DIVERSITY AND MARINE RESOURCE MANAGEMENT : WHAT CAN WE LEARN FROM THE RESULTS OF ECOLOGICAL STUDIES ON FISHES?

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Resource management is still nowadays dominated by population dynamic approaches and its derivatives. These approaches have proven to be useful in many circumstances but they have limitations which have lead in some cases to severe problems. For instance one may attribute at least in part to these approaches the crashes of important fisheries such as the North-West Atlantic cod in Canada and USA or the orange roughy fishery in the south-west Pacific (Pitcher, 2001; Roberts 2002). Without entering in the many criticisms which can be made it should be noted that these approaches: i- require a very good knowledge of the resource and its environment; ii- have problems to manage more than a couple resources at the same time in the same area; iii -are based on past events to predict future potential harvests. I do not think that we should throw altogether the ideas of these approaches but we should remember that they can not represent the entire solution and should be integrated in a much larger picture.

A new concept has emerged in the past three decades, ecosystem management. This time instead of looking at a handful of resources one tries to consider many aspects at the same time, among others: major and minor resources, trash fish, benthic environment, coastal and pelagic environment, fishing, other uses such as tourism, and the socio-economical context. Needless to say that if resource management stumbled in the past with models considering only a very limited number of species, there is presently no model available to yield precise indications on how to manage resources in this new way. The time has certainly not yet come for such models, if however we may one day pretend to build some which are realistic. Instead of models one will try to define management units which will be considered as basic elements in a large puzzle which combines three major components: the environment, biodiversity and the socio-economic context, all three components displaying strong interdependence (Figure 1). The aim of the present article is to consider some of the issues linked to the biodiversity component of this approach.

within this archipelago as second order sub-regions. For each order one may define a gamma diversity. For instance the total Indo-Pacific tropical region has probably around 6000 taxa of coastal fishes, the Tuamotu archipelago which is at the eastward limit of this region has approximately 650 coastal species and the island of Rangiroa, part of the Tuamotu has around 450 species.

Alpha diversity is given by the number of species found in a local habitat. The definition of "local habitat" is however a little subjective, but two criteria may be retained: 1- there should be a boundary to the habitat; 2- the habitat should be a "functioning entity".

Beta diversity is not truly a diversity but rather a diversity gradient. It measures the average difference in alpha diversity from one locality to the next. This can be understood in different ways/ It can be for instance the difference in number of species between two localities (the usual definition) but it may also take into account the species composition and count the number of different species between two localities. There are many formulas to estimate beta diversity, a review can be found in Koleff et al. (2003).

II – Relationships between diversity levels

As will be seen later local diversity is a major driver for several ecosystem services. It is therefore important to see if this local diversity can be predicted in some ways from large scale information. In other words is there a relationship between local and regional diversity?

This question has been considered by many and theory (Hillbrand & Blenckner, 2002) indicates that there is necessarily a relationship between alpha and gamma diversity, the species found on a local scale deriving necessarily from a regional species pool. There are very few studies trying to relate alpha to gamma diversity for marine fishes. The following example is extracted from the IRD data base and is not yet published. The first step is to compare regional gamma diversity with the gamma diversity of islands within these regions (Figure 2). This analysis is based on 65 checklists of reef fishes from the tropical Pacific biogeographic area. Ten regions were defined based on the species composition of these checklists. Two results are of interest here, first there is a general increase of island diversity with regional diversity, second there is a large variance within region. This variance will be analyzed a little further but is mainly due to island size and isolation. The second step is the comparison between gamma diversity at the island level and local diversity (Figure 3). The latter is represented by the diversity measured on isolated coral reefs. The major feature is an

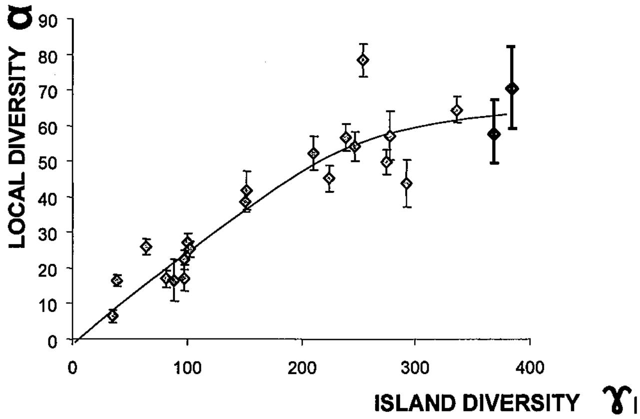

Figure 3: relationship between alpha diversity (number of reef fish species on a standard site of $500m^2$) and insular diversity (number of reef fish species on an island)

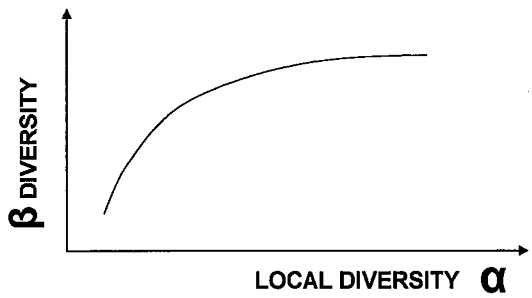

Figure 4 : relationship between beta diversity and local (alpha diversity) in the case of reef fishes as deduced from Figure 3

III- MAJOR FACTORS AFFECTING DIVERSITY

One may ask which factors act on diversity. Let's examine the case of coastal fishes. Two major types of factors may be defined: i- large scale factors; ii- local scale factors. Large scale factors comprise factors such as island size, degree of isolation of the island, latitude, distance to biodiversity centers, whereas local factors may comprise reef type, depth, fishing level, substrate composition such as algae, rock or sand covers.

Gamma diversity will be influenced only by large scale factors. Latitude is a well known factor, with usually a decrease of gamma diversity as one leaves the equator. This trend is usually attributed to a will have more internal similarity than larger or less isolated islands. Similarly areas at higher latitudes or further from the centers of biodiversity will have more internal similarity than areas closer tot the equator or to the biodiversity centers. To give some pragmatic cases, one may consider the Mediteranea - Black Sea area. The maximum diversity will probably be found near the communication with the Atlantic Ocean and the formal communication with the Red Sea, the latter being also the southern most area in this biogeographical region. In opposition areas such as the northern part of the Adriatic sea or the northern part of the Black sea will likely support lower diversity and higher similarity because of higher latitudes and larger isolation. This means that if one whishes to protect diversity this can be done with smaller areas in the latter areas.

IV- Diversity and ecosystem services

Diversity by itself would not interest much people in general. What is of interest to most of us are the services linked to this diversity. These services are numerous and it would be very ambitious to try to list them all. In the following we will concentrate on a restricted number of these services which have received much attention from the scientific community: i- biomass and production; ii- stability-resistance and resilience of ecological systems.

Biomass is the amount of matter per unit area. For coastal marine resources it is usually expressed as g / m^2. Measurements of this biomass are not always easy even for coastal fishes which represent probably the best known wild marine resource. Problems with measuring biomass come from the high specificity of most fishing techniques and the fact that underwater observation (visual or with videos) can not take into account all the species present, many species being either too small, cryptic or too shy to be observed by these means. Therefore one has usually access to only a fraction of the entire biomass present. One should remember that similar problems exist with our appreciation of alpha diversity, therefore at present our understanding of the relationship between biomass and diversity are still in its infancy. Most of what is known on these relationships comes from mesocosm experiments essentially conducted on grass type plants (Hector et Loreau 2005). Additional information exists also from several other biomes, but to my knowledge very little is known on these relationships on a large scale. There is however some information for reef fishes from the tropical Pacific islands which confirm most of the findings coming from

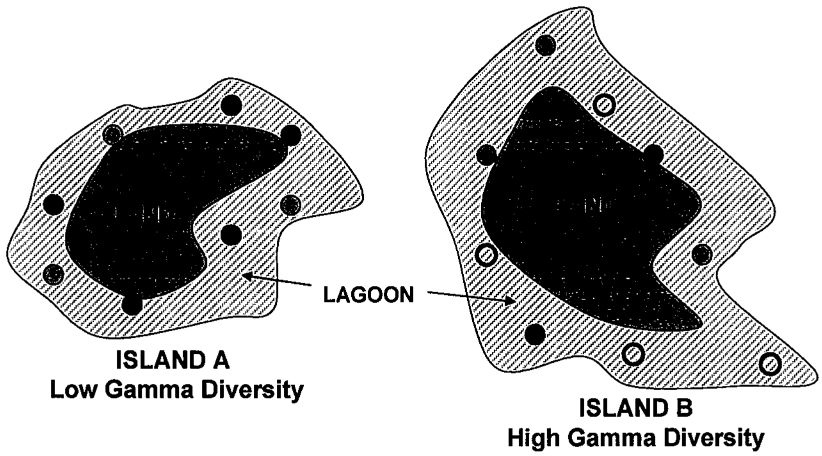

Figure 6 : localities on two hypothetic island with different alpha diversity. Black circles: low alpha diversity; Grey circles: medium alpha diversity; Open circles: high alpha diversity.

The second service of interest to most coastal resources is production. Production can be defined as the increase in biomass per unit of time. Production is therefore related to biomass, especially in exploited systems, as production can then be more or less assimilated to yield when the systems are sustainable. Most of what is known on the relationships between production and diversity comes from experimental approaches on grasslands. Little has been so far published on the relationships between production and diversity in other systems in particular for coastal marine fishes. In most cases production is proportional to biomass (Ernest et al. 2003), higher biomass meaning in general higher production for a given alpha diversity level. In the absence of real data it is difficult to assess what would be really observed according to gamma diversity but it is likely that one should observe relationships as those indicated on Figure 7. One would in particular predict for localities with low alpha diversity a slightly higher production in the area with low gamma diversity compared to the area with high gamma diversity. However localities with high alpha diversity will only be found on the area with high gamma diversity and those localities will support the highest production. One would also expect production to be concentrated on a few species in the area of low gamma diversity compared to the area with high gamma diversity (Figure 8), in particular it is likely that the species displaying the highest production will be in the area with low gamma diversity.

variance of its biomass through time. Perturbations will usually induce a variation of alpha diversity and therefore biomass. One may define resistance as the amount of perturbation needed for the assemblage to loose a certain proportion of its diversity or biomass. In other words an assemblage that looses less diversity or biomass than another assemblage for a given type and level of perturbation will be considered as more resistant (system 1 has higher resistance than system 2 on Figure 9). Once this loss of diversity or biomass has occurred it will take time for the assemblage to recover and come back to its initial state. The time needed for this recovery is a measure of the resilience. The shorter the time needed and the more resilient a system will be (system 1 has higher resilience than system 2 on Figure 9)..

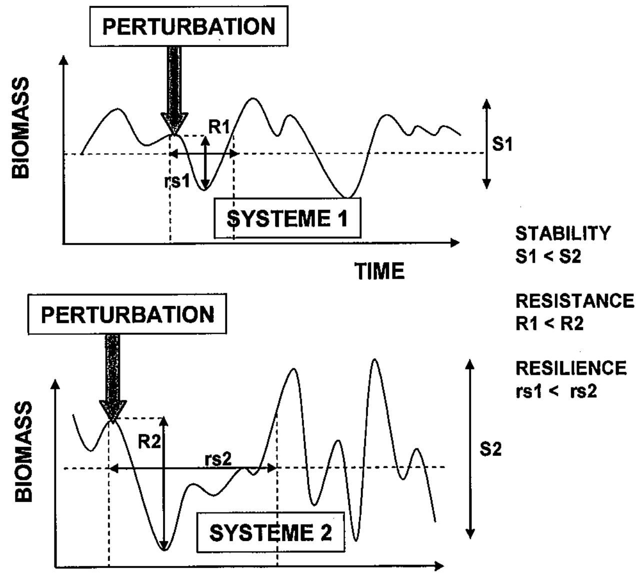

Figure 9: stability, resistance, resilience. S1 and S2 vertical arrows indicating the magnitude of the variance in biomass through time. R1 and R2 vertical arrows indicating the magnitude of the change in variance next to a perturbation. rs1 and rs2 horizontal arrows indicating the magnitude of the time needed for the biomass to come back to its initial level after a perturbation. System 1 is supposed to have a higher diversity than system 2.

The ability of assemblages to recover from perturbation is an essential property. At present we still have little practical knowledge on how complex systems react to perturbations as the latter come in multiple understanding of the functioning of ecosystems is still very primitive, especially in the case of extremely diverse ones as found in tropical coastal marine environments. One may simplify an ecosystem as a network of organisms with complex energy flows between them. Alteration of these flows may be acceptable within certain limits beyond which the system may either collapse or change state. Depending on the components of the system the critical flows may be found at various levels of the network. Based on these levels three major types of control are proposed at present (Cury et al. 2003) : bottom up, top-down and "wasp waist" controls.

V-1- Bottom-up controls

Many marine ecosystems are typically driven by their primary production components, i.e. plankton or its nutrient sources. An increase in primary production leads to an increase in plankton (first phyto-plankton, then zooplankton) which will in turn feed forage organisms (mainly fish) which themselves will be preyed by top predators (Figure 10).

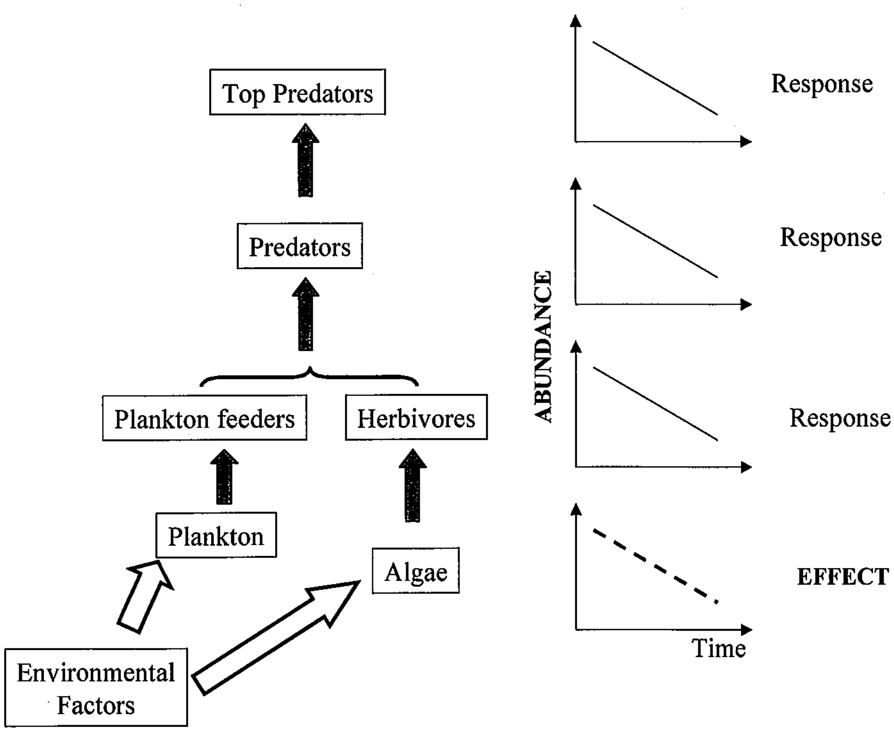

Figure 10 : Bottom-up control (adapted from Cury et al. 2003) in a marine system simplified to four trophic levels. The environmental factors decrease the growth of algae or the abundance of phytoplankton

dam (Caddy, 2000). This collapse was due to the very sharp drop in nutrient input from the Nile river which allowed high primary production and consequently a regular source of food for plankton feeding sardines. Similar changes are known from other river systems, such as in the China Sea, Japan or Mediterranean (see Caddy, 2000 for a review).

V-2- Top down controls

Predators play a very important role in aquatic systems. It is estimated that fishing mortality represents only a fraction of mortality by predation (Bax, 1991) in these systems. Thus the effects of fishing on predators may seriously alter the control that predators have over a range of preys and consequently alter the whole system. This top-down control (Figure 11) is not necessarily unidirectional, i.e. large fish eating small fish. A famous example is given by the relationships between cods and herrings in the North-Atlantic. Adult cods are predators of herrings. However, cod larvaes are predated by herrings, thus resulting in a double-way predation between these two species (Stokes, 1992). This type of interaction can become very complex, especially in very diverse systems such as coral reefs, prey and predators frequently swapping their roles, mainly based on body size. It would therefore be difficult to try to understand all the possible effects of changes in predations on a fish community. There is seldom a one way effect, i.e. the removal of one predator will promote its major prey species, but rather a set of complex interactions. May et al. (1979) indicate that in the North Sea the relative abundance of various species changed but the overall catch remained rather stable (considering the increase in fishing effort). This was explained by the decrease consequent to fishing of pelagic fish (herring and mackerel) which controlled the recruitment of benthic species (mainly cod and allied species) by eating the larvae of these benthic species during their planktonic phase. One should however remember that in general an increase in fishing effort and therefore the decrease in the abundance of the largest predators brings to a decrease of the overall trophic level of a system, as demonstrated by Pauly et al. (1998) on a global scale and by numerous authors on a local scale.

Even though predation is by far not the only explanation for the relationship between stability and complexity within a system, it certainly plays an important role. As mentioned above predation is linked to size in marine systems and large fish will tend to prey on the most available preys in terms of size. This will have a stabilizing effect on size distribution within the system and consequently on diversity (Shin and Cury 2001). This size relationship between preys and predators within marine systems is also illustrated by size-abundance diagrams. Typically

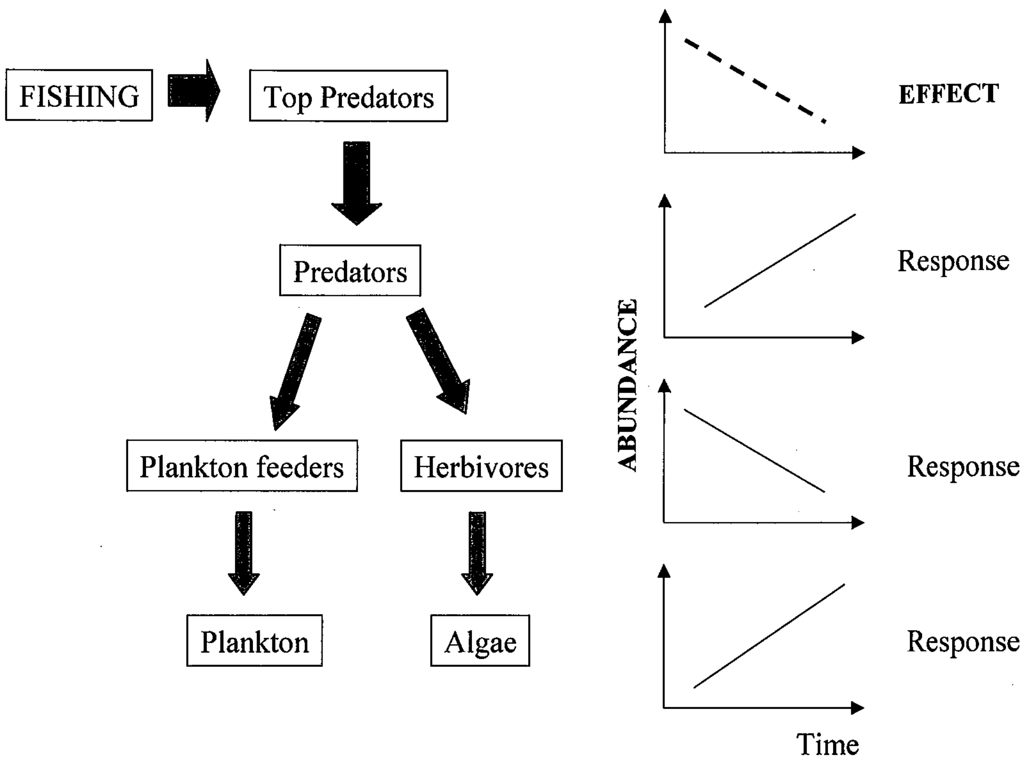

Figure 11 : top-down control in marine ecosystems (adapted from Cury et al. 2003) simplified to four trophic levels. The decrease in top predators (induced in the present example by fishing) will allow predators to increase. This in turn has a negative effect on grazers (plankton feeders and herbivores in this case), the ultimate consequence being an increase in plankton abundance and algae growth.

V-3- Wasp waist controls

Cury et al. (2000) proposed a third type of control within marine systems, "wasp-waist" control (Figure 12). This concept is based on observations made on large pelagic systems such as off Peru, California or SW Africa. In these systems one may observe that small plankton feeding fish species exert at the same time a top-down control on plankton and a bottom-up control on predators (mainly fish, marine birds and pinnipeds). The response of the plankton to a change in these plankton feeding species is usually rapid. On the opposite the predators of these fish tend to have life-history characteristics which buffer the consequences of rapid changes in their preys. This can be done by switching to other prey species, by moving to other feeding grounds, by

Technology is evolving at a very fast pace these days and there has been numerous applications in improving our estimates of abundance, biomass and diversity of coastal fishes. It would probably take books to document them all, therefore in the following just a few examples will show some of the present trends.

A basic technique in estimating diversity, abundance or biomass is to allocate sampling effort according to a preset stratification. This stratification usually reflects known or supposed gradients in the spatial distribution of the objects to sample. In terrestrial environments stratification is usually done according to the definition of habitats obtained from aerial photography or satellite imagery. Underwater these methods are also very useful but they are limited to shallow waters, as even in very clear waters it is very difficult to map habitats beyond depths of 15m. Sounders have been used for a long time to map sea bottom topography, but until rather recently the width of the sea bottom covered by the sounder was rather narrow and it took long cruises to accurately map an area. The development of multi-beam sounders, side-sweeping and wide-angle beams have allowed to considerably increase the accuracy of the mapping and with far less boat time. In addition it is now possible to have indications on the nature of the bottom (e.g. its rugosity, hardness, thickness or homogeneity). These progresses allow considerable improvement in the quality of the maps, even shallow areas being now mapped with accuracy.

The combination of accurate habitat mapping with diversity sampling have lead to accurate mapping of the diversity at a much finer scale than ever before (Harborne et al. 2006; Pittman et al. in press). An example of how this is applied is given by Mellin et al. (2007) (Figure 13). In this case the island to sample was first pictured at high resolution (1.5m pixels). Then the substrate was evaluated from these pictures by analyzing the combinations of information from the pixels and ground truth stations. This allowed mapping substrate variables such as algae or sand cover, the proportion of hard bottom or the abundance of corals with a resolution of 35m pixels. Similarly a depth map was also constructed in the same way. Then information from fish sampling stations were combined with depth and substrate information by a GLM (General Linear Model) in order to attribute to each depth and substrate combination (stratum) an average diversity and abundance. This allowed a first mapping of diversity and abundance with a low resolution (35m pixels). Interpolation methods (Triangular Irregular Networks) allowed afterwards refining these maps to a much finer scale (1.5m pixels).

in the presence of a diver. These systems allow to estimate the distance at which fish are observed and also to estimate their size. This information allows density and biomass estimates with much higher accuracy than most fishing methods. However there are still numerous problems with these techniques. For instance in areas with high species diversity or high rugosity it remains difficult to assess the number of species. In such circumstances it may also become very time consuming to analyze the images. These techniques are however a major improvement for waters which are not easily accessible by divers (too deep, too dangerous) and represent a complementary sampling tool in areas usually sampled by divers. Another advantage of these methods is that they do not harm the environment or the resources.

VII - Marine reserves as a basic ecosystem management tool

Ecosystem management is still in its infancy and to date only a limited number of management tools have emerged from this concept. The major concept is probably the use of marine protected areas (MPA) to enhance habitat quality as well as the diversity, abundance and biomass of its inhabitants. There are many types of MPAs and they may be used in many different ways. There are numerous reviews on how MPAs may change diversity, abundance, biomass, size frequency or behavior of fish not only within the MPAs but also outside the boundaries of the MPAs (Roberts and Polunin, 1991, 1993; Côté et al. 2001; Roberts et al. 2001; Agardy et al. 2003; Halpern and Warner, 2002; Russ 2002; Halpern 2003). In most cases MPAs will generate an increase in the alpha diversity of coastal fishes within the MPAs. This increase is however usually limited and will in most cases affect preferentially species targeted by fishing. Increases by MPAs in abundance, biomass and average size of species targeted by fishing is widespread. These increases have been proven inside the MPAs but increases outside the boundaries of the MPAs are not easily demonstrated (Roberts 2001). Species which are not targeted by fishing may display various tendencies. In some cases there may be an increase linked to the improved habitat quality. In other cases as the species targeted by fishing are often carnivorous or piscivorous, the increase of the latter will generate a decrease of their preys, i.e. herbivorous and planktivorous species. This may have cascading effects on the environment (e.g. a decrease in herbivores may generate an increase in algae cover which in turn will change habitat quality) and the resources.

MPAs do not however always generate such changes. In some cases (see Kulbicki et al. in press) changes brought by the MPA may be

One of the major problems with the scientific aspects of ecosystem management is the lack of a sound and unique theoretical background to frame our knowledge and construct decisions. There are multiple theories trying to explain the causes and consequences in the variations of biodiversity but none at present can explain the entire range of what is observed. One of the major problems with theories in this field is that theoretical work is quite often in advance on field observations and many theoretical propositions lack field observations to support them or the field evidence is restricted to small scale experiments, mostly using plants, which may not be relevant to other biomes.

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