

## **Biodiversity**

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### **Abstract**

The word biodiversity is used to explain the variety of life on Earth, and is considered at different levels of biological organization including genes, species and ecosystems.

Biodiversity is most often understood in terms of the number of species or other taxa and can be considered at different spatial scales such as Whittaker's definitions of alpha, beta and gamma diversity. Biodiversity is not distributed evenly over the world, leading to Myers concept of biodiversity hotspots.

The importance of biodiversity was one of the key subjects of the 1992 World Summit held in Rio de Janeiro, Brazil, which resulted in the Convention on Biological Diversity (CBD). The goals of the CBD are "the conservation of biological diversity, the sustainable use of its components, and the fair and equitable sharing of the benefits from the use of genetic resources". Nevertheless, human actions have caused huge losses in biodiversity, including the disruption of ecosystem processes, habitat destruction, species extinction and the eroding of genetic diversity within species.

In order to understand and conserve biodiversity we need to measure it effectively, with species richness being the most frequently used measure of biodiversity. At the moment around 1.75 million species have been identified and estimates for the total number vary from 3 to 100 million. Identifying, naming and examining the relationships between species depends on highly skilled taxonomists and the general lack of taxonomic expertise and infrastructure has been called the taxonomic impediment. The Global Taxonomy Initiative has developed a programme of work that attempts to reverse this impediment, whilst molecular techniques such as DNA bar-coding provide an important way forward.

The National Botanic Garden of Wales is given as a case study for the role of a new botanic garden in conserving biodiversity.

### 1.1. What is biodiversity?

Biodiversity is the variety of life on earth and includes variation at all levels of biological organisation from genes to species to ecosystems. Genetic, organismal and ecological diversity are all elements of biodiversity with each including a number of components (Table 1) (Gaston & Spicer 2004).

All of these elements of biodiversity have led to a large number of formal definitions; Delong (1996) reviewed 85 different definitions. An important and widely used definition is that included within the Convention on Biological Diversity (CBD). This treaty was signed by over 150 nations at the United Nations Conference on Environment and Development, held in Rio de Janeiro, Brazil, in 1992. It defines biodiversity as “the variability among living organisms from all sources including, *inter alia* [among other things], terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems”.

### 1.2. Measuring biodiversity

In order to think about fundamental questions associated with biodiversity, such as where it occurs, how fast it is disappearing or how it can be maintained; we first need to be able to measure it. This is actually very difficult to do as biodiversity is a multidimensional concept that cannot be reduced to a single number (Purvis & Hector 2000). Imagine two islands with different organisms: island A has 6 reptiles, 1 bird and 1 mammal. Island B has 4 reptiles and 4 mammals. We could say that island A is more diverse as it has 3 different taxa whilst island B has only 2, but island B has a more even spread of the two taxa. Neither measure is wrong as ‘richness’ and ‘evenness’ are both facets of biodiversity and no single number can incorporate both without loss of information. Purvis & Hector (2000) describe three facets of biodiversity that can be measured:

- Numbers: e.g. the number of genes, populations, species or taxa in an area.
- Evenness: a site containing 1000 species may not seem very diverse if 99.9% of the species are the same. Many diversity indices have been developed such as Simpson’s and Shannon’s diversity indices that attempt to convey the extent to which individuals are distributed among species. There are also equivalent measures for genetic diversity such as measures of heterozygosity that incorporate both allele number and relative frequencies.
- Difference: some pairs of alleles, populations, species or taxa may be very similar whilst others are very different. For example, if populations within a species are very different they may be considered as different sub-species, management units or evolutionary significant units. Some differences may be considered to be more important than others, for example, ecological differences between species may be

important for ecosystem function. All of these kinds of differences are likely to be at least partly reflected by phylogenetic diversity among organisms, which is the sum total of the branch lengths in the evolutionary tree (phylogeny) that links the organisms together. If you sample the phylogeny in different places you will find different things.

Although biodiversity can be measured in lots of different ways the most commonly used measure is that of species richness, there are a number of reasons for this (Purvis & Hector 2000; Gaston & Spicer 2004):

1. Species often keep their genes to themselves and thus can have independent evolutionary trajectories and unique histories; it thus makes biological sense to measure species richness rather than a higher taxonomic grouping.
2. It is often easier to count the number of species compared to other measures of biodiversity. Humans tend to be able to recognise species and these are the units typically used in folk knowledge, practical management and political discourse. Humans can visualise variation in biodiversity as variation in species richness.
3. There is a substantial body of information already available on species, for example, in museums and herbaria.
4. Species richness can act as a 'surrogate' for other measures of biodiversity. In general as long as the number of species involved is moderate, greater numbers of species will tend to have more genetic diversity and will tend to have greater ecological diversity as more niches, habitats or biomes will be represented.

There are however some disadvantages in the use of species richness as a measure of biodiversity. One of these is that the number of species that you count depends on the species concept that you adopt. For example, using the biological species concept 40 – 42 species of birds-of-paradise are recognised in Australasia; if the phylogenetic species concept is used this increases to 90 species (Gaston & Spicer 2004). Another limitation arises if species richness is used synonymously with biodiversity without emphasising the fact that species richness represents just one element of what biodiversity is.

We also need to consider the spatial scale over which species richness can be considered, with a distinction commonly being made between alpha, beta and gamma diversity. Alpha diversity refers to diversity within a particular area, community or ecosystem and is typically measured as the number of species within that area. Beta diversity is the species diversity between areas and involves comparing the number of species that are unique to each area. Gamma diversity is a measure of the overall diversity across a region (Gaston & Spicer 2004).

### 1.3. How many species are there?

The diversity of life on Earth has increased over time but it is incredibly difficult to know how many extant species there currently are. Due to the enormity of the task indirect measures are used to estimate the number of extant species and the number varies depending on the assumptions used in the estimation. We are still discovering new species all of the time. A new species of large mammal is still discovered roughly every three years and an average day sees the formal description of around 300 new species across the whole range of life (Purvis & Hector 2000). 13.5 million is a frequently quoted working estimate for the number of species on Earth with a lower estimate of 3.5 and higher estimate of 111.5 million species (Gaston & Spicer 2004). Figure 1 shows one estimate of named and unnamed species for a number of taxonomic groups (MEA 2005). This highlights the high proportion of species that are as yet unnamed, it also illustrates that diversity is not equally represented within the taxonomic groups; different groups vary widely in their abundance as well as species number. Take the nematodes for example, Cobb (1914) noted that "If all matter in the universe except the nematodes were swept away, our world would still be dimly recognisable, and if, as disembodied spirits, we could investigate it, we should find its mountains, hills, vales, rivers, lakes and oceans represented by a film of nematodes". The actual number of species of nematode has been estimated to be between 1 million to 100 million species, with a conservative estimate of  $10^{19}$  free living nematode individuals (Gaston & Spicer 2004).

### 1.4. Mapping biodiversity

In general as the size of an area increases so does the number of species found within it. This species-area relationship is commonly represented as:

$$\log S = \log c + z \log A$$

S is the number of species

A is the area

z and c are constants known as the Arrhenius relationship

Relationships of this type typically explain more than 50% of the variation in species richness between different areas, with the slope of the relationship, z, ranging from 0 to 0.5 (most commonly 0.25 to 0.30). This means that a 90% reduction in the habitat in an area will result in the loss of approximately 50% of the species that live in that habitat, whilst a loss of 99% of the habitat will lead to the extinction of 75% of the species. The constant, z, varies widely however depending on factors such as islands versus continents, latitude and with the range of sizes of areas (Gaston & Spicer 2004).

Although larger areas typically contain more species, different areas of the world vary widely in the diversity found within them. Myers *et al.* (2000) introduced the concept of biodiversity hotspots; these are areas with exceptionally high numbers of endemic species and very high levels of habitat loss. A number of conservation organizations such as Conservation International state that these areas should be conservation priorities. There are currently 34 biodiversity hotspots recognized each holding at least 1,500 endemic plant species and having lost 70% of their original habitat area. The hotspots include: Madagascar and the Indian Ocean islands; the coastal forests of Eastern Africa; the Caribbean Islands and the Mediterranean Basin. The combined area of all the hotspots covers only 2.3 % of the Earth's land surface ([www.biodiversityhotspots.org](http://www.biodiversityhotspots.org)).

### **1.5. Value of biodiversity**

Humans cannot exist without biodiversity as we use it directly and indirectly in a number of ways (Figure 2). Direct use includes things like food, fibres, medicines and biological control, whilst indirect uses includes ecosystem services such as atmospheric regulation, nutrient cycling and pollination. There are also non-use values of biodiversity, such as option value (for future use or non-use), bequest value (in passing on a resource to future generations), existence value (value to people irrespective of use or non-use) and intrinsic value (inherent worth, independent of that placed upon it by humans) (Gaston & Spicer 2004).

Many of these uses of biodiversity are not incorporated in economic accounts and this leads humans to under-value biodiversity. Ecosystem services and resources such as mineral deposits, soil nutrients, and fossil fuels are capital assets but traditional national accounts do not include measures of the depletion of these resources. This means a country could cut its forests and deplete its fisheries, and this would show only as a positive gain in GDP (gross national product) without registering the corresponding decline in assets (wealth) (MEA 2005).

The relationship between biodiversity and ecosystem function is clear but a major question in ecology is how much biodiversity is required to maintain ecosystem function (Purvis & Hector 2000; Gaston & Spicer 2004). Gaston & Spicer (2004) summarize three main ways that ecosystem function can respond to reductions in species richness (figure 3).

- 1: Redundancy: there is a minimum number of species required to carry out ecosystem processes and beyond this species are equivalent and their loss of little significance.
- 2: Rivet-popping: the loss of a few species may have no apparent effect on ecosystem processes but beyond certain thresholds ecosystem services will fail.
- 3: Idiosyncrasy: species have complex and varied roles so changes in diversity will cause changes in ecosystem functioning where the direction and magnitude of change is unpredictable.

The design and interpretation of some of the experiments used to test these possible relationships is very contentious but a number of experiments have found relationships that suggest that there is some degree of ecological equivalence between species which fits the redundancy model (Gaston & Spicer 2004).

## **1.6. Loss of biodiversity**

Humans have increased the species extinction rate by as much as 1,000 times over background rates typical over the planet's history. 10–30% of mammal, bird, and amphibian species are currently threatened with extinction (MEA 2005) (Figure 4). Purvis & Hector (2000) use a simple calculation to illustrate that recent rates of species loss are unsustainable. If we assume that there are around 14 million species on Earth at present, then each year the tree of life grows by an extra 14 Myr of branch length. The average age of extant species is nearly 5 Myr (this data is from primates and carnivores, species in other groups may well be older). So the tree can 'afford' at most about three species extinctions per year without shrinking overall. There have been roughly this many documented species extinctions per year since 1600 and many extinctions will not have been documented. Last century saw the extinction of 20 mammalian species, a pruning of the mammalian tree that would require at least 200 centuries to redress.

The largest assessment of the effect of humans on the Earth's ecosystems was started in 2000 and called the Millennium Ecosystem Assessment (MEA). It found that over the past 50 years, humans have changed ecosystems more rapidly and extensively than in any comparable period of time in human history and that this has resulted in a substantial and largely irreversible loss in the diversity of life on Earth. It stresses that the loss of species and genetic diversity decreases the resilience of ecosystems, and that human impacts such as over-harvesting, climate change, invasive species, and nutrient loading push ecosystems toward thresholds that they might otherwise not encounter (MEA 2005).

## **1.7. Causes of biodiversity loss**

The Millennium Ecosystem Assessment identifies habitat change, climate change, invasive species, over-exploitation and pollution as the primary drivers leading to loss of biodiversity (MEA 2005) (Figure 5).

### **1.7.1. Habitat change**

Humans have had an effect on every habitat on Earth, particularly due to the conversion of land for agriculture. Cultivated systems (areas where at least 30% of the landscape is in croplands, shifting cultivation, confined livestock production, or freshwater aquaculture) now

cover one quarter of Earth's terrestrial surface. Habitat loss also occurs in coastal and marine systems, though these changes are less well documented. Trawling of the seabed, for instance, can significantly reduce the diversity of benthic habitats. (MEA 2005) (Figure 6)

### **1.7.2. Climate change**

Observed recent changes in climate, especially warmer regional temperatures, have already had significant impacts on biodiversity and ecosystems, including causing changes in species distributions, population sizes, the timing of reproduction or migration events, and an increase in the frequency of pest and disease outbreaks. By the end of the twenty-first century, climate change and its impacts are likely to be the dominant direct driver of biodiversity loss and changes in ecosystem services globally (MEA 2005).

### **1.7.3. Invasive Species**

The spread of invasive alien species has increased because of increased trade and travel. While increasingly there are measures to control some of the pathways of invasive species, for example, through quarantine measures and new rules on the disposal of ballast water in shipping, several pathways are not adequately regulated, particularly with regard to introductions into freshwater systems (MEA 2005) (Figure 7).

### **1.7.4. Overexploitation**

For marine systems, the dominant direct driver of change globally has been overfishing. Demand for fish as food for people and as feed for aquaculture production is increasing, resulting in increased risk of major, long-lasting collapses of regional marine fisheries. 50% of the world's commercial marine fisheries are fully exploited whilst 25% are being overexploited. For example, the Atlantic cod stocks off the east coast of Newfoundland collapsed in 1992, forcing the closure of the fishery, the depleted stocks may not recover even if harvesting is significantly reduced or eliminated (figure 8) (MEA 2005).

### **1.7.5. Pollution (especially nutrient loading)**

Since 1950, human mediated increases in nitrogen, phosphorus, sulphur, and other nutrients (nutrient loading) has emerged as one of the most important drivers of ecosystem change in terrestrial, freshwater, and coastal ecosystems, and this driver is projected to increase substantially in the future. For example, humans now produce more biologically available nitrogen than is produced by all natural pathways combined. Aerial deposition of reactive nitrogen into natural terrestrial ecosystems, especially temperate grasslands, shrub-lands, and forests, leads directly to lower plant diversity; excessive levels of reactive nitrogen in

water bodies, including rivers and other wetlands, frequently leads to algal blooms and eutrophication in inland waters and coastal areas (figure 9). Similar problems have resulted from phosphorus, the use of which has tripled between 1960 and 1990. Nutrient loading will become an increasingly severe problem, particularly in developing countries and particularly in East and South Asia.

### **1.8. Conserving biodiversity – what actions can be taken?**

The Millennium Ecosystem Assessment (MEA 2005) lists the following actions that have been at least partly successful in reducing biodiversity loss and can be further strengthened in the future:

- Protected areas.
- Species protection and recovery measures for threatened species.
- *Ex situ* and *in situ* conservation of genetic diversity (e.g. genebanks).
- Ecosystem restoration.
- Payments and markets for biodiversity and ecosystem services (e.g. for ecotourism or carbon sequestration).
- Incorporating considerations of biodiversity conservation into management practices in sectors such as agriculture, forestry, and fisheries.
- Capture of benefits by local communities (i.e. ensuring local people benefit from the conservation of the biodiversity around them).
- Increased co-ordination among multilateral environmental agreements and between environmental agreements and other international economic and social institutions (i.e. ensuring that ecosystem services are considered in all international agreements and treaties and that those concerning biodiversity co-ordinate with those focusing on other areas such as economics and trade).
- Public awareness, communication, and education.
- Enhancement of human and institutional capacity for assessing the consequences of ecosystem change for human well-being and acting on such assessments.
- Increased integration of sectoral responses (i.e. biodiversity issues in agriculture, fishery, and forestry management in many countries are the responsibility of independent ministries, these ministries need to establish processes that encourage the development of cross-sectoral policies).
- Elimination of subsidies that promote excessive use of ecosystem services.
- Sustainable intensification of agriculture.
- Slowing and adapting to climate change.
- Addressing unsustainable consumption patterns.
- Slowing the global growth in nutrient loading.
- Correction of market failures and internalization of environmental externalities that lead to the degradation of ecosystem services. (Because many ecosystem services



are not formally traded, markets fail to provide appropriate signals that might otherwise contribute to their efficient allocation and sustainable use. In addition, many of the harmful trade-offs and costs associated with the management of one ecosystem service are borne by others and so are not weighed in sectoral decisions regarding the management of that service).

- Integration of biodiversity conservation and development planning.
- Increased transparency and accountability of government and private-sector performance in decisions that affect ecosystems, including through greater involvement of concerned stakeholders in decision-making.
- Scientific findings and data need to be made available to all of society.

### **1.9. Biodiversity and Taxonomy**

Article 7 of the CBD requires the parties to the Convention to identify and monitor biological diversity, particularly those aspects important for conservation and sustainable use. Parties are also required to monitor activity which could have significant adverse impacts on the conservation and sustainable use of biological diversity and to maintain and organise data derived from identification and monitoring activities ([www.cbd.int](http://www.cbd.int)).

The third conference of the parties of the CBD (COP 3) identified a "taxonomic impediment": namely a scarcity of sufficient taxonomic skills, resources and information needed to help fulfil the objectives of the CBD. In response to this the Global Taxonomy Initiative (GTI) was launched in order to try and reverse this impediment [www.cbd.int/gti](http://www.cbd.int/gti). A programme of work was developed with the following objectives:

- Assess taxonomic needs and capacities at national, regional and global levels for the implementation of the Convention.
- Provide focus to help build and maintain the human resources, systems and infrastructure needed to obtain, collate, and curate the biological specimens that are the basis for taxonomic knowledge.
- Facilitate an improved and effective infrastructure/system for access to taxonomic information; with priority on ensuring countries of origin gain access to information concerning elements of their biodiversity.
- Within the major thematic work programmes of the Convention include key taxonomic objectives to generate information needed for decision-making in conservation and sustainable use of biological diversity and its components.
- Within the work on cross cutting issues of the Convention include key taxonomic objectives to generate information needed for decision-making in conservation and sustainable use of biological diversity and its components.

A number of key strategy documents also highlight the importance of taxonomy for conserving biodiversity. For example, the Global Strategy for Plant Conservation (GSPC) has as its first target: "A widely accessible working list of known plant species, as a step towards a complete world flora" (GSPC 2002).

In order to overcome the taxonomic impediment it is vitally important that organisations whose primary purpose is taxonomy and the conservation of biodiversity are active and have the resources required to carry out their work: this includes botanic gardens, museums and zoological collections.

New developments in molecular biology can also assist with overcoming the taxonomic impediment, the most important of these being DNA bar-coding. DNA sequences from a uniform locality on genomes can be a barcode of life for identifying species. The DNA barcode provides an additional master key to knowledge about a species with a public library of sequences linked to named specimens available on-line. The Consortium for the Barcode of Life (CBOL) give the following ten reasons for DNA bar-coding (Stoeckle *et al.* 2004; [www.barcoding.si.edu/](http://www.barcoding.si.edu/)).

*"1. Works with fragments.* Bar-coding can identify a species from bits and pieces. When established, bar-coding will quickly identify undesirable animal or plant material in processed foodstuffs and detect commercial products derived from regulated species. Bar-coding will help reconstruct food cycles by identifying fragments in stomachs and assist plant science by identifying roots sampled from soil layers.

*2. Works for all stages of life.* Bar-coding can identify a species in its many forms, from eggs and seed, through larvae and seedlings, to adults and flowers.

*3. Unmasks look-alikes.* Bar-coding can distinguish among species that look alike, uncovering dangerous organisms masquerading as harmless ones and enabling a more accurate view of biodiversity.

*4. Reduces ambiguity.* Written as a sequence of four discrete nucleotides - CATG – along a uniform locality on genomes, a barcode of life provides a digital identifying feature, supplementing the more analogue gradations of words, shapes and colours. A library of digital barcodes will provide an unambiguous reference that will facilitate identifying species invading and retreating across the globe and through centuries.

*5. Makes expertise go further.* The bewildering diversity of about 2 million species already known confines even an expert to morphological identification of only a small part of the plant and animal kingdoms. Foreseeing millions more species to go, scientists can equip themselves with bar-coding to speed identification of known organisms and facilitate rapid recognition of new species.

6. *Democratizes access.* A standardized library of barcodes will empower many more people to call by name the species around them. It will make possible identification of species whether abundant or rare, native or invasive, engendering appreciation of biodiversity locally and globally.

7. *Opens the way for an electronic handheld field guide, the Life Barcoder.* Bar-coding links biological identification to advancing frontiers in DNA sequencing, miniaturization in electronics, and computerized information storage. Integrating those links will lead to portable desktop devices and ultimately to hand-held bar-coders. Imagine the promise of a schoolchild with a bar-coder in hand learning to read wild biodiversity, the power granted to a field ecologist surveying with a bar-coder and global positioning system, or the security imparted by a port inspector with a bar-coder linked to a central computer!

8. *Sprouts new leaves on the tree of life.* Since Darwin, biologists seeking a natural system of classification have drawn genealogical trees to represent evolutionary history. Bar-coding the similarities and differences among the nearly 2 million species already named will provide a wealth of genetic detail, helping to draw the tree of life on Earth. Bar-coding newly discovered species will help show where they belong among known species, sprouting new leaves on the tree of life.

9. *Demonstrates value of collections.* Compiling the library of barcodes begins with the multimillions of specimens in museums, herbaria, zoos and gardens, and other biological repositories. The spotlight that bar-coding shines on these institutions and their collections will strengthen their ongoing efforts to preserve Earth's biodiversity.

10. *Speeds writing the encyclopedia of life.* Compiling a library of barcodes linked to vouchered specimens and their binomial names will enhance public access to biological knowledge, helping to create an on-line encyclopedia of life on Earth, with a web page for every species of plant and animal.”

## **2.0. Case study: National Botanic Garden of Wales: the role of a new botanic garden in conserving biodiversity**

The National Botanic Garden of Wales (NBGW) was the first national botanic garden to be created in the new millennium. Its mission statement is to: “develop a viable world-class national botanic garden dedicated to the research and conservation of biodiversity and its sustainable utilisation, to lifelong learning and to the enjoyment of the visitor”. The development of a new conservation and research programme began in October 2007. At present NBGW is contributing to biodiversity conservation in the following ways.

- Research programme on the ecology, taxonomy and conservation of the Welsh flora, working on a number of endangered species in collaboration with research and

conservation organisations throughout the UK. Future plans include the development of a molecular lab for conservation genetics and taxonomy research.

- *Ex-situ* plant collection in excess of 5000 species, including a dedicated systematics garden.
- National Nature Reserve next to the garden that contains a wide range of habitat types of conservation importance. This provides a focus for *in-situ* conservation and for research into habitat management and restoration.
- The importance of plants and their conservation is highlighted to 150,000 visitors a year (including the provision of formal education sessions to 20,000).
- NBGW provides a centre for undergraduate to PhD level students in the areas of plant conservation and taxonomy to gain experience and carry out research.
- Beginning to develop a botanical library and herbarium that can be used by staff and visiting specialists.

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Table 1: Elements of biodiversity (adapted from Gaston & Spicer 2004)

Genetic diversity	Organismal diversity	Ecological diversity
Nucleotides	Individuals	Populations
Genes	Populations	Niches
Chromosomes	Subspecies	Habitats
Individuals	Species	Ecosystems
Populations	Genera	Landscapes
	Families	Bioregions
	Orders	Biomes
	Classes	
	Phyla	
	Kingdoms	

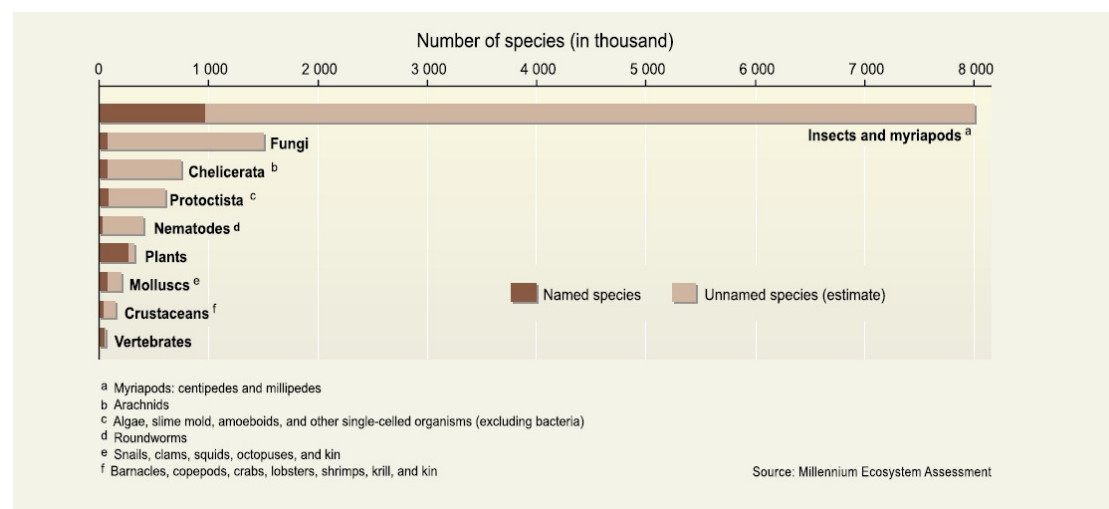


Figure 1: Number of named and estimated number of unnamed species in different taxonomy groups, from MEA (2005).

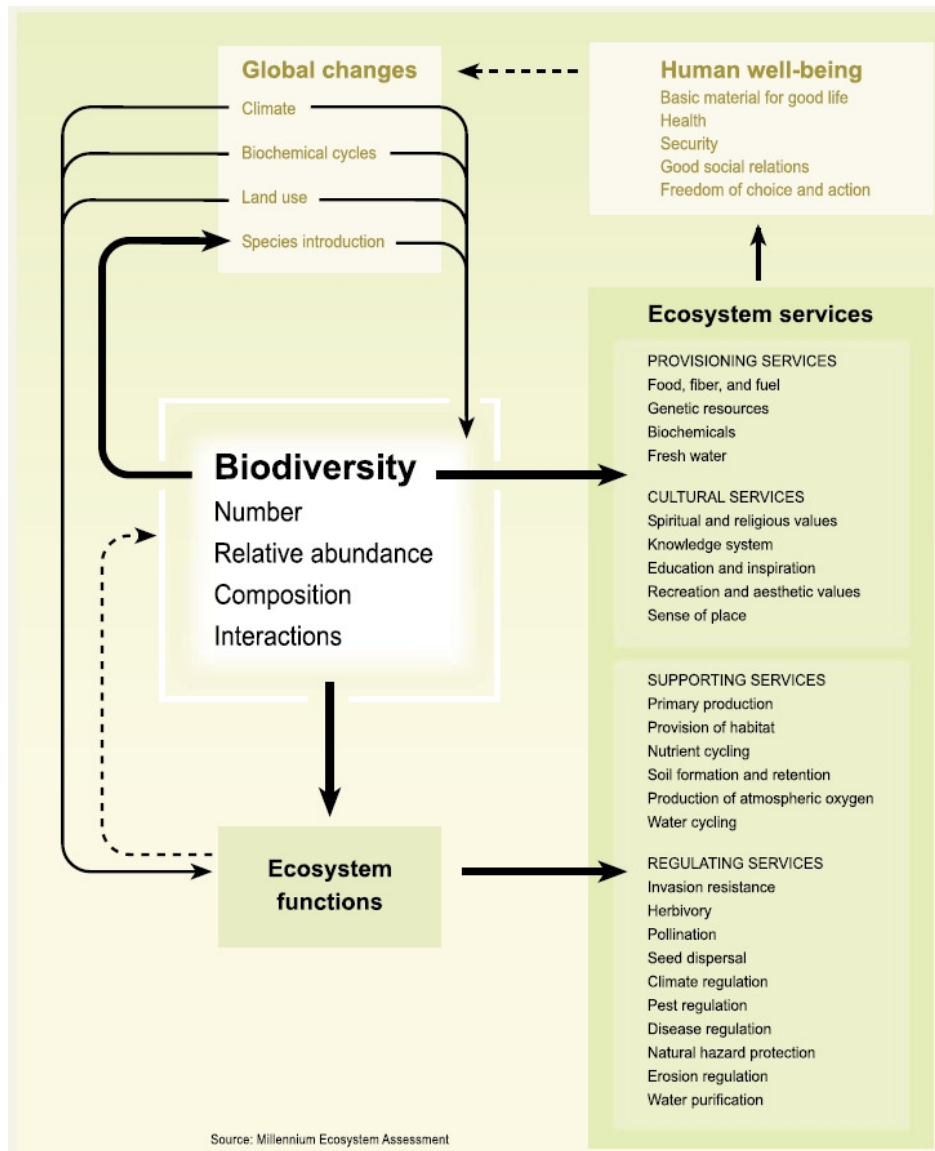


Figure 2: Relationship between biodiversity, ecosystem function and human well-being, from MEA (2005).

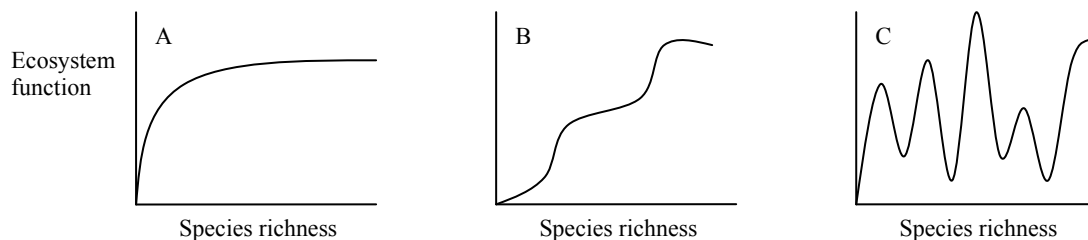


Figure 3. Possible relationships between species richness and ecosystem function: A: Redundancy B: Rivet-popping C: Idiosyncrasy (adapted from Gaston & Spicer 2004).

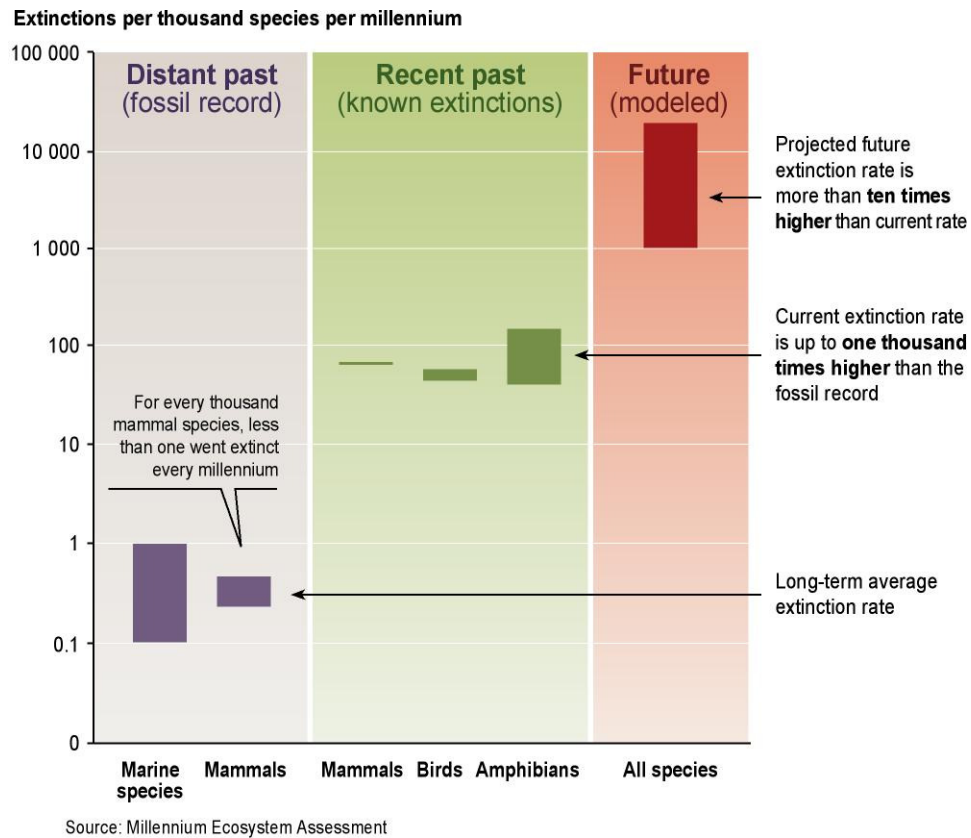


Figure 4. Past and future numbers of species extinctions, from MEA (2005).



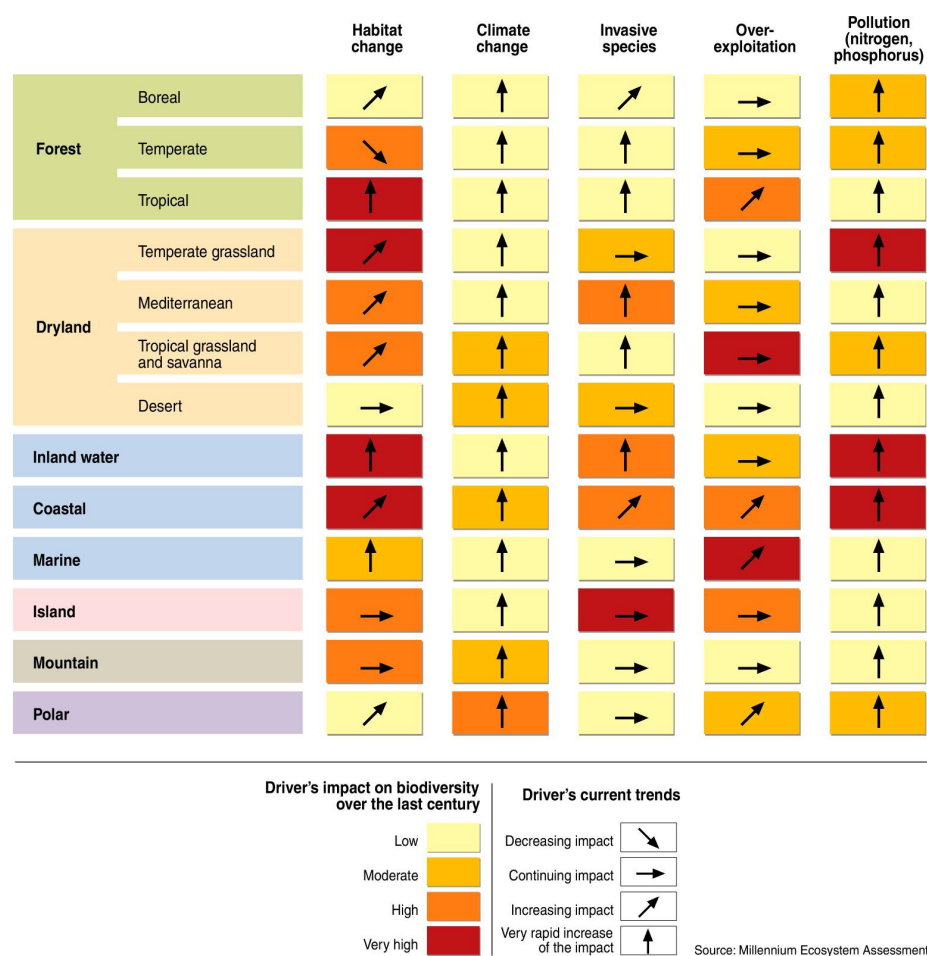


Figure 5 Impact of the main drivers of biodiversity loss over the last century and current trends, from MEA (2005).

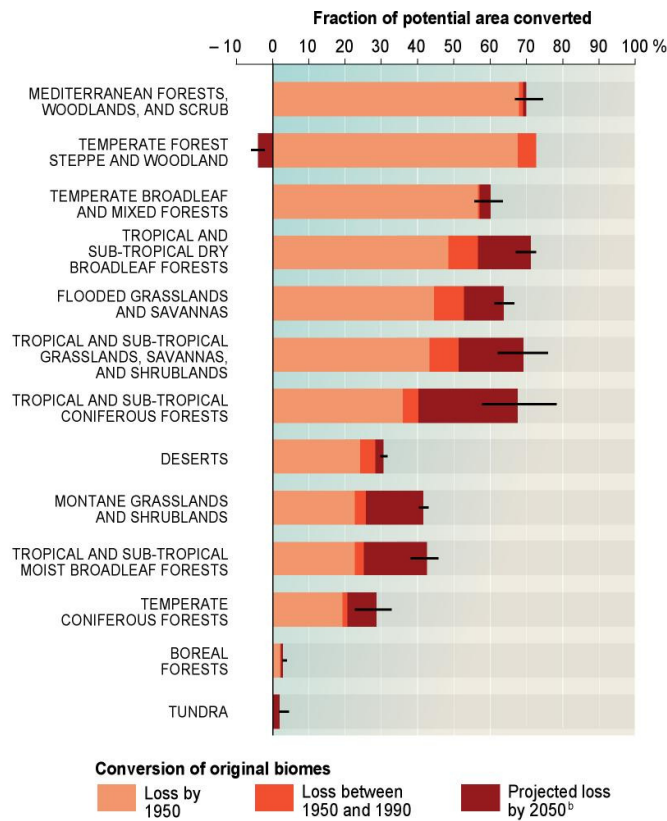


Figure 6. It is not possible to estimate accurately the extent of different biomes prior to significant human impact, but it is possible to determine the “potential” area of biomes based on soil and climatic conditions. This figure shows how much of that potential area is estimated to have been converted by 1950 (medium certainty), how much was converted between 1950 and 1990 (medium certainty), and how much would be converted between 1990 and 2050 (low certainty). Most of the conversion of these biomes is to cultivated systems, from MEA (2005).

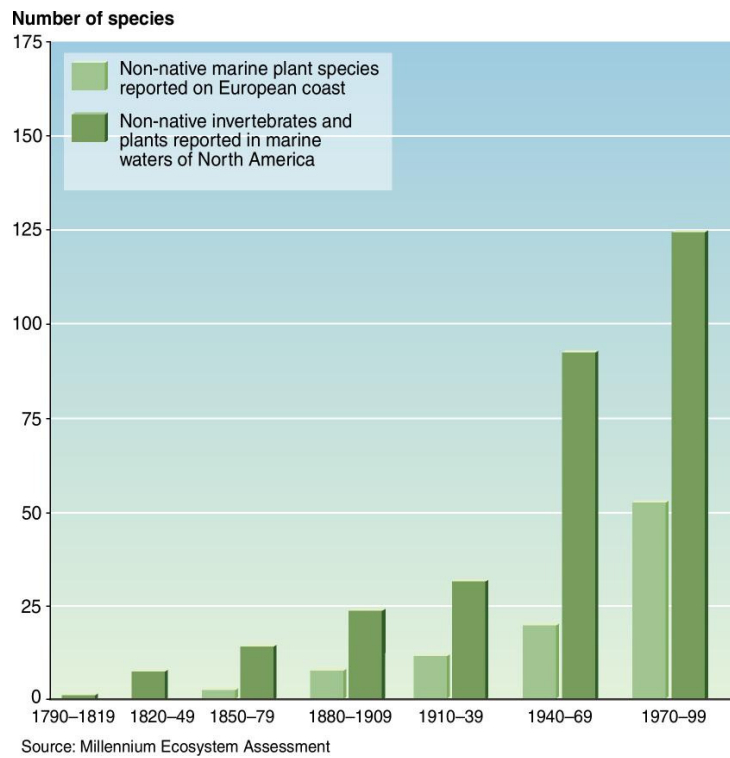


Figure 7. Increases in non-native species, from MEA (2005).

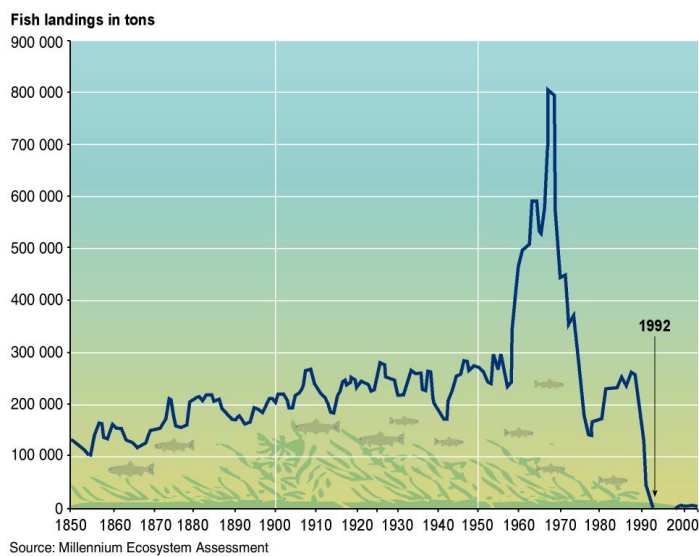
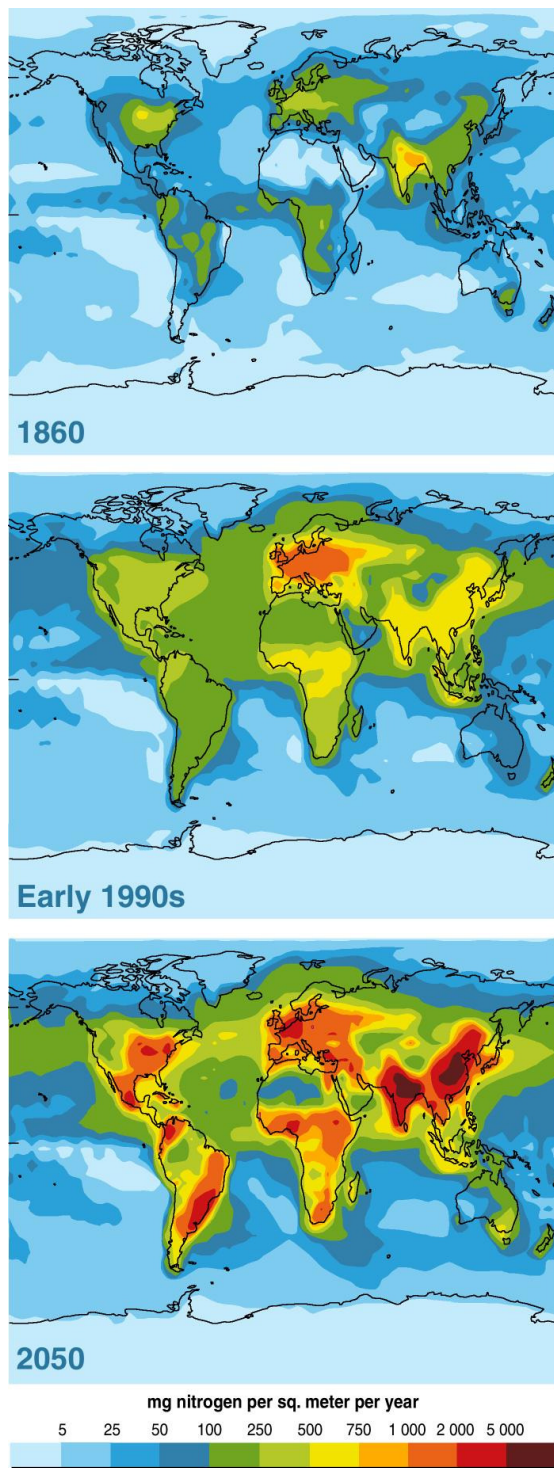


Figure 8. Atlantic cod stocks off the east coast of Newfoundland (MEA 2005).



Source: Galloway et al. 2004

Figure 9. Estimated total reactive nitrogen deposition from the atmosphere (wet and dry) in 1860, early 1990s, and projected for 2050 (milligrams of nitrogen per square metre per year), from MEA (2005).