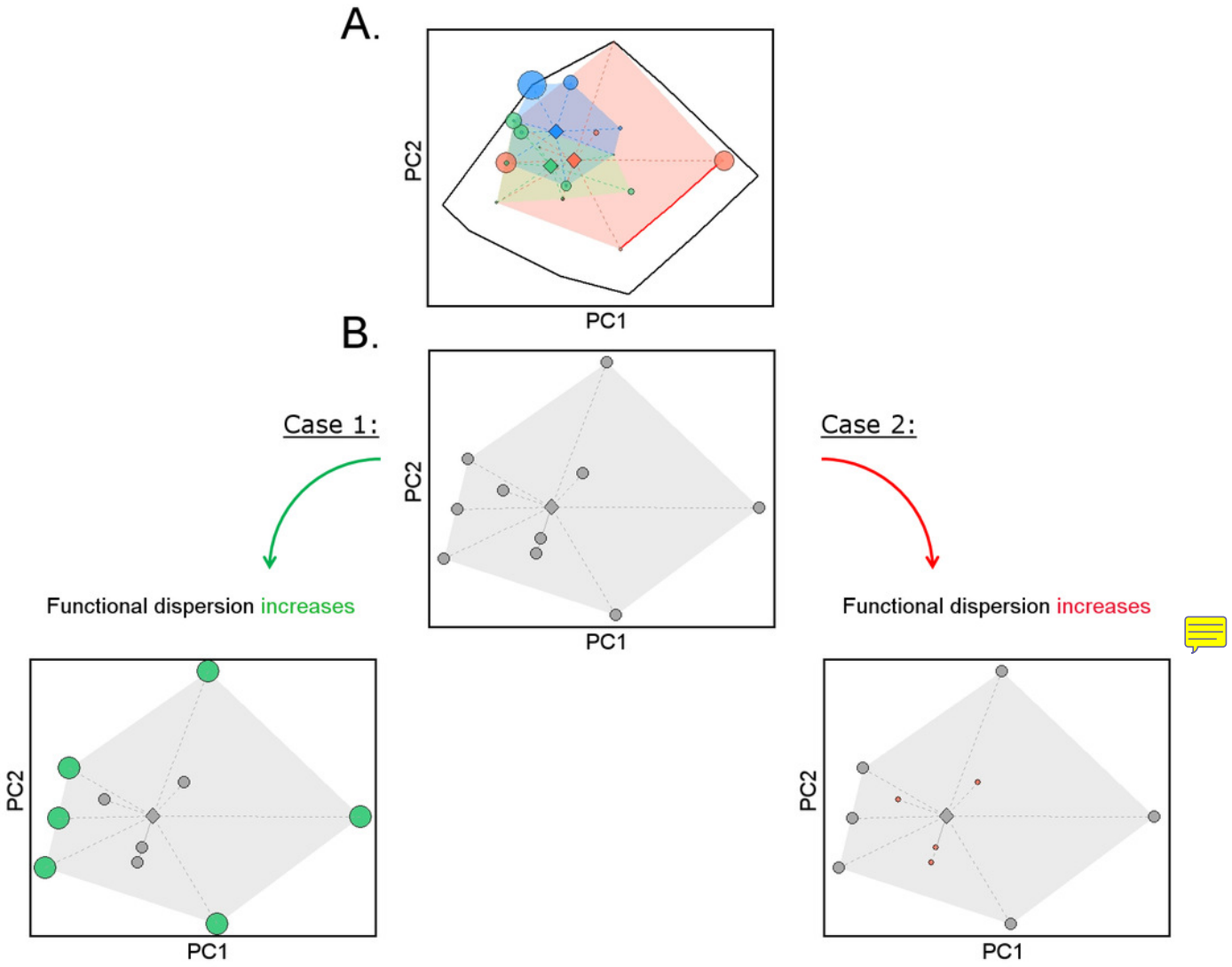

A.
PC2
PC1
B.
Case 1:
Case 2:
PC2
PC1
Functional dispersion increases
Functional dispersion increases
PC2
PC1
PC2
PC1

Figure 3

Figure 3. Comparison of fish diversity between the levels of use in PNZMAES.

The density and biomass have been log-transformed (base 2). The red asterisk indicates a significant difference ong the levels of use. The boxplots depict the mean, 2nd and 3rd quartiles, the confidence interval (95%) and the outlier dots).

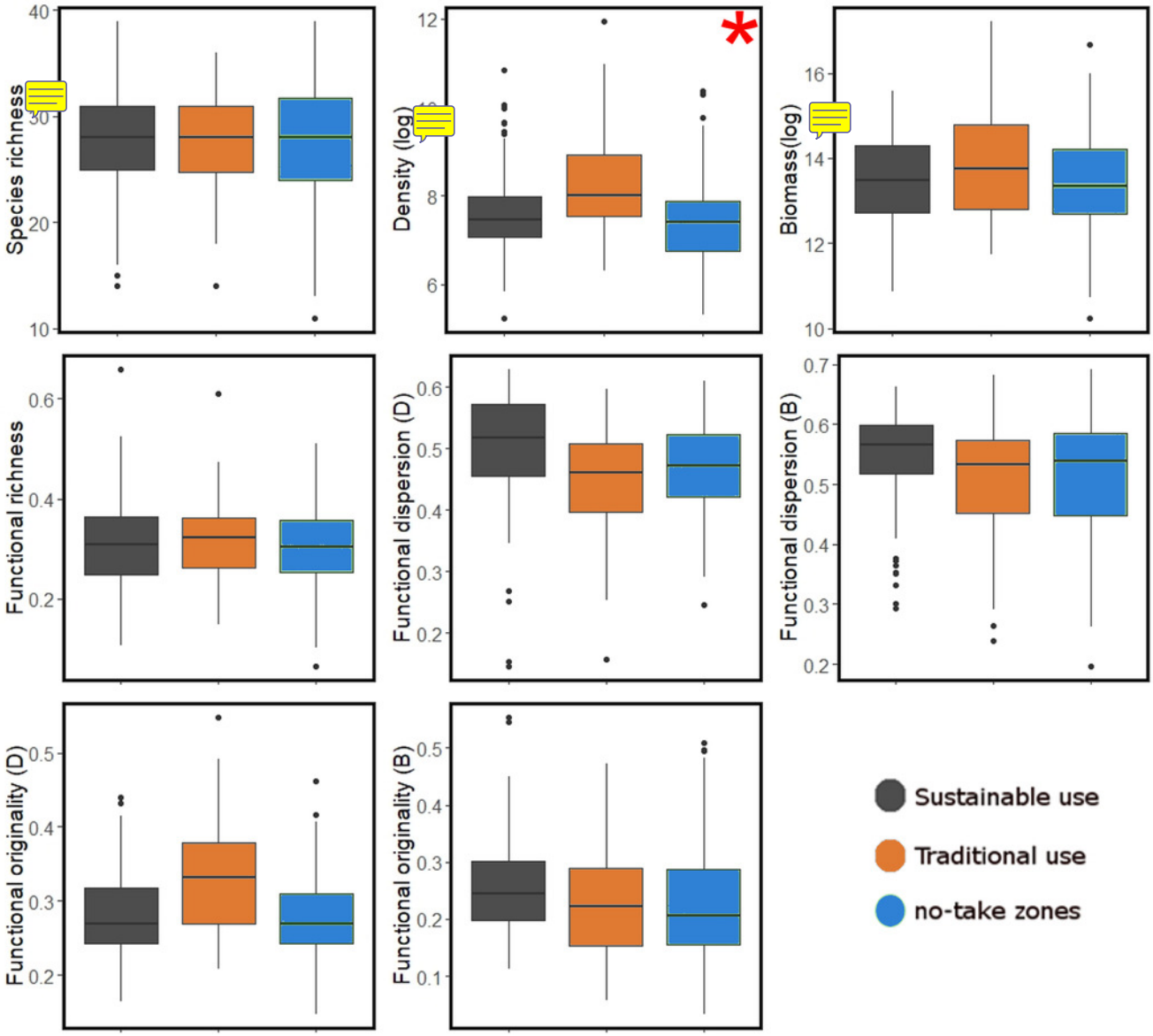

Species richness
Density (log)
Biomass(log)
Functional richness
Functional dispersion (D)
Functional dispersion (B)
Functional originality (D)
Functional originality (B)
Sustainable use
Traditional use
no-take zones

Figure 4

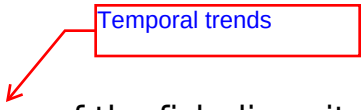


Figure 4. ~~Evolution~~ of the fish diversity along a 13-year study period in PNZMAES.

Regression lines are showed for each index. A jitter position has been added to handle overplotting of the data. The colors of regression lines are according to the level of use in the park, i.e., grey: sustainable, brown: traditional, and blue: no-take zones. The coefficients estimates (mean ± 95% confidence interval) of the LMMs considering the 11 sites are showed.Coefficients have been standardized for vizualisation. Green and red circles show significant positive and negative changes, respectively. Grey symbols indicate no significant changes.

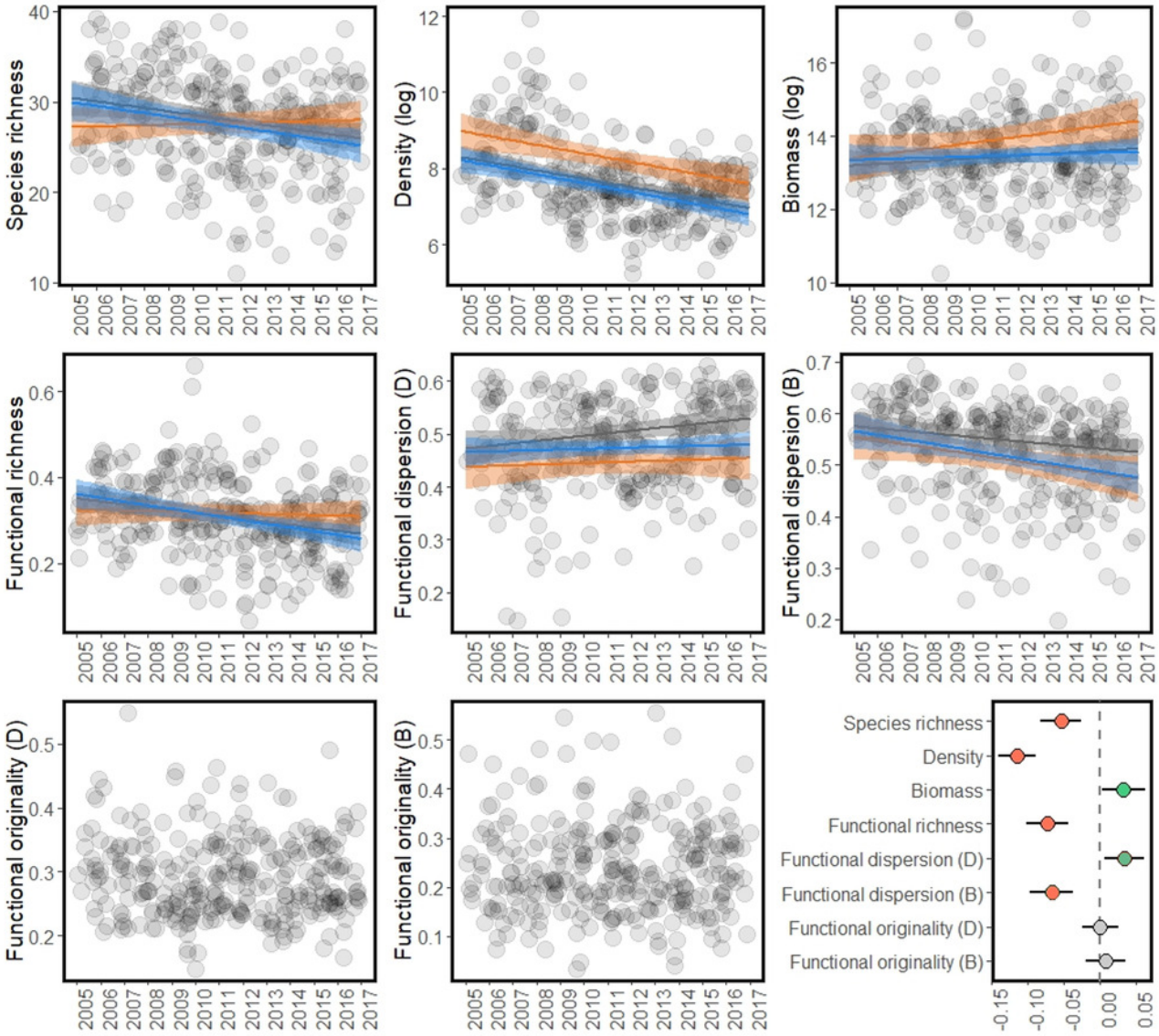
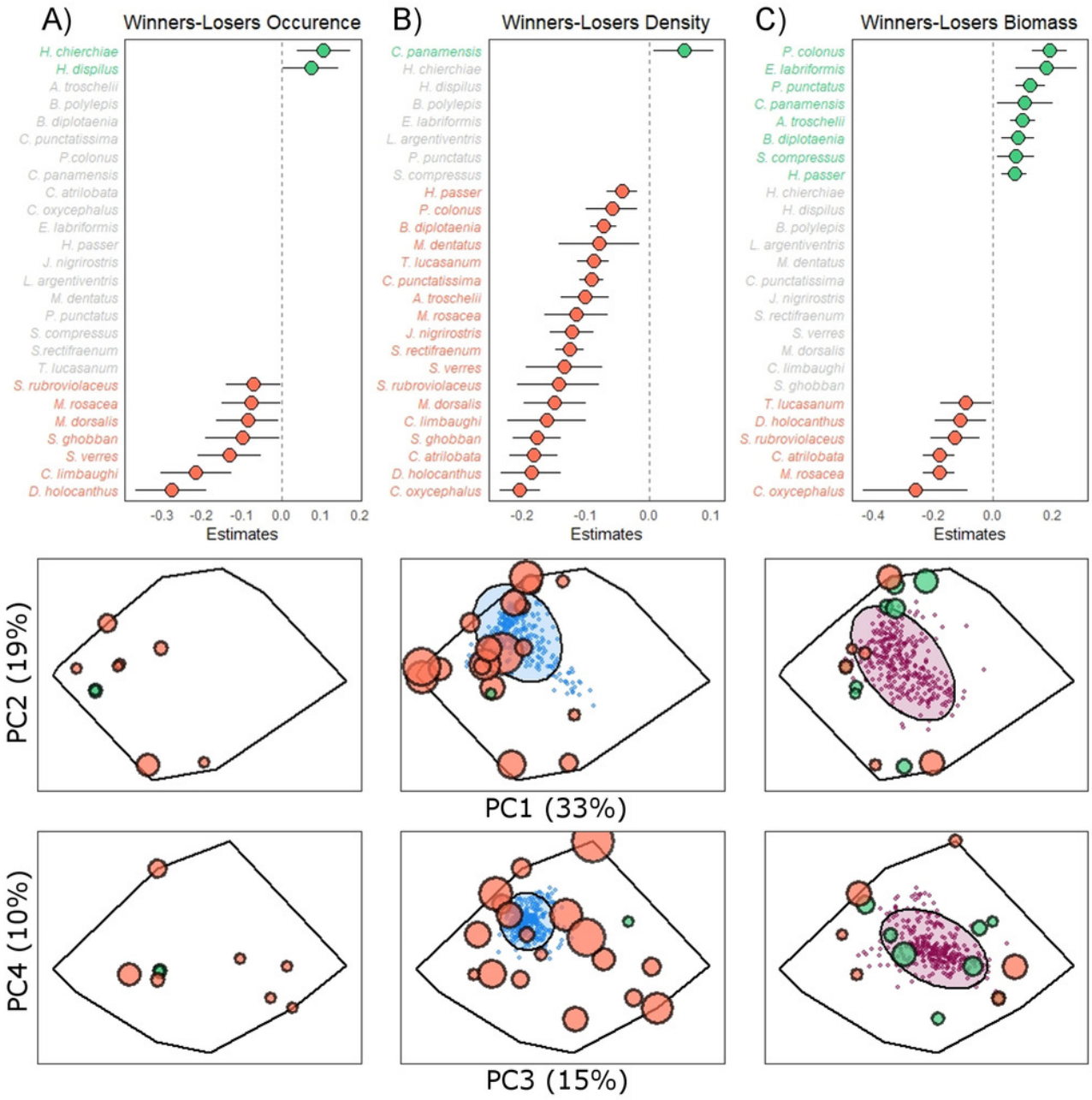

Species richness
Density (log)
Biomass (log)
Functional richness
Functional dispersion (D)
Functional dispersion (B)
Functional originality (D)
Functional originality (B)
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
Species richness
Density
Biomass
Functional richness
Functional dispersion (D)
Functional dispersion (B)
Functional originality (D)
Functional originality (B)
-0.15
-0.10
-0.05
0.00
0.05

Figure 5

Figure 5. Winners and losers species along a 13-year study period in PNZMAES.

From A) to C), the winners and losers species in term of occurrence, density, and biomass. The mean coefficient estimates (± 95% confidence interval) of the GLMMs showed the effect of the years on the common species (present in at least 50% of the transects). Only the parameters of the species for which a significant effect was found and for which the models were validated are showed.een and red circles indicate significant positive and negative values, respectively.The position in the functional space of the winners and losers species are showed in the functional space for the occurrence, density, and biomass. The size of the dots is proportional to the z-values of the models. For the density and biomass functional space, the average-weight centroids (one per transect) are indicated by blue and purple dots, respectively. The 95% confidence interval ellipses of the centroids values are illustrated.


A)
Winners-Losers Occurence
H. chierchiae
H. dispilus
A. troschelii
B. polylepis
B. diplotaenia
C. punctatissima
P.colonus
C. panamensis
C. atrilobata
C. oxycephalus
E. labriformis
H. passer
J. nigrirostris
L. argentiventris
M. dentatus
P. punctatus
S. compressus
S.rectifraenum
T. lucasanum
S. rubroviolaceus
M. rosacea
M. dorsalis
S. ghobban
S. verres
C. limbaughi
D. holocanthus
-0.3 -0.2 -0.1 0.0 0.1 0.2
Estimates
B)
Winners-Losers Density
C. panamensis
H. chierchiae
H. dispilus
B. polylepis
E. labriformis
L. argentiventris
P. punctatus
S. compressus
H. passer
P. colonus
B. diplotaenia
M. dentatus
T. lucasanum
C. punctatissima
A. troschelii
M. rosacea
J. nigrirostris
S. rectifraenum
S. verres
S. rubroviolaceus
M. dorsalis
C. limbaughi
S. ghobban
C. atrilobata
D. holocanthus
C. oxycephalus
-0.2 -0.1 0.0 0.1
Estimates
C)
Winners-Losers Biomass
P. colonus
E. labriformis
P. punctatus
C. panamensis
A. troschelii
B. diplotaenia
S. compressus
H. passer
H. chierchiae
H. dispilus
B. polylepis
L. argentiventris
M. dentatus
C. punctatissima
J. nigrirostris
S. rectifraenum
S. verres
M. dorsalis
C. limbaughi
S. ghobban
T. lucasanum
D. holocanthus
S. rubroviolaceus
C. atrilobata
M. rosacea
C. oxycephalus
-0.4 -0.2 0.0 0.2
Estimates
PC2 (19%)
PC1 (33%)
PC4 (10%)
PC3 (15%)