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Insights into the diversity of the biodiversity concept

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Abstract. Biodiversity is not a monodimensional but a multidimensional concept. It refers to the variety of life, encompassing levels of complexity from within species to across ecosystems. Biodiversity therefore includes diversity within species (genetic diversity), between species (species diversity), between higher taxonomic units (phyletic diversity), between ecosystems (ecodiversity) and diversity in the functional role of species within ecosystems (functional diversity), from the local (sample) to the global scale. Finally, biodiversity encompasses the proportional distribution of the individuals among the species (heterogeneity diversity or evenness). This complexity of levels and scale makes it impossible to assess the state of diversity using a single measure. Different measures can suggest different conclusions. For example, a given impact can increase α-species diversity and decrease γ-species diversity; patterns of species diversity and diversity measured at higher taxonomic levels are not concordant. It may therefore be naïve, risky and/or erroneous to use single measures of diversity for management or conservation purposes.

Keywords: biodiversity, genetic diversity, species diversity, functional diversity, heterogeneity diversity, scale.

Résumé. **Sur la diversité du concept de biodiversité.** La biodiversité est un concept multidimensionnel qui englobe la diversité du vivant dans toutes ses dimensions, du gène à l'écosystème. La biodiversité inclut donc la diversité au sein des espèces (diversité génétique), entre espèces (diversité spécifique), entre niveaux taxonomiques supérieurs à l'espèce, du genre au phylum (diversité phylétique), entre écosystèmes et paysages (écodiversité) et la diversité des fonctions que remplissent les espèces au sein des écosystèmes (diversité fonctionnelle). La diversité spécifique est le nombre d'espèces, de l'échelle locale du relevé (diversité ponctuelle) à celle de l'écosystème (diversité α), de l'ensemble des écosystèmes d'une région (diversité γ) ou d'une province biogéographique (diversité ε. Enfin, la biodiversité peut décrire la distribution d'abondance des espèces (diversité d'hétérogénéité). La diversité β mesure le renouvellement des espèces (ou des taxons supérieurs à l'espèce) entre relevés, écosystèmes ou régions. Cette complexité des niveaux et des échelles, qu'englobe le concept de biodiversité, rend impossible l'utilisation d'une mesure unique pour la décrire. En effet, les mesures de la biodiversité, à ses différents niveaux et échelles, peuvent donner l'impression que les résultats sont contradictoires. Un impact donné, naturel ou d'origine humaine, peut par exemple accroître la diversité α et diminuer la diversité γ, accroître la diversité d'un taxon et diminuer celle d'un autre taxon ; la diversité mesurée au niveau spécifique peut ne pas être en concordance avec celle mesurée à un niveau taxonomique plus élevé. Il est donc naïf, risqué et/ou erroné d'utiliser une seule approche de la biodiversité (il s'agit généralement de la diversité spécifique) pour les besoins de la gestion et de la conservation des milieux naturels. En outre, il est important de noter que le nombre d'espèces ne traduit absolument pas la valeur d'un habitat : une décharge d'ordures est plus riche en espèces que beaucoup d'habitats à grande valeur patrimoniale.

Mots clés : biodiversité, diversité génétique, diversité spécifique, diversité fonctionnelle, équitabilité, échelle.

Introduction

'Biodiversity' is today a popular expression, widely used not only by scientists, but also by political leaders, civil servants, conservationists, environmentalists ('greens') and the public at large. The term actually encompasses a wide spectrum of concepts, sometimes worlds away from its popular definition.

The term 'biological diversity' was used first by Dasmann (1968). Thomas Lovejoy, in the foreword to the book 'Conservation Biology' (Soulé and Wilcox, 1980) introduced the term to the scientific community. The term's contracted form 'biodiversity' was coined by Wilson (1988) in the proceedings of the National Forum on Biological Diversity. It gained in popularity after the 'United Nations Conference on Environment and Development' (UNCED), also known as the Rio Summit, Rio Conference and Earth Summit, held in Rio de Janeiro (Brazil) from 3 June to 14 June 1992.

Since then, both the term and the concept of biodiversity have achieved widespread use among biologists, conservationists, politicians and concerned citizens. The term is often used to reflect concern for the natural environment, nature conservation and species extinctions.

In the course of their more than 40-year lifespan, the meaning of the terms 'biological diversity' and 'biodiversity' have greatly evolved. The way their meaning has shifted in the environmentalist's jargon is completely different from their evolution within the scientific community. As a result, misunderstandings are all too frequent between environmentalists and scientists. Misunderstanding also occurs within the scientific community, between those who refer to biodiversity as it was originally defined and those who refer to its current definition, or to one of its current definitions, more exactly to the suite of concepts they encompass.

This review, which follows the previous attempts of Whittaker (1972), Gray (2000) and Sala and Knowlton (2006), analyses the above issues, proposes a uniform terminology for the range of concepts biodiversity encompasses and highlights the fact that using a single measure of biodiversity, e.g. species richness at a given habitat or geographic scale, cannot assess the overall state of biodiversity.

The modern concept of biodiversity

Biodiversity means the variety of life, encompassing levels of complexity from within species to across ecosystems. Biodiversity therefore includes diversity within species, diversity between species, diversity between ecosystems and diversity in the functional role of species within ecosystems (Sala and Knowlton, 2006). Biodiversity also encompasses the scale, from local and regional to global (Table I; Ramade, 1994; Gray, 2000; Sala and Knowlton, 2006). The geographic scale matters a great deal for biodiversity estimates (Warwick, 1998; Ellingsen, 2001; Willis and Whittaker, 2002). In addition, biodiversity encompasses the proportional distribution of the individuals among the species, the so-called heterogeneity diversity or evenness (Gray, 2000). Biodiversity is therefore a multidimensional concept (Fig. 1).

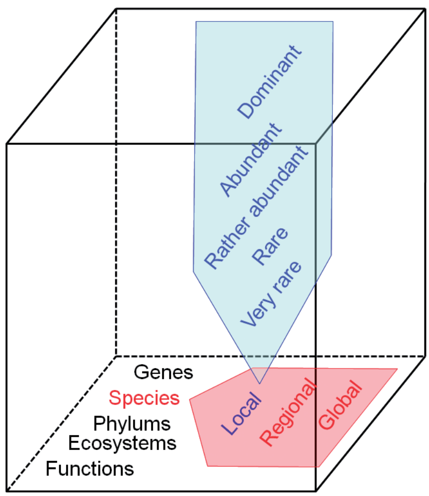

Figure 1. Biodiversity is a multidimensional concept. Dimension 1: from genes to ecosystems, landscapes/seascapes and functions. Within each taxonomic and organizational level (e.g. species), dimension 2 (scale). Within each scale level (e.g. local), dimension 3 (proportional distribution).

Taxonomic and ecological diversity

Genetic diversity

Genetic diversity means, within a species, the genetic differences between individuals and populations (Féral, 2002). For example, the *Salmonella enterica* (*Bacteria*) species, the agent of serious diseases such as typhoid and paratyphoid fevers, includes more than 2 400 known pathogenic serotypes (Lemarchand and Lebaron, 2002). *Poa annua* (Poaceae, Magnoliophyta) populations from closed habitats perform better under the less favorable conditions imposed by cutting and/or competition than those from open habitats, whereas this situation is reversed in their absence (McNeilly, 1981). In *Arrhenaterum elatius* (Poaceae), populations from closed habitats (e.g. forests) have selected a lower rate of seed production than those from open habitats (Gauthier *et al*., 1999).

Table I. Dimensions and measures of biodiversity. From Sala and Knowlton (2006).

Scale	Compositional	Structural	Functional
Species/populations	Within-species genomic diversity, divergence, disparity	Abundance	Within-species gene expression and divergence
Communities/eco-systems	α-diversity, β-diversity	Ecodiversity, evenness, disparity, ecodiversity spectra (β-diversity), food web complexity	Functional diversity
Regional to global	γ-diversity, community/ ecosystem diversity	Ecodiversity spectra (β-diversity)	Functional diversity

Species diversity

Species diversity (= species richness) squares with the most popular perception of the concept of biodiversity (Boero, 2010). It means the taxonomic diversity at the level of the species (generally *sensu* the Linnean taxonomy), i.e. the number of species at a given scale of space (sample, habitat, ecosystem, landscape/seascape).

A species is often defined as a group of organisms capable of interbreeding and producing fertile offspring (sexual reproduction). In many cases, this definition is adequate. However, sexual reproduction only concerns eukaryotes. In addition, it is unknown in many eukaryote taxa, such as ascomycetes (Fungi, opisthokonts) and bdelloids (rotifers, metazoa, opisthokonts). Finally, as far as fossils are concerned, of course interbreeding cannot be checked (Le Guyader, 2002; Meselson and Welch, 2007; Hayden, 2008).

For the above mentioned reasons, differing measures of the species concept are often used, such as morphology and similarity of DNA. OTUs (Operational Taxonomic Units), a species surrogate, are usually defined in prokaryotes as less than 97% similarity DNA sequences (e.g. *in* Fu *et al.,* 2010).

Phyletic diversity

Phyletic diversity means the taxonomic diversity at a level higher than the species level: genus, tribe, family, order, class, phylum, kingdom and domain. At the species, genus and family levels, the marine diversity is lower than the terrestrial one (Sala and Knowlton, 2006; Benton, 2009; Mora *et al.,* 2011).

Three domains of Life are usually delineated: *Bacteria, Archaea* and eukaryotes; however, a fourth domain is suspected, harboring the giant viruses such as Mimiviridae (Raoult *et al.*, 2004; Claverie *et al*., 2009). As far as kingdoms are concerned, *Bacteria, Archaea* and eukaryotes encompass respectively five, two (*Crenarchaeot*a and *Euryarchaeota*) and ten (Archaeplastida, Rhizaria, Alveolates, Stramenopiles, Haptobionta, Cryptobionta, Discicristates, Excavates, Opisthokonta and Amoebobionta) kingdoms (Baldauf, 2003; Boudouresque *et al*., 2006; Baldauf, 2008; Boudouresque, 2011; Boudouresque *et al.,* 2011).

At the phylum level ('deep diversity'), the diversity of the marine realm is higher than that of the terrestrial one, which is logical, since Life began in the sea, 3 850-3 500 Ma[1] ago, and conquered continents as recently as 475 Ma ago (Wellman *et al.,* 2003). For example, 35 phylas of Metazoa (Opisthokonta) dwell in the marine environment, of which 14 are exclusively marine (e.g. Chaetognatha, Ctenophora, Cycliophora, Echinodermata, Kinorhyncha, Loricifera, Pogonophora, Vestimentifera), while only 1 (Onychophora) is exclusively terrestrial (Grassle *et al.,* 1990; Morris, 1993; Heip, 1998; Dayton, 2003; Sala and Knowlton, 2006).

Phylogenetic diversity

Phylogenetic diversity is of interest because, for a given number of taxa, their belonging to the same higher taxon (e.g. birds) or to several higher taxa (e.g. birds, lizards, mammals, etc.) matters (Fig. 2 and 3). Phylogenetic diversity is defined and calculated as the sum of the lengths of all those branches that are members of the corresponding minimum spanning path, in which 'branch' is a segment of a cladogram, and the minimum spanning path is the minimum distance between the two nodes (Faith, 1992; Fig. 3).

Ecological diversity

Ecological diversity means the spatial diversity: patches within an ecosystem, ecosystem diversity and landscape/seascape diversity (Ros, 2003). Ecological diversity is often known under the contracted form ecodiversity. It is easy to approach where ecosystem limits are clear-cut, either naturally or due to human impact, as commonly occurs in European land environments. In contrast, ecological diversity is not a useful concept where species composition steadily changes

[1] Ma = million years.

(continuum; Boudouresque, 1970, 1971) along an ecological gradient (e.g. salinity, temperature), such as in the open sea pelagic environment. Beta diversity (see below) can be used to compare species and phyletic diversity between patches, ecosystems and landscapes/seascapes.

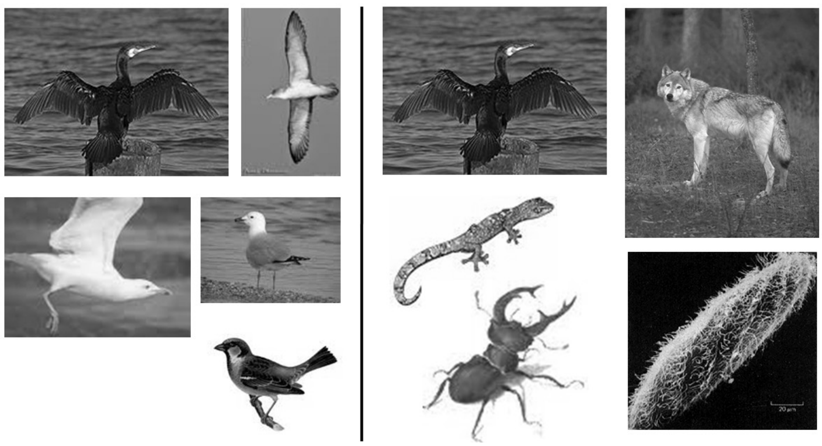

Figure 2. Phylogenetic diversity matters. For a given number of taxa (here five), it is not equivalent whether they all belong to the same higher taxon (birds; left) or to several higher taxa (birds, lizards, mammals, insects – metazoa, kingdom opisthokonts – and ciliates – kingdom alveolates -; right) This example is fictitious.

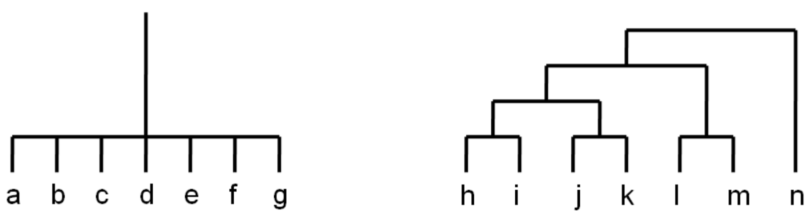

Figure 3. Phylogenetic diversity differs, for a given number of taxa (here 7), according to the mean path length between every taxon and all the others. Phylogenetic diversity of the a through g habitat (left) is lower than that of the h through n habitat (right). This example is fictitious.

Functional diversity

Functional diversity was defined as the value and range of functional traits of the organisms in a given ecosystem (Tilman *et al.,* 2001; Mason *et al.,* 2005). The reason why the concept of functional diversity emerged is the recognition that taxonomic measures of biodiversity (species diversity, i.e. the number of species, or their relative abundance, i.e. heterogeneity diversity or species evenness; see below) fail to provide adequate insight into the consequences of species loss for ecosystems (Naeem, 2003).

A species' contribution to ecosystem processes is determined by many traits, e.g. **(i)** its efficiency to fix CO_2 (C3, C4 and CAM primary producers), **(ii)** the nature of the photosynthetic pigments and therefore the width of the light spectrum it can use (e.g. chlorophylls *a*, *b*, *c*, *d*, bacteriochlorophylls, phycobilines), **(iii)** the ability to fix N_2 (molecular nitrogen), **(iv)** mixotrophy, i.e. the ability to shift from autotrophy to heterotrophy, or the obligation to perform both photosynthesis and predation, such as the Dinobionta *Karlodinium armiger*, **(v)** the way heterotrophic organisms acquire organic matter (e.g. predation, parasitism, suspension feeding, filter feeding), and **(vi)** the number of trophic levels (Naeem, 2003; Duffy, 2006; Sala and Knowlton, 2006; Berge *et al.,* 2008). The above mentioned trait variation between species forms the basis for a permanent differentiation of function that enhances collective performance of the ecosystem (complementary effect) (see Loreau, 2003).

Scale pattern of the diversity: point, alpha, gamma and epsilon diversity

Species diversity (= species richness), the most popular meaning of the concept of biodiversity, and phyletic diversity (genus through domain) encompass several scales: point, alpha, gamma and epsilon-diversity; they measure the number of species, genera, families, etc. at a given scale.

Point-diversity means the number of species (or higher-level taxa) within a sample (Whittaker, 1972; Gray, 2000; Sala and Knowlton, 2006). Here, a sample is a subset of the ecosystem, in the ideal case a representative subset; its surface area, or volume, is then equal to or higher than the minimum area or the minimum volume, and depends upon the type of the ecosystem (Gounot and Calleja, 1962; Gounot, 1969; Weinberg, 1978; Boudouresque and Belsher, 1979; Rumohr *et al*., 2001). It is worth noting that a 'representative' sample never means that all the species (or higher-level taxa) of the ecosystem are actually present within it, but rather that many, or the most abundant ones, are found within it; larger areas or volumes tend to contain larger numbers of species (or higher-level taxa), so that the relationship between number of species (or higher-level taxa) and surface area (or volume) does not have any asymptote (Connor and McCoy, 1979; Williamson *et al*., 2001).

The alpha (α) diversity is the cumulative number of species (or higher-level taxa) of samples within an ecosystem, in a given region (Fig. 4; Whittaker, 1972; Gray, 2000).

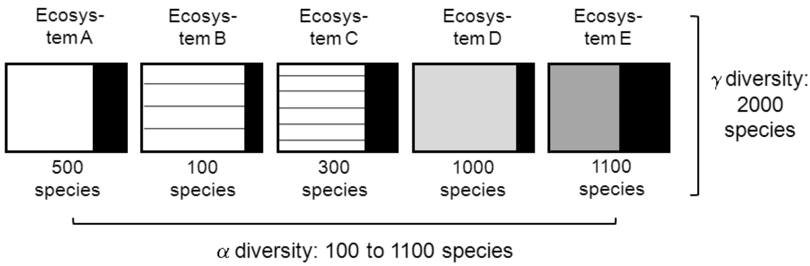

Figure 4. Five ecosystems (A, B, C, D, E) and (below) the number of species (α-species diversity) they harbor in a given region (e.g. Provence or the northern Gulf of California). The size of the rectangles is not proportional to the number of species they harbour. In white, stripped and grey, the species specific to an ecosystem. In black, the percentage of species they share with one or several other ecosystems. Due to these shared species, γ-species diversity (right) is not the sum of the α-diversity of the five ecosystems. Fictitious data.

The gamma (γ) diversity is the cumulative number of species (or higher-level taxa) of a larger unit (e.g. a set of ecosystems, a landscape/seascape, an island, a region) (Fig. 4; Whittaker, 1972; Gray, 2000; Sala and Knowlton, 2006). Due to the fact that some species (or higher-level taxa) are shared by several ecosystems, γ-diversity is not the sum of the α-diversity of every individual ecosystem. For example, the g-species diversity of Rhodobionta, Chlorobionta and Phaeophyceae (Chromobionta) in the Hyères Gulf and Islands (Provence, France) is of 335 species (Belsher *et al.,* 1976).

Finally, the epsilon (ε) diversity is the total species (or higher-level taxa) diversity of a group of areas of γ-diversity, e.g. a large biogeographical province, such as the British Islands or the Mediterranean Sea (Whittaker, 1972; Gray, 2000). For example, the ε-species diversity of the Mediterranean Sea is approximately of 17 000 species (Coll *et al*., 2010).

Heterogeneity diversity

Beta diversity

Beta diversity measures how diversity changes between samples, ecosystems, landscapes/seascapes or across time.

Some species (or higher-level taxa) are characteristic of an ecosystem: they are absent or rare from all other ecosystems. Other taxa are shared by two, several or all ecosystems. The β-diversity (or turnover diversity) is the degree of change in taxon composition between ecosystems (or habitats, or samples), along a transect, or within a landscape/seascape or a geographical area (e.g. Provence) (Gray, 2000). The β diversity is high when a few taxa are shared by the ecosystems (or habitats, or samples) of an area; in contrast, it is low when many taxa are common to many ecosystems (habitats, samples) (Fig. 5).

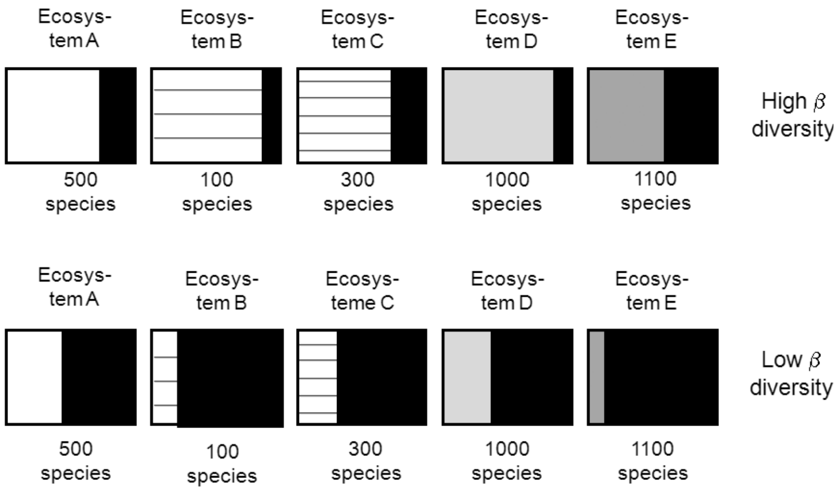

Figure 5. Five ecosystems (A, B, C, D, E) and the number of species they harbor in a given region (e.g. Provence or the northern Gulf of California) (=-species diversity). The size of the rectangles is not proportional to the number of species they harbour. In white, stripped and grey, the species specific to an ecosystem. In black, the percentage of species they share with one or several other ecosystems. Above, this percentage is relatively low, resulting in a high ß-diversity. Below, this percentage is high, resulting in a low ß-diversity. Fictitious data.

To measure the β diversity between two ecosystems, habitats or samples A and B, the following index has been proposed by Wilson and Shmida (1984). It varies between 0 (all taxa are common to A and B) and 1 (no taxon is common to A and B):

$$\beta - \text{diversity} = \frac{G_{A\text{-}B} + L_{A\text{-}B}}{S_A + S_B}$$

Where $G_{A\text{-}B}$ = the number of taxa gained (i.e. newly encountered) from A to B,

$L_{A\text{-}B}$ = the number of taxa lost from A to B,

S_A = the number of taxa within the ecosystem (habitat, sample) A,

S_B = the number of taxa within the ecosystem (habitat, sample) B.

(Formulation has been changed from that in the original Wilson and Shmida's article)

Evenness

The evenness measures the distribution of species (or higher-level taxa) abundance within a sample, an ecosystem or a landscape/seascape. It encompasses not only the number of species (or higher-level taxa), but also the proportional distribution of the individuals among the taxa (Gray, 2000). The most commonly used evenness index (J'; Pielou, 1976; Heip *et al.,* 1998) is based upon the Shannon-Wiener diversity index (H'; Heip *et al.,* 1998; Frontier, 1999):

$$H' = - \sum_{i=1}^{i=s} pi \log2\, pi$$

where s is the total number of species (or higher-level taxa), $p_i = n_i/N$, n_i = number of individuals of the i^{th} taxon and N = total number of individuals.

$$J' = H'/H_{max}$$

where H' is the Shannon-Wiener diversity index and H_{max} is maximum diversity index, i.e. log s (s = total number of taxa).

The evenness index varies between 1 (all taxa have the same abundance) and ~0 (most individuals belong to one taxon, the other taxa being represented by only one individual). There are many other indices of evenness (Hill, 1973; Heip *et al.,* 1998; Levin and Gage, 1998; Gray, 2000).

Biodiversity: a multitude of metrics and a variety of replies

The concept of biodiversity encompasses not a single but a multitude of meanings. Biodiversity is *par excellence* a multidimensional concept. The choice of a meaning (qualitative or quantitative, compositional or functional, scale, etc.) depends primarily on one's goals and interests. Biodiversity can therefore be measured in different and complementary ways and therefore have different metrics (Sala and Knowlton, 2006).

This complexity of meanings, scale and units makes it impossible to assess the state of biodiversity using a single measure. Most studies dealing with biodiversity report the simplest measure of biodiversity, that is, species diversity (= species richness). Although species diversity may be useful (as long as the spatial scale is provided) for comparisons between ecosystems, or within ecosystems over time, it may not give a good measure of the structure, function and degree of disturbance of these ecosystems. Moreover, different measures can suggest different, contrasting conclusions (Willis and Whittaker, 2002; Sala and Knowlton, 2006). A naïve approach to the biodiversity concept could lead to regarding such conclusions as diametrically opposed.

For example, at the phylum level (phyletic diversity), the known diversity of the marine realm is higher than that of the terrestrial one (see above), while the contrary is true at the species level (species diversity). Insects, which represent more than a half of the known species living on Earth, are only terrestrial. As far as Magnoliophyta (flowering plants, kingdom Archaeplastida) are concerned, 250 000-400 000 species dwell on continents vs only 64 (seagrasses) in the marine environment (Thorne, 2002; Scotland and Wortley, 2003; Hartog and Kuo, 2006; Boudouresque *et al.,* 2009). At Port-Cros islands (Port-Cros, Bagaud and the islets La Gabinière and Le Rascas), hundreds of terrestrial species of Magnoliophyta were recorded, vs 3 marine species, namely *Posidonia oceanica, Cymodocea nodosa* and *Zostera noltei* (e.g. Jahandiez, 1929; Belsher, 1975).

Ecosystems with relatively low α-species diversity (e.g. sandy marine bottoms, desert habitats) can have a high β-species diversity when compared to adjacent ecosystems.

A disturbance or a stress (see definition below and *in* Boudouresque *et al.,* 2009 and Pergent *et al.,* 2012), e.g. pollution or introduced species (see definition *in* Boudouresque and Verlaque, 2002), can enhance α-species diversity within one ecosystem while reducing it within an adjacent ecosystem subject to the same disturbance (or stress). As far as γ-species diversity is concerned, the disturbance (or stress) which enhances α-species diversity for a given ecosystem can reduce γ-species diversity at region scale (Fig. 6; Boudouresque, 2008). For example, in French Riviera habitats colonized by the introduced species *Caulerpa taxifolia* (Viridiplantae, Archaeplastida), a general decrease in teleost ('fish') species richness was observed in habitats with a high initial structural complexity (e.g *Posidonia oceanica* seagrass meadows and rocky substrates), and an increase in sandy habitats which had a low initial structural complexity (Harmelin-Vivien *et al.,* 1999, 2001).

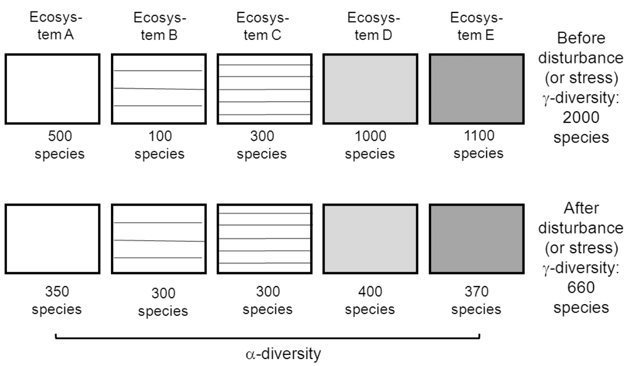

Figure 6. A disturbance (or stress), e.g. an introduced species, which reduces α-species diversity within an ecosystem (A, D and E), can increase it within another (B). In both cases (decline or increase), the γ-species diversity can be reduced. Fictitious data.

In the same way, six non-flying mammal species, all of them endemic, were dwelling in terrestrial habitats in Corsica (γ-species diversity), ~10 000 years ago, before human colonization of the island (Fig. 7). Other endemic non-flying mammals were also occupying the other Mediterranean large islands: Sardinia (e.g. the dwarf mammoth *Mammuthus lamarmorae,* the Lagomorpha *Prolagus sardus*), Sicily (e.g. the dwarf elephant *Elephas falconeri,* the dwarf hippopotamus *Hippopotamus pentlandi*), Malta (e.g. the dwarf elephant *Elephas melitensis,* the dwarf hippopotamus *Hippopotamus melitensis*), Crete (the dwarf mammoth *Mammuthus cretiosus* and the dwarf deer *Candiacervus ropalophorus*) and Cyprus (e.g. the dwarf elephant *Elephas cypriotes* and the pigmy hippopotamus *Hippopotamus minor*) (Mennessier, 1998; Pascal *et al*., 2006; Poulakakis *et al.,* 2006; Blondel *et al*., 2010). All in all, more than fifty species were living in Mediterranean large islands (ε-species diversity). Nearly all of these species were quickly doomed to extinction by the arrival of Man on these islands (the so-called *blitzkrieg*), with the exception of shrews *Crocidura sicula* (Sicily), *C. zimmermanni* (Crete), *C. cypria* (Cyprus) and the mouse *Mus cypriacus* (Cyprus) (Blondel *et al*., 2010). They were replaced by a set of some twenty introduced species, virtually the same everywhere (Fig. 5; Pascal *et al*., 2006). As a result, island γ-species diversity greatly increased (~3.5-fold in Corsica: from ~6 to ~20 species), while Mediterranean islands ε-species diversity conspicuously decreased (from ~50 to ~20 species).

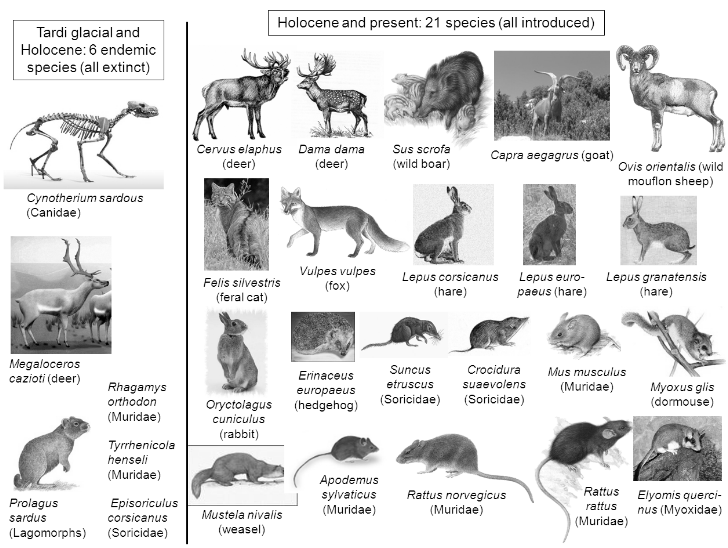

Figure 7. Left. The past γ-species diversity of non-flying terrestrial mammals of Corsica: 6 species, all endemic. For 3 species of Muridae and Soricidae, no picture was available. **Right**. The present γ-species diversity: 21 species, all introduced. Scale generally changes between pictures. Human impacts (extinctions and introductions) therefore increased 3.5-fold the Corsican γ-species diversity.

Species diversity should take into account all the species of a sample, an ecosystem or a region, from *Bacteria* and *Archaea* to e.g. unicellular eukaryotes, Fungi, Magnoliophyta (flowering plants), birds and mammals. For practical reasons, namely the difficulty of bringing together specialists of every taxon, most biodiversity studies only deal with one or a few taxa (e.g. *Archaea*, Rhodobacterales, Dinobionta, Bryophyta, ferns or flowering plants; Richard *et al*., 2000; Hugonnot, 2007; Guillou *et al.,* 2008; Herfort *et al.,* 2009; Fu *et al.,* 2010). Scientists are usually aware that the species diversity of a taxon may be relatively high while that of another taxon, within the same sample, ecosystem or region, may be low. In addition, responses to a natural or human induced disturbance rarely exhibit parallel trends among taxa. When trophic levels are dominated by a taxon or a set of taxa, opposite trends resembling trophic cascades can occur (Sala *et al.,* 1998). For example, within the Scàndula Natural Reserve (Corsica), with a high diversity and density of 'fish' preying on benthic 'invertebrates', a mean of 9 macro-invertebrate species per ~100 m^2 transect was observed; outside the reserve, in the Bay of Galeria, with poorer 'fish' populations, the mean number of macro-invertebrates per ~100 m^2 transect was ~17 (Boudouresque *et al*., 1992).

Some scientists erroneously consider as a vacant ecological niche any habitat where their taxon of interest (e.g. macrophytes, or bats) is absent. For example, in the intertidal zone of Galicia (Spain), the large introduced Phaeophyceae *Undaria pinnatifida* (photosynthetic Stramenopile, ~1 m long), has developed very dense populations; according to Cremades Ugarte *et al.* (2006), there is no problem, since it occupies a 'vacant ecological niche'; for these authors, who are phycologists (i.e. specialists of MPOs[1]), it is obvious that the lack of large Rhodobionta (red algae) and Phaeophyceae (brown algae) makes the niche 'vacant'; in their unvoiced opinion, it is clear that a mat of cyanobacteria, a turf of dwarf MPOs, limpets, winkles, barnacles and crabs, do not participate in the biodiversity and cannot edify a respectable ecosystem! Another example, in a French National Park (the Port-Cros National Park, Provence and French Riviera, Mediterranean Sea), is provided by bat specialists; they proposed the setting up of shelters and drinking troughs, in order to enhance bat populations, naturally low in the area, under the pretext that, outside the National Park, some bats are threatened species; apart from the fact that the purpose of a National Park is anything but to constitute a zoo, the bat specialists were not aware that bats consume enormous amounts of

[1] MPOs : Multicellular Photosynthetic Organisms, a polyphyletic group of organisms which encompasses most Rhodobionta (red algae; Archaeplastida), Ulvophyceae (Chlorobionta, Archaeplastida), most Streptobionta (Archaeplastida, including Embryophyta) and Phaeophyceae (brown algae: Stramenopiles).

insects, some of them possibly threatened and of patrimonial interest, and that consuming nocturnal insects can remove a resource for a threatened amphibian species, native within the National Park, the frog *Discoglossus sardus*.

Biodiversity and disturbances

The word 'disturbance' is often used by authors in a rather vague way. For this reason, its meaning will be defined hereafter. In a given ecosystem, a disturbance is the result of a short-lasting and unpredictable change in a forcing parameter (physical, chemical and/or biological) whose range of impact is greater than the inertia or resilience of one or more key species, ecosystem engineer, guild or functional compartment (Boudouresque *et al*., 2009; Pergent *et al.*, 2012). 'In a given ecosystem' means that a forcing cannot be defined *per se* as a disturbance; for example, the deposition of a 1-cm thick layer of sediment in Mediterranean subtidal habitats may constitute a disturbance for a coralligenous ecosystem but not for a *Posidonia oceanica* seagrass meadow (Boudouresque *et al.,* 2009). 'Unpredictable' means that cyclical predictable events (e.g. daily, tidal and seasonal) are not disturbances. 'Short-lasting' means that a permanent change of a forcing parameter which is greater than the inertia or the resilience of the ecosystem shall be referred to as a 'stress' (Boudouresque *et al*., 2009). 'Inertia' is the greatest magnitude of the forcing that elicits no response in some specified variable (either because the ecosystem really is unaffected by that forcing or because other processes allow the forcing to be resisted), so that the chosen variable (population or ecosystem) does not change (GESAMP, 1995). 'Resilience' is the greatest magnitude of the forcing that can be tolerated by the variable, so that the population or the ecosystem recovers to previous control values (GESAMP, 1995). A 'key species' is a species the impact of which on its community or ecosystem is great, and much greater than would be expected from its abundance; in other words, its effect on the ecosystem is out of all proportion to its relative abundance (Power and Mills, 1995; Bond, 2001). In conclusion, if the intensity of the forcing does not cause a significant change in the characteristic of interest, there is not a disturbance: the ecosystem has resisted the forcing (Connel and Sousa, 1983; Short and Wyllie-Echeverria, 1996; Boudouresque *et al.,* 2009; Pergent *et al.*, 2012).

According to the Intermediate Disturbance Hypothesis (IDH; Connell, 1978), in the absence of disturbance, inferior competitors are excluded from the ecosystem, until disturbance creates a gap, releasing them from competition. Inferior competitors are also excluded through competition and extinction due to frequent or severe mortalityinducing disturbance; it is for intermediate levels of disturbance that species diversity peaks (Fig. 8; Lubchenko and Menge, 1978; Bythell *et al.,* 2000; Hastwell and Huston, 2001; Valdivia *et al*., 2005; Ballorain, 2010). The Dynamic Equilibrium Model (DEM; Huston, 1979) accounts for some discrepancies of the Intermediate Disturbance Hypothesis, i.e. species diversity being at its highest for either low or high regimes of disturbance. The DEM predicts that the effects of disturbance on species diversity are influenced by the environmentally determined (e.g. water and nutrient availability) growth rates: species diversity is maximized at low, intermediate or high levels of disturbance, depending on whether the environmentally determined growth rates are low, intermediate or high, respectively (Fig. 8; Hastwell and Huston, 2001).

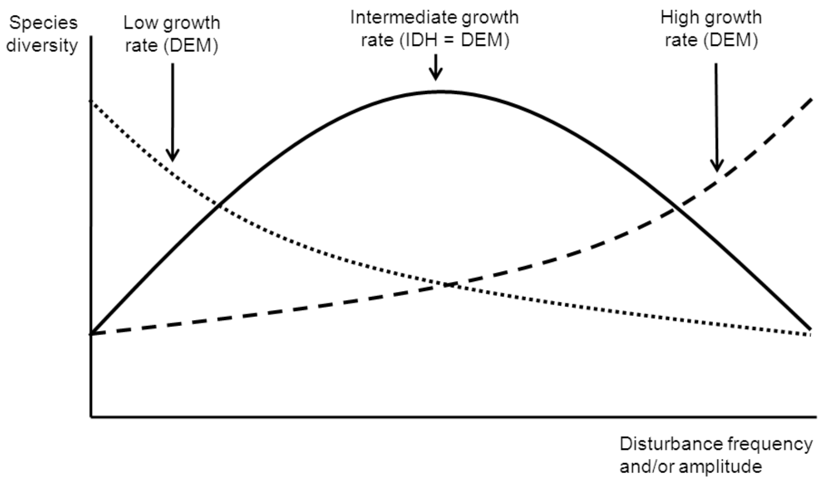

Figure 8. IDH (Intermediate Disturbance Hypothesis): species diversity peaks at intermediate disturbance intensity (unbroken line). DEM (Dynamic Equilibrium Model) accounts for high species diversity at low disturbance regime when resource availability and growth rate are low (dotted line), and high species diversity at high disturbance regime when resource availability and growth rate are high (broken line).

Conclusions

The term of biodiversity encompasses a wide spectrum of concepts and meanings. These meanings can be seen as conflicting but are actually complementary and are part of a consistent theoretical corpus.

Biodiversity is often seen by politicians, civil servants and naïve environmentalists as the number of species: the more species are present, the healthier is the ecosystem. Apart from the fact that scale matters (the number of species can be high at the scale of the sample and low at the scale of a region), the patrimonial value and the health of an ecosystem do not only depend upon the number of species. What matters is not ‘how many species?’ but ‘what are the species?’ It is important to note that a dumping area may be more species-rich than some high heritage value ecosystems, such as coastal rocks terrestrial habitats, which are species-poor but rich in endemic species.

Biodiversity is measured by a variety of metrics, at the taxonomic level (from genes and species to phyla; what is the taxon or the set of taxa taken into consideration?), at the ecological level (from patch to ecosystem), at the spatial scale (from the sample to the regional and global scale) and at the heterogeneity level (how abundant are the present taxa). Each level, scale and taxon provides a specific reply; these replies do not necessarily show parallel trends, so that the different replies may seem to be conflicting.

Many politicians, civil servants and environmentalists expect a simple (if not simplistic or Manichean) reply, a single index which sums up all the facets of biodiversity: Is the impact under consideration good or bad for biodiversity? Is the ecosystem healthy or disturbed? Unfortunately, such a comprehensive index not only does not exist, but also is utopian, that is to say it cannot exist. It may therefore be naïve, risky and/or erroneous to use single measures of biodiversity for management or conservation purposes, as often occurs in the environmentalist world.

Only comprehensive multi-scale and multi-level scientific studies of the biodiversity, designed in response to a precise concern or problem, can provide a response, of course complex, to the problem under concern.

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