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# Functional diversity in fish assemblages of the Tropical Eastern Pacific Ocean: A review of two decades of progress in the functional diversity approach

# Diversidad funcional en el ensamblaje de la ictiofauna del Océano Pacífico Oriental Tropical: Una revisión de dos décadas en su enfoque

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## ABSTRACT

**Background**. One of the most relevant topics in ecology and evolution is understanding the relationship between biological and functional diversity at the ecosystem level; both important in the evolutionary processes and the structuring of complex communities. **Goals.** In this essay, the explanatory hypotheses focused on global patterns of the distribution of species are described along with selected hypotheses relating species richness/biodiversity to ecosystem function, and the differentiation of the terms guild and functional group are discussed. **Methods.** Both biodiversity and functional diversity are key in the evolutionary processes and the structuring of complex communities and thus examples of functional equivalence of convergent evolution derivatives are presented in terms of the form and ecological habits of fishes of the Tropical Eastern Pacific Ocean. Finally, the importance of redundancy in ecosystem functioning is examined as well as the impact of environmental disturbances on ecosystem function. **Results**. In general, systems with low species richness and redundancy within functional groups are more vulnerable to disturbances. However, despite the extensive effort to understand the relationship between species richness/biodiversity and ecosystem functioning, there is no consensus on the effect of species loss on the functioning of the ecosystem. Some hypothesize that each species is unique and plays a unique role in the ecosystem whereas alternate hypotheses indicate that species overlap in function supporting sustainability at the ecosystem level, such that the removal of one species function may be replaced by another. **Conclusions**.The most widely accepted concept is that a greater number of species increases the efficiency in the use of resources and also provides resilience against environmental changes or impacts through functional redundancy.

**Keywords**: biological diversity, ecological redundancy, evolutionary convergence, functional equivalence

## RESUMEN

**Antecedentes.** Un tema relevante en ecología y evolución es la relación entre la diversidad biológica y la funcional a nivel del ecosistema; ambas importantes en los procesos evolutivos y la estructuración de comunidades complejas. **Objetivos.** Discutir hipótesis explicativas centradas en los patrones globales de la distribución de las especies junto con hipótesis seleccionadas que relacionen la riqueza y la biodiversidad de especies con la función del ecosistema. Diferenciar los términos de gremio y grupo funcional. **Metodología.** Presentar ejemplos de equivalencia funcional de los derivados de evolución convergente en términos de la forma y los hábitos ecológicos de los peces del océano Pacífico oriental tropical. Examinar la importancia de la redundancia en el funcionamiento de los ecosistemas, así como el impacto de las perturbaciones ambientales en la función del ecosistema. **Resultados.** En general, los sistemas con baja riqueza de especies y redundancia dentro de grupos funcionales son más vulnerables a las perturbaciones. Sin embargo, a pesar del extenso esfuerzo por comprender la relación entre la riqueza de especies/biodiversidad y el funcionamiento del ecosistema, se encontró que no existe consenso sobre el efecto de la pérdida de especies en el funcionamiento del ecosistema. Algunos suponen que cada especie es única y desempeña un papel particular en el ecosistema, mientras que las hipótesis alternativas indican que las especies se superponen en función de la sustentabilidad a nivel de ecosistema, de modo que la eliminación de la función de una especie puede ser reemplazada por la de otra especie. **Conclusiones**. El concepto más ampliamente aceptado es que un mayor número de especies aumenta la eficiencia en el uso de los recursos y también brinda resistencia contra los cambios o impactos ambientales a través de la redundancia funcional.

**Palabras clave:** convergencia evolutiva, diversidad biológica, equivalencia funcional, redundancia ecológica

## INTRODUCTION

Biological classification (taxonomy) aims to simplify and order the diversity of life into coherent units called taxa; however, there is currently no consensus among taxonomists concerning which classification scheme to use (Ruggiero *et al.*, 2015). Simply, taxonomy integrates diverse, character-based data in a phylogenetic framework, which allows the use of this knowledge of shared biological properties of taxa but there is still strong debate over their accounting for evolutionary divergence or information content other than the branching pattern (Stuessy & Hoerandl, 2014). In contrast to taxonomy and phylogeny approaches to Earths biodiversity, a central issue in population and community ecology is species' geographical distribution and range size, which are important components needed for a better understanding of biodiversity. Generally, studies have focused on two different aspects: (1) patterns in species' range size distributions (Gaston, 1996; MacPherson, 2003); and (2) the effect of latitude on species' range sizes, *e.g.* Rapoport's rule (Stevens, 1989; 1996).

However, in contrast to earlier research on mechanisms driving known biodiversity patterns (Winemiller *et al.*, 2015; Pianka *et al.*, 2017), recent work highlights that evolution works on ecological similarities (redundancy) and differences (complementarity) of individuals and not on the number of species (Cadotte *et al.*, 2013). A number of early studies that simultaneously examined aspects of species biodiversity and functional diversity (reviewed in Tilman *et al.*, 1997) have shown that species biodiversity is an important indicator of ecosystem functioning but functional diversity and species composition together are most important in grassland ecosystems. Functional diversity (trait-based) is generally defined as "morpho-physio-phenological traits which impact fitness indirectly via their effects on growth, reproduction, and survival, the three components of individual performance" (Violle *et al.*, 2007). There is also evidence that functional traits strongly link to species composition and shifts in ecosystem processes (Villéger *et al.*, 2010) and that the choice of functional traits is key to quantifying functional diversity and its use to examine anthropogenic modifications of ecosystems. This relationship is strong when many species have unique functional traits that are important in ecosystem functioning, whereas if many species have similar characteristics (redundancy), the relationship between species biodiversity and functional diversity is weak.

Natural or human-induced environmental modifications (*e.g.*, fishing, climate change, habitat fragmentation) have had drastic impacts on habitats and species and thus biodiversity and ecosystem function worldwide (Costanza *et al.*, 1997; Vitousek *et al.*, 1997; Lotze *et al.*, 2006; Halpern *et al.*, 2008). These impacts are generally focused on habitat modification or loss as it relates to species loss and biodiversity reduction since it has long been postulated that habitat is the 'template for ecosystem strategies' (Southwood, 1977; Ferraro & Cole, 2010; Ferraro, 2013) and that habitat provides the organizing structure for ecosystem functionality. However, there are generally two approaches to assessing local and regional community assembly relative to diversity and ecosystem function: 1) taxonomic (phylogenetic); and 2) functional (trait-based) (Cadotte *et al.*, 2013; Winemiller *et al.*, 2015; Pianka *et al.*, 2017).

The traditional approach is to examine changes by using species richness/biodiversity metrics but more recently a growing literature on functional diversity and its importance in better understanding ecosystem function (Violle *et al.*, 2007; Villéger *et al.*, 2010; Parravicini *et al.*, 2014) is emerging, and, in particular, relative to species invasions and habitat degradation, and fishing pressure (Pecuchet *et al.*, 2017; Silva-Junior *et al.*, 2017; Villéger *et al.*, 2017). For example, it has been shown in coral reef fish communities that functional diversity is lower than taxonomic diversity because of redundancy (Villéger *et al.*, 2012, 2013; Mouillot *et al.*, 2014) which suggests that one cannot use taxonomic diversity to predict changes in functional diversity nor one cannot use taxonomic diversity alone to assess habitat degradation and subsequent ecosystem functional capacity relative to stable and sustainable ecosystems (Villéger *et al.*, 2014; Loiseau & Gaertner, 2015; Pecuchet *et al.*, 2017; Silva-Junior *et al.*, 2017).

The study of functional traits important to the community ecology and, by extension, ecosystem function has been most noticeable in plant communities worldwide with fewer examples in other taxa, including fishes and avifauna (Villéger *et al.*, 2017). As a result of our empirical perception, we tend to assign a key role to a relatively small number of generally abundant and larger species, considering that their conservation is enough to maintain ecosystem processes and thus services. However, it was found that rare or unique species with the highest risk of extinction have, in some cases, a quantifiably important impact toward maintaining the functioning of the ecosystem, acting as key species (Lyons *et al.*, 2005; Mouillot *et al.*, 2013; Friedman *et al.*, 2016; Escobar-Toledo *et al.*, 2017).

Recent examination of freshwater, estuarine and marine fishes has illustrated the value of examining these communities based on functional traits in order to address pressing ecological issues associated with climate change, overfishing, invasive species, and habitat loss or alterations (Mouillot *et al.*, 2014; Parravicini *et al.*, 2014; Villéger *et al.*, 2014; Chuang & Peterson, 2016; Pecuchet *et al.*, 2016, 2017; Rodrigues-Filho *et al.*, 2017; Silva-Júnior *et al.*, 2017).

With this essay, we aim to (1) summarize patterns of fish species richness/biodiversity and distribution in the Tropical Eastern Pacific Ocean (TEP), (2) provide a selective review of hypotheses relating fish species richness/ biodiversity/functional diversity to ecosystem function, and (3) review the importance of redundancy in ecosystem function and the impact of environmental disturbances. This essay will focus on marine fishes of the TEP but may provide examples from freshwater and estuarine fishes, and other vertebrate groups to illustrate a point.

## MARINE FAUNAS TROPICAL EASTERN PACIFIC

The shallow, warm-water marine faunas of the world are traditionally divided into the Indo-West Pacific, Eastern Pacific, and western and eastern Atlantic regions (Ekman, 1953; Briggs, 1974). The Isthmus of Panama was established as one of the greatest natural events of the Cenozoic, driving profound biotic transformations on land and in the oceans, so faunas on the east and west sides are closely related and sister species are common (O'Dea *et al.*, 2016). Furthermore, the TEP is divided from the rest of the Pacific by a wide expanse of deep ocean, with very few islands, coupled with cold water masses flowing along west coasts of both North and South America towards the equator. This is not a complete barrier to shallow-water invertebrate dispersal, but rather is a filter, allowing only those larvae with an exceptionally long life to be transported from the central tropical Pacific (Scheltema, 1988).

There is a substantial variation in species composition from north to south through the TEP region, but boundaries among biogregraphical provinces are not always well defined. For example, mainly on ichthyological evidence, Briggs (1974) define four main provinces (Fig. 1), and places a boundary in the Gulf of Tehuantepec to separate the Mexicana province (Sinaloa to Oaxaca, on the coast of Mexico) and the Panamic province (Nicaragua to Ecuador, including Cocos and Malpelo). The Revillagigedo Islands was considered as part of the offshore Ocean Island province. However, the northern boundary of the Panamic province is debatable, the southern boundary is clearly defined by the cold Peruvian Current diverting offshore around Punta Aguja, Peru. Briggs (1974) set the northern boundary of the Mexican province in the Gulf of California and on Baja California at about 23°N. The Galapagos Islands are treated as a separate faunistic region and included in the offshore Ocean Island province along with the Revillagigedo and Clipperton Islands. The province of Cortez (southern Baja and the central Gulf of California) is isolated from its counterpart in the Mexican province by the Gap of Sinaloa, a band of 370 km of sandy and muddy shoreline extending between Topolobampo and Mazatlan, Mexico, whereas the Mexican province is separated from its counterpart in the Panamic province by the gap of Central America, a large 1,000 km section of coastline sand between the Gulf of Tehuantepec (south of Mexico) and El Salvador (Hastings, 2000).

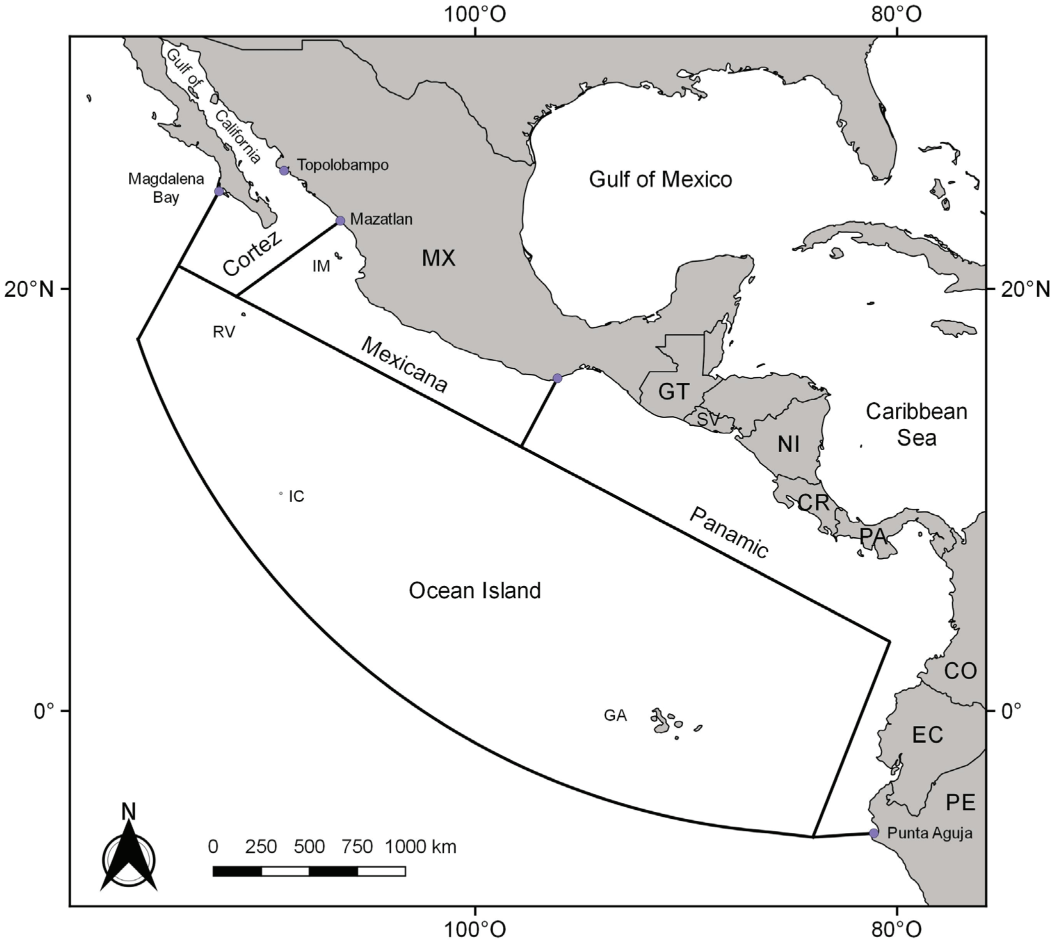

Figura 1.

Biogeographically, the TEP is fascinating in several respects. Its marine shore biota is most similar to that of the tropical western Atlantic, but, as a result of the independent evolution of their faunas in very different environments over the past 3.5 million years, the two regions share relatively few fish species (Rosenblatt, 1967; Castellanos-Galindo *et al.*, 2013). The TEP includes five oceanic islands or archipelagos whose fish faunas are relatively well known (McCosker & Rosenblatt, 1975; Robertson & Allen, 1996; Grove & Lavenberg, 1997; Garrison, 2000; Galland *et al.*, 2017). These islands harbor subsets of the mainland fauna, a significant number of insular endemics, and numerous species that also occur on the western side of the east Pacific barrier (Leis, 1984). The geographic isolation of the TEP has resulted in its having the highest level of regional endemism among shore fishes of any comparably sized region in the world. About 85 percent of its fishes are found nowhere else, although many of them regularly or periodically cross the thermal barrier to the north and are found in California (*e.g.*, during El Niño events; Lea & Rosenblatt, 2000). Although less well documented, a similar periodic transgression of the southern terminal barrier presumably also occurs.

Many TEP fish species have wide distributions within the region. Others have more limited distributions, with the Panamic province and the Cortez province serving as centers of regional endemism (Fig. 1). Precise distributions of many species of fishes between these provinces, along with the coast of southern Mexico southward to Honduras, are not well documented. Some species, particularly small, benthic reef fishes, support the recognition of a third, Mexicana province located between the Cortez and Panamic province (Hastings, 2000), as suggested by several studies on the systematics of coastal fishes (*e.g.*, Hubbs, 1952; Briggs, 1955; Springer 1959; Stephens, 1963).

## SPECIES RICHNESS / BIODIVERSITY AND DISTRIBUTION PATTERNS OF THE TEP FISHES

Species richness/biodiversity is distributed irregularly among ecosystems across biospheres. For example, there are 34 phyla alive in the marine environment, 17 in freshwater, and only 15 on land (Briggs, 1994; Mora *et al.*, 2011). The contrast is higher when considering only animals, as there are 32 marine phyla and only 12 terrestrial fauna (Benton, 2001). However, although the ocean has the greatest wealth of phyla and it is about 300 times larger than the Earth's terrestrial environment, species richness/biodiversity of the terrestrial realm is 25 times greater than the one found in the marine environment (Briggs, 1994; Mora *et al.*, 2011). This difference in species richness/ biodiversity is probably caused by three key conditions (Benton, 2001). First, land offers more endemism opportunities because of the effect of geographic isolation and independent evolution; marine environment barriers are not as efficient at reducing the possibility of endemism and diversification (*e.g.*, soft barriers; Cowman & Bellwood, 2013). Second, terrestrial habitats are more diverse and heterogeneous, with large fluctuations in temperature and humidity throughout the day both seasonally and latitudinally; the physical marine environment is more stable compared to land. Third, the size of primary producer's plays an important role as marine primary producers are mostly unicellular organisms that serve as food source for benthic and pelagic animals, but are unable to provide important habitat for other species of animals and plants like in terrestrial systems (Briggs, 1994; Mora *et al.*, 2011).

Fishes worldwide consist of about 33,395 known species (Eschmeyer & Fong, 2013). They have very diverse latitudinal, longitudinal, and bathymetric distributions and very complex morphological, biological and behavioral characteristics such that it is possible that both allopatric and non-allopatric speciation processes are involved in the formation of this biodiversity. How disjunct distributions (*e.g.*, distributions composed of multiple geographically discrete and widely spaced populations) arise is an interesting question in biogeography and has long been subject of the dispersalist–vicariance debate (Cowman & Bellwood, 2013; Cowman, 2014). Dispersalist theories emphasize the importance of species traits and dispersal in explaining the occurrence of highly isolated populations, whereas vicariant theories invoke landscape evolution and fragmentation of a species' ancestral range as the principal drivers of these biotic patterns. Species with geographically disjunct ranges are important for understanding the factors controlling species' distributions, population connectivity, and the process of allopatric speciation (Ronquist, 1997; Cowen & Spongaugle, 2009; Cowman, 2014). In both cases, allopatric speciation can take place if the gap in a species' range sufficiently limits gene flow (Crisp *et al.*, 2010).

In the Mexican Pacific Ocean, two geological events have played a key role in the formation of the current fish fauna - the formation of the Gulf of California and the rise of the Isthmus of Panama (Jacobs *et al.*, 2004). The formation of the Gulf of California dates about 5-8 mya during the Pliocene-late Miocene (De la Cruz-Agüero, 2000). The geological formation of Baja California divided a group of fish species that are disjunct populations on the Pacific coast and in the northern Gulf of California (Table 1); these eleven species represent an interesting case for studies of incipient speciation (Bernardi *et al.*, 2003). The origin of these species from Magdalena-Almejas Bay and San Ignacio Lagoon is explained by the existence of interpeninsular Pleistocene-Holocene channels (0.115 - 2.6 mya) on sandy plains that connected the Pacific with the Gulf of California.

The geological development and endemism of species of tropical lineage support this hypothesis (Castro-Aguirre *et al.*, 1995, 2005; De la Cruz-Agüero, 2000). In fact, most of the disjunct species of the Pacific and Gulf of California (Table 2) show few morphological and color differences, but in some cases divergence has been detected, as in members of the genus *Leuresthes, Gillichthys*, *Girella,* and *Hypsoblennius* (Crabtree, 1983; Orton & Buth, 1984; Huang & Bernardi, 2001; Bernardi, 2014). Bernardi *et al.* (2003) analyzed 12 species with disjunct populations and found that eight species had strong genetic differences between populations of the Gulf of California and the Pacific and four of them are in the process of incipient speciation, indicating that the physic separation of populations (considered as the first step towards speciation) is very commonly responsible for the creation of new geminate species.

In the TEP, families that experienced wide speciation patterns are Gobiidae (111 species), Sciaenidae (82 species), Serranidae (56 species), Labrisomidae (48 species), Gobiesocidae (43 species), Ophichthidae (41 species), Haemulidae (37 species), Labridae (36 species), Carangidae (35 species), Chaenopsidae (34 species), and Muraenidae (33 species). A number of these species groups can be partitioned into habitat-based subcategories like soft-bottom environments, coastal pelagic environments, estuarine, coastal lagoons, coastal pelagic zones, coral reef and rocky intertidal habitats where redundancy is higher, and subtidal habitats (Table 3). Another remarkable example of adaptive radiation in the TEP is the moray eels of the genus *Gymnothorax*, with 11 indigenous species; some species inhabit subtidal reefs (*G. angusticeps* (Hildebrand & Barton, 1949)*, G. castaneus* (Jordan & Gilbert, 1883)*, G. dovii* (Günther, 1870)*, G. mordax* (Ayres, 1859)*, G. panamensis* (Steindachner, 1876)*, G. porphyreus* (Guichenot, 1848), and *G. serratidens* (Hildebrand & Barton, 1949)), and other soft bottoms (*G. equatorialis* (Hildebrand, 1946)*, G. eurygnathos* Böhlke, 2001*, G. phalarus* Bussing, 1998, and *G. verrilli* (Jordan & Gilbert, 1883)). This genus has been enriched with the addition of species of Indo-Pacific or trans-Pacific affinity (*G. buroensis* (Bleeker, 1857)*, G. flavimarginatus* (Rüppell, 1830)*, G. javanicus* (Bleeker, 1859)*, G. meleagris* (Shaw & Nodder, 1795)*, G. pictus* (Ahl, 1789) and *G. undulates* (Lacepède, 1803)), currently consisting of 17 species in total for TEP (Table 3).

Speciation events and the great topographic and bathymetric biodiversity have turned the Gulf of California into one of the most diverse regions of the TEP with about 875 species of fish, 92 of which are endemic (Thomson *et al.*, 2000); it is regarded as a center of origin along with the Central America landscape (Mora & Robertson, 2005).

According whith O'Dea *et al*. (2016), the formation of the Isthmus of Panama resulted in the absence of further gene flow between shallow marine animal populations after 3.2 millon years (mid-Pliocene) by the interrupted the communication between the Pacific and Atlantic and particularmente causing the effective isolatiion of fish populations, resulting in the formation of new species as well as the disappearance of others (Castro-Aguirre *et al.*, 1995).

It is hypothesized that the presence of a marine Pleistocene gap in the area of Panama (1.8-2 mya), initiated the divergence of some transisthmian species of the genus *Anisotremus* (Tavera-Vargas, 2006). While 85% of the coastal fish fauna of the TEP is derived from taxa present before the rising of the Isthmus of Panama, the low percentage of common species in the two regions of the American continent (> 100 sister species, pairs or transisthmian; see Table 4) is the result of independent evolution of their faunas in very different environments (Rosenblatt, 1967; Robertson *et al.*, 2004; Aguilar-Medrano, 2018). In some genera, the sister species have been separated taxonomically by minor morphological differences or genetic differences, such as the Pacific machete and Atlantic ladyfish (*Elops affinis* Regan 1909 - *E. saurus* Linnaeus, 1766), Pacific sleeper and bigmouth sleeper (*Gobiomorus maculatus* (Gunther,1859) - *G. dormitor* Lacepede, 1800), the Pacific fat sleeper and fat sleeper (*Dormitator latifrons* (Richardson, 1844) - *D. maculatus* (Bloch, 1792)), Atlantic and Pacific spadefish (*Chaetodipterus faber* (Brousonnet, 1782) - *C. zonatus* (Girard, 1858)), the Panamic banged blenny and the red-lip blenny (*Ophioblennius steindachneri* Jordan & Evermann, 1898 - *O. macclurei* (Silvester, 1915)). For the latter, a new species (*O. clippertonensis* Springer, 1962) has been recognized for Clipperton Atoll, a small isolated island at the western edge of the TEP (Allen & Robertson, 1997). In contrast, for some, the separation into two species is not possible or even questionable including the nurse shark *Ginglymostoma cirratum* (Bonnaterre, 1788), the lemon shark *Negaprion brevirostris*, the leatherjacket *Oligoplites saurus* (Poey,1868) the yellowfin mojarra *Gerres cinereus* (Walbaum, 1792) and the fringed flounder *Etropus crossotus* Jordan & Gilbert 1882; these are remarkably similar in external morphology, but also in their behavior and ecology (Castro-Aguirre *et al.*, 1995; Thomson *et al.*, 2000).

Table 1. Fish incipient speciation examples in the Mexican Pacific Ocean. Numbers= information from references below.

| **Family** | **Species** | **Common name** | **Habitat** | **Reference** |
|---|---|---|---|---|
| Atherinidae | *Atherinops affinis* (Ayres, 1860) | Topsmelt silverside | [1]Nearshore generalist | Bernardi *et al.* (2003) |
| Scorpaenidae | *Sebastes macdonaldi* (Eigenmann & Beeson, 1893) | Mexican rockfish | [1]Shallow generalist | Bernardi *et al.* (2003) |
| Haemulidae | *Anisotremus davidsonii* (Steindachner, 1876) | Xantic sargo | Rocky-sand bottom | Bernardi *et al.* (2003)<br>Bernardi & Lape 2005 |
| Sciaenidae | *Cheilotrema saturnum* (Girard, 1858) | Black croaker | Near sand bottom | Bernardi *et al.* (2003) |
| Embiotocidae | *Zalembius rosaceus* (Jordan & Gilbert, 1880) | Pink seaperch | Offshore deeper water | Bernardi *et al.* (2003) |
| Labridae | *Halichoeres semicinctus* (Ayres, 1859) | Rock wrasse | [2]Shallow nearshore, algal-covered substrata | Bernardi *et al.* (2003) |
| Blennidae | *Hypsoblennius jenkinsi* (Jordan & Evermann, 1896) | Mussel blenny | [3]Holes and crevices in rocky areas, in burrows of boring clams or tubes of marine worms, and in mussel beds | Bernardi *et al.* (2003) |
| Gobidae | *Gillichthys mirabilis* Cooper, 1864 | Longjaw mudsucker | Bays and coastal sloughs, burrowing in shallow mud substrate in tidal flats and bays including coastal lagoons | Bernardi *et al.* (2003) |
| Paralichthyidae | *Paralichthys californicus (Ayres, 1859)* | California flounder | [1]Shallow generalist | Bernardi *et al.* (2003) |
| Pleuronectidae. | *Pleuronichthys ocellatus* (Starks & Thompson, 1910) | Ocellated turbot | Offshore over sand and sandy mud soft substrates | Bernardi *et al.* (2003) |
| Pleuronectidae. | *Pleuronichthys verticalis* Jordan & Gilbert, 1880 | Hornyhead turbot | [1]Nearshore soft bottom | Bernardi *et al.* (2003) |

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Table 2. Examples of some fishes that exhibit disjunct or geographically discontinuous ranges between the Gulf of California and outer Pacific Coast.

| Family | Species | Common name | Geographical distribution | Source |
|---|---|---|---|---|
| Atherinidae | *Leuresthes tenuis* (Jenkins & Evermann, 1889) | Gulf grunion | The California grunion, is a common inhabitant of the inshore waters of the northeastern Pacific. This pelagic, schooling fish is usually found from just behind the surf line to a depth of about 18 m. It ranges from San Francisco to Magdalena Bay, Baja California, but is rarely found north of Point Conception in southern California. | (Miller & Lea 1972; Eschmeyer *et al.,* 1983; Love, 1996). |
| Atherinidae | *Leuresthes sardina* (Ayres, 1860) | California grunion | The California grunion ranges from Monterey Bay, California, to Magdalena Bay, Baja California Sur. | (Walker, 1952; Moffatt &Thomson. 1975). |
| Kyphosidae | *Girella nigricans* (Ayres, 1860) | Rudderfish, Opaleye | This species is endemic to the Eastern Pacific, and is found from California to southern Baja, and an isolated population in the central and northern Gulf of California. | Allen & Robertson (2010a) |
| Kyphosidae | *Girella simplicidens* Osburn & Nichols, 1916 | Gulf opaleye | Gulf of California; abundant in the northern Gulf, but scarce in the southern portion. | Robertson & Allen (2015) |
| Blennidae | *Hypsoblennius gentilis* Girard, 1854 | Bay blenny | This species is endemic to the Eastern Pacific, and is found from Monterey, California, USA to the northern and central Gulf of California. | Bessudo *et al.* (2010) |
| Chaenopsidae | *Chaenopsis alepidota* (Gilbert, 1890) | Orangethroat pikeblenny | This species is endemic to the Eastern Pacific, and has a disjunct distribution. It is found in southern California, USA and northern Baja California, Mexico and in the western and north-eastern Gulf of California. | Bessudo *et al.* (2010b) |
| Serranidae | *Paralabrax maculatofasciatus* Steindachner, 1868 | Spotted sand bass | The spotted sand bass has a historic range from Mazatlan, Baja California, to Monterey in Central California. Dense populations also occur in the northern portions of the Gulf of California. | (Allen *et al.*,1995; Stepien *et al.,* 2001) |
| Gobiidae | *Gillichthys mirabilis* Cooper, 1864 | Longjaw mudsucker | Inhabits sloughs and estuaries from Tamales Bay just north of San Francisco Bay to sites throughout Baja California. | Gracey (2008) |
| Haemulidae | *Anisotremus davidsonii* Steindachner, 1876 | Xantic sargo | This species is endemic to the Eastern Pacific, and is found from central California to central Baja, and the northwestern and eastern Gulf of California. | Allen *et al.* (2010b) |
| Gobiidae | *Lythrypnus dalli* (Gilbert, 1890) | Blue-banded goby | This species is endemic to the Eastern Pacific, ranging from Monterey Bay to the tip of Baja, and the Gulf of California to northern Peru, including the Malpelo, Galapagos, and Guadalupe Islands, at depths ranging from intertidal to 64 m, is most abundant in rocky subtidal habitats along the coast and offshore islands of southern California and northern Baja California, Mexico. | (Miller & Lea, 1972, 1976; Wiley, 1976; Van Tassell *et al.* 2010c) |
| Kyphosidae | *Hermosilla azurea* (Jenkins & Evermann, 1889) | Zebra-perch sea chub | This species is endemic to the Eastern Pacific, and is found from Monterey, California to Baja California, and in the Gulf of California. | Allen *et al.* (2010c) |
| Labridae | *Halichoeres semicinctus* (Ayres, 1859) | Rock wrasse | This species can be located from the Gulf of California, Mexico to Point Conception, California. | Miller & Lea (1972) |
| Labridae | *Semicossyphus pulcher* (Ayres, 1854) | California sheephead | The California sheephead is found from Monterey Bay, California, to the northern Sea of Cortez, Mexico, including the California Channel islands and the isolated Guadalupe Island, Mexico. | (Miller & Lea, 1972; Present, 1987; Poortvliet *et al.*, 2013) |
| Scorpaenidae | *Sebastes macdonaldi* (Eigenmann & Beeson, 1893) | Mexican rockfish | Mexican rock fish is the Northeast Pacific rockfish with the southernmost distribution, ranging from Point Sur, Central California, to offshore banks off Bahía Magdalena, Baja California. The species distribution is discontinuous since it has not been reported further south at the entrance to the Gulf of California. Within the gulf, Mexican rockfish is found near Guaymas and in Bahía de Los Angeles. | (Moser, 1971; Chen, 1975; Thomson *et al.*, 2000) |

Tabla 2. Continúa.

| Family | Species | Common name | Geographical distribution | Source |
|---|---|---|---|---|
| Pleuronectidae | *Pleuronichthys verticalis* (Jordan & Gilbert, 1880) | Hornyhead turbot | The hornyhead turbot is a common resident flatfish on the mainland shelf from Magdalena Bay, Baja California, Mexico to Point Reyes, California at depths from 9 to 201 m. | (Miller & Lea 1972; Eschmeyer *et al.*, 1983) |
| Embiotocidae | *Zalembius rosaceus* (Jordan & Gilbert, 1880) | Pink seaperch | Northern California to central Baja California, plus an isolated population in the upper and central Gulf of California. | Eschmeyer *et al.* (1983). |
| Scorpaenidae | *Scorpaena guttata* Girard, 1854 | Scorpionfish | California to lower Baja, with an isolated population in the upper half of the Gulf of California. | (Eschmeyer *et al.*, 1983; Love *et al.*, 1987; Eschmeyer & Alvarado, 2010) |
| Percichthydae | *Stereolepis gigas* Ayres, 1859 | Giant seabass | Their historical range is from Humboldt Bay, CA to Baja Mexico (Point Abreojos) and into the northern Gulf of California. However, they are primarily found south of Point Conception in shallow rocky reefs. | (Domeier, 2001; Cornish, 2004; Hawk & Allen, 2014) |
| Agonidae | *Xeneretmus ritteri* Gilbert, 1915 | Stripefin poacher | Eastern Central Pacific: Malibu in southern California, USA to central Baja California, Mexico; isolated population in northern Gulf of California. | Eschmeyer *et al.* (1983) |
| Pleuronectidae | *Hypsopsetta guttulata* (Girard, 1856) | Diamond turbot | Is an estuarine flatfish ranging from Cape Mendocino to Bahía Magdalena on the Pacific coast of North America, and from Bahía Concepción to Guaymas in the Gulf of California. | (Miller & Lea, 1972; Lane, 1975; Present, 1987). |

The *Stathmonotus* blennies provide a clear example of allopatric speciation. This genus is represented by three species in the TEP, the Gulf worm blenny *S. sinuscalifornici* (Chabanaud, 1942) from the province of Cortez, the Mexican worm blenny *S. lugubris* (Bohlke, 1953) from the Mexicana province and the Panamanian worm blenny *S. culebrai* Seale, 1940 from the Panamic province. Hastings (2000) proposed two hypotheses to explain the speciation of the genus. First, the final rise of the Isthmus of Panama isolated a population into the Caribbean, which was widely distributed in the region or initially restricted to the Panamic province, later dispersing throughout the Tropical Pacific Ocean (TPO). Subsequently, the gap of Sinaloa isolated *S. sinuscalifornici* from the other members of the genus of the TEP, then the gap in Central America isolated *S. lugubris*, and *S. culebrai*. The alternative hypothesis proposes that speciation of the Caribbean species (*S. gymnodermis* Springer, 1955, *S. hemphillii* Bean, 1855 and *S. stahli* (Evermann & Marsh, 1899)) occurred before the final rise of the Isthmus of Panama, in which case the divergence within the TEP could start before the final rise of the Isthmus. This hypothesis is reinforced because in all other paired species of blenny, sister species are phenotypically very similar which is consistent with a short time period since its divergence (Lin & Hastings, 2013).

Furthermore, there are 190 trans-Pacific species, 126 coastal species, and 64 oceanic pelagic species representing about 12% of the fish fauna of the TPO in the TEP (Robertson & Allen 1996; Robertson *et al.*, 2004). The conditions that favor the establishment and residence of these species are not clear, although the horizontal ocean temperature gradients tend to restrict the latitudinal ranges of species, whereas extending their ranges longitudinally has fewer restrictions. According to Briggs (1961) and Margalef (1972), the strong interspecific competition that is generated in a very integrated ecosystem like the western Pacific (an ecosystem of high biodiversity) can cause outward emigrations and colonization, which are directed towards the central and eastern Pacific (areas of low biodiversity). A similar case is observed in the fish fauna of coral and rocky reefs of the TPO where richness is high and therefore the degree of competition as well. In this way, several species inhabit these systems (*e.g.*, *Chaetodon humeralis* Gunther, 1860, *Diodon holocanthus* Linnaeus, 1758, and *Hippocampus ingens* Girard, 1858) or emigrate to soft bottom systems for feeding (*e.g.*, *Haemulon flaviguttatum* Gill,1862, and *H. maculidauda* (Gill,1862). However, movement of species from reef systems to soft bottoms is rare, since they can hardly compete for resources with resident species.

In the offshore Ocean Island province of the TEP, an interesting case occurs. Briggs (1961) remarks that for the Indo-Pacific migrant fishes it is easier to recruit to oceanic islands populations because these areas represent less competition than the mainland. A migrant group of fishes is well represented in the Revillagigedo Islands (18°49’ N 112°46’ W; some 390 km southwest of Cabo San Lucas, Baja California del Sur, Mexico; Fig. 1) with 21% of the fauna (Castro-Aguirre & Balart, 2002) and in the Clipperton Atoll (10°17’ N, 109°13’ W) with about 75% of species (Robertson & Allen, 1996). This atoll has been regarded as a bridge that connects the coastal biota of the TEP and western Pacific (Robertson & Allen, 1996). Only 99 species of shore fish are endemic to oceanic islands and – 30% of the remaining has self-sustaining insular populations (Robertson & Allen, 1996, 2002) which may favor the colonization of trans-Pacific species.

Table 3. Examples of some families of marine fish with wide speciation patterns in the Tropical Eastern Pacific Ocean.

| **Habitat type** | **Family** | **Genus** | **Common name** | **Species** |
|---|---|---|---|---|
| Soft-bottom | Cynoglossidae | *Symphurus* | Tonguefish | *S. atramentatus* Jordan & Bollman, 1890,*S. atricaudus* (Jordan & Gilbert, 1880),*S. callopterus* Munroe & Mahadeva, 1989, *S. chabanaudi* Mahadeva & Munroe, 1990, *S. diabolicus* Mahadeva & Munroe, 1990; *S. elongatus* (Günther, 1868), *S. fasciolaris* Gilbert, 1892, *S. gorgonae* Chabanaud, 1948*, S. leei Jordan &* Bollman, 1890, *S. melanurus* Clark, 1936, *S. melasmatotheca* Munroe & Nizinski, 1990, *S. microlepis* Garman, 1899, *S. ocellaris* Munroe & Robertson, 2005, *S. oligomerus* Mahadeva & Munroe, 1990, *S. prolatinaris* Munroe, Nizinski & Mahadeva, 1991, *S. undecimplerus* Munroe & Nizinski, 1990, *S. varius* Garman, 1899, *S. williamsi* Jordan & Culver, 1895. |
|  | Sciaenidae | *Stellifer* | Drums | *S. chrysoleuca* (Günther, 1867), *S. ephelis Chirichigno F., 1974, S. ericymba* (Jordan & Gilbert, 1882), *S. fuerthii* (Steindachner, 1876), *S. mancorensis Chirichigno F., 1962, S. melanocheir* Eigenmann, 1918, *S. minor* (Tschudi, 1846), *S. oscitans* (Jordan & Gilbert, 1882), *S. pizarroensis* Hildebrand, 1946, *S. walkeri* Chao, 2001, *S. wintersteenorum* Chao, 2001, *S. zestocarus* Gilbert, 1898. |
| Coastal Pelagic | Engraulidae | *Anchoa* | Anchovy | *A. analis* (Miller, 1945), *A. argentivittata* (Regan, 1904), *A. chamensis* Hildebrand, 1943, *A. compressa* (Girard, 1858), *A. curta* (Jordan & Gilbert, 1882), *A. delicatissima* (Girard, 1854), *A. eigenmannia* (Meek & Hildebrand, 1923), *A. exigua* (Jordan & Gilbert, 1882), *A. helleri* (Hubbs, 1921), *A. ischana* (Jordan & Gilbert, 1882), *A. lucida* (Jordan & Gilbert, 1882), *A. mundeola* (Gilbert & Pierson, 1898), *A. mundeoloides* (Breder, 1928), *A. nasus* (Kner & Steindachner, 1867), *A. panamensis* (Steindachner, 1876), *A. scofieldi* (Jordan & Culver, 1895), *A. spinifer* (Valenciennes, 1848), *A. starksi* (Gilbert & Pierson, 1898), *A. walkeri* Baldwin & Chang, 1970. |
| Intertidal zone | Gobiesocidae | Gobiesox | Skilletfish | *G. adustus* Jordan & Gilbert, 1882, *G. aethus* (Briggs, 1951), *G. canidens* (Briggs, 1951), *G. crassicorpus* (Briggs, 1951), *G. daedaleus* Briggs, 1951, *G. eugrammus* Briggs, 1955, *G. fluviatilis* Briggs & Miller, 1960, *G. fulvus* Meek, 1907, *G. juradoensis* Fowler, 1944, *G. maeandricus* (Girard, 1858), *G. marijeanae* Briggs, 1960, *G. mexicanus* Briggs & Miller, 1960, *G. milleri* Briggs, 1955, *G. multitentaculus* (Briggs, 1951), *G. papillifer* Gilbert, 1890, *G. pinniger* Gilbert, 1890, *G. potamius* Briggs, 1955, *G. rhessodon Smith, 1881, G. schultzi* Briggs, 1951, *G. stenocephalus* Briggs, 1955, *G. woodsi* (Schultz, 1944). |
|  |  | *Tomicodon* | Clingfishes | *T. absitus* Briggs, 1955, *T. abuelorum* Szelistowski, 1990, *T. bidens* Briggs, 1969, *T. boehlkei* Briggs, 1955, *T. chilensis* Brisout de Barneville, 1846*, T. eos* (Jordan & Gilbert, 1882), *T. humeralis* (Gilbert, 1890), *T. myersi* Briggs, 1955, *T. petersii* (Garman, 1875), *T. prodomus* Briggs, 1969, *T. vermiculatus* Briggs, 1955, *T. zebra* (Jordan & Gilbert, 1882). |
|  | Labridae | *Halichoeres* | Wrasse | *H. adustus* (Gilbert, 1890), *H. aestuaricola* Bussing, 1972, *H. chierchiae* Di Caporiacco, 1948, *H. discolor* Bussing, 1983, *H. dispilus* (Günther, 1864), *H. insularis* Allen & Robertson, 1992, *H. malpelo* Allen & Robertson, 1992, *H. melanotis* (Gilbert, 1890), *H. nicholsi* (Jordan & Gilbert, 1882), *H. notospilus* (Günther, 1864), *H. salmofasciatus* Allen & Robertson, 2002, *H. semicinctus* (Ayres, 1859). |
| Subtidal reef | Muraenidae | *Gymnothorax* | Morays | *G. angusticeps* (Hildebrand & Barton, 1949), *G. castaneus* (Jordan & Gilbert, 1883), *G. dovii* (Günther, 1870), *G. mordax* (Ayres, 1859), *G. panamensis* (Steindachner, 1876), *G. porphyreus* (Guichenot, 1848), *G. serratidens* (Hildebrand & Barton, 1949), *G. equatorialis* (Hildebrand, 1946), *G. eurygnathos* Böhlke, 2001, *G. phalarus* Bussing, 1998, *G. verrilli* (Jordan & Gilbert, 1883), *G. buroensis* (Bleeker, 1857), *G. flavimarginatus* (Rüppell, 1830), *G. javanicus* (Bleeker, 1859), *G. meleagris* (Shaw, 1795), *G. pictus* (Ahl, 1789), *G. undulates* (Lacepède, 1803). |

Finally, tropical trans-Pacific fishes occur on both sides of the world's largest deep-water barrier to the migration of marine shore organisms, the 4,000km to 7,000km-wide Eastern Pacific Barrier. They include 64 epipelagic oceanic species and 126 species of shore fishes known from both the TEP and the central and West Pacific. However, although trans-Pacific species are characterized by long larval stages, surprisingly, species with appropriate characteristics have not yet managed to colonize the TEP. While the region has a poor fauna, indigenous species are adapted to a very dynamic ocean environment with wide temperature fluctuations and salinity, heavy sediment discharges, reduced tidal ranges, many areas of upwelling, diverse estuarine-lagoon systems, a very narrow continental shelf, few islands and coral reef formations, extensive oxygen minimum layer, and especially the El Niño Southern Oscillation (Boschi, 2000; Glynn & Ault, 2000; Hastings, 2000; Lea & Rosenblatt, 2000; Robertson & Cramer, 2009; Aguilar-Medrano, *et al*., 2015).

The latter two phenomena are probably intolerant conditions for alien species. Fish migrations of the TEP to the western Pacific (Hawaii and the Marquesas islands) are also known but in a smaller proportion (1:3; Robertson *et al*., 2004) and are characteristic of a high number of pelagic species or species associated with floating objects (Table 5). While trans-Pacific species contribute to an increase in species richness/biodiversity of the TEP, these species have different ecological characteristics compared to the local fauna, except in a few cases such as the genera *Acanthurus* and *Ctenochaetus*, and the two species of the genus *Arothron*. Despite these, there is no evidence of the invaders having biological or ecological characteristics that offer adaptive capabilities that may provide an advantage over members of the native fauna (Robertson *et al*., 2004).

## SELECTED REVIEW OF RICHNESS / BIODIVERSITY HYPOTHESES AND ECOSYSTEM FUNCTION

Species richness depends solely on the number of species and thus the speciation processes whereas biodiversity depends on the abundance of each species in the ecosystem (Willig & Presley, 2017). Overall, there are about 50 hypotheses relating biodiversity to ecosystem function through simple hypothetical relationships that generally do not exemplify the true complexity of relationships in ecosystems (Naeem, 1998; Naeem *et al*., 2002; Thibaut & Connolly, 2012). All of these studies use sets of traits (morphological, physiological, phenological, ethological and biochemistry convergence, or similar trophic characteristics; Violle *et al*., 2007; Cadotte *et al*., 2013; Laureto *et al*., 2015; Villéger *et al*., 2017) to separate and enumerate species phylogenetically or functionally; these traits may link phylogenetic lineages and ecological processes in ecological and evolutionary time (Willig & Presley, 2017; Floeter *et al*., 2018).

Collectively, a functional trait is defined as one that can be measured in an organism and which is related to an effect on one or more ecological processes or a response to one or more environmental variables (Naeem & Li, 1997; Tilman, 2001; Diaz *et al*., 2007; Martín-López *et al*., 2007; Cadotte *et al*., 2013; Winemiller *et al*., 2015). This strategy used to represent the relationship between biodiversity and ecosystem function is a useful approach to simplify complex ecosystems based on a set of traits into units that facilitate comparative study among communities and are a low-resolution proxy to predict changes in the ecosystem. These traits can be compared directly or through calculation of functional diversity (*e.g.*, Winemiller *et al*., 2015; Villéger *et al*., 2017) that can further our understanding of the mechanisms and processes shaping patterns of biodiversity. Regardless of definitions, the functioning of ecosystems is carried out by the joint action of physical processes and natural attributes (solar radiation, evaporation, rainfall, currents, tides, etc.), the activities of the species (nitrogen fixation, feeding, breeding, growth, competition, migration, waste excretion, etc.), and the effects their activities have on the physical and chemical conditions of their environment. Thus, the function of an ecosystem is not singularly determined by the phylogenetic biodiversity of biota (Floeter *et al*., 2018), but the functional traits of individuals, the distribution and abundance of these individual, and their biological activity (Naeem & Wright, 2003; Violle *et al*., 2007; Cadotte *et al*., 2013; Díaz *et al*., 2013; Laureto *et al*., 2015; Villéger *et al*., 2017).

In recent years, the concept of functional groups has gained considerable popularity, particularly in plant ecology. Unlike the phylogenetic classifications, the approach is based on groups of functional traits that are ecologically significant and provide flexible classifications (Diaz *et al*., 2002; Villéger *et al*., 2017; Violle *et al*., 2007). Many of these ideas stem from Southwood (1977) who presented a view that habitat features provide the template for recurring properties of biotic communities and that habitats could be viewed as ecological periodic tables organizing communities. In fact, Lopez de Casenave (2001) indicates that the functional groups could represent the basic building blocks of communities and become the standard currency of the ecologists in their efforts to understand community relations. The forerunner that considered organismal traits in the classification of plants of ancient Greece into trees, shrubs and herbs was Theophrastus (300 BC; Diaz *et al*., 2002). In animals, Root (1967) was the first to employ classifications based on bird feeding strategies; these were called "guilds" and defined as a group of species that exploit a basic common resource in a similar way. Guilds or functional groups are comprised by generalist and opportunistic species with ambiguous boundaries that may in some cases be arbitrary (Root, 2001).

Pianka (1980) characterized guilds as arenas of intense interspecific competition with strong interactions, but weak interactions with the rest of their community. In contrast, Silvestre *et al.* (2003) indicates species belonging to a functional group would be those that exploited the resources within the n-dimensional niche in different ways, with a preference for certain portions of the food supply, differences in spatial occupation, or are active during different periods of the day. Furthermore, in tropical environments the effects of competition within functional groups appear minimized by the provision of non-limiting resources and the plasticity of behavioral strategies adopted by each species, avoiding agonistic encounters.

Some authors mistakenly use guild as a synonym of functional group. However, while functional groups simultaneously employ many traits related to the role of the species in the ecosystem, guilds are only based on the classification of a particular attribute (*e.g.*, feeding, reproduction, etc.). Elton (1927) was one of the first to use the term niche in the sense of the "functional state of the organism within its community" and defined the niche as "the basic function of an organism in the community because of relationships with food and their enemies." Subsequently, Root (2001) proposed to replace the Eltonian niche with "guild". This change produced contradictions that occur when several similar species are said to occupy the same niche; niche as a category is supposed to be a property of individual species (Blonder *et al.*, 2014). Therefore, species exploit niches while guilds exploit niche corners (Root, 2001). In contrast, the more ecological traits of species (Winemiller *et al.*, 2015) are employed to form functional groups, the closer we come to the definition of the niche; the fewer variables we have in the grouping of species, the closer we will approach the definition of guild (Root, 1967). Thus, Hutchinson (1957) suggested that niche could be viewed as the n-dimensional hypervolume within which the environment allows the individual or the species to survive indefinitely. Hutchinson also differentiated the maximum fundamental niche: "the hypervolume inhabited abstractly "when the species is not restricted by competition or other limiting biotic interactions, and the realized (true) niche: the smallest hypervolume occupied" under specific biotic constraints (Odum & Barrett, 2006; Blonder *et al.*, 2014; Pianka *et al.*, 2017).

Finally, the guild approach has been developed emphazing different life-history traits such that there is now a need to review the use of guild. The wide use of the guild approach has involved increasing overlap and/or confusion between different studies, which therefore increases the need for standardization while at the same time providing the opportunity to reconsider the types of guilds and their use worldwide. In fact, this term has lost its accuracy since its introduction, and has acquired a variety of meanings, ranging from functional analogs, ecological species, community guild, structural guild, functional guild, ecological species group, functional group, functional type, and many more (see Lopez de Casenave, 2001 for a review).

Until 2010, more than 90% of the studies using functional classifications were focused on terrestrial ecosystems. Of these, about 45% were plants, over 40% derived from experimental studies, and more than 30% were focused on the lifestyle of the species (Naeem & Wright 2003; Blaum *et al.*, 2011). In plants, two main approaches are used to form functional groups on the basis of environmentally significant traits (Diaz *et al.*, 2002), which can be generalized for animal studies (Barnett *et al.*, 2007). The *a priori* strategy based on a single character or a very small number of traits to define different groups. The definition of groups is required prior to the study in question (subjective classification, Jaksic, 1981; Terborgh & Robinson, 1986; Blondel, 2003; Naeem & Wright, 2003) and *a posteriori* method, which is based on the collection of information on a number of traits and the subsequent identification of functional groups from the simultaneous consideration of all these traits through multivariate statistics (Winemiller *et al.*, 2015; Pianka *et al.*, 2017). Typically, the functional groups and the most relevant traits are not defined before starting the study, but arise as a result of the study (objective classification; Hawkins & MacMahon, 1989; Simberloff & Dayan, 1991; Naeem & Wright, 2003; Winemiller *et al.*, 2015; Pianka *et al.*, 2017) regarding the environment or particular influence on ecosystem processes responses (Hooper *et al.*, 2002).

The type and number of traits used in functional classifications vary according to the scale of analysis and research objectives. Clearly, identifying key ecological traits involved in the processes of ecosystems is a major challenge to understand how species biodiversity affects ecosystem function. In general, most species within a specific ecosystem have similar environmental tolerances and occupy similar niches (Elliott *et al.*, 2007). Naeem & Wright (2003) indicated that the relationship between taxonomic biodiversity and functional diversity is sensitive to the character response and effect employed, function being assessed, the degree of redundancy and uniqueness of species, biotic interactions and trophic structure, and the biogeographic factors controlling species composition, distribution and abundance. Thus, if rare species are redundant, then ecosystem function may be insensitive to the loss of some of them, while the opposite happens if the rare species is unique. Redundancy and uniqueness may vary depending on the trait measured and effect response employed (Tilman *et al.*, 1997; Petchey & Gaston, 2006; Villéger *et al.*, 2010, 2014). In fish, morphology plays an important role in determining the type of prey consumed and morphological variation can lead to changes in foraging ability and a subsequently differential exploitation of food resources (Karpouzi & Stergiou, 2003; Cruz-Escalona *et al.*, 2005).

For example, the caudal fin generates propulsion and is important in maintaining swimming speed over long sustainable periods and also provides speed and acceleration (Fulton, 2007). However, the existence of species with different requirements and different evolutionary histories hinders determining a standard functional classification scheme to define functional groups. Some traits may be expressed by one or a few species in an association, whereas, others may have many unique traits, but it should be noted that some functional traits differently ontogenetically within a species (Vilà, 1998; Naeem & Wright, 2003; Winemiller *et al.*, 2015).

This variation challenges the classifications in functional *a priori* groups. For example, the classic fish example is the pinfish *Lagodon rhomboides* (Linnaeus, 1766) that presents an orderly progression of changes in trophic preferences (Livingston, 2002). One-year-old young recruits (< 20 mm standard length, SL) are primarily planktivorous, but as they grow (21-33 mm SL) they have a gradual transition to benthic carnivores, feeding on amphipods, mysids, and harpacticoid copepods, and at ~60 mm SL, they prefer amphipods, shrimp, algae and detritus. Fish between 61-120 mm SL eat crabs, shrimps and bivalve molluscs and once they exceed 120 mm SL they generally feed on seagrass, being practically herbivorous. The transition from one feeding stage to the next is gradual, but, in general, related to stages of growth associated with ontogenetic changes in morphology (dimension of the mouth, teeth, and size of the stomach) and body shape (Livingston, 2002).

Some authors suggest that there is a degree of predictability in the process of convergence. If there are similar resources in two geographically isolated locations, it is possible that a group of similar species may eventually converge despite phylogenetic differences (Schluter & Ricklefs, 1993; Winemiller *et al.*, 2015; Pianka *et al.*, 2017). However, despite ecosystems having quite similar structure, the organization of the species niches may be different; that is, a function performed by a species in an ecosystem can be equivalent within a second similar ecosystem, but in a third ecosystem, its function can be divided among several species, or included as part of the functions of another species (Smith & Smith, 2001). Furthermore, as a result of convergent evolution, some groups of plants and animals worldwide with independent evolutionary histories but under similar environmental conditions, adapt to similar ecological niches, and thus represent ecological equivalents (Whittaker & Levin, 1975; Pianka, 2000).

Table 4. Examples of sister species of marine fish with wide speciation in the Tropical Eastern Pacific Ocean.

| Family | Sister species | Common name | Distribution |
|---|---|---|---|
| Elopidae | *Elops affinis*, Regan, 1909 | Pacific ladyfish, machete | This species is present in the eastern Pacific stretching from southern California to Peru, including Isla del Coco (Adams *et al.,* 2012; Eschmeyer & Fong, 2013). |
| | *Elops saurus*, Linnaeus, 1766 | Atlantic ladyfish, northern ladyfish, tenpounder | The species is only distributed in the Western Atlantic from southern New England (but uncommon north of Cape Hatteras, NC) south to Florida, and throughout the Gulf of Mexico to the Yucatan Peninsula (McBride & Horodysky 2004; McBride *et al.*, 2010; Adams *et al.,* 2012). *Elops saurus* was recently split into two species, *E. saurus* and *E. smithi* (McBride *et al.*, 2010). |
| Eleotridae | *Gobiomorus maculatus* (Günther, 1859) | Pacific sleeper | This species is endemic to the Eastern Pacific, and is found from the tip of Baja California and the mouth of the Gulf of California, Mexico to northern Peru, including the Galapagos and Cocos Islands (Van Tassell, 2010a). |
| | *Gobiomorus dormitor*, Lacepède, 1800 | Bigmouth sleeper | This species is distributed in the western Atlantic from Bermuda, southern Florida, in the Bahamas from Andros Island, in the Gulf of Mexico from Louisiana (USA) down along Mexico to Cuba, throughout the Caribbean except the Cayman Islands and the northern Lesser Antilles, and along the Central and South American coast from Quintana Roo, Mexico to Touros, Brazil (Gilmore, 1992; McEachran & Fechhelm, 2005, Page &Burr, 2011). It can be found a considerable distance upstream at altitudes up to 300 m (Hildebrand, 1935). This species is most abundant in the Caribbean region, but is also common in tributaries to the southern Gulf of Mexico (Gilmore, 1992; Pezold *et al.*, 2015). |
| | *Dormitator latifrons* (Richardson, 1844) | Pacific fat sleeper | This species is endemic to the Eastern Pacific, and is found from southern California, USA and the Gulf of California, Mexico to Ecuador, including the Galapagos Islands (Van Tassell, 2010b). |
| | *Dormitator maculatus* (Bloch, 1792) | Fat sleeper | This species is distributed in the western Atlantic from North Carolina (USA) south along the U.S. and in the Bahamas, throughout the Gulf of Mexico and Caribbean Sea to southeastern Brazil. It has been recorded as far north as Massachusetts, however, rarely occurs past North Carolina. It can be found up to nine meters depth (Robins & Ray, 1986; Rezendes-Medina, 1973; Felder *et al.*, 2009; Nordlie, 2012). It is not known from the Cayman Islands. In the southern Gulf of Mexico is has been recorded from Pantanos de Centla, Mexico in Arroyo Punteada, the dredged canal San Román, the drains Narváez Norte and Narváez Sur, the lagoons Cantemoc, Concepción, El Coco, El Guanal, El Viento, Landeros, Larga, Los Ídolos, Punteada, El Sauzo, San Isidro, San Isidro El Jobo, San Pedrito, the Grijalva Centro River and the first section of the Ribera, Alta River (Usumacinta River) in 28.4°C and PSS 0.6, on average (Macossay-Cortez *et al.*, 2011; Aiken *et al.*, 2015). |
| Ephippidae | *Chaetodipterus zonatus* (Girard, 1858) | Pacific spadefish | This eastern Pacific species is found from southern California to the Gulf of California to northern Peru, and Malpelo (Smith-Vaniz *et al.*, 2010). |
| | *Chaetodipterus faber* (Broussonet, 1782) | Atlantic spadefish | Atlantic spadefish species is distributed in the western Atlantic from Massachusetts south along the U.S. coast, Bermuda, the Bahamas, throughout the Gulf of Mexico and Caribbean Sea, and along the South American coast to southern Brazil. Its depth range is 0-30 m (Dooley *et al.*, 2015). |
| Blenniidae | *Ophioblennius steindachneri*, Jordan & Evermann, 1898 | Panamic banged blenny | This species is endemic to the Eastern Pacific, and is found from central Baja California and the northern Gulf of California, Mexico to Peru, and including the Revillagigedo, Cocos, Malpelo and Galápagos Islands (Bessudo *et al.*, 2014). |
| | *Ophioblennius macclurei*, (Silvester, 1915) | Redlip blenny | Redlip Blenny is distributed in the western Atlantic from the Gulf of Mexico in Vermillion Bay, Louisiana south to the Yucatan, Cuba, and Florida Keys, the Bahamas, and throughout the Caribbean Sea. It is also found on offshore reefs and banks in the eastern and northwestern Gulf of Mexico from Florida in the Dry Tortugas, off Texas, Veracruz, Mexico, and on Alacranes Reef off Yucatan (McEachran & Fechhelm, 2005; Williams, 2014). |

Table 5. Examples of tropical trans-Pacific fishes. Asterisks = information from reference below.

| Family | Specie | Common name | Distribution | Habitat |
|---|---|---|---|---|
| *Sphyrnidae | *Sphyrna zygaena*, (Linnaeus, 1758) | Smooth hammerhead | Cirncumglobal in tropical and temperate seas; California to Mexico, Colombia to Chile. | A coastal-pelagic and semi-oceanic hammerhead often sighted near Surface. |
| **Carangidae | *Decapterus muroadsi* (Temminck & Schlegel, 1844) | Amber-striped scad, Mexican scad | An Indo-Pacific species; southern California to the tip of Baja, Ecuador to Chile, the Revillagigedos and Galapagos. | The Amberstriped scads are a coastal pelagic species found at depths up to 1,050 feet. Adults are pelagic, in oceanic and inshore waters forming schools. |
| *Echinorhinidae | *Echinorhinus cookei*, Pietschmann, 1928 | Prickly shark | A subtropical to temperate Pacific species; Oregon to Chile. | Demersal, 10-1100 m depth. Reef associated (reef + edges-water column and soft bottom). Soft bottom (mud/sand/gravel/beach) |
| Mugilidae | *Mugil cephalus*, Linnaeus, 1758 | Striped mullet | This species is widespread throughout the tropics and sub-tropical seas to warm temperate regions. | This species is pelagic near shores, it sometimes forages in lagoons, estuaries and lower courses of rivers and can tolerate freshwater. It is known to breed in its third year of life: adults school in estuaries then move out to sea to spawn in coastal surface water, before returning to estuaries and freshwater (Harrison and Senou 1999). Juveniles feed on zooplankton, larger individuals filter algae, detritus, sediment and small invertebrates. |
| Lobotidae | *Lobotes pacificus*, Gilbert, 1898 | Pacific tripletail | Southern California to the Gulf of California to Perú, Coccos islands. | Occurs in bays and brackish estuaries or sometimes well out to sea around floating objects; juveniles sometimes in flotsam, they may lay on their side at the Surface and mimic a drifting dark leaf. |
| **Carangidae | *Caranx caballus*, Günther, 1868 | Green jack | Green jack are widely distributed along the Pacific coast of the Americas, from southern California, USA, to Peru (Mair *et al.* 2012; Robertson and Allen 2008). | Often caught in open water between the islands on spoons or feather lures trolled by fishermen. |
| **Carangidae | *Seriola rivoliana*, Valenciennes, 1833 | Almaco jack | Througout tropical and subtropical waters, in the eastern Pacific from Oceanside, California to Perú, and Galápagos. | Open water or near escarpments, occasionally moving into more shallow waters to feed. Species associated with floating objects. |
| **Carangidae | *Uraspis helvola* (Forster, 1801) | Whitemouth jack | This species is widely distributed in the Indo-West Pacific but rarely collected. Verified records from the Western Central Pacific area are pending and if *U. secunda* is a junior synonym, this species is also widely distributed throughout the Atlantic. In the Eastern Central Atlantic, *Uraspis helvola* occurs off St. Helena and Ascension Islands, and there is also a record from off Cape Verde. In the Indo-West Pacific, this species occurs from off South Africa, Mozambique, Somalia, the Red Sea, off Oman and Bahrain, Sri Lanka, the Andaman Sea, the northern South China Sea, the Hawaiian Islands and offshore islands of the tropical eastern Pacific. Records from the Philippines south to Australia need verification. | A pelagic schooling species that prefers waters over the continental shelf, and around islands (Smith-Vaniz & Williams, 2015). The depth range for this species is 50 to 300 m (Jiménez Prado & Béarez, 2004). |
| *Khiphosidae | *Kyphosus ocyurus*, (Jordan & Gilbert, 1882) | Bluestriped sea-chub | From southern California to Perú (excluding the bulk of the Gulf of California) and all the oceanic islands. Occasional specimens have also reached Tahiti and Hawai, and there is a resident population in the Marquesas Islands of Polynesia. | Most common around offshore islands, also frequently seen near floating logs far out to sea. |

Tabla 5. Continúa.

| Family | Specie | Common name | Distribution | Habitat |
|---|---|---|---|---|
| Scombridae | *Euthynnus lineatus*, Kishinouye, 1920 | Black skipjack | The occurrence of black skipjack is sometimes reported in the logbooks of commercial tuna fishing vessels, although this species is not taken by these vessels. A search of the tuna boat log- book records of the Inter-American Tropical Tuna Commission revealed that this species has been encountered, at various times, nearly everywhere along the coast from the middle of Baja California to Guayaquil Bank, off northern Peru. They have frequently been reported from the Gulf of California, the Revillagigedo Islands, all along the coast of Mexico and Central America, and the Galapagos Islands. In addition, black skipjack have occasionally been reported from Clipperton and Cocos Islands and there is a single report from Shimada Bank (l6°52’N by 17°30’W), 1.80 miles southwest of Clarion Island. | This species is associated with floating objects. |
| Ballistidae | *Balistes polylepis, Steindachner, 1876* | Finescale triggerfish | In the eastern Pacific, this species ranges from northern California to the Gulf of California to central Chile and all the offshore islands. It also occurs in Hawaii (may be a vagrant), where it may be establishing a population, and seen in the Marquesas islands in 1999. | This reef-associated species occurs in rocky reefs, boulder strewn slopes, and adjacent areas of sand. Adults are demersal; and young are pelagic. It feeds on sea urchins, small crustaceans, and mollusks. This species is known to occur to 50m but may occasionally be found deeper. This species is associated with floating objects (Nielsen *et al.*, 2010). |

**Grove, J.S. & R.J. Lavenberg. 1997. The fishes of the Galápagos Islands. Stanford University Press, Stanford, California

*Robertson, D.R. & G.R., Allen. 2008. Shore fishes of the Tropical Eastern Pacific. Panamá: Smithsonian Tropical Research Institute. Retrieved from: http://www.neotropicalfishes.org/sftep; www.stri.org/sftep.

For example, members of the Labridae are one of the most structurally and functionally diversified fish families on coral and rocky reefs around the world, having evolved a diverse array of skull forms for feeding on diverse prey ranging from molluscs, crustaceans, plankton, detritus, algae, coral, and other fishes (Westneat *et al.*, 2005). Despite the importance of labrids to coastal reef ecology, Westneat *et al.* (2005), determined a repeated phylogenetic pattern of functional divergence in local regions of the labrid phylogenetic tree that produces an emergent family-wide pattern of global convergence in jaw function. The divergence of close relatives, convergence among higher clades, and several unusual ‘breakthroughs’ in skull function characterize the evolution of functional complexity in these diverse groups of reef fishes. Finally, closely related species are not necessarily similar morphologically and functionally as Steneck (2001) illustrated that taxonomically unrelated species, which are similar in anatomy, ethology, physiology and function within natural communities, have evolved similar functional traits under similar environmental conditions from disjunct geographic locations. For example, feeding behavior and diet associations between Brazilian offshore rocky reef and freshwater lake communities showed a great similarity despite the taxonomic differences between preys (Sazima, 1986). The feeding behavior of about a third of the fish in each community was ecologically equivalent, even though the author excluded species with close phylogenetic relationships (*e.g.*, Belonidae). Despite having very different floristic and faunal communities, there were a number of similar structural and functional characteristics; the similarity in the feeding strategy in some species was very strong, including behavior, appearance, and structure of the alimentary tract.

The territorial behavior exerted by species of the Pomacentridae and Serranidae families in reef systems is similar to species of Characidae and Cichlidae families in lakes (Sazima, 1986). However, each system has species with specific tactics, such as cleaning characteristic of reef systems, and piranha attacks on large predators and scavengers in lakes. In both communities, species richness was similar (rocky reefs: 64 species, 35 families, and 10 orders vs Lakes: 61 species, 16 families and 5 orders), but the marine reefs were taxonomically more diverse (3.9 vs 1.9 genera per family). These observations support the idea that associations of unrelated species have the ability to evolve into a suite of behavioral, structural, and functional organization patterns, based, in part, on similarity in environmental selective pressures on functional traits (Whittaker & Levin, 1975; Pianka, 2000).

Several generalities have been recognized in regard to biodiversity and species’ distribution patterns. One of the most important is the “latitudinal gradient in species richness” which suggests the existence of high species richness at low latitudes (the tropics) that gradually decreases towards higher latitudes (Willig & Bloch, 2006; Willig & Presley, 2017). This gradient is maintained in terrestrial, marine and freshwater ecosystems and is more pronounced in taxa with higher species richness. Over 30 scenarios have been proposed to explain this trend (*e.g.*, average domain-climatic stability, spatial heterogeneity, species-energy, historical disturbance, among others), but none has gained general acceptance and the issue is still debated (Willig *et al.*, 2003; Willig & Presley, 2017).

Briggs (2006) proposed an explanation of the latitudinal pattern of biodiversity in the marine environment based on historical events and the types of speciation involved. According, tectonic events during the Jurassic period (~ 200 mya) caused the separation of Pangea and the combination of four significant factors stimulated the increase in marine biodiversity. These are (1) an increase in sea level, (2) the formation of biogeographic barriers, (3) an increase in the areas of continental shelves, and (4) an increase in global temperature. Then, between the Cretaceous (~ 145 mya) and the Tertiary periods, sea level and the temperature dropped, and a mass extinction occurred which extinguished about half of the species of the planet; the recovery took two million years. During the Cenozoic (~ 66 mya to present), the present temperature gradient from the tropics to the poles was established as well as the consequent global gradient of organic biodiversity.

The first key process that contributed to the increase of biodiversity of the Cenozoic was the formation of biogeographic regions and provinces due to the temperature gradients, promoted by tectonic movements and changing ocean currents. Subsequently, four centers of evolutionary origin (Antarctica, the North Pacific, eastern Indonesia, and the southern Caribbean) are suggested to be the main sources of diversification in the marine environment, increasing biodiversity in other parts of the world (Briggs, 2007). The centers of origin hypothesis (Briggs, 2000; 2006; 2007) assumes that interspecific interactions (competition, predation, etc.) are the main determinants of the number of coexisting species in a habitat, that all available energy is used by the resident species, and that only through finer subdivision of habitat may increase the richness of a community (Pianka, 2000; Ruggiero, 2001; Ruggiero *et al.*, 2015). However, adjustment of the centers of origin hypothesis indicates that species richness at the local scale is increased by processes that occur at the regional scale (Ruggiero, 2001). Thus, typical processes of speciation and migration occurring within biogeographic provinces can add species to these communities without speciation and niche differentiation at the local scale.

The species occupying centers of origin appear to be highly competitive, well adapted, and have the necessary genetic resources to adjust to environmental changes. When species extend their distribution ranges, they can displace less competitive species, and in turn, are exposed to a variety of barriers that can disrupt their genetic integrity (Briggs, 2007). Eventually, the barrier can result in allopatric speciation and ultimately, the generation of new species. Populations of geographical provinces isolated by physical barriers contribute to the overall richness/biodiversity of populations of endemic species produced by allopatric speciation.

The characteristic sympatric speciation within centers of origin and the allopatric speciation of peripheral provinces seem to be the main sources of marine biodiversity. However, Krebs (2003) notes that environmental factors control natural selection in temperate and polar areas, whereas in the tropics, biological competition is more important for evolution. This concept reflects that the core processes for the functioning of ecosystems can be maintained by very few species and questions if there is really a relationship between biodiversity and ecosystem function (Tilman *et al.*, 2014). Finally, although the centers of origin hypothesis (Briggs, 2007) is often supported by certain patterns of species distribution (Mora *et al.*, 2003), it is often not considered valid on multiple grounds by some experts (Morrone, 2002); thus, it is necessary to be taken with caution. In contrast, the species-energy hypothesis (Hillebrand, 2004a) based on a great number of indirect variables such as air temperature, sea temperature, radiation, biomass, productivity, and potential and actual evapotranspiration, which reflect the availability of energy, has been widely accepted in marine environments. However, the major disadvantage of this hypothesis, is that it presents no mechanism that links the energy transfer to biodiversity (Hillebrand, 2004a).

Because increased species richness is a well-established pattern across many taxa and is pervasive in time and space (Willig & Presley, 2017), it is likely that a number of mechanisms are required to generate latitudinal gradients and may be species and habitat dependent; gradients appear not to be based solely on variation in species richness. For example, the evolutionary time hypothesis (Rohde, 1992) that assumes that tropical areas favor high rates of speciation and low rates of extinction because they have a larger geographic area, greater productivity (energy), increased spatial heterogeneity, and a greater geological stability. Furthermore, the area hypothesis predicts that species richness and biodiversity is generally associated with a high susceptibility to allopatric speciation through geographical barrier formation, high probability of covering more niches, and higher total population size (Rosenzweig, 1992; Ruggiero, 2001; Ruggiero *et al.*, 2015).

This hypothesis agrees well with observations of fossil record indicating that tropical areas are centers of evolution, with greater evolutionary speed than mild climate areas (Hillebrand, 2004b). However, the latitudinal gradient in species richness has a few exceptions to the observed spatial pattern. An interesting example (Bolton, 1994) is the green (Chlorophyta), brown (Phaeophyta) and red (Rhodophyta) macrophytic algae that has a tendency to increase towards the poles, attributed to competition for suitable habitats with tropical coral reef species. Another latitudinal gradient related to the distribution range of the species is the “Rapoport’s rule.” This suggests a progressive increase in the size of the geographic ranges of species with latitude, a pattern that is explained as an effect of selection for greater species climate tolerance inhabiting higher latitudes (Stevens, 1989). As species inhabiting temperate-cold regions are adapted to greater climatic variability than tropical species, this allows them to extend their geographical distribution. A similar pattern occurs in marine fish where fishes that live near the ocean surface are distributed in narrow depth ranges, while fishes in deeper areas are distributed over wide ranges (Stevens, 1989; Hughes *et al.*, 2002; Macpherson, 2003; Tittensor *et al.*, 2010; Willig & Presley, 2017).

In parallel, it has been identified that biodiversity also decreases with altitude, aridity, depth, and environmental homogeneity, among other factors. A model based on planktonic foraminifera (Allen *et al.*, 2006) indicated that environmental temperature affects the metabolic speed of individuals and influences in the divergence rate and therefore the tempo of speciation. This indicates that the environmental temperature may be an important controlling factor in speciation rates and, in turn, helps explain the overall decline in species richness with increases in latitude (Briggs, 2007). However, although the temperature is a good indicator of speciation rates, this does not explain why the distribution range can differ in the longitudinal plane. Finally, Allen & Gillooly (2006) reported positive correlations between species richness and speciation rates for some groups of plankton, indicating that the speciation rate varies with species abundance; overall, new species, genera and families evolve under conditions of high biodiversity.

Based on these models and the idea that “biodiversity generates biodiversity,” Briggs (2007) argues that a high rate of speciation developed a high concentration of species in the Indo-Pacific and the southern Caribbean Sea, and that outward migration to warm-temperate latitudes occurred and from there the migration reaches the poles. One trophic strategy driving such a pattern in tropical centers of origin, is herbivory which is a widespread feeding strategy but is rare in temperate waters. Cold waters are a complicated physiological barrier relative to the increase in energy demand; thus, Briggs (2006) suggests some groups have shifted into a type of omnivorous feeding or perform seasonal changes between herbivorous and carnivorous habits. In some locations, between 57 and 79% of the species depends on their diet of algae and sea grasses (Kieckbusch *et al*., 2004).

This suggests that a considerable portion of the tropical marine biodiversity can be attributed to the presence of species that tend to evolve by means of ecological specializations, using low energy food sources. This shift towards an alternative food supply under high competition suggests that sympatric speciation may partially drive evolution in the tropics. The processes of sympatric speciation (or parapatric) are suggested to be faster than allopatric processes (Bush & Butlin, 2004), indicating that the exponential increase in biodiversity during the Cenozoic might be mainly due to the production of centers of origin (Busch & Butilin, 2004; Mittelbach *et al*., 2007).

## IMPORTANCE OF FUNCTIONAL REDUNDANCY IN ECOSYSTEM FUNCTION AND THE IMPACT OF ENVIRONMENTAL DISTURBANCES

Naeem *et al*. (2002) grouped the biodiversity and ecosystem functioning hypotheses that emerged as mechanisms into three classes according to how the relationship is modified by removing or adding species that can include temporally or trait-based trait redundancy. First, species are mostly redundant. This premise assumes that systems are sensitive to variation in biodiversity and implies that the loss of species is compensated by other species or by the incorporation of alien species that do not add new functions to the system. The basis of this premise is a classification of species into functional groups formed by redundant species (Walker, 1992). Functional redundancy is based on the premise that some species perform the same function in communities and ecosystems, and can, therefore, be replaced with little impact on ecosystem processes (Walker, 1992; Rosenfeld, 2002).

For the maintenance of ecosystem functions, a minimum number of species is required in each functional group or ecosystem stability may become reduced or lost to the extent that the functional groups disappear (Lawton & Brown 1993); thus, to ensure stable ecosystem functions, redundancy is required. Second, species are mostly unique which implies that each species contributes to ecosystem functioning in a unique way, therefore, species loss or addition causes a noticeable change in ecosystem function and stability (Naeem *et al*., 1994; Naeem & Li, 1997; Pratchett *et al*., 2011).

Keystone species or ecosystem engineering species are often cited as examples of unique species. Engineer species modify the available resources for the other members of the community through the modification of the habitat (*e.g*., oysters or beaver dam builders; Lawton, 1994). These species have a disproportionate functional impact (positive or negative depending on the processes under study) on community or ecosystem abundance and biodiversity (Scherer-Lorenzen, 2005). Third, the impacts of species are context-dependent and therefore idiosyncratic or unpredictable (Fariña *et al*., 2003). The idiosyncratic response hypothesis (Lawton, 1994) argues that the impact based on the loss or addition of a species in an ecosystem can be insignificant or highly significant, depending on environmental conditions (*e.g.*, fertility, food availability, disturbance regime, etc.), the nature of the added or loss species, and the nature of the species with which it interacts.

To illustrate how the functional redundancy of species in a community depends on the environmental context (premise three above), Wellnitz & Poff (2001) developed a theoretical scenario based on a hypothetical feeding guild formed by three lotic species (A, B and C). These three species belong to a guild of grazers and current velocity is vital to their permanence. These species are potentially redundant at low velocities since they feed on algae and associated organisms and detritus, with overlap in their fundamental niche. On average, all three species have the same effect on the rate at which algae are removed from the substrate. However, the relative importance of each species in this process changes dramatically as velocity increases with their functions being similar under low speed conditions, but not redundant at intermediate and high current velocities. Thus, if we conclude that the three species are redundant based on their functional contributions in the low velocity or the average value of the three gradients, and then we remove species C, the community would lose an important functional component in the system. Unfortunately, there are a limited number of studies that address this type of issue that provides an unlimited overview of the functions of the species, and thus may give a false diagnosis of redundancy.

Studies that do address such changes or impacts indicate variable results depending on duration/frequency of disturbances and these are scale-dependent (local, regional). For example, Bellwood *et al*. (2006) conducted an experimental study in the Great Barrier Reef, simulating changes from a macroalgae-dominated to a coral- and epilithic-dominated state, inducing the reversal of the dominance of macroalgae through functional herbivorous fishes. Surprisingly, the reversal through direct removal of macroalgae was not the result of grazing parrotfish (Scaridae) and surgeonfish (Acanthuridae), the most common herbivorous reef fish, or any of the other 43 herbivores species in the area, but primarily from a single species, the batfish *Platax pinnatus* (Linnaeus, 1758) (Ephippidae, that was previously listed as zoobentivore). The species was observed consistently ingesting large pieces of *Sargassum* (the dominant macroalgae) and algae. The batfish is relatively rare in the Great Barrier Reef (1.6 individual/ha), but it has the ability to remove 12,750 kg/yr; however, the importance of removing macroalgae by this species was unknown.

This species, according to Bellwood *et al*. (2006), represents a ‘sleeping’ functional group-species or group of species able to perform a particular function role but only under certain exceptional circumstances. This case highlights the importance of identifying and protecting these species or species groups that support resilience and regeneration of complex ecosystems. Similarly, the green humphead parrotfish, *Bolbometopon muricatum* (Valenciennes, 1840), from the Indo-Pacific, was primarily responsible for bioturbation of coral reefs, each fish consumes about five tons of carbonate coral reef per year, corresponding to about half of the live coral (Bellwood *et al*., 2003, Bellwood & Choat, 2011). Overfishing of this species has changed the dynamics of accretion of reefs (Bellwood *et al*., 2003; Bellwood & Choat, 2011).

Coral reef ecosystems are increasingly subject to severe, large-scale disturbances caused by climate change (*e.g*., coral bleaching) and other more direct anthropogenic impacts causing coral loss; these cause changes in habitat structure, which has additional effects on abundance and biodiversity of coral reef fishes (Wilson *et al*., 2006). Declines in the biodiversity and abundance of coral reef fishes are of considerable concern, given the subsequent loss of ecosystem function (reviewed in Pratchett *et al*., 2008). Pratchett *et al*. (2011) reviewed the effects of coral loss throughout the world on the biodiversity of fishes and also on individual functional responses of fishes. Extensive (> 60%) coral loss led to declines in fish biodiversity; most fishes declined in abundance following disturbances that caused > 10% declines in local coral cover. Response biodiversity, which is considered critical in maintaining ecosystem function and promoting resilience, was very low for corallivores, but was much higher for herbivores, omnivores and carnivores. They indicated that sustained climate change poses a significant threat to coral reef ecosystems and biodiversity hotspots are no less susceptible to projected changes in biodiversity and function (Pratchett *et al*., 2011). Although there is no global agreement on the effects of species loss on ecosystem functioning, it has been noted that deforestation, introduction of exotic species, habitat destruction, isolation or fragmentation of habitats and pollution can contribute to local, regional and global extinction of species causing an inevitable ecosystem degradation and loss of services to society (Sodhi *et al*., 2009).

However, Cheal *et al*. (2008) suggested that coral reef fish biodiversity may not be a reliable indicator of reef resilience but predicted declines in coral cover due to global warming are likely to cause changes in the observed structure of reef fish communities; the nature of these changes and associated functional capacity to assist ecosystem recovery will vary among reefs because of differences in functional diversity. Finally, Denis *et al*. (2017) based on the 1983 severe coral reef bleaching data off Tikus Island Indonesia, found clear signs of coral assemblage complexity recovery approaching pre-El Niño conditions five years after the event. They also noted that, independent of the changes in species richness, this return in structural complexity was accompanied by a global decrease in species number associated with functional redundancy (each morphological entity) and an increase in the functional vulnerability (number of unique single-species/functional groups). They suggested an overall functional erosion of the coral assemblage and indicated that the role of the coral reef habitat could be strongly imperiled under repeated or synergistic disturbances.

Currently, there has been a surge of studies examining the relationship between phylogenetic (species) biodiversity, functional diversity, and ecosystem sustainability (*e.g.*, Cowman, 2014; Floeter *et al*., 2018) using different approaches and relative to a better understanding of anthropogenic-induced impacts on sustainability. Although there are multiple definitions (Naeem & Li, 1997; Tilman, 2001; Diaz *et al*., 2007; Martín-López *et al*., 2007; Cadotte *et al*., 2013; Winemiller *et al*., 2015), all agree on the importance of evaluating the functional role of species within an ecosystem. The approaches vary but most are through multidisciplinary and multivariate studies (Schulze & Mooney, 1994; Winemiller *et al*., 2015; Pianka *et al*., 2017; Floeter *et al*., 2018) where functional groups are defined according to the concept that species with high overlap of information on ecological and morphological traits are placed together and thus play similar ecological roles (Alvarez-Filip & Reyes-Bonilla, 2006; Cadotte *et al*., 2013; Winemiller *et al*., 2015; Pianka *et al*., 2017).

Each group is characterized by its own unique combination of functional features and outcomes provide a manageable number of groups that maximize the biological coherence of its members (Field *et al*., 1982; Simberloff & Dayan, 1991; Petchey & Gaston, 2002; Winemiller *et al*., 2015). Recently, Floeter *et al*. (2018) documented that functional traits and the environment influence phylogenetic lineages, such that acquiring a functional trait may drive evolution of other traits or behaviors and that an improvement of our understanding of mechanisms of species assemblages are enhanced using both metrics in coral reef fish communities.

In theory, the presence of multiple dominant or subordinate species increases the functional redundancy within each functional group and provides ecosystem resilience to respond or adapt to disturbances (Giller & O'Donovan, 2002). Further, functional redundancy also reduces the likelihood of invasion of exotic species (Naeem *et al*., 1994; Walker *et al*., 1999; Steneck, 2001; Rosenfeld, 2002; Hooper *et al*., 2005). The greater the number of functionally similar species, each with different responses to environmental constraints, the greater the likelihood that at least one species survives against possible disturbances (Walker, 1992, 1995; Naeem, 1998; Diaz *et al*., 2013).

For example, let us assume that an ecosystem is facing a drought, then a fire, and then is on flood. According to the functional diversity hypothesis, the ecosystem will have species that can tolerate drought, some that are fire-tolerant, and some that are resistant to flooding. If true, then two scenarios are likely: 1) the ecosystem may show resistance, remaining unchanged because species richness moderates the damage; or 2) the ecosystem may show resilience, quickly returning to its original state because tolerant species contribute to recovery and compensate for the functional loss of other species who showed less resistance (Naeem, 2002).

After removing a species within a fully formed group, reduced redundancy makes the remaining species increase their density to offset the functional contribution of the lost species. For example, in algae when a compensating effect between species of the same functional group is observed; biomass remains relatively constant despite fluctuations in species abundance (Steneck, 2001). Functional redundancy is good because it increases ecosystem resilience (Walker, 1992; Cheal *et al*., 2008) and important functional groups comprised of a few or a single species deserve attention regarding conservation priority because their functions may be rapidly lost (Walker, 1992).

## CONCLUSIONS

The analysis of functional diversity is a powerful and complementary tool to the classic indices of biological biodiversity (richness, dominance, equity, etc.) and taxonomic biodiversity indices (taxonomic biodiversity, taxonomic differentiation, average taxonomic differentiation, variation in taxonomic distinction). Biodiversity indicates richness and proportions, taxonomic biodiversity reflects the structure and phylogenetic variability, and functional diversity suggests the role of species in the ecosystem. Moreover, functional diversity studies can be used as a tool to predict the functional consequences of invasions or invasion front speciation events (Chuang & Peterson, 2016) and biotic changes caused by humans like overfishing, habitat loss, and climate change (Heenan & Williams, 2013; Villéger *et al*., 2017). The functional diversity approach offers an opportunity for a better understanding of coral reef ecosystem responses, and the associated fish communities, to natural and anthropogenic disturbances.

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