ELSEVIER

Ecological Economics 29 (1999) 183–202

ECOLOGICAL ECONOMICS

COMMENTARY

# Linking Nature's services to ecosystems: some general ecological concepts

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**Abstract**

I present a selected review of ecological concepts that are important for understanding how nature's services are linked to their support system, the ecosystem. The paper is mainly aimed at an audience of non-biologists to facilitate cooperation among disciplines. A list of services compiled from the literature is classified according to ecological criteria that relate to the properties of the services. These criteria are: (1) if the goods or services are produced and maintained within the ecosystem or shared with other ecosystems; (2) if the goods or object of the service are living or inorganic material; and (3) what biological unit is associated with production and maintenance, i.e. an individual, a species, a group of species, an entire community, the ecosystem, the landscape or on a global scale. Using these criteria I have identified and selected three major groups of ecosystem services for which some common ecological concepts apply. These are: (1) the maintenance of populations; (2) the use of ecosystems as filters of externally imposed compounds; and (3) the property of biological units to create organization through selective processes. These three categories are examined and exemplified in detail. © 1999 Elsevier Science B.V. All rights reserved.

*Keywords:* Biodiversity; Ecosystem functioning; Ecological concepts

## 1. Introduction

As global resources increase in scarcity, many ecologists have now begun to enunciate in ways clear to a general audience what has long been

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PII: S0921-8009(99)00011-7

known within the profession: that Nature provides ‘life support services’ at virtually every scale, that many are free of charge (not captured by markets), and that many are irreplaceable by technology (Costanza et al., 1997). Human domination of major portions of the biosphere (Vitousek et al., 1997) already affects many species as well as global biogeochemical cycles (Charlson et al., 1992) and the resulting decline in services provided by some ecosystems has raised great concern among ecologists (Fujita and Tuttle, 1991; Ehrlich and Wilson, 1991; Watanabe, 1994; this issue). The need for managing the natural capital of the human society in a sustainable way is thus of high priority.

To understand the options available to sustainably manage an ecosystem service and the costs associated with these, it is important to understand the underlying basic ecological mechanisms that link a certain product or service of Nature to its support system, the ecosystem. Such knowledge is also important to estimate the qualitative reliability of the service, i.e. the capacity to ‘work upon demand’ (Naeem, 1998), and the sensitivity of this reliability to human-accelerated environmental change. Because this is a transdisciplinary undertaking, information has to be shared across research fields to facilitate understanding and cooperation. In this paper I do not attempt to present a primer of ecology but rather to present some selected ecological concepts that are of importance in understanding the properties and dynamics of ecosystem services from an ecological viewpoint. To do so, I first describe the rationales for choosing ecosystems as a natural unit of study. Then I present an analysis and classification of recognized ecosystem services from an ecological perspective. Based on this analysis, I have selected three major groups of ecosystem goods or services for which I examine and exemplify the main ecological concepts that are needed to understand how these are linked to their support system, the ecosystem.

## 2. What are ecosystems really?

Many ecologists agree that ‘ecosystem’[1] ranks among the most useful concepts in ecology, especially for the analysis of environmental issues (Cherrett, 1989). This might not seem intuitively obvious at times, as ecosystem services are often affiliated with some conspicuous species, i.e. timber with particular tree species, pollination with honeybees, denitrification with a group of special bacteria, or eco-tourism with some spectacular animals such as whales or large predators. However, ecosystems not only contain those species that we regard as very beneficial, but also myriads of less well-known species which provide much of the biotic support system for the more conspicuous species. Our knowledge of these ‘unsung heroes’ (Daily, 1997) is often imperfect, yet we likely rely on their function when we use a service provided by the ecosystem. The physical environment that was included by Tansley (1935) in the definition of the term ecosystem is a key aspect including not only the biotic community but also minerals or soil, chemical compounds, temperature, light, wind, waves, etc. For some ecosystems, the spatial extent is easily defined, such as for lakes, or for systems that are created by particular species such as corals or kelp. Other ecosystems have diffuse borders that gradually change into some other type of ecosystem, for example, grassland-savanna, or deciduous-coniferous forests. Even though the definitions of ecosystem boundaries may be diffuse, for the purpose of this paper I will refer to entities or processes as either internal or external to the ecosystem.

[1] “But the more fundamental conception is, as it seems to me, the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom” (Tansley, 1935).

## 3. Identifying three main categories of ecosystem services

I have derived a list of recognized services (Table 1) from three publications (Barbier et al., 1994; Costanza et al., 1997; Daily, 1997). These are classified according to certain ecological criteria: (1) are the goods or the object of the service internal to the ecosystem or shared with other systems? (2) are the goods or object of the service of biotic or abiotic origin? and (3) at which level of ecological hierarchy are the goods or services maintained? The importance of the scale of ecological hierarchy in understanding ecological processes has been strongly advocated in ecology (Levin, 1992). I have therefore emphasized this aspect in the classification of ecosystem services as presented in Table 1. By applying these criteria to currently recognized services of Nature, I argue that at least three general types of services can be distinguished that have certain similarities in terms of the ecological properties and how they are maintained.

- First, there are services for which the goods or services are associated with certain species or a group of similar species and for which the goods or the target of the service is internal to the ecosystem. These services are often related to the growth or maintenance of a particular species. Examples of such services include valuable foods and goods such as fish, timber, pharmacutical chemicals, and flowers, all of which are produced by natural or cultivated species. Honeybees, many other insects, and several birds and bats pollinate cultivated crops. The dispersal of seeds or nutrients as done by e.g. flying foxes, birds, or other fruit-eating animals or key predators, can control pests or other destructive organisms. Colorful displays such as in peacock or flowers provide aesthetic beauty as do mass effects of flower fields, bird flocks, fish schools, or for example a herd of zebras. The presence of potentially dangerous animals such as wolves, lions, tigers, or white sharks provide opportunities for adventure and life memories. All of the above are examples of services produced by individual organisms, species, or a group of similar species. To maintain populations of certain species at desirable levels, one must know how these specific groups of organisms are dependent on other species and how the physical environment affects them. In the following section on maintenance of population densities, I examine four key concepts from population and community ecology, i.e. regulation of intrinsic rates, direct and indirect interactions with other species, density dependent versus independent mechanisms of population regulation, and resource limitation.
- A second category consists of services that regulate some exogenous chemical or physical input, i.e. the system itself cannot affect the magnitude of the input. The maintenance of these services is associated with the entire community or the ecosystem itself rather than with particular species. Such services are thus a result of processes that drive material and energy flows in ecosystems. The biota takes a significant part in most global cycles of chemical compounds such as water, $CO_2$, nitrogen, etc. As a result, ecosystems not only alter the chemical environment but also the geological, hydrological, and climatic conditions. For example, vegetation plays an important role in moderating the pulse of water in rivers following a storm, toxins may be diluted and decomposed or buried, nitrogen is denitrified in certain ecosystems, and soil fertility is renewed through passive or active weathering of minerals. One may draw the analogy of ecosystems as filters such as used in engineering signal processing. They modulate imposed environmental signals, for example a change in magnitude of a chemical compound, by processing or transforming them, and then either store these or release the compound again. In the second section on processing and transformation of external inputs, I will examine how the function of ecosystems as a filter or a true sink for a chemical compound is maintained through the internal network of flows and reservoirs or stocks. I will also mention how ecosystems can flip between alternate states and how this might affect their function as filters.

Table 1
A list of ecosystem services compiled from literature and classified according to selected ecological criteria (Open symbols indicates ambiguous classification)

| Services or goods | | | | Production/maintenance level | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Internal[b] | Abiotic | Goods | Individual | Species | Functional group[c] | Community[d] | Ecosystem | Landscape | Global cycles | Example of production unit | Assigned type[a] |
| | ● | ● | Water | | | | | ● | ● | ● | Temperate forests | |
| | ● | | Timber | ● | ● | ● | | | | | Spruce in temperate forests | 1 |
| | ● | | Food | ● | ● | ● | | | | | Cod in the North Pacific ocean | 1 |
| | ● | | Clothing | ● | ● | ● | | | | | Cotton agriculture systems | 1 |
| | ● | ● | Stone, minerals | | | | | ● | ● | ● | Coral reefs | |
| | ● | ○ | Fuel[e] | ○ | ○ | ○ | ○ | ○ | ○ | ○ | Trees | 1 |
| | ● | | Pharmaceuticals | ● | ● | | | | | | Fungi that produce penicillin | 1 |
| | ● | | Genetic information | ● | ● | | | | | | Wild varieties of cultured crop species | 1 |
| | ● | ○ | Ornamental objects | ● | ● | | | | | | Shellfish | 1 |
| Object of service | | | Regulatory services | | | | | | | | | |
| *Benefits* | | | | | | | | | | | | |
| Fruit development | ● | | Pollination | ● | ● | ● | | | | | Flying foxes on Carribbean islands | 1 |
| Habitats | ● | | Provision of structure | ● | ● | | | | | | Kelp forests | 1 |
| *Problem* | | | | | | | | | | | | |
| Pest species | ● | | Biological control | ● | ● | ● | | | | | Birds control budworm outbreaks | 1 |
| Foreign species | | ● | Resistance against invasion | | | | ● | ● | ● | | Communitites at climax | 2 |
| UV | ● | ● | UV protection by ozone | | | | | | | ● | Ozone produced by lightening | |
| Temperature | | ● | Climate regulation by gases | | | | | | | ● | Oceans as potential carbonsinks | 2 |
| Precipitation | | ● | Mitigation of floods and droughts | | | | | ● | ● | | Watersheds with undisturbed forests | 2 |
| Erosion forces[f] | | ● | Preventing erosion | | | | ● | ● | ● | | Savanna vegetation | 2 |
| Eutrophication | | ● | Denitrification | | | ● | ● | ● | ● | | Coastal softbottoms | 2 |
| Toxins | | ● | Detoxification | | | ● | ● | ● | ● | | Mussels in coastal zones | 2 |
| Waste | | ○ | Decomposition and recycling | | | | ● | ● | ● | | Garden compost | 2 |
| Low production | ● | ● | Nutrient regeneration | | | | ● | ● | ● | | Agriculture soil | 2 |
| Extreme weather | | ● | Moderation of extremes | | | ● | ● | ● | ● | | Coral reefs as wavebreakers | 2 |

Table 1 (Continued)

| Services or goods | | | | Production/maintenance level | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Internal[b] | Abiotic | Goods | Individual | Species | Functional group[c] | Community[d] | Ecosystem | Landscape | Global cycles | Example of production unit | Assigned type[a] |
| | | | Information services | | | | | | | | | |
| *Benefits* | | | | | | | | | | | | |
| Aestetic appreciation | ○ | ○ | Conspicuous patterns, spectacular behaviour | ○ | ○ | ○ | ○ | ○ | ○ | ○ | Autumn colors in maple forests, whales | |
| Religious inspiration | ○ | ○ | Complexity beyond our understanding | ○ | ○ | ○ | ○ | ○ | ○ | ○ | The eye, Big Bang | |
| Cultural inspiration | ○ | ○ | Dramatic landscapes | ○ | ○ | ○ | ○ | ○ | ○ | ○ | Provence | |
| | | | Support services | | | | | | | | | |
| Self-regeneration | ● | | Species maintenance and regeneration | ● | ● | | | | | | Horses and cattle | 3 |
| Evolution | ● | | Natural selection and genetic variabillity | ● | ● | ● | ● | ● | ● | ● | Directed adaptation to climate changes | 3 |
| Organization | ● | | Selective processes and variabillity | | | | ● | ● | ● | | Succession of hurricane scars in forests | 3 |

[a] The type assignment refers to the three following sections in the paper in which major ecological concepts are examined and examplified.
[b] The goods or services may be either entirely internally processed (●) or shared with other systems.
[c] A group of species that have similar ecological function.
[d] The living part of an ecosystem, i.e. without the physical environment.
[e] Can be living or fossil organic material or physical, such as wind or waves.
[f] For example: precipitation, cattle, wind.

- The third category of services is related to the organization of biotic entities. Organization is a key aspect of biological processes at virtually all scales, i.e. from the way gene sequences are organized to networks of energy and material flows at the level of ecosystems. Biological organization can be any non-random pattern, structure, or interaction network in time or space, or morphology, color, etc. Biological patterns and structure expressed in organism morphology may have great market value in themselves such as with flowers, fur coat patterns, and seashells. Furthermore, the organization of genes through natural selection, the spatial distribution of a population through dispersal and competitive exclusion, or the development of food webs and ecosystems through invasion and extinction processes, is fundamental to Nature's functioning and ability to adapt to changing conditions. These types of services are so fundamental that they are often overlooked or taken for granted even though it is adaptability and self-organization that makes ecosystems, and the services provided by them, resilient against a certain degree of natural and human induced disturbances. Thus, these services may be called support services. Since biological organization is somewhat abstract to non-biologists as well as to many within the profession, and yet so fundamental, I point out in a separate section how the generation of biological organization takes place in nature.

These categories represent three major fields in ecology that have well-established theoretical foundations, i.e. population/community ecology and ecosystem research, and/or new frontiers in ecological theory such as for biological organization (Levin et al., 1997; Levin, 1998). The review and examples I am going to present here are a summary of some selected basic theories for these research fields from an anthropogenic perspective. The sections presented in this paper will not at all cover all the services that are presented in Table 1, or that have been recognized but are not listed here. Even so, I argue, it might be constructive for economists to have a review at hand describing how ecosystem services are actually maintained by ecosystems in general. There is also a need for ecologists to understand what criteria are needed to set a value on a natural object or function and how along the human scale, e.g. the individual, the community, institutions, nations or global interests, we may perceive these differently.

## 4. Maintenance of population densities

The regulation of a given population is often of value for humans. Organisms are embedded within one or more food webs which in turn are part of an ecosystem (Tansley, 1935; Winemiller and Polis, 1996). Interactions with other species or resources may be used to maintain populations at desired levels to provide or secure this service in a cost-effective manner. For example, food-web management in lakes through stocking or removal of specific species can improve both fishing and water quality (Carpenter and Kitchell, 1993). Other policies include habitat restoration or provision of artificial substrate (Branden et al., 1994; Andersen, 1995). However, food-web management is not an easy task, as there are usually interactions among several species as well as interference from environmental variables such as weather; often, interactions with other species are non-linear and may cause population dynamics that are difficult to predict. Thus a large degree of ecological knowledge about the specific ecosystem and the interactions of the target population with other species is needed to provide sound management advice. But even well studied systems may contain surprises, as shown in the first example below. Here I will first describe some ecological concepts that are of general importance for the regulation of populations, secondly demonstrate how these concepts work using two examples, and then discuss some policies that might promote better management and reliability of this particular service in the future.

There are many aspects of population regulation that should be considered in practical management. Four important concepts for understanding population regulation are presented here. These are:

- Regulation of intrinsic rates by the physical environment;
- Direct and indirect interactions;
- Density dependency of species interactions; and
- Resource limitation.

### 4.1. Regulation of intrinsic rates by the physical environment

Species are ultimately constrained by their optimal performance. For example, the maximum generation time is strongly correlated to the body size of the organism. However, optimal conditions seldom occur in nature and thus physical factors, such as temperature, light, or availability of water, regulates the performance of species.

### 4.2. Direct and indirect effects

Species interactions may vary in strength, depending on their nature. As a trivial example, a predator can be highly dependent on the abundance of a specific prey item if this is the exclusive food source, but much less dependent on it if the prey type is just one of many choices. In the latter case, the interaction between a particular prey and the predator can be dependent on other prey items and also on other predators that compete for food (Abrams et al., 1996). Such indirect effects (exemplified in Box 1) are common in food webs (Menge, 1995) and make prediction of population dynamics very difficult unless the nature of interactions in a particular food web is well understood. To understand the dynamics of any species, it is important to pinpoint the strongest interactions with other species and to decide how many species have to be considered simultaneously in order to make good predictions.

### 4.3. Density dependency of species interactions

Today, after some decades of dispute, many ecologists agree that natural intrinsic regulation of populations occurs to a large extent through density dependent mechanisms (Turchin, 1995). Density dependence is the dependence of per capita population growth rate on present and/or past population densities (Murdoch and Briggs, 1996). The dynamics of a specific population is a balance of several such processes, e.g. birth and immigration rates add to population density while predation, emigration, and mortality from old age or disease decrease it over time. A comprehensible way of showing such density dependence and the resulting dynamics is by a simple diagram, in which the change in population density is plotted as a function of the present density of the population (Fig. 1). For example, if the net rate of change (thick line) is positive, the density will over time increase as indicated with arrows. Eventually, provided resource availability is maximal, any population will be constrained around some high density, also called the carrying capacity. This phenomenon was made well-known by Pearl and Reed (1920) and is referred to as logistic growth. There are many factors, environmental or biological, that can cause variations in the functions that determine population change. Therefore, ecologists no longer regard this carrying capacity as a fixed state, but rather as a range

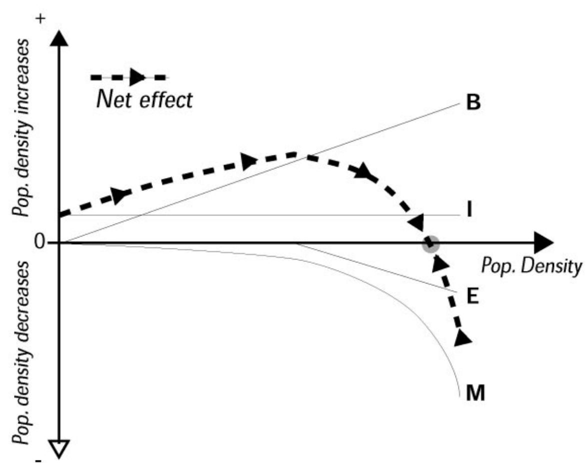



Fig. 1. A population regulated by processes of births (B), immigration (I), mortality (M) and emigration (E). All processes except immigration are dependent on the density of the population. In this example, births are a linear function of density, mortality a non-linear one, and emigration is triggered when density reaches a certain threshold level. The net effect of all four processes combined is shown as a dashed line and the arrows denote the direction of population change at any given density. The gray circle indicates the density of the steady state.

within which the population densities will fluctuate over time (Murdoch, 1994; Turchin, 1995).

### 4.4. Resource limitation

The maximum growth rate of a population constrains its potential rate of increase, also called the intrinsic rate of increase. To achieve this rate of growth, all resource requirements must be met. Actual growth of a population is in nature often limited by some resource and it is often that essential resource type, that is present at the lowest concentration relative to the demand of the organism, which will be the limiting resource according to the law of the minimum (Liebig, 1842; Tilman, 1982). As a consequence, there will be a close relationship between the limiting resource and the population that is dependent on this particular resource. However, in some situations, multiple resources may interact in limiting population growth.

### 4.5. Example 1: control of sea urchins by otters

I will use an example of the interaction between otters and sea urchins in Alaska to illustrate food web manipulation through management of a predator, also called top-down regulation in the ecological literature (deMelo et al., 1992). Specifically, I want to demonstrate how density dependent predation can regulate a population and note the potential limitations. I will only present a very simplified version of the problem to illustrate some of the dynamics of the system. Levin (1988), Lubina and Levin (1988) and Estes and Duggins (1995) provide more detailed analyses.

The sea otter population was strongly influenced by hunting and went locally extinct over most of its former range. The reestablishment of otters has therefore been limited by immigration from refuges. The disappearance of sea otters was accompanied by the extirpation of kelp by sea urchins, which in turn led to less productive shorelines in terms of shellfish and other harvestable products. The loss of kelp forests also removed an important physical buffer, leading to an increase in coastal erosion. Reestablished sea otter populations have reversed this effect and I explore below why this has worked so well thus far.

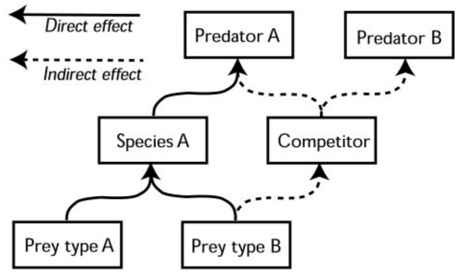
There are some important features of this set of species. First, sea otters love to eat sea urchins but usually do not depend on them for survival because they are generalist feeders, feasting on various fruits of the sea. When urchins are present, these are a preferred food item. Second, sea urchins graze heavily on kelp and, provided with a large food supply, reproduce quickly and can reach very large numbers.

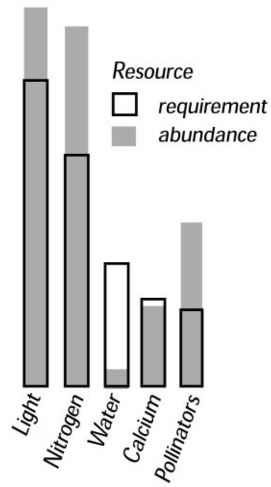
The basic concept of this system of species can be understood by looking at the population dynamics of the sea urchins. For clarity I will assume that local immigration is balanced by emigration, and omit these processes until later. I also assume that there is an established kelp forest present, and that the management aim is to maintain this state. Provided with unlimited food (which can be assumed is the case when urchins enter an established kelp forest) the urchin population grows at the maximum intrinsic rate of increase permitted by environmental conditions such as temperature. Thus, without otters, the urchin population will increase towards carrying capacity, which could potentially cause eradication of the kelp forest.

The aim of this example is to examine how to maintain low abundances of sea urchins by reestablishing sea otters and we need therefore to be concerned about how sea otters find and consume urchins at low densities. This is related to the functional response of the sea otter. The functional response of a predator is the relation between density of a given prey type and the amount of that prey found and consumed by the predator (Holling, 1959); this is a form of density dependent mortality from the perspective of the prey. In Box 1 this response is shown for a typical vertebrate predator. Note that there is saturation of the killing rate at high densities, because of the limited time an otter can search for and handle each urchin, and also, because of satiation, its daily ration is limited.

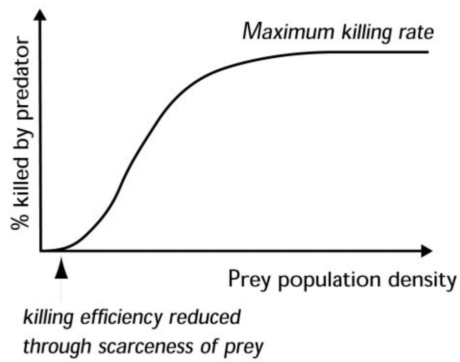
**Box 1. -Regulation of natural populations-**

Both **direct and indirect effects** occur in food-webs. Indirect effects affect species A through an effect on some direct interaction. Direct effects are e.g. mortality caused by Predator A or consumption of Prey type B.




**Law of the minimum:** The maximum growth rate of an organism is limited by that resource type that is present at its lowest abundance in relation to the requirement of the species, in this case, water.




**Density dependence** of interactions between species are often nonlinear and thus can produce complex dynamics. The above diagram examplifies an interaction between a prey population and some predator. At low densities of prey, the predator spends most time searching and thus, killing rate is low. As search time decreases with increasing prey density killing rate increases until the prey-handling capacity of the predator is reached.

The rate of change of the sea urchin population at low densities has two components: (1) natural rate of increase without otter predation; and (2) mortality caused by otters. Total otter predation is proportional to the density of otters as shown in the left panel of Fig. 2. The management goal in this case is to ensure a sufficient density of sea otters to control the urchin population. The net effect of these two processes is shown in the right panel of Fig. 2. At a certain density of urchins, the otters will not be able to counteract the birth rate of the urchins, i.e. the urchin population will escape control by its predator. We can call this critical point the point of escape, or P.o.E. This means that there is a need to maintain the P.o.E above the range of possible variations in urchin density that could be caused by environmental variability or other species. Once they have escaped from control, urchins will increase up to carrying capacity as long as there is enough food

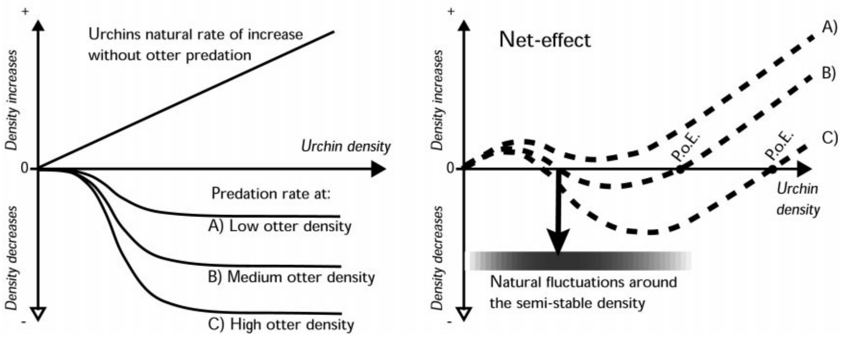



Fig. 2. The processes that govern the development of urchin density at low densities. Left panel: the rate of increase without mortality caused by otters and three scenarios for different otter-induced mortalities are shown. Right panel: the combined effect of non-otter and otter predation processes is shown for three different scenarios. At low otter density (A), the urchin population will increase over the entire range. At medium otter density (B), the urchin population is forced towards a low level (indicated by arrow) unless natural fluctuations happen to increase these over the critical point of escape (P.o.E.) at which the otters cannot control the urchin population any more. Increasing otter density to high levels (C) can increase the safety margin of the P.o.E.

present. There is also the theoretical possibility that high densities of urchins can lead to high emigration rates, which in turn could cause a rapid increase in urchin populations at neighboring sites above the controllable level. Such an effect might under some circumstances propagate spatially, a phenomenon known as a traveling wave (Kolmogorov et al., 1939) which can spread along the coastline and eradicate the kelp forests.

To maintain kelp forests on coasts it is important to maintain a stable otter population, which is capable of controlling the urchin population with good margins relative to the P.o.E. To do so, one has to focus on the otter's habitat and its interactions with other species including humans and predators. Recently killer whales (*Orca Orca*) have begun to consume many otters since the normal food resources of these whales have declined due to human overfishing of off-shore waters. To understand whether this effect might cause a decline in the otter population beneath the critical density, this interaction has to be studied in more detail. Thus, in this example, the maintenance of a healthy kelp forest requires understanding of population regulation across trophic and spatial scales, and species from sea urchins to whales.

Maintaining high abundances of some particular organism type is desirable whenever the presence of a species benefits or promotes a desired service. In this case, usually the crucial point is density dependent regulation of population growth mediated by the scarceness of some resource. In an early publication from the science of agriculture, Liebig (1842) formulated the law of the minimum. This states that the growth rate of a crop will be limited by that essential nutrient which occurs at the lowest density in relation to the proportional demand of the crop species. In some cases this principle can be extended to include not only nutritional aspects, but also other essential resources, such as nesting sites or shelter. There might even be a delicate trade-off between the service and the resource that is crucial for a species, which in turn is important for the desired service. I will illustrate this with an example of crop pollination.

### 4.6. Example 2: pollination of crops

Pollination has been one of those natural services that have been taken for granted by many people and thus surprise is caused as alarming headlines warn of huge economic losses due to insufficient pollination of crops (Watanabe, 1994). The ongoing pollination crisis in the USA is a combination of introduced diseases, use of pesticides and hybridization with Africanized bees, with the combined result of a 20% reduction of managed honey bee colonies between 1990 and 1994 (Buchman and Nabhan, 1996). But also, to a large extent the crisis is due to changes in landscape patterns (Aizen and Feinsinger, 1994; Watanabe, 1994). Wholesale conversion of land to agriculture and residential/industrial uses has decreased habitats favorable for natural and introduced pollinators, which have a potential value in pollination service in the order of US$4.1–6.7 billion a year (Southwick and Southwick, 1989).

A huge field of flowering crops should obviously be able to sustain a high density of natural pollinators. However, even though the nutritional demands are fulfilled ad absurdum, crucial nest sites, often associated with certain wild plants or undisturbed soil, are too sparse in the modern agricultural landscape to provide sufficient opportunities for successful larval development. Thus the birth rate of some pollinator species will be limited to low densities by the scarcity of nesting sites; carrying capacity will also thereby be highly reduced.

Attempts to maintain populations at levels where production rates are highest are a most elaborate undertaking, on a road marked with management failures, e.g. in fisheries (Ludwig et al., 1993; Hutchings and Myers, 1995). As optimal management of harvested populations is 'the' classic issue of ecological and environmental economics I will not consider this issue in any detail here. However, it is worth noting that management decisions based on single-species population models often have proven to be insufficient for securing sustainable harvest rates (Hilborn and Walters, 1992) suggesting that multi-species models are required (Christensen, 1991; Larkin, 1996). Another critical point for sustainable harvesting is to reduce the lag between harvesting statistics and implementation of new policies based thereon. The time scale of the administrative process, or preferably the behavior of the fishing fleet itself, should be be adapted to the time scale at which the harvested population responds. A large discrepancy between these time scales makes exploitation of the system inherently unstable (May, 1981; Hilborn and Walters, 1992).

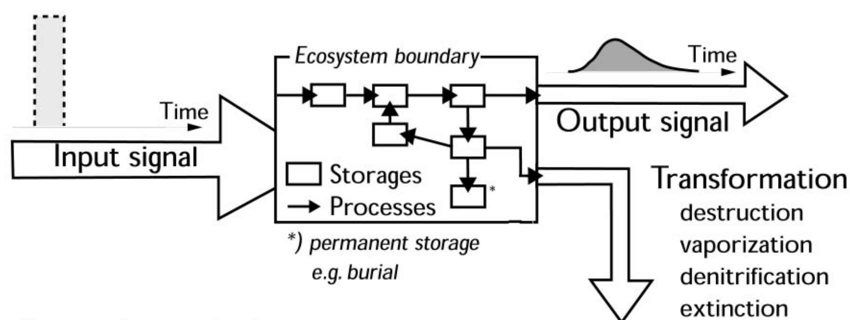
Managing populations involves the formidable task of understanding and monitoring a multitude of processes that are sustained by ecosystems, which not only naturally undergo succession and transition but also are subject to human induced environmental change. The general concepts described above outline some basic mechanisms of population regulation, but will be insufficient for making any reliable predictions for practical purposes. To improve predictive capacities of theoretical models, which are to be used in management decisions, both the population and the environmental variables have to be considered in more detail and preferably site-specifically. A state-of-the-art approach is currently in progress in the Everglades (FL) restoration project in the US. In this project an environmental map, including vegetation, temperatures, water depth, etc, is produced based on spatially explicit hydrology models and topography data. In parallel, scientists are using experimental and field observations to construct models for several endangered species; these simulate stochastically the basic behavior of individuals in terms of movement patterns, food seeking strategies, and requirements for reproductive activities. Specific species under investigation are the snail kite, wood stork, Florida panther and white-tailed deer. These individual-based models are then used in simulations in which the environmental map is used as a site-specific scenario. After validation of these models has been completed, decision-makers can begin to ask questions regarding predicted environmental impacts of specific actions, such as changes in water flows or urbanization projects. Although many assumptions and simplifications have to be made in the process of constructing these simulation tools, they provide the best scenario and location specific predictions that ecologists can currently produce. Constant validation and refinement might over time yield tools that provide valuable advice for management.

## 5. Processing and transformation of external inputs

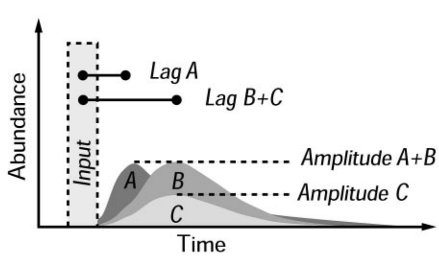
Too often, human enterprise considers little else than economic and social aspects. Equally often, society must later face the consequences in terms of degradation of ecosystems, for instance by xenobiotic compounds released without proper knowledge of their environmental consequences. But also, there are natural variations and extremes in chemical or physical properties of the environment. In the following I shall refer to both anthropogenic impacts and natural variations as environmental signals. Here I define an environmental signal to be a variation in some quantity over time, which is imposed on the system externally. That is, the system itself does not generate the signal. This can, for example, be a pulse of nutrients into a lake, an increasing trend of atmospheric carbon dioxide entering a forest, the release of an exotic species into an ecosystem, or the arrival of a storm front over a watershed. The ability of ecosystems to process and regulate such signals is of great value as substitution by artificial techniques would be very costly, e.g. as shown by Folke et al. (1994) and Gren et al. (1997) for nutrient retention.

A system can either transform an externally imposed quantity or transport it through the system with more or less of a time lag. For example, dissolved inorganic nitrogen entering a lake (input signal) can be incorporated into biomass or buried in the sediment (storage) or transformed into nitrogen gas (transformation), but some fraction is also remineralized or left unaffected and leaves the system in the dissolved inorganic phase with the drainage. In Box 2, a quantity of some substance is imposed on the system and the time-dependent release of this substance from the system can have certain properties. If the quantity is only processed and not transformed, the area under the curve is not changed, that is, the same

**Box 2.** -Ecosystems as filters-




Compounds or species that enter an ecosystem are processed within an internal network. As a result, this compound or species can be 1) released from the system again with more or less modulated signal characteristic, 2) transformed or, 3) stored within the system. Only the latter two may be considered as sinks for this compound. The capacity of the system to remove compounds is thus determined by the internal structure and can be estimated as the difference in volume (area under the curves) between the input and the output signal.




The output signal from the system may be time delayed in relation to the input signal (i.e. the lag), may have different amplitude (e.g. peak water flows in rivers), or different volume (area underneath the curves) if transformation or a change in storage has taken place.

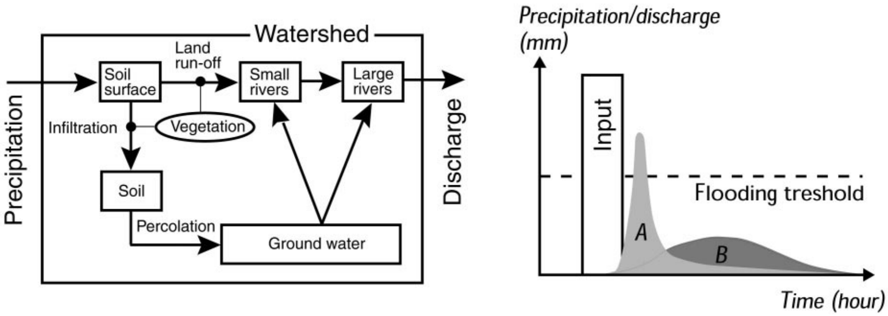



Fig. 3. The fate of precipitation over a watershed is illustrated as internal pathways between reservoirs and the potential effect of vegetation on the discharge (left). The hydrograph of a watershed without vegetation has a short time lag and high amplitude, as much water will flow directly into rivers because of high surface run-off (A). When vegetation is dense, water infiltrates the soil and enters the large groundwater reservoir, creating a longer lag and lower amplitude in the release of water into rivers and other water bodies.

amount that entered the system is also released again. If some or all of the substance is transformed into something different while in the ecosystem, for example by assimilation by organisms, storage or decomposition, the amount released may be less than the input. In that case the ecosystem functions as a sink for the substance of interest. Further, there may be a delay in the release, i.e. a time lag.

The result of this type of service is thus a regulation of materials and energy that enter and pass through the ecosystem. To understand the sensitivity of this function in relation to human impacts and the possibilities to sustain these, one has to understand the underlying mechanisms and the pathways within the ecosystem. In the following I show how the processing of matter by different systems can be influenced by its internal structure, i.e. storages and flows, and how particular processes can be dependent on very specific conditions that are in turn determined by other processes upheld by the ecosystem.

### *5.1. Example 3: flood management*

Flooding is a cause of great economic loss worldwide (Dunne and Leopold, 1978). In many cases, human alteration of the landscape has greatly reduced the capacity of the watershed to buffer flooding. This example helps to explain how water storages and flows within a natural ecosystem provide this type of ecosystem service, i.e. the prevention of flooding following a storm front. Calculation of flood hazards is a major concern in environmental planning (Dunne and Leopold, 1978). Methods by which the amplitude of a downstream pulse created by a storm can be reduced are many, and have been widely debated in the literature, e.g. Leopold and Maddock (1954) and Hoyt and Langbein (1955). I will only discuss two aspects: the importance of vegetation and soil properties, and the use of reservoirs or other storage systems.

There are many ways in which vegetation can influence the behavior of the simple system illustrated in Fig. 3, left panel. In general, dense vegetation will decrease land run-off as well as increase percolation into groundwater due to (1) increased infiltration properties of the soil, (2) increased water holding capacity of the soil due to higher content of organic matter, and (3) direct removal by water from the soil by the plants' roots for transpiration. Thus vegetation increases the reservoir capacity of the soil, thereby diminishing and delaying the flow of surface and groundwater into streams and rivers. Water that has entered the river system of the drainage basin will be transported downstream into larger and larger tributaries. Although the scheme in Fig. 3 simplifies this continuum into two discrete reservoirs—small and large rivers—this simple model can illustrate the effect. As the outflow from a natural reservoir is positively related to the water volume, any increases in the inflow of water will

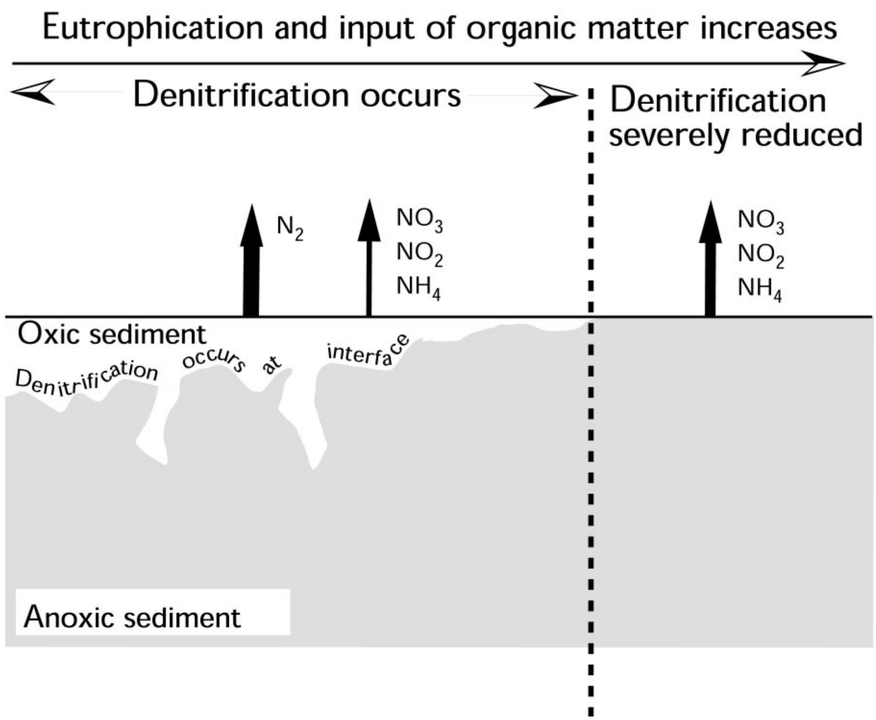



Fig. 4. Removal of nitrogen through denitrification in sediments as a function of eutrophication (increases towards the right end). Organic matter is deposited from the water column and consumes oxygen through degradation. As oxygen consumption increases with eutrophication, the sediment becomes completely oxygen free and the ecosystem switches into another state in which nitrogen is recirculated instead of transformed into nitrogen gas.

first lead to an increase in the water volume and then the discharge will start to increase as well. As shown in Fig. 3, right panel, this creates a lag between the incoming and outgoing pulse. With little vegetation, infiltration will be low and surface run-off high, creating curve A (Fig. 3, right panel). With dense vegetation, more precipitation can be infiltrated into the large groundwater reservoir, prolonging the discharge according to hydrograph B. Management by the use of reservoirs is done primarily through damming but also by channeling, which increases depth, width, and consequently the volume; another strategy is the straightening of rivers, which increases the rate of outflow at the expense of the time lag. Much of the debate and controversy is treated in the references mentioned previously and I will not get into more detail here. Nevertheless, flood management illustrates well the use of natural or artificial reservoirs as filters of external environmental pulses.

### *5.2. Use of ecosystems as filters and sinks of matter*

Human use of non-renewable resources has altered major global biogeochemical cycles as, for example, those of carbon and nitrogen, by the exploiting of natural resources that would naturally be considered as permanent storages over an ecological time scale (Charlson et al., 1992). This has resulted in accumulation of chemicals above pristine levels and altered responses of recipient ecosystems in terms of shifts in function and structure. Often, these responses are unwanted and/or unexpected. There is clearly a need for pollutant reduction policies, but additionally, the capacity of natural ecosystems to function as filters and storage for these compounds has become of considerable interest (Jansson et al., 1998). This type of ES uses the property of transformation and storage by ecosystems.

As shown in Box 2, there are only two possible true sinks for chemical compounds provided in an ecosystem: (1) transformation into a non-harmful compound, and (2) storage in either living or dead biomass, e.g. burial. Note that the material stored can be exchanged over time as long as the net increase compared to non-human-altered levels is maintained. For example, although incorporation of chemical compounds into biomass can increase due to increased $CO_2$ or nitrogen concentrations, this can only lead to a net-sink of these compounds if the loss rate (output) from both living or dead biomass is less than what is incorporated over time. If there is potential for a substantial increase in compound storage, such as burial in deep sea sediments, replanting of tropical forests, or redevelopment of harvested bogs and fens, and these storages can be sustained over a long enough time period, such an option is of great value. Sometimes, however, transformation of the compound can be a very effective process as illustrated by nitrogen removal through denitrifying bacteria in coastal zones.

### *5.3. Example 4: the denitrifying process in coastal zones*

Increased nutrient loading into coastal zones has great impact on water quality and on benthic ecosystems (Cederwall and Elmgren, 1990). To a considerable extent, benthic ecosystems can function as a sink for nitrogen by transforming nutritious nitrogen into nitrogen gas provided that the physical and biological conditions are favourable. Nitrogen removal in sediments can only occur at surfaces between an oxygen-free environment and environments in which oxygen is present. The concentration of oxygen is to a large extent affected by biological activity and deposition of organic material as outlined in Fig. 4. Burrowing animals promote oxygen transport into the deeper sediment layers, thereby increasing the surface at which denitrification can occur and the efficiency of the denitrifying process (Henriksen et al., 1983). The rate of deposition of organic material also increases the denitrification rate as long as there is an interface between oxygen free and oxygenated layers within the sediment. However, breakdown of organic material consumes oxygen and thus, as is often reported from eutrophicated coastal zones, creates bottom habitats that are completely free of oxygen. In this case the denitrifying process is severely reduced and the capacity of the coastal zone to buffer eutrophication can be reversed. This can become a reinforcing process that might have profound effects far into the open sea in terms of algal blooms that could potentially even be harmful to off-shore fisheries. Thus, there are complex interactions between species that provide the right physical and biological conditions, human induced environmental change, and the denitrifying bacteria that do the job.

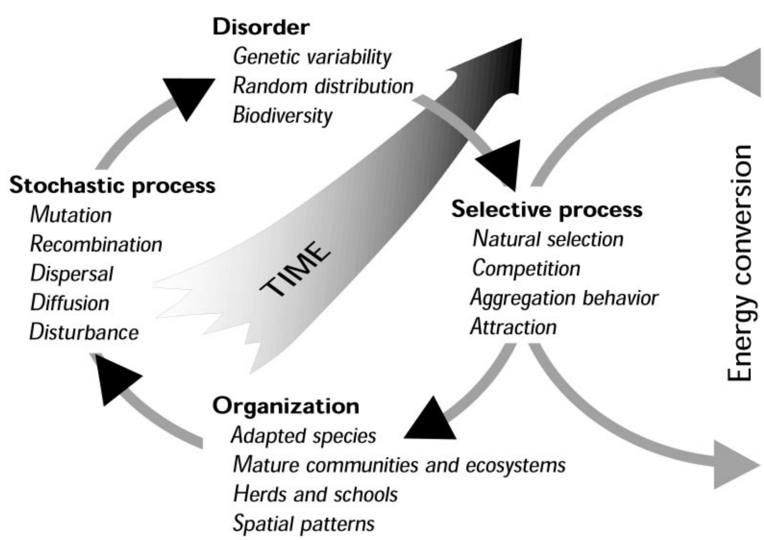
Few ecosystem services are so important to the future of our environment as the capacity of the earth's ecosystems to store carbon. An immense effort is currently devoted to understanding how the earth's ecosystems will respond to the change in increased atmospheric carbon dioxide (Wisniewski and Lugo, 1992). Will the global carbon storage increase, that is, will there be more living and dead biomass produced than consumed and will organic matter be buried into sediments at higher rates? Most important, will an increased storage of carbohydrates be persistent over a very long time (200 + years) or will the global carbon cycle just increase turn-over rates? This giant, uncontrolled experiment by humankind is today in its initial phase. Modeling efforts are trying to simulate the continuation of the input signal, i.e. future $CO_2$ production through such activities as burning of fossil fuels, deforestation and cement production, and the corresponding response of the major biomes of the globe, i.e. temperate and tropical forests and oceans (Mintzer, 1992; Bazzaz et al., 1996).

## 6. Biological organization

The creation of organization is an important aspect of most biological systems. If the main ingredients are provided, that is, opportunities (variability), energy, materials, and some selective process, one can observe the result as generated structure at virtually any scale. The study of biological structure formation is one of the most active fields of research in many biological disciplines today, spanning from molecular biology to ecosystems (Levin et al., 1997). Here, I define organization as some non-random pattern, structure, or interaction network in time, space, or any type of aspect such as morphology, color, etc. Organization thus contains a certain degree of regularity, meaning that the underlying mechanisms are not entirely stochastic and are sustained through biological processes (Levin, 1998). Examples of biologically organized entities include the genomes of organisms, non-random spatial distributions of species, the network of energy and matter flows in ecosystems, schools and herds, patterns on furs, coral reefs, migration patterns, flowers and so forth. Biological organization (including genetic information formed by evolutionary processes) is created by a selective process that acts on a gradient, i.e. on a multitude of choices or opportunities (Box 3). Whereas the stochastic processes often tend towards disorder (entropy), the selective processes require continuous inputs of energy (in biological cells this fuel is ATP (adenosine triphosphate), and on a larger scale, ecosystems run on solar energy or occasionally on hydrothermal energy). In evolutionary processes, natural selection determines whether any specific set of genes that make up an organism will be passed on to the next generation. The variability in the properties of different individuals belonging to one species is the gradient on which this process acts.

In a very general sense, the process of biological structure generation involves “a recursive ‘dialog’

Box 3. -Biological organization-




Variability is created by a stochastic process that to some degree degrades organization and thus increases disorder. Biological organization occurs over time through an energy-consuming selective process that acts on this gradient or variability. Thus, sustaining a certain degree of variability and diversity is essential for biological organization to function.

between the parts and the whole: the parts create a macroscopic pattern that in turn modifies the boundary conditions in which the parts interact" (Bascompte and Sole, 1995). Such a 'recursive dialog' is also the basis for the famous Red Queen hypothesis for evolutionary processes (Van Valen, 1973). In Alice in Wonderland (Carroll, 1866), the Red Queen was forced to move forever in order to be able to stay in one place. By analogy, the Red Queen hypothesis proposes that a species will adapt to a changing environment in order to avoid extinction. But as a result of such adaptations, the environment is in turn also affected, and this might cause a change in the direction of natural selection to which the species then has to respond again. One of the most important consequences of this stepwise selective process is the dependence of any given state on its unique history, so called path-dependency (Levin, 1998). If the organization process is disrupted by a disturbance, it may under certain circumstances reorganize again. For example, if a forest is clear-cut, it may over time develop into a similar forest again, provided that seeds of the former organisms are present or that they can invade the habitat from refuge populations. The property of reorganization over ecological time can be interpreted as resilience (Holling, 1992). Since this property is a result of adaptive properties at many different scales of an ecosystem, one can call ecosystems 'complex adaptive systems' (Levin, 1998).

Reorganization of ecosystems does not always have to lead to a similar state, though. Some ecosystems seem to be less resilient than others. For example, savannas may, because of overgrazing, change into open grasslands and do not develop into a savanna easily again (Walker, 1993). Shallow lakes dominated by clear water and large bottom-growing algae may become turbid and dominated by free-floating microalgae following a eutrophication event or alteration in water level (Scheffer and De Boer, 1995). The same applies over much longer time scales for evolutionary processes. Major groups of organisms seem to evolve again if preceding organisms have become extinct. For example, corals have developed at least twice in the history of the world albeit in slightly different designs (Eldredge, 1996). Also, similar types of organisms may develop on different continents from different taxa; for example the placental wolf had its homologous counterpart in Australia, yet the latter evolved from marsupial ancestors. Other species that have become extinct may not have been replaced by organisms with similar ecological functions as yet. Thus, biological organization is a uni-directional process, it cannot be reversed or repeated, but it may follow a similar path if disturbed. The ability of biological systems to follow this path of succession is of utmost importance for the ability of ecosystems to perform certain functions and thus to provide goods and services. To sustain healthy ecosystems, one has to understand what criteria are needed for biological organization to take place.

### 6.1. Example 5: succession of ecosystems

When an ecosystem initially develops, the number and properties of species that can invade the pristine habitat will determine its succession (time-course of development). The size of this species pool limits the variability from which the parts, which will compose the network of energy and matter pathways in the ecosystem, are selected. Ecosystems are not designed for any particular species, but rather are the result of species assemblages. However, this assemblage is not a completely random collection of species because selective processes operate, foremost competition for resources. Species that most efficiently harvest resources or can prevent other species from attaining them under prevailing environmental conditions will be successful and may out-compete the latter. Thus, as the cumulative number of species that have invaded the habitat increases over time, the chance that any established species will be replaced by a more competitive one also increases. As a result, resources in ecosystems are generally more efficiently used as succession proceeds. In that sense, succession through species replacement creates a structure, or organization, that is different from an assemblage of species drawn randomly from the pool of potential invaders. This organization can eventually be destroyed by both natural (e.g. fires, storms, flooding, pest outbreaks) or anthropogenic events. These can disrupt the process of succession and move the system towards a state with less internal organization and initiate a new phase of succession (Gunderson et al., 1997). From this follows that the availability and variability in performance of species that can enter an ecosystem is crucial for its functioning (Tilman et al., 1997). Ecosystems are usually defined on a spatial scale that exceeds the scale of the local population, but not necessarily that of the whole species (Hughes et al., 1997). Thus, as ecosystems are degraded and populations become extinct, other populations of the same species that are located elsewhere become increasingly important for the reorganization of the ecosystem. The more species that have a similar function and potentially may invade the ecosystem, the higher the rate of invasions and thus the rate at which the succession of the ecosystem proceeds. An important point is therefore, that in general, species richness is potentially a limiting factor for the rate of ecosystem succession and regeneration.

Biological organization is probably the most undervalued and least understood ecosystem service of the three classes of ecosystem services I have described. Yet, from the basic principles of how such organization is formed, one can strongly argue that opportunity, or variety, is a key aspect that is linked to the rate and quality of the formation of biological organization. This property also seems to be relatively scale invariant, i.e. it is as true for adaptation of species to changing environments as to ecosystem succession. As an ecologist, it is difficult to understand why the importance of opportunity and diversity in biological systems is so hard to communicate to the general public, while it is seems so treasured in conventional economics and markets.

## 7. General discussion

The use of ecosystem services as a concept has great advantages as a tool of communication between disciplines. But also, this concept has to be usable within disciplines if it is to remain scientifically credible. The types of services examined in this paper have strong foundations in ecological theory or are frontier fields. However, not all services fall into the simplified scheme used here nor are all possible services listed in Table 1 or even recognized yet at all. One group of services that has not been dealt with in this paper is that referred to as information services in Table 1. I have found these very difficult to put into an ecological context and therefore rather refrained from doing so. Admittedly, however, these types of services may well be among the most important regarding how nature has determined the path of human history. Religious and cultural identity plays a great role in the development and interactions between human populations. That these aspects are linked to nature's services may be illustrated by an early appreciation written by one of the greatest naturalists, Carl Linneus, in the early 17th century during his travels[2]:

> As one sits here in summertime and listens to the cuckoo and all the other bird songs, the crackling and buzzing of insects, as one gazes at the shining colors of flowers, doth one become dumbstruck before the Kingdom of the Creator.

## Acknowledgements

Karin Limburg has been a great help in fixing the manuscript and steering the idea into something publishable. Several ideas have sprung from discussions with Dennis Swaney and Ragnar Elmgren. Glenn-Marie Lange, Simon Levin and two anonymous referees have provided very valuable comments.

[2] Original text: "När man sätter sig här på sommaren och lyssnar på göken och alla andra fåglars sång, insekternas gnissel och surr, när man betraktar blommornas lysande och glada färger, då bliver man helt förstummad inför skaparens rikedom" (from Linneus diaries).

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