

---

## Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve

D. Mouillot<sup>a,\*</sup>, J.M. Culioli<sup>b</sup>, D. Pelletier<sup>c</sup>, and J.A. Tomasini<sup>a</sup>

<sup>a</sup> UMR CNRS-IFREMER-UM2 5119 ECOLAG, Université Montpellier 2 CC 093, 34095 Montpellier Cedex 5, France

<sup>b</sup> Réserve Naturelle des Bouches de Bonifacio, Office de l'Environnement de la Corse, Avenue Jean Nicoli, 20 250 Corte, France

<sup>c</sup> IFREMER, Laboratoire MAERHA, BP 21105, 44311 Nantes Cedex 03, France

\*: Corresponding author : D. Mouillot, email address : [david.mouillot@univ-montp2.fr](mailto:david.mouillot@univ-montp2.fr)

---

### Abstract:

Changes in biodiversity may disrupt the ecological functions performed by species assemblages. Hence, we urgently need to examine the implications of biodiversity loss not only in terms of species conservation but also in terms of sustainability of ecosystem services. The ability of protected areas to maintain local species richness has been clearly demonstrated. However, preserving goods and services provided by ecosystems requires not only the conservation of species richness but also the conservation of the most 'original' species, i.e. the ones with the highest average rarity of their attributes which are likely to perform some unique functions in ecosystems. We proposed a new conservation of biological originality (CBO) index as well as associated randomization tests to quantify the ability of protected areas to maintain viable populations for the most original species. As an application, we used long-term fisheries data collected in the Bonifacio Strait Natural Reserve (BSNR) to determine the species which benefited from the protection reinforcement in 1999. We also estimated a set of 14 ecomorphological functional traits on the 37 fish species caught in the BSNR and we obtained a functional originality value for each species. As a result, we found that functional originality was significantly protected in the fish assemblage of the BSNR: species with the most original functional trait combinations became more abundant after 1999. Our finding suggests that protecting most original species is an insurance against functional diversity erosion in the BSNR. More generally, our new index can be used to test whether protected areas may protect preferentially the most original species and whether restorative management promotes the reestablishment of the most original species with particular habitat requirements.

**Keywords:** Marine reserve; Functional trait; Functional originality; Randomization test; Fish assemblage; Indicator species; Biological indicator

# 1. Introduction

---

In a natural world increasingly transformed by human activities, there is more and more evidence for declining trends in biodiversity for both terrestrial (Thomas et al., 2004) and marine realms (Roberts and Hawkins, 1999). A few major sources of ecological alterations may be identified from the long list of factors explaining these trends. For terrestrial ecosystems, changes in land use have probably had the largest effect, followed by climate change, nitrogen deposition, biotic exchange and elevated carbon dioxide concentration (Sala et al., 2000). For aquatic ecosystems, the most important factors are certainly climatic change, biotic exchange and overfishing; the latter being the most direct human disturbance to all coastal ecosystems (Jackson et al., 2001). Land use change has also significant impact on inland, estuarine and near shore coastal waters (e.g. Ramos Miranda et al. 2005).

The causes of biodiversity loss are well established and the consequences of such dramatic declines or alterations have spurred considerable research and tremendous debate (reviewed in Hooper et al. (2005)). Indeed biodiversity should be preserved not only for aesthetic reasons and for its direct usefulness, but also for its indirect benefits through services that species provide to ecosystems (Chapin et al., 2000). For instance, it has been experimentally demonstrated that, locally, species richness *per se* positively influences ecosystem functioning and some fundamental properties of ecosystems such as productivity, resistance to invasion, stability and resilience (e.g. Loreau et al. 2001). Thus, as alterations of biodiversity may disrupt ecological functions performed by species assemblages (Hughes et al., 2003), it is urgent to carefully examine the implications of biodiversity loss not only in terms of species conservation but also in terms of sustainability of ecosystem services upon which human welfare depends.

Protected areas are indisputably the primary tool for *in situ* biodiversity conservation across the world (Ravenel and Redford, 2005) with more than 100,000 sites covering nearly 11.7 per cent of the land surface of the planet and about one per cent of the marine environment (Bishop et al., 2004). However, protected areas have been set up with respect to species and habitat considerations rather than based on considerations about the functioning of ecological systems. For instance, in protected areas, biodiversity is almost exclusively assimilated to species richness (the number of species coexisting on a site) while the definition of biodiversity includes various facets of the diversity of life (Purvis and Hector, 2000). It is thus worth noting that the most widely used measure of biodiversity ignores what makes species different in an assemblage (Cousins, 1991): their relative abundances and their biological traits. Yet, these two facets of biodiversity, which are based on differences among species, are known to influence ecosystem functioning. They are generally measured by two indices: (i) evenness, which measures the relative distribution of abundance among species and is positively related to resistance against invasion (Wilsey and Polley, 2002); and (ii) functional diversity, which measures the value and range of functional traits in organism assemblages, is now widely recognized as a main driver of ecosystem processes in both terrestrial (Petchey et al., 2004) and aquatic (Waldbusser et al., 2004) environments. Beyond protecting species richness against erosion, we should thus ask the question of whether protected areas are able to maintain these other facets of biodiversity.

When considering differences among species to assess the diversity of an assemblage we can assume that the species that contributes more to the biological diversity of this assemblage is the one with the most original features, i.e. the one with the highest average rarity of its attributes (Pavoine et al., 2005). From this standpoint, losing the most original species is more likely to result in losing some unique biological features such as life-history traits, morphological attributes or behaviours. This is obvious for some species-poor taxonomic groups (e.g. rhinoceros and kiwis) (Purvis et al., 2000). In turn, the loss of some rare biological features may significantly disrupt ecosystem functioning. For instance only a few species of parrotfish, with particularly long and strong jaws, can substantially erode reef carbonate of dead corals (Bellwood and Choat, 1990). When such species are threatened by overfishing (like in Caribbean coral reefs) the bioerosion of dead corals by fish decreases. As a result, the increased spatial extent of dead coral may prevent new coral settlement on fragile or unstable foundations (Bellwood et al., 2004). The absence of species able to play the same role as eroding parrotfish thus makes the preservation of their functionally original attributes essential to the recovery of coral reef ecosystems. More generally, the degree of functional originality of species within an assemblage determines the strength and

shape of the relationship between taxonomic and functional diversity (Micheli and Halpern, 2005). Extinction of species which are functionally equivalent to some others in the assemblage has less impact on functional diversity than the extinction of the most original species (Figure 1).

Our article aimed to evaluate the ability of protected areas to maintain viable populations for the most “original” species. This question was investigated using fisheries data from a long-term monitoring programme in the Bonifacio Strait Natural Reserve (BSNR thereafter). We proposed a new Conservation of Biological Originality (CBO) index and tested the hypothesis that biological originality was significantly protected in the BSNR. Our results illustrate how protection against human impact in coastal areas preferentially benefits the most original fish species in terms of ecomorphological traits. The usefulness of our new index within a wider context of biological conservation and restoration of original features (phylogenetic, functional, life-history traits) will be discussed.

## 2. Materials and Methods

---

### 2.1. Data collection

The data used were those from traditional artisanal fisheries in the Lavezzi Islands Reserve (LIR) within the BSNR (80,000 ha) (France, Mediterranean Sea, Corsica Island). This BSNR was created in September 1999 and encompasses the LIR created in 1982 (Mouillot et al., 1999; Mouillot et al., 2002). This latter area is characterized by a predominantly rocky substrate and *Posidonia oceanica* seagrass beds at shallow depths. Since 1982, the area corresponding to the LIR has been partially protected from spearfishing and other recreational fishing activities whereas traditional trammel net fisheries are tolerated. In 1999, protection was strengthened (i) at the local level (LIR) with the prohibition of longlines for tourists and with an additional 90 ha no-take area for a total of 5050 ha, and (ii) at the regional level with the creation of the BSNR: no take areas were created within the perimeter of the reserve and the limitation of recreational fishing activities was extended. See <http://www.parcmarin.com/> for more details about the legislation.

An artisanal fleet composed of small boats (average length 9 meters) fished on the continental shelf or in its vicinity. Generally, trammel nets were set for 24 hours at depths ranging from 20 to 60 meters. The mesh size used was fine-knit for fish (7-9 nodes for 25 cm long, 9 being the smallest authorized). Data were collected during the warm season (water temperature > 17° C between April and September) for two distinct periods of time: 1992-1993 (before BSNR establishment) and 2000-2003 (after BSNR establishment). Fish landings were randomly sampled from the boats fishing in the Lavezzi Islands Reserve. Since the same geographical area (and the same habitat) was available for fishermen (except 90 ha out of 5050 ha) before and after the BSNR establishment, the hauls remained comparable between the two periods in terms of species relative abundances and levels of occurrence.

All species caught were measured and their total weight was estimated using size class correspondences (Bauchot and Pras, 1980). To standardize collected data, Catch Per Unit of Effort (CPUE) was estimated, expressed in grams by piece of net (50 m) and per fishing day, here 24 hours ( $\text{g.p}^{-1}.\text{d}^{-1}$ ). Overall, 37 species were sampled including teleosts and elasmobranchs (Table 1). This pool of species included most of species known to live in the BSNR, excluding very small fish species (adult size < 10 cm) such as Gobiidae and Blenniidae and very large transient species such as tuna. Thus our study was restricted to a non-random sub-sample of species occurring in the BSNR, those caught by trammel nets. However these species represented the main fish biomass.

### 2.2. Winner versus loser species

Species termed ‘winner’ species were defined as those which significantly benefited from the BSNR establishment while ‘loser’ species were those that were significantly less present and less abundant since the BSNR establishment. Note that we did not observe any new species after

BSNR establishment. In order to determine winner versus loser species between the two periods (1992-1993 to 2000-2003), we used the indicator species approach proposed by Dufrene and Legendre (1997) rather than usual statistical tests such as ANOVA. The interest of this approach is to include both occurrence and abundance of species whereas classical tests only rely on species abundances. Moreover it can be used with data containing a high proportion of tied zero scores, presenting a non-normal distribution and exhibiting a wide variability. Mouillot et al. (2002) showed the advantages of this method over classical tests for data sets encountered in marine biology (visual census or fishery data) where tied zero scores are highly represented in sampled data.

The indicator species index (*IndVal*) combined the relative abundance of a species (denoting its *specificity*) with its relative frequency of occurrence during a period (denoting its *fidelity*). These two components were included in our study to determine winner vs. loser species because protecting a species can promote both its mean abundance and its frequency of occurrence across samples. To take into account this duality, indicator values were calculated for each species *j* and for each period *k* (1992-1993 or 2000-2003) as:

$$IndVal_{kj} = 100 \times A_{kj} \times B_{kj}$$

where  $A_{kj}$  was a measure of *specificity* and  $B_{kj}$  a measure of *fidelity* according to the formulae:

$$A_{kj} = Abundance_{kj} / Abundance_{+j}$$

and

$$B_{kj} = Nsamples_{kj} / Nsamples_{k+}$$

In our case,  $Abundance_{kj}$  was the mean CPUE (in  $g.p^{-1}.d^{-1}$ ) of species *j* for the samples of period *k*.  $Abundance_{+j}$  was the sum of the mean CPUE (in  $g.p^{-1}.d^{-1}$ ) of species *j* within the whole sampling programme (two periods).  $Nsamples_{kj}$  was the number of samples during period *k* where species *j* was present and  $Nsamples_{k+}$  was the total number of samples during this period (for more details see Dufrene and Legendre (1997), McGeoch and Chown (1998) and Mouillot et al. (2002)). The indicator value of species *j* for a period *k* ( $IndVal_{kj}$ ) was maximum (100 %) when the total abundance of species *j* was observed in fish landing records (samples) belonging to this period *k* only. The largest value of  $IndVal_{kj}$  observed over the two periods for a species *j* was  $IndVal_j = \text{Max}(IndVal_{kj})$ .

The indicator species analysis (step 1 in Fig. 2) relied on permutation tests of *IndVal*. Samples were randomly permuted between periods to obtain a distribution for  $IndVal_j$ . We then compared the observed  $IndVal_j$  value to the null distribution of  $IndVal_j$  values in order to obtain the p-value which is the type I error (Dufrene and Legendre, 1997). A species was a significant indicator for one period if we rejected the null hypothesis with a p-value lower than 5% (unilateral test). The calculations of *IndVal* values and associated tests were implemented using PC-ORD 4.0 for Windows (McCune and Mefford, 1999); 9,999 permutations were performed.

The winner species were those which had significant higher indicator values for the second period (2000-2003), i.e. those which were significantly more abundant and more frequent in the samples of the second period (after BSNR establishment and protection reinforcement in the LIR) than in the first one. Loser species were those with significantly higher indicator values for the first period, i.e. those which were significantly less abundant and less frequent after the BSNR establishment. Species with no significant indicator values were considered to be stable, i.e. their frequencies and abundances were not significantly influenced by the BSNR establishment.

### 2.3. Functional originality

To characterize the functional originality of each species, 14 functional traits were measured, providing information on three aspects of fish functional niche: diet, prey capture mode and position in the water column (Dumay et al., 2004; Mason et al., 2007; Mouillot et al., 2007) (Table 1). Because of allometric effects, fish species traits were standardized by biomass (Adite and Winemiller, 1997; Winemiller, 1991), with the exception of gut length which was standardized by standard length according to Cleveland and Montgomery (2003) and Kramer and Bryant (1995). Finally, 14 mean functional traits were obtained for each species considering that intraspecific variability was much lower than interspecies variability (Dumay et al., 2004). Only adult specimens were used to obtain trait measurements, to avoid complications associated with ontogenetic trait

variation. We considered, on average, 8 individuals per species (from 2 to 20) to estimate a mean value per species for each functional trait. We then obtained the species functional trait matrix (Figure 2).

Based on this standardized species trait matrix, we used the procedure recently proposed by Pavoine et al. (2005) to estimate the level of biological originality for each species. This procedure was initially proposed to measure phylogenetic originality using phylogenetic trees where the length of branches shared by two species indicates the expected number of features that these species have inherited from their common ancestor. Instead of phylogenetic trees we used functional trees and we adapted the procedure of Pavoine et al. (2005) (step 2 in Fig. 2).

We first estimated a Mahalanobis distance between any two species. A hierarchical clustering (the unweighted pair-group clustering method using arithmetic averages: UPGMA) of the distance matrix produced a functional dendrogram comprising the 37 species. We then estimated the square root of the distances between all pairs of species based on branch lengths of this dendrogram. This measure produced an ultrametric distance between species pairs ( $d_{ij}$ ) which was a circum-euclidean distance (see Pavoine et al. 2005 for more details) with the following property:

$$\sqrt{d_{ij}} \leq \max(\sqrt{d_{ik}}, \sqrt{d_{kj}}),$$

where  $i, j$  and  $k$  were three distinct species.

The originality values of species were the weights that maximize the expected dissimilarity between two species randomly drawn from the pool. The maximal value was obtained when the most functionally distinct species had the highest weight and the most redundant species had the lowest weight. Indeed, the expected functional dissimilarity between two species randomly sampled according to their weight was maximal when the most functionally dissimilar species had the greatest weights. The ultrametric distance ensured that all end nodes were equidistant from the root of the tree which was necessary to correctly estimate species weights that maximized the expected dissimilarity between species pairs. More details were provided in Pavoine et al. (2005). In addition to the functional originality values we carried out a Principal Component Analysis based on the species by trait matrix to figure out the relative position of species in the functional space.

## 2.4. Conservation of Biological Originality indices

We proposed two new Conservation of Biological Originality (CBO) indices (Step 3 in figure 2). First, winner species, which exhibited a significant increase in indicator value between the two periods, were given a weight of +1, while loser species were given a weight of -1, and species with no significant trend between the two periods were given a weight of 0. From this initial weighting of species, a first index was calculated using species originality values ( $o_i$ ):

$$CBO = \frac{\sum_{i=1}^S o_i \times w_i}{\sum_i o_i},$$

where  $w_i$  was the weight of species  $i$  defined above and  $S$  was the number of species. This index ranges between -1 and +1. When all species are winner species, all weights have a value of +1 and  $CBO=1$ . When all species are loser species, all weights have a value of -1 and  $CBO=-1$ .  $CBO=0$  indicates that there is no significant trend in originality for the assemblage over the period studied.  $CBO$  tends to be positive when the most original species are winner species over the period studied, while it tends to be negative when these most original species are loser species over the period studied.  $CBO$  is much less sensitive to species with low originality values as they have a low weight.

Since the distribution of originality values is uneven with many species having very low values while few others have high values we proposed, in addition, another Conservation of Biological Originality index: CBOR. Compared to the first CBO index, the originality of each species was replaced by its rank along the originality gradient ( $r_i$ ), i.e. the less original species received rank 1 while the most original species received rank  $S$  (the total number of species):

$$CBOR = \frac{\sum_{i=1}^S r_i \times w_i}{\sum_i r_i}$$

This index also ranges between -1 and +1 with a similar ecological meaning as CBO. The main difference with CBO is that the impact of species on the index estimation is related to their ranks along the originality scale and not to their originality values, thus this second index is more robust.

## 2.5. Two null hypotheses tested by randomisation

As a single index value was calculated for a given area, there is a limited ecological meaning to interpret CBO value *per se*. Instead, one needs to assess whether the measured value of CBO (or CBOR) is significantly different from those expected under suitable null hypotheses. To this aim, we designed two complementary null hypotheses that place different restrictions on how samples and species may be randomized.

Tokeshi (1986) points out that, during the selection of a null model to test a hypothesis, it is essential to keep every feature of the randomized data as it is in the observed data, except the feature that the study aims to test. First we wanted to test whether the value of observed CBO value was significant with respect to the diagnostic of winner versus loser species, i.e. with respect to sample periods. The corresponding null hypothesis was that, for each species, abundance did not change between the two periods. Under this hypothesis, CBO would not be significantly affected by random permutations of the samples (here fish landings) between the two periods, the originality values for each species being kept constant. The null distribution of CBO was obtained by calculating the empirical distribution of CBO values for a large number of sample permutations (here fish landings) between the two periods (step 4 in Figure 2).

Secondly we wanted to test whether the level of CBO observed between two periods was significant with respect to species originality values. The corresponding null hypothesis was that CBO values did not depend on species originalities. Under this hypothesis, CBO would not be significantly affected by random permutations of originality values among species, the couples of abundance values for a given species being kept constant. The null distribution of CBO values corresponded to the level of Conservation of Biological Originality index expected if originality values were randomly distributed among species (step 5 in Figure 2).

By combining the matrix containing abundance patterns of species during the two periods and the originality matrix, we first calculated the observed CBO index between the two periods (step 5 in Figure 2). We then randomly swapped the factor to be tested (abundance or originality values) to obtain a randomized CBO index between the two periods. We repeated this randomization procedure 9,999 times to obtain a null distribution for the CBO (or CBOR) index between the two periods. We then compared the mean observed CBO index to the null distribution in order to obtain the *p*-value which was the type I error (probability of rejecting the null hypothesis whereas it is true (Manly, 1998)). We repeated this procedure four times, one for each CBO index and one for each null hypothesis tested (step 6 in Figure 2).

## 3. Results

---

428 fish landings were sampled in the Lavezzi Island Reserve during the two periods, 246 in 1992-1993 and 182 in 2000-2003. The overall mean CPUE increased significantly between the two periods from 656.5 g.p<sup>-1</sup>.d<sup>-1</sup> (SD=441.7) in 1992-1993 to 823.6 g.p<sup>-1</sup>.d<sup>-1</sup> (SD=582.7) in 2000-2003 (*F*=11.38; *ddl*=1,426; *p*=0.001).

A total of 37 fish species were sampled including a majority of teleosts and some elasmobranchs (Table 2). The coefficient of variation of trait values among individuals of the same species was

very low (<10%) except for biomass (86%). The coefficient of variation of trait values among species varied from 15% for eye position to 159% for body biomass. For instance, mean species biomass ranged from 60 grams (*Diplodus annularis*) to 5,120 grams (*Seriola dumerlii*). Thus, we needed to standardize trait values to give the same weight to each functional trait in functional originality estimation.

Species were then classified according to their functional originality values (Table 2). The most original species was the Greater Amberjack (*Seriola dumerlii*) followed by the Brown Ray (*Raja miraletus*) and the John Dory (*Zeus faber*). Greater Amberjack is a pelagic piscivorous fish characterised by a high swimming ability, large mouth size and relatively small gut length. The Brown Ray has a very original flat body form with a low ratio of maximal body depth to standard length and a low ratio of maximal body depth to body width. The John Dory was the most laterally flat fish in our species pool with an orientation of the mouth higher than +45° allowing it a high manoeuvrability between rocks and to catch its prey above it in the water column. Conversely the less original species belonged to either Labridae (*Labrus merula*, *Labrus viridis* and *Symphodus tinca*) or Sparidae (Genus *Diplodus*) which comprised the largest number of species in the reserve.

We found a CBO index equal to 0.42 and a CBOR index equal to 0.28. Using the first null hypothesis (swapping samples between the two periods) we found that both CBO and CBOR indices were statistically higher than expected if samples were randomly allocated between the two periods ( $p < 0.001$ ) (Figs. 3A and 3B). After randomly swapping the originality values among species under our second null hypothesis, the observed CBO index was not statistically different from our randomized CBO values (Figure 3C) ( $p = 0.0569$ ). Conversely, we obtained an observed CBOR index higher than expected under the second null hypothesis ( $p = 0.0057$ ) (Figure 3D). Taken together, our results showed that functional originality was significantly protected in the BSNR.

Although an increase of 25% in the total fish biomass caught by local fishermen was observed after the BSNR establishment, this increase was not evenly distributed among fish species. Amongst the 37 species, 13 and 3 species were significantly identified as *winner* species and *loser* species, respectively, by the Indicator Species test, while the 21 remaining species were statistically stable between the two periods (Table 2). There was consistency for some genera (the two *Pagellus* species were winner, the two *Labrus* were loser while the four *Diplodus* species were stable through time) but not for all (*Scorpaena* sp.).

Among the five most functionally original species, four were significantly more present and more abundant after 1999 (*Raja miraletus*, *Scyliorhinus canicula*, *Solea vulgaris* and *Zeus faber*). In addition, the three species which did not benefit from BSNR establishment (*Spicara Maena*, *Labrus viridis*, *Labrus merula*) were among the more functionally redundant species (originality values ranging in 0.002-0.004) since they shared many traits with other coexisting species. There were, however, no losers with originality values  $> 0.01$  and half of the species with originality values  $> 0.01$  were winners; whilst only a quarter were species with originality values  $< 0.01$ .

The PCA shows the functional relatedness among species in a reduced two-dimension space (Figure 4). This plot highlights that some species were functionally redundant while some others had a very uncommon combination of functional traits. Most of species located near the boundaries of the functional space filled by the assemblage benefited from the protection with an increase in both abundance and presence (e.g. *Raja miraletus*, *Scyliorhinus canicula*, *Solea vulgaris* and *Zeus faber*).

Originality values were not significantly correlated to the mean abundance of species for any of the two periods ( $r = -0.108$ ,  $p = 0.525$  for 1992-1993 and  $r = -0.046$ ,  $p = 0.788$  for 2000-2003). The most functionally original species were neither the most abundant nor the less abundant ones in the BSNR. Hence, the observed result was not simply a consequence of an increasing abundance of rare species which would be the most original species. *Raja miraletus* was the seventh most abundant species in fish catches while being the second most original one for functional traits. The main difference observed between the two indices lay in the range of originality values. In our case the most original species (*Seriola dumerlii*) was 80 times as original as the less original species (*Labrus viridis*) (Table 2). As a result, the CBO value was almost insensitive to the less original species while the two or three most original species highly contributed to the final value. Instead,

CBOR gave relatively more weight to the less original species even if *Seriola dumerilii* influenced the index 37 times more than *Labrus viridis* did.

## 4. Discussion

---

Marine reserves have been proposed as management tools to limit human pressures on resources and the local environment in order to sustain ecosystem functioning. Indeed, the potential benefits of marine reserves in terms of fishing mortality reduction (Jennings, 2001), of restoring trophic interactions (Guidetti, 2006), of fish biomass increase (Polunin and Roberts, 1993) and of spillover to adjacent fisheries (Goni et al., 2006) have been supported (but see Gardmark et al. (2006)). However, the utility of marine reserves as fisheries-management tools has been rarely demonstrated except for areas in the vicinity of the reserve (Russ et al., 2004; Stelzenmuller et al., 2007). Using MPAs for fisheries management is still controversial and the issue is whether establishment of protected areas have positive or negative impacts on fisheries (e.g. Hilborn, 2002; Gell and Roberts, 2003). One important, undesirable effect of protected area implementation is that fishing effort, excluded from these areas, is redirected to unprotected areas, at the risk of higher fishing pressure (Ashworth and Ormond, 2005; Murawski et al., 2005). For the BSNR, after the intensification of the protection in 1999, we observed an increase of 25% in the total fish biomass (equates to a 167.1 grams by piece of 50 meters and by day) caught by local fishermen inside the BSNR over a period of 10 years. To our knowledge this is the first time that a direct benefit in terms of CPUE to an artisanal fishery has been demonstrated within a protected area.

In addition to an increase of biomass (estimated through CPUE), we observed that the reserve enhanced biological originality within the fish assemblage. Our null models revealed that the observed level of CBO index was significantly higher than expected both (i) when abundance data were randomly distributed between the two periods (for both indices CBO and CBOR) and (ii) when originality values were randomly distributed among species (only for CBOR). Taken together, these results mean that most of the original species benefited from the protection, as illustrated in figure 4. The protection of functional originality has some relation with the level of functional diversity that is maintained (Figure 1). Nowadays, more and more studies show that functional diversity rather than species diversity enhances ecosystem functioning such as productivity (Tilman et al., 1997), resilience to disturbances (Bellwood et al., 2004) and regulation in the flux of matter (Waldbusser et al., 2004). As functional diversity increases with the volume of the functional space occupied by species assemblages (Mason et al., 2005) we can expect functional diversity to be maintained by protecting the most original species, i.e. the most extreme species in that functional space. Indeed, the edge of the volume corresponding to the functional space filled by the fish assemblage in the BSNR was reinforced against erosion after the intensification of the protection: species with particular functional trait combinations were less prone to decline (Figure 4). As these original species were expected to accomplish some particular functions in the system, their protection would enhance the level of functional diversity in the assemblage. For instance *Sarpa salpa*, which was the only strict herbivorous fish species present in the BSNR (longest gut length ratio, small mouth gape), made an important contribution to the functional volume filled by the fish assemblage. Any change in the abundance of this species would have a strong impact on ecosystem functioning through grazing activity (Tomas et al., 2005). Our findings have some implications for a process-based management of the BSNR because the increasing abundance of the most original species is an insurance against functional diversity erosion (Figure 4).

We propose two hypotheses to explain why the most original species would benefit more from protection in general. First, we know that the distribution of species is largely influenced by habitat, and that human impact on habitats can significantly modify the composition of coastal assemblages (i.e. Guidetti et al., 2002; Pihl et al., 2006). According to niche theory, coexisting species are the best competitors in their own ecological niche and compete for alternative resources and different habitats. Thus, the number of species is limited by the number of niches available and a large spectrum of niches is needed to maintain or increase species richness. Following this theory the most functionally original species are certainly the most specialized species (Bellwood et al., 2006b) and thus may have particular requirements to survive. For example, *Sarpa salpa* is strictly herbivorous and feeds mainly on *Posidonia oceanica* in the BSNR. Their high degree of specialization makes these species more sensitive to the destruction or loss of habitats. Hence, the



occurrence and abundance of these biologically original species would benefit from the protection or the restoration of habitats.

Second, we know that interspecific competition is more intense among species sharing many traits in common because they have the same requirements; this was coined as the limiting similarity principle (MacArthur and Levins, 1967). We know that protected areas yield higher densities and biomasses for populations than outside (e.g. Rakitin and Kramer, 1996). Consequently, the competition intensity would increase after the establishment of protection through density-dependent body growth (Gardmark et al., 2006) and resource limitation (McClanahan and Kaunda-Arara, 1996). As functionally original species have particular niches with low functional overlap with the rest of the assemblage (Mouillot et al., 2005) they may escape from competitive interactions for their particular resources or their particular habitats. In turn, these species would benefit more from protection in terms of abundance because they would escape competition.

In the BSNR we did not retain the first hypothesis to explain our findings because no major habitat alterations were reported before the establishment of the reserve in 1999 as the Lavezzi Islands were protected since 1982. The second hypothesis was more plausible to explain why the most original species benefited from protection. Landing data clearly showed an increase of 25% for fish catches. We can thus expect an increasing density of fish as well as an increase in competitive interactions in such a low productive ecosystem typical of the Mediterranean Sea. The process of limiting similarity has not been demonstrated for fish assemblages (Grossman et al., 1998; Mouillot et al., 2007; Peres-Neto, 2004) but see Olden et al. (2006). However these studies were conducted in estuarine or continental waters. Competitive interactions in open sea waters are still difficult to assess but our study suggests that, at a regional scale, the most functionally original species would benefit from protection by avoiding increasing competition due to an increasing fish density and biomass.

We are aware that all fish species living in the BSNR were not included in our study and it may influence originality values that we observed. Indeed, originality is a measure relative to a species pool and these values have no meaning out of this context. Thus, our result is limited to the 37 fish species caught by trammel nets in the BSNR. Other species such as crustaceans (*Palinurus elephas*) were not considered whereas large amounts of these are caught by nets. These 37 species represent the largest fraction of fish biomass in the BSNR and influence greatly ecosystem functioning such as the secondary production available for fisheries.

#### **4.1. The influence of exotic species**

The main pitfall of our index is related to the presence of exotic and invasive species. Two major recent publications clearly demonstrate that exotic species which are biologically distinct from the native pool of species are more likely to become invasive species than exotic species which are biologically close to native species. Using respectively life-history traits and phylogenetic data, Olden et al. (2006) and Strauss et al. (2006) show that exotic species which are less related to native ones have a higher ability for invasion success. Using our new indices, one may conclude that an ecosystem where exotic species with particular combinations of traits become invasive (increasing in abundance and spatial distribution area) would enhance biological originality and functional diversity because the CBO value would increase. However, invasive species may disturb the system and ultimately provoke species extirpation (Olden et al., 2006). To overcome this pitfall we suggest correcting our indices when exotic species are included in analysis. We propose to use opposite  $w_i$  values for exotic species: significantly winner exotic species will have a weight ( $w_i$ ) of -1, significantly loser exotic species will have a weight of +1 while exotic species with no significant trend between two periods will have a weight of 0. Thus, if an exotic species becomes invading, CBO will decrease whereas if this exotic species becomes rare, CBO will increase. The impact of an exotic species on CBO will be proportional to its biological originality, CBO being more sensitive to highly original exotic species which are potentially the strongest invaders (Olden et al., 2006; Strauss et al., 2006) able to disturb native species and ecosystem functioning.

## 4.2. Future application of indices

Our approach has important application to the wider context of resilience-based management of ecosystems and restoration ecology. A challenging issue is to determine the ability of ecosystems to durably provide goods and services upon which human welfare depends. It is feared that pressures on ecosystems will become more intense and that alterations will be more frequent as a result of ongoing changes, such as climate warming and anarchic land use. Thus, the question is no longer whether ecosystems will face more and more disturbances but whether they will be able to come back to an initial state after disturbances, i.e. whether they will be able to be resilient. To this aim, developing new metrics that account for ecological processes underlying ecosystem dynamics is a priority for ecosystem management (Hughes et al., 2005). Since returning to an initial state is often not attainable in ecological restoration (too high intensity of degradation) one may target successive equilibrium states (e.g. Jeppesen et al., 2007). During these steps, ecosystems are supposed to meet the habitat requirements for species with more and more particular niches and functional attributes (van Kleef et al., 2006). Thus CBO and CBOR indices could be used to assess the effects of restoration management through the capacity of species assemblages to harbour more original species among those available in the regional pool.

An emerging approach to conservation management highlights the need to take into account ecological roles and key processes undertaken by particular species (Bellwood et al., 2006a). The underlying idea is that the focus of conservation must shift from species with patrimonial or commercial values to species that support some essential processes and thus sustain ecosystem services. For instance, Bellwood et al. (2006a) demonstrate that the reversal from a macroalgal-dominated to a coral- and epilithic algal-dominated ecosystem was surprisingly driven by a single batfish species (*Platax pinnatus*) while the 43 herbivorous fishes in the local fauna played only a minor role. Indeed, this batfish species has the ability to remove and ingest large amounts of macroalgae (Bellwood et al., 2006a) and no other herbivorous fish studied in this experiment is able to provide the same function. Thus, the functional “originality” of this batfish species makes it of conservation priority because its absence or its low density in coral ecosystems would prevent a reversal shift from a macroalgal-dominated to a coral-dominated state. More generally, within the context of process-oriented management of ecosystems, functional originality certainly deserves attention. Solan et al. (2004) demonstrated that the impact of species loss on ecosystem functioning is closely related to the covariation between species functional traits and their extinction risks. When species with particular traits go extinct first, we may expect greater ecosystem-level consequences following biodiversity loss. Thus, our new index and the associated null models provide a management tool to follow the trend of biological originality in ecosystems which governs a large part of ecosystem processes.

## Conclusion

---

Through this study we propose new indices, with associated randomization tests, which quantify the ability of protected areas to preserve an overlooked facet of biodiversity - biological originality – which was not considered in other classical community-based indicators (Claudet et al., 2006). These indices can be used in any context where biotic indicators are needed to detect changes due to environmental impact. These indices are also highly versatile as they can be used with any phylogenetic, taxonomic or functional tree representing differences among species. Furthermore an emerging approach highlights the importance of key processes undertaken by some functionally original species (Bellwood et al., 2006a). This perspective implies the focus from conservation of targeted, emblematic and patrimonial species to conservation of functional entities that support essential ecosystem services. Here we have shown, using new flexible statistical tools, that protected areas may protect preferentially the most original species, at least in the fish assemblage of the Bonifacio Strait Natural Reserve. This finding has to be tested in other systems.

## Acknowledgements

---

We thank Guy-François FRISONI, manager of the Bonifacio Strait Marine Reserve and R. PANTALACCI and J. POLVERINI, director and president of the 'Office de l'Environnement de la Corse' respectively, for facilities and financial support concerning scientific surveys of in the BSNR. Fishermen of the Bonifacio Strait Natural Reserve, D. RIGO, V. ORSONI, N. CASALTA and M.C. SANTONI contributed to collect the data. This study was funded by a LITEAU II, LITEAU III (PAMPA) and two ANR (GAIUS and AMPHORE) financial supports from the French government. J.A. GARCIA-CHARTON provided useful comments on a first draft of the manuscript. Two reviewers as well as the Editor improved the manuscript through constructive criticisms. A.B. Gill, Marine and Aquatic Editor, provided many minor modifications which clarified the manuscript.

## References

---

- Adite, A., Winemiller, K.O., 1997. Trophic ecology and ecomorphology of fish assemblages in coastal lakes of Benin, West Africa. *Ecoscience* 4, 6-23.
- Ashworth, J.S., Ormond, R.F.G., 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of no-take zone. *Biological Conservation* 121, 333-344.
- Bauchot, M.L., Pras, A., 1980. Guide des poissons marins d'Europe. Delachaux et Niestlé, Lausanne.
- Bellwood, D.R., Choat, J.H., 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environmental Biology of Fishes* 28, 189-214.
- Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. *Nature* 429, 827-833.
- Bellwood, D.R., Hughes, T.P., Hoey, A.S., 2006a. Sleeping functional group drives coral-reef recovery. *Current Biology* 16, 2434-2439.
- Bellwood, D.R., Wainwright, P.C., Fulton, C.J., Hoey, A.S., 2006b. Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B-Biological Sciences* 273, 101-107.
- Bishop, K, Dudley, N., Phillips, A., Stolton, S., 2004. Speaking a Common Language: The uses and performance of the IUCN System of Management Categories for Protected Areas, Cardiff University, IUCN-The World Conservation Union and UNEP-World Conservation Monitoring Centre.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234-242.
- Claudet, J., Pelletier, D., Jouvenel, J.Y., Bachet, F., Galzin, R., 2006. Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. *Biological Conservation* 130, 349-369.
- Cleveland, A., Montgomery, W.L., 2003. Gut characteristics and assimilation efficiencies in two species of herbivorous damselfishes (Pomacentridae: *Stegastes dorsopunicans* and *S. planifrons*). *Marine Biology* 142, 35-44.
- Cousins, S.H., 1991. Species diversity measurement: choosing the right index. *Trends in Ecology and Evolution* 6, 190-192.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345-366.
- Dumay, O., Tari, P.S., Tomasini, J.A., Mouillot, D., 2004. Functional groups of lagoon fish species in Languedoc Roussillon, southern France. *Journal of Fish Biology* 64, 970-983.
- Gardmark, A., Jonzen, N., Mangel, M., 2006. Density-dependent body growth reduces the potential of marine reserves to enhance yields. *Journal of Applied Ecology* 43, 61-69.
- Gatz, A.J.J., 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* 21, 91-124.
- Gell, R., Roberts, C.M., 2004. Benefits beyond boundaries: the fishery effects of marine reserve. *Trends in Ecology and Evolution* 18, 448-455.
- Goni, R., Quetglas, A., Renones, O., 2006. Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. *Marine Ecology Progress Series* 308, 207-219.
- Grossman, G.D., Ratajczak, R.E., Crawford, M., Freeman, M.C., 1998. Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. *Ecological Monographs* 68, 395-420.
- Guidetti, P., 2006. Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. *Ecological Applications* 16, 963-976.
- Guidetti, P., Fanelli, G., Frascchetti, S., Terlizzi, A., Boero, F., 2002. Coastal fish indicate human-induced changes in the Mediterranean littoral. *Marine Environmental Research* 53, 77-94.
- Hilborn, R., 2002. Marine reserves and fisheries management. *Science* 15, 1233-1235.
- Holcik, J., Banarescu, P., & Diana, E. (1989). General introduction to fishes. In *The freshwater fishes of Europe - General introduction to fishes - Acipenseriformes* (ed J. Holcik), Vol. 1/2, pp. 19-59. AULA Verlag, Wiesbaden.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75, 3-35.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* 301, 929-933.

Hughes, T.P., Bellwood, D.R., Folke, C., Steneck, R.S., Wilson, J., 2005. New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology and Evolution* 20, 380-386.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629-638.

Jennings, S., 2001. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* 10, 209-231.

Jeppesen, E., Sondergaard, M., Meerhoff, M., Lauridsen, T.L., Jensen, J.P., 2007. Shallow lake restoration by nutrient loading reduction - some recent findings and challenges ahead. *Hydrobiologia* 584, 239-252.

Kramer, D.L., Bryant, M.J., 1995. Intestine Length in the Fishes of a Tropical Stream .2. Relationships to Diet - the Long and Short of a Convoluted Issue. *Environmental Biology of Fishes* 42, 129-141.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., Wardle, D.A., 2001. Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294, 804-808.

MacArthur, R., Levins, R., 1967. Limiting Similarity Convergence and Divergence of Coexisting Species. *American Naturalist* 101, 377-387.

Mahon, R. (1984) Divergent structure in fish taxocenes of north temperate streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 41, 330-350.

Manly, B.F.J., 1998. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, Second Edition edn. Chapman & Hall, London.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111, 112-118.

Mason, N.W.H., Lanoiselee, C., Mouillot, D., Irz, P., Argillier, C., 2007. Functional characters combined with null models reveal inconsistency in mechanisms of species turnover in lacustrine fish communities. *Oecologia* 153, 441-452.

McClanahan, T.R., Kaunda-Arara, B., 1996. Fishery Recovery in a Coral-Reef Marine Park and Its Effect On the Adjacent Fishery. *Conservation Biology* 10, 1187-1199.

McCune, B., Mefford, M.J., 1999. *PC-ORD. Multivariate Analysis of Ecological Data*, Version 4. MjM Software Design, Glenden Beach, Oregon, USA.

McGeoch, M.A., Chown, S.L., 1998. Scaling up the value of bioindicators. *Trends in Ecology and Evolution* 13, 46-47.

Micheli, F., Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters* 8, 391-400.

Mouillot, D., Culioli, J.M., Lepretre, A., Tomasini, J.A., 1999. Dispersion statistics and sample size estimates for three fish species (*Symphodus ocellatus*, *Serranus scriba* and *Diplodus annularis*) in the Lavezzi Islands Marine Reserve (South Corsica, Mediterranean Sea). *Marine Ecology: PSZN* 20, 19-34.

Mouillot, D., Culioli, J.M., Chi, T.D., 2002. Indicator species analysis as a test of non-random distribution of species in the context of marine protected areas. *Environmental Conservation* 29, 385-390.

Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B., Chi, T.D., 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. *Oecologia* 145, 345-353.

Mouillot, D., Dumay, O., Tomasini, J.A., 2007. Limiting similarity, niche filtering and functional diversity in coastal lagoon fish communities. *Estuarine, Coastal and Shelf Science* 71, 443-456.

Murawski, S.A., Wigley, S.E., Fogarty, M.J., Rago, P.J., Mountain, D.G., 2005. Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science* 62, 1150-1167.

Nikolski, G.V. (1933) On the influence of the rate of flow on the fish fauna of the rivers of central Asia. *Journal of Animal Ecology*, 2, 266-281.

Olden, J.D., Poff, N.L., Bestgen, K.R., 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* 76, 25-40.

Pavoine, S., Ollier, S., Dufour, A.B., 2005. Is the originality of a species measurable? *Ecology Letters* 8, 579-586.

Peres-Neto, P.R., 2004. Patterns in the co-occurrence of fish species in streams: the role of site suitability, morphology and phylogeny versus species interactions. *Oecologia* 140, 352-360.

Petchey, O.L., Hector, A., Gaston, K.J., 2004. How do different measures of functional diversity perform? *Ecology* 85, 847-857.

Pihl, L., Baden, S., Kautsky, N., Ronnback, P., Soderqvist, T., Troell, M., Wennhage, H., 2006. Shift in fish assemblage structure due to loss of seagrass *Zostera marina* habitats in Sweden. *Estuarine, Coastal and Shelf Science* 67, 123-132.

Polunin, N.V.C., Roberts, C.M., 1993. Greater biomass and value of target coral reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* 100, 167-176.

Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288, 328-330.

Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212-219.

Rakitin, A., Kramer, D.L., 1996. Effect of a Marine Reserve On the Distribution of Coral Reef Fishes in Barbados. *Marine Ecology Progress Series* 131, 97-113.

Ramos Miranda, J., Mouillot, D., Flores Hernandez, D., Sosa Lopez, A., Do Chi, T., Ayala Perez, L., 2005. Changes in four complementary facets of fish diversity in a tropical coastal lagoon after 18 years: a functional interpretation. *Marine Ecology Progress Series* 304, 1-13.

Ravenel, R.M., Redford, K.H., 2005. Understanding IUCN protected area categories. *Natural Areas Journal* 25, 381-389.

Roberts, C.M., Hawkins, J.P., 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* 14, 241-246.

Russ, G.R., Alcalá, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. *Ecological Applications* 14, 597-606.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity - Global biodiversity scenarios for the year 2100. *Science* 287, 1770-1774.

Sibbing, F.A., Nagelkerke, L.A.J., 2001. Resource partitioning by Lake Tana barbs predicted from fish morphometrics and prey characteristics. *Reviews in Fish Biology and Fisheries* 10, 393-437.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L., Srivastava, D.S., 2004. Extinction and ecosystem function in the marine benthos. *Science* 306, 1177-1180.

Stelzenmuller, V., Maynou, F., Martin, P., 2007. Spatial assessment of benefits of a coastal Mediterranean Marine Protected Area. *Biological Conservation* 136, 571-583.

Strauss, S.Y., Webb, C.O., Salamin, N., 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103, 5841-5845.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145-148.

Tilman, D., Knops, J., Weldin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277, 1300-1302.

Tokeshi, M., 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology* 55, 491-506.

Tomas, F., Turon, X., Romero, J., 2005. Seasonal and small-scale spatial variability of herbivory pressure on the temperate seagrass *Posidonia oceanica*. *Marine Ecology Progress Series* 301, 95-107.

van Kleef, H.H., Verberk, W., Leuven, R., Esselink, H., van der Velde, G., van Duinen, G.A., 2006. Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* 565, 201-216.

Waldbusser, G.G., Marinelli, R.L., Whitlatch, R.B., Visscher, P.T., 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. *Limnology and Oceanography* 49, 1482-1492.

Watson, D.J. & Balon, E.K. (1984) Ecomorphological analysis of fish taxocenes in rainforest streams of northern Borneo. *Journal of Fish Biology*, 25, 371-384.

Wilsey, B.J., Polley, H.W., 2002. Reductions in grassland species evenness increase dicot seedling invasion and spittle bug infestation. *Ecology Letters* 5, 676-684.

Winemiller, K.O., 1991. Ecomorphological Diversification in Lowland Fresh-Water Fish Assemblages from 5 Biotic Regions. *Ecological Monographs* 61, 343-365.

## Tables

Table 1. Morphological parameters measured and their relevance for functional considerations (\* = parameters standardized by the biomass after using  $\log(x+1)$  transformation, # parameter standardized by the standard length)

Parameter	Functional interest
Biomass	The biomass of the fish indicates the size of the body, the energy content and the impact on the food web
Caudal ratio	The length/height ratio of the caudal fin indicates fish propulsion (ambush or pursuit catching mode)
Eye diameter *	This parameter is linked to visual acuity
Eye position	Ratio of the distance between the bottom of the head to the eye's centre to the head depth in line with the eye's centre. Related to vertical habitat preferences (Mahon, 1984; Watson and Balon, 1984)
Oral gape height	The oral gape gives information on maximum prey size
Mouth protrusion length *	This related to prey catching mode (aspiration, ambush or gulping).
Height of gill raker *	This reflects the capacity of fish species to filter plankton
Ratio of maximal body depth to standard length	Related to swimming ability through hydrodynamics (Gatz, 1979; Sibbing & Nagelkerke, 2001) and turning ability (Nikolski, 1933)
Ratio of maximal body depth to body width	Idem Hydrodynamics (Gatz, 1979; Sibbing and Nagelkerke, 2001)
Caudal peduncle length #	Swimming speed and endurance (Holcik et al., 1989)
Position of the Mouth	Ratio of the distance between the extremity of the mouth and the bottom of the head to the head depth in line with the eye's centre. Related to the prey catching mode
Orientation of the mouth	Method of food acquisition (Dumay et al., 2004; Sibbing and Nagelkerke, 2001). This parameter is semi-quantitative: - 90 to - 45° (-3) ; - 45 to - 30° (-2) ; - 30 to - 10° (-1) ; - 10 to 10° (0) ; 10 to 30° (1) ; 30 to 45° (2) and 45 to 90°(3).
Teeth	Tooth were coded from 0 to 5 along a gradient of their utility in prey capture mode: (0) nothing , (1) cardiform, (2) viliform, (3) vomerine, (4) incisiform and (5) caniniform.
Gut length #	The gut length is directly linked to fish diet

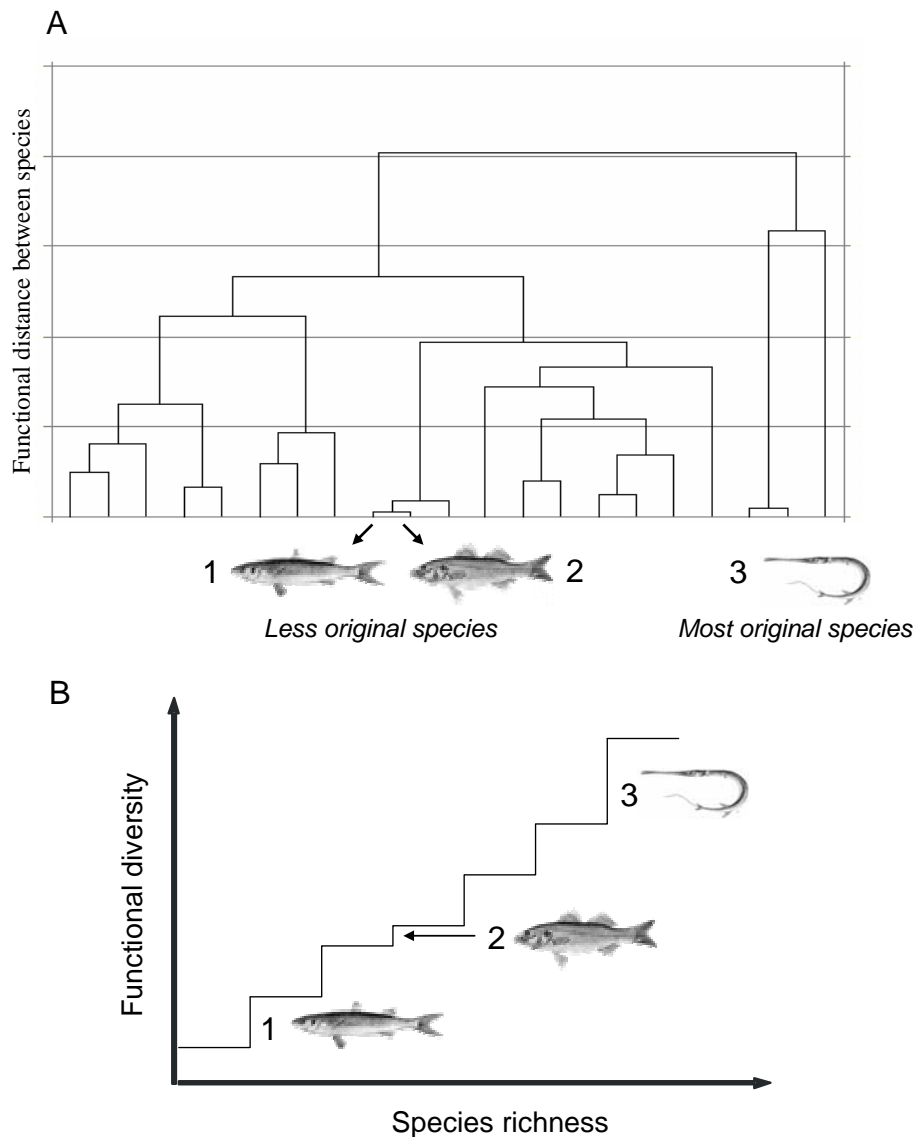


Table 2. Species observed in the samples with their scientific name, species code and originality values. W for winner species (benefit from BSNR establishment) and L for loser species. The weight is 1 for winner species, -1 for loser ones, and 0 for species that are neither winner nor loser. The rank is given according to originality values which are provided on a continuous scale (no tied ranks needed).

Species name	Species code	Originality ( <i>oi</i> )	Status	Weight ( <i>wi</i> )	Rank ( <i>ri</i> )
<i>Seriola dumerilii</i>	Sdu	0.130		0.00	37
<i>Raja miraletus</i>	Rmi	0.121	W***	1.00	36
<i>Zeus faber</i>	Zfa	0.114	W***	1.00	35
<i>Solea vulgaris</i>	Svu	0.082	W**	1.00	34
<i>Scyliorhinus canicula</i>	Sca	0.075	W*	1.00	33
<i>Sphyaena sphyaena</i>	Ssp	0.072		0.00	32
<i>Uranoscopus scaber</i>	Usc	0.069		0.00	31
<i>Sarpa salpa</i>	Ssa	0.047		0.00	30
<i>Conger conger</i>	Cco	0.031		0.00	29
<i>Muraena helena</i>	Mhe	0.031	W***	1.00	28
<i>Mullus surmuletus</i>	Msu	0.028	W*	1.00	27
<i>Trigla lucerna</i>	Tlu	0.028		0.00	26
<i>Merluccius merluccius</i>	Mme	0.024		0.00	25
<i>Scorpaena scrofa</i>	Ssco	0.022	W*	1.00	24
<i>Phycis phycis</i>	Pph	0.022	W*	1.00	23
<i>Dentex dentex</i>	Dde	0.012		0.00	22
<i>Sparus aurata</i>	Sau	0.012		0.00	21
<i>Boops boops</i>	Bbo	0.008		0.00	20
<i>Oblada melanura</i>	Ome	0.008		0.00	19
<i>Epinephelus marginatus</i>	Ema	0.007	W*	1.00	18
<i>Sciaena umbra</i>	Sum	0.007		0.00	17
<i>Scorpaena porcus</i>	Spo	0.006		0.00	16
<i>Trachinus draco</i>	Tdr	0.004	W*	1.00	15
<i>Pagellus erythrinus</i>	Per	0.004	W***	1.00	14
<i>Pagellus acarne</i>	Pac	0.004	W***	1.00	13
<i>Spondylisoma cantharus</i>	Sca	0.004	W***	1.00	12
<i>Spicara maena</i>	Sma	0.004	L**	-1.00	11
<i>Serranus scriba</i>	Ssi	0.004		0.00	10
<i>Serranus cabrilla</i>	Sca	0.004		0.00	9
<i>Pagrus pagrus</i>	Ppa	0.003		0.00	8
<i>Diplodus vulgaris</i>	Dvu	0.003		0.00	7
<i>Diplodus annularis</i>	Dan	0.003		0.00	6
<i>Labrus merula</i>	Lme	0.002	L*	-1.00	5
<i>Diplodus puntazzo</i>	Dpu	0.002		0.00	4
<i>Diplodus sargus</i>	Dsa	0.002		0.00	3
<i>Symphodus tinca</i>	Sti	0.002		0.00	2
<i>Labrus viridis</i>	Lvi	0.002	L***	-1.00	1

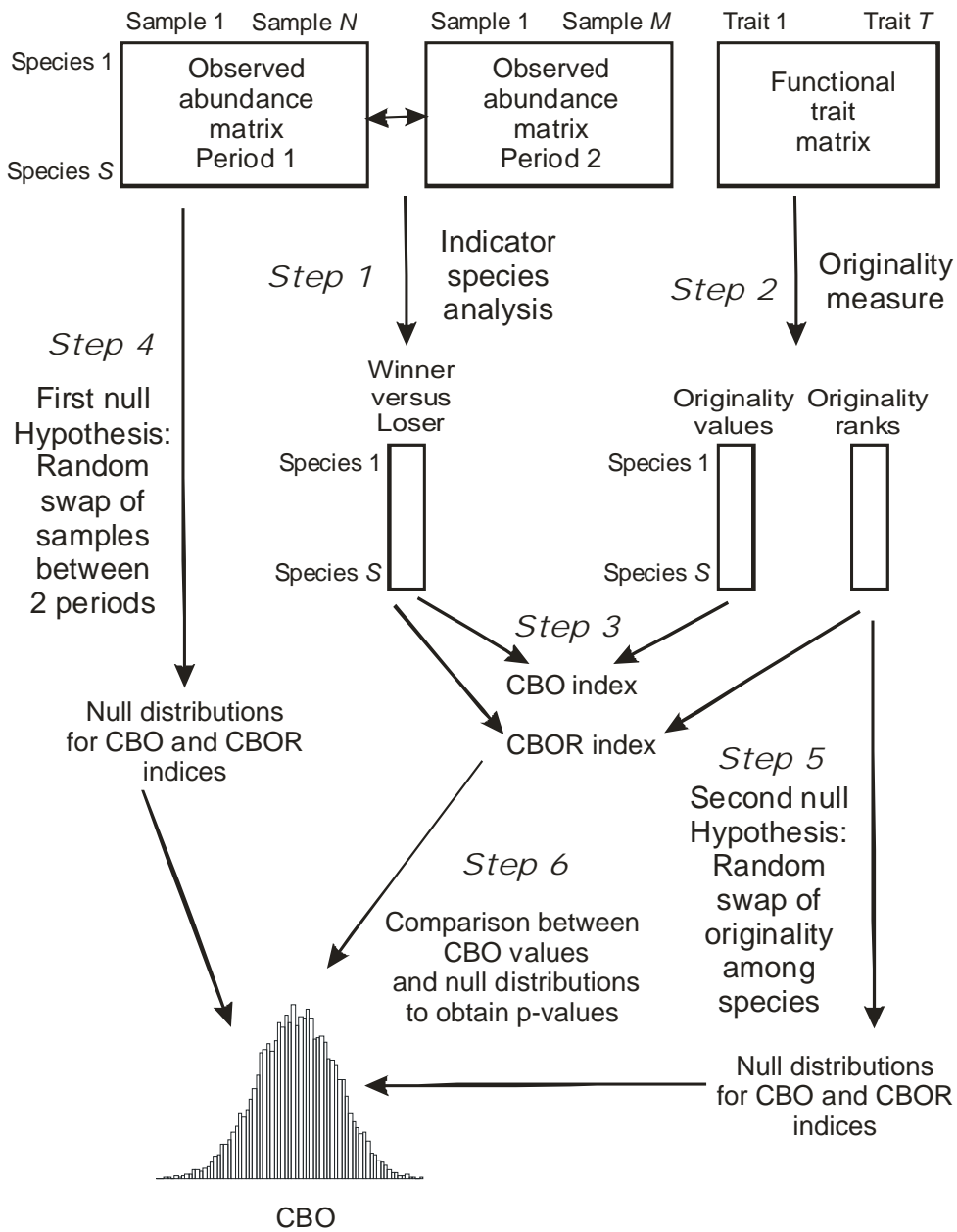
\*  $p < 0.05$ ; \*\*  $p < 0.01$ ; and \*\*\*  $p < 0.001$ .

## Figures



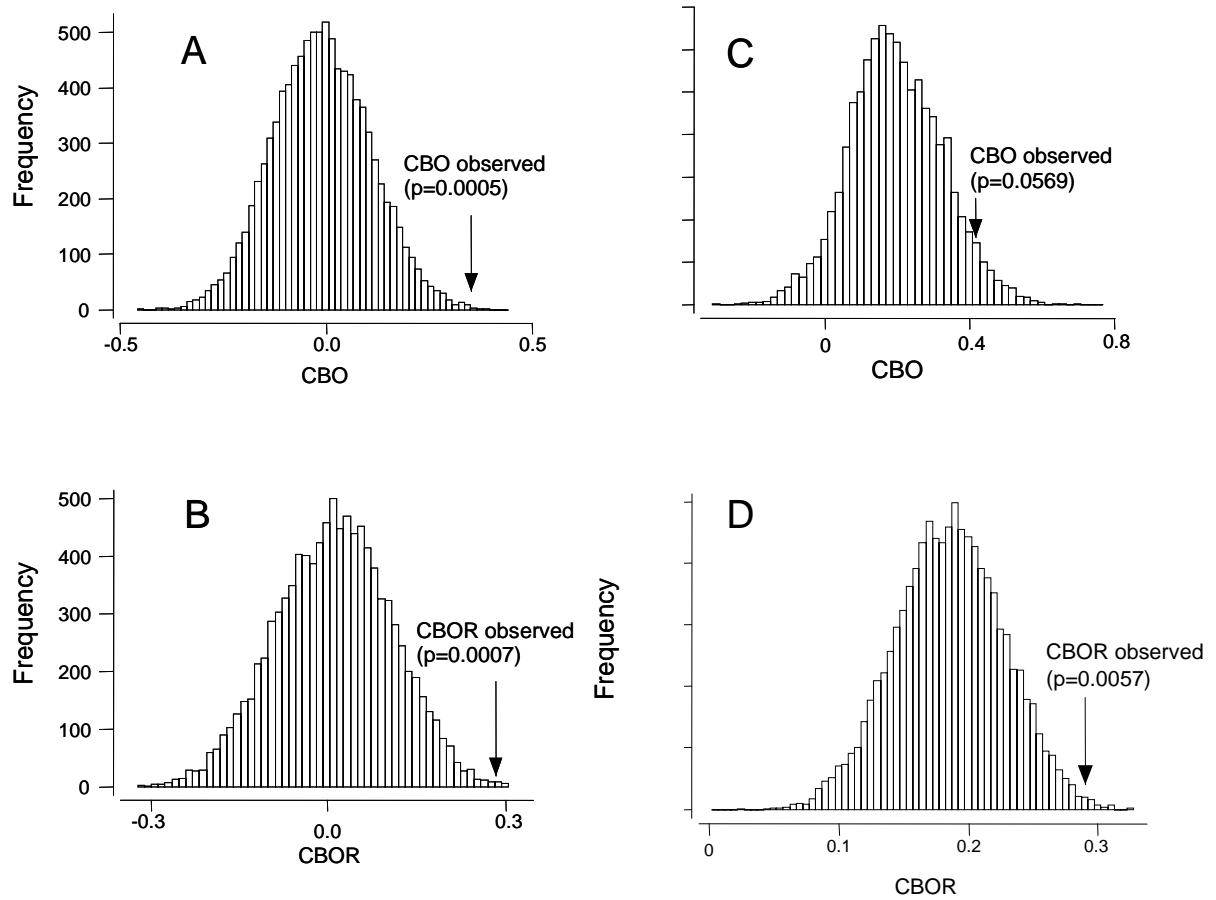
**Figure 1**

Figure 1. (A) Location of the the most original species (3) and the less original species (1 and 2) on a dendrogram based on functional distances between species. (B) Species 1, 2 and 3 contribute in a different way to the relationship between functional diversity and species richness. Each species contribute to 1 on the species richness axis (whatever their originality value) while their contribution on the functional diversity axis depends on their originality compared to the species already considered. As an illustration, the loss of the most original species (3) would decrease substantially functional diversity while the loss of species 2 does not affect substantially functionally diversity as a redundant species (1) is already present in the assemblage.



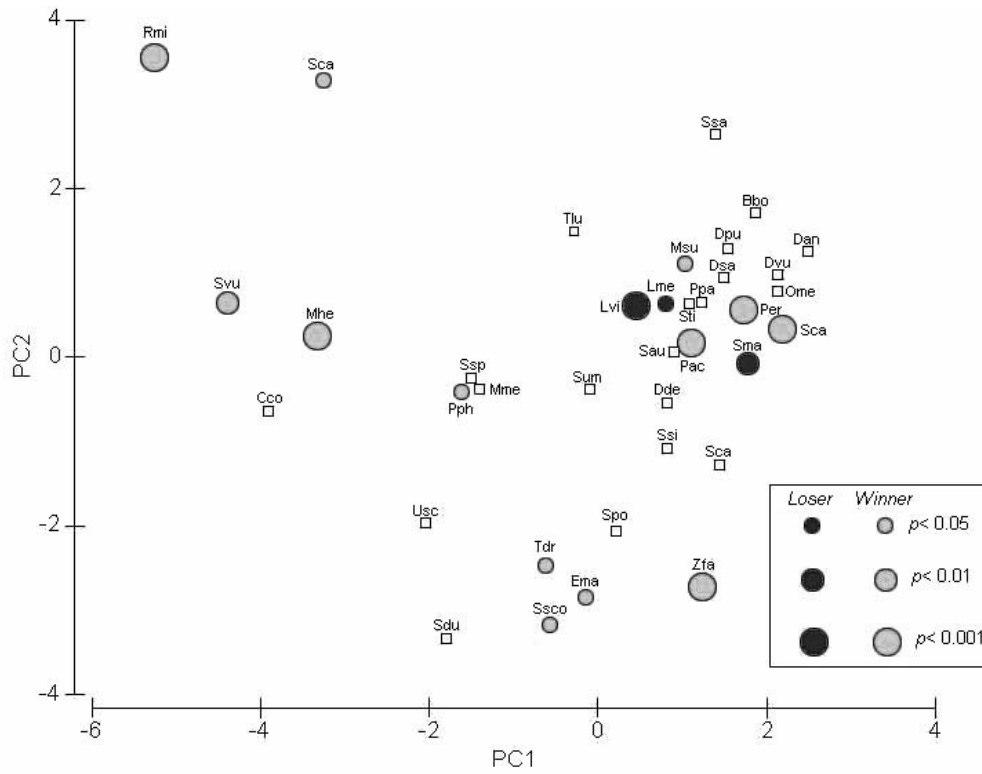
**Figure 2**

Figure 2. Summary of the different steps providing the estimation of the new Conservation of Biological Originality indices (CBO and CBOR based on ranks) and testing them using two null hypotheses.



**Figure 3**

Figure 3. Conservation of Biological Originality indices (CBO for A and C and CBOR for B and D) were estimated using two null models: (A and B) abundance data were randomly distributed between the two periods, (C and D) originality values were randomly distributed among species. The observed CBO value is higher than expected under the first null model (A), while the observed CBOR value is higher than expected under each of the two null models (B and D).



**Figure 4**

Figure 4. Position of the 37 species (codes are in table 1) in 2 functional dimension plot provided by Principal Component Analysis performed on the species by functional traits matrix. The two first axes explain 48.9 % of the total variation. Winner species are in grey while loser species are in black.