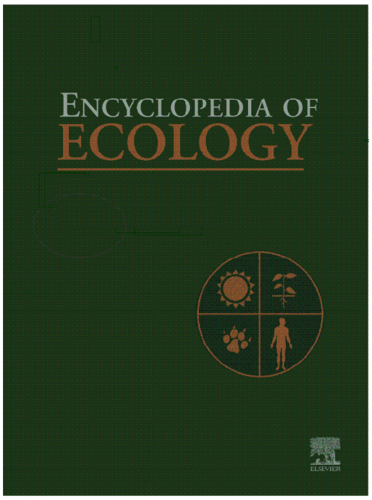

A K Salomon. Ecosystems. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), General Ecology. Vol. [2] of Encyclopedia of Ecology, 5 vols.
pp. [1155-1165] Oxford: Elsevier.

Ecosystems

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What Is an Ecosystem?

Coined by A. G. Tansley in 1935, the term 'ecosystem' refers to an integrated system composed of a biotic community, its abiotic environment, and their dynamic interactions. A diversity of ecosystems exist through the world, from tropical mangroves to temperate alpine lakes, each with a unique set of components and dynamics (Figure 1). Ecosystems can be classified according to their components and physical context yet their classification is highly dependent on the spatial scale of scrutiny. Typically, boundaries between ecosystems are diffuse. An 'ecotone' is a transition zone between two distinct ecosystems (i.e., the tundra–boreal forest ecotone).

History

Over 70 years ago, Sir Arthur Tansley (Figure 2) presented the notion that ecologists needed to consider 'the whole system', including both organisms and physical factors, and that these components could not be separated or viewed in isolation. By suggesting that ecosystems are dynamic, interacting systems, Tansley's ecosystem concept transformed modern ecology. It led directly to considerations of energy flux through ecosystems and the pathbreaking, now classic work of R. L. Lindeman in 1942, one of the first formal investigations into the functioning of an ecosystem, in this case a senescent lake, Cedar Creek Bog, in Minnesota. Inspired by the work of C. Elton, Lindeman focused on the trophic (i.e., feeding) relationships within the lake, grouping together organisms of the lake according to their position in the food web. To study the cycling of nutrients and the efficiency of energy transfer among trophic levels over time, Lindeman considered the lake as an integrated system of biotic and abiotic components. He considered how the lake food web and processes driving nutrient flux affected the rate of succession of the whole lake ecosystem, a significant departure from traditional interpretations of succession.

By the late 1950s and early 1960s, system-wide energy fluxes were quantified in various ecosystems by E. P. Odum and J. M. Teal. In the late 1960s, Likens, Bormann, and others took an ecosystem approach to studying biogeochemical cycles by manipulating whole watersheds in the Hubbard Brook Experimental Forest to determine whether logging, burning, or pesticide and herbicide use had an appreciable effect on nutrient loss

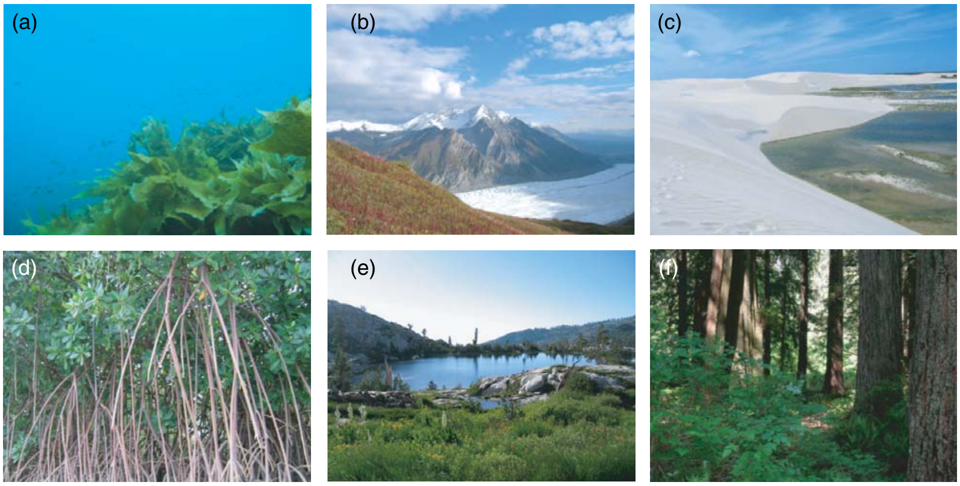

Figure 1 (a) Kelp forest, (b) subarctic alpine tundra, (c) tropical coastal sand dune, (d) tropical mangrove, (e) alpine lake, and (f) temperate coastal rain forest. Photos by Anne Salomon, Tim Storr, and Tim Langlois.

A. G. Tansley

Figure 2 Sir Arthur G. Tansley coined the term ecosystem in 1935. From *New Phytologist* 55: 145, 1956.

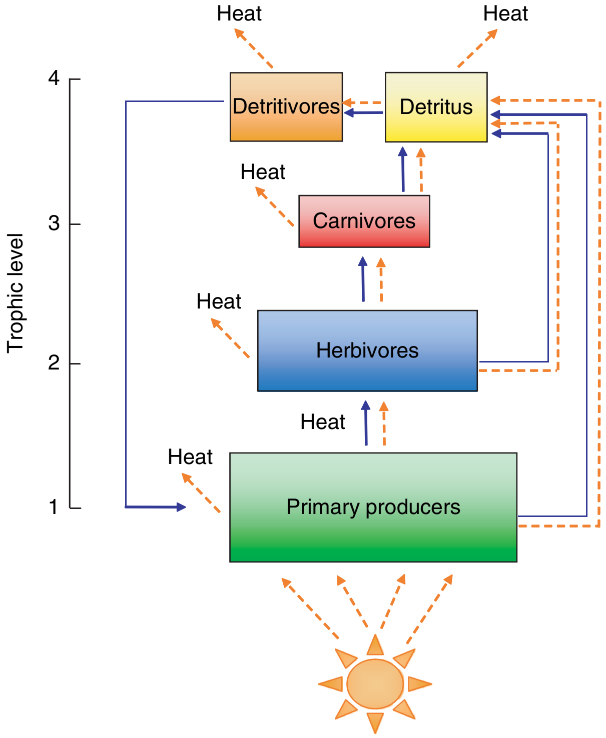

Figure 3 Energy flows and material cycles in an ecosystem. Materials move through the trophic levels and eventually cycle back to the primary producers via the decomposition of detritus by microorganisms. Energy, originating as solar energy, is transferred through the trophic levels via chemical energy and is lost via the radiation of heat at each step. Adapted from DeAngelis DL (1992) *Dynamics of Nutrient Cycling and Food Webs*. New York, NY: Chapman and Hall.

from the ecosystem. This research set an important precedent in demonstrating the value of conducting experiments at the scale of an entire ecosystem (see the section entitled ‘Whole ecosystem experiments’), a significant advancement which continues to inform ecosystem studies today.

Ecosystem Components and Properties

Ecosystems can be thought of as energy transformers and nutrient processors composed of organisms within a food web that require continual input of energy to balance that lost during metabolism, growth, and reproduction. These organisms are either ‘primary producers’ (autotrophs), which derive their energy by using sunlight to convert inorganic carbon into organic carbon, or ‘secondary producers’ (heterotophs), which use organic carbon as their energy source. Organisms that perform similar types of ecosystem functions can be broadly categorized by their ‘functional group’. For example, ‘herbivores’ are heterotophs that eat autotrophs, ‘carnivores’ are heterotrophs that eat other heterotrophs, while ‘detritivores’ are heterotrophs that eat nonliving organic material (detritus) derived from either autotrophs or heterotrophs (Figure 3). Herbivores, carnivores, and dertitivores are collectively known as ‘consumers’.

Classifying organisms according to their feeding relationships is the basis of defining an organism’s ‘trophic level’; the first trophic level includes autotrophs; the second trophic level includes herbivores and so on. Ecosystem components that make up a trophic level are quantified in terms of biomass (the weight or standing crop of organisms), while ecosystem dynamics, the flow of energy and materials among system components, are quantified in terms of rates.

Typically, ecologists quantifying ecosystem dynamics use carbon as their currency to describe material flow and energy to quantify energy flux. Material flow and energy flow differ in one important property, namely their ability to be recycled. Chemical materials within an ecosystem are recycled through an ecosystem’s component. In contrast, energy moves through an ecosystem only once and is not recycled (Figure 3). Most energy is transformed to heat and ultimately lost from the system. Consequently, the continual input of new solar energy is what keeps an ecosystem operational.

Solar energy is transformed into chemical energy by primary producers via photosynthesis, the process of converting inorganic carbon (CO_2) from the air into organic carbon ($C_6H_{12}O_2$) in the form of carbohydrates. Gross primary production is the energy or carbon fixed via photosynthesis over a specific period of time, while net primary production is the energy or carbon fixed in

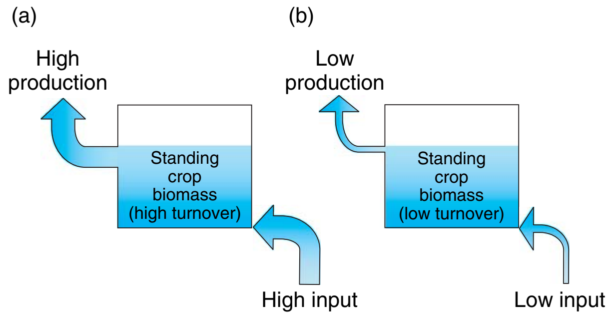

Figure 4 Standing crop biomass is not always correlated to production rates. Here, two hypothetical species with populations at equilibrium, where input equals output, have an equivalent standing crop biomass but differ in their turnover rates. Population (a) has high input, high production, and high turnover rates, whereas population (b) has low input, low production, and low turnover rates. In reality, populations are rarely at equilibrium so standing crop biomass fluctuates depending on input rates and the amount of production consumed by higher trophic levels. Adapted from Krebs C (2001) *Ecology: The Experimental Analysis of Distribution and Abundance*, 5th edn. San Francisco: Addison-Wesley Educational Publishers, Inc.

photosynthesis, minus energy or carbon which is lost via respiration, per unit time. Production by secondary producers is simply the amount of energy or material formed per unit term.

A careful distinction needs to be made between production rates and static estimates of standing crop biomass, particularly because the two need not be related. For example, two populations at equilibrium, in which input equals output, might have the same standing stock biomass but drastically different production rates because turnover rates can vary (**Figure 4**). For example, on surf swept shores from Alaska to California, two species of macroalgal primary producers grow in the low rocky intertidal zone of temperate coastal ecosystems (**Figure 5**). The ribbon kelp, *Alaria marginata*, is an annual alga with high growth rates, whereas sea cabbage, *Hedophyllum sessile*, is a perennial alga with comparatively lower growth rates. Although they differ greatly in their production rates, in mid-July, during the peak of the growing season, these two species can have almost equivalent stand crop biomasses.

Ecosystem Efficiency

The efficiency of energy transfer within an ecosystem can be estimated as its 'trophic transfer efficiency', the fraction of production passing from one trophic level to the next. The energy not transferred is lost in respiration or to detritus. Knowing the trophic transfer efficiency of an ecosystem can allow researchers to estimate the primary production required to sustain a particular trophic level.

For example, in aquatic ecosystems, trophic transfer efficiency can vary anywhere between 2% and 24%, and average 10%. Assuming a trophic efficiency of 10%, researchers can estimate how much phytoplankton production is required to support a particular fishery. Consider the open ocean fishery for tuna, bonitos, and billfish. These are all top predators, operating at the fourth trophic level. According to world catch statistics recorded by the Food and Agriculture Organization, in 1990, 2 975 000 t of these predators were caught, equivalent to 0.1 g of carbon

Figure 5 (a) In the low intertidal zone of temperate coastal ecosystems, (b) the ribbon kelp, *Alaria marginata*, is an annual alga with high growth rates, whereas (c) the sea cabbage kelp, *Hedophyllum sessile*, is a perennial alga with lower growth rates. During the peak of the growing season, these two species can have a similar stand crop biomass but differ greatly in their production rates because one is an annual and the other is a perennial. Photo by Anne Salomon and Mandy Lindeberg.

per m^2 of open ocean per year. To support this yield of tuna, bonitos, and billfish, researchers can calculate the production rates of the trophic levels below, assuming a trophic efficiency of 10% and equilibrium conditions. Essentially, to produce of $0.1\,\mathrm{gC\,m^{-2}\,yr^{-1}}$ of harvested predators (tuna, bonitos, and billfish) requires $1\,\mathrm{gC\,m^{-2}\,yr^{-1}}$ of pelagic fish to have been consumed by the top predators, $10\,\mathrm{gC\,m^{-2}\,yr^{-1}}$ of zooplankton to be consumed by the pelagic fishes, and $100\,\mathrm{gC\,m^{-2}\,yr^{-1}}$ of phytoplankton. Note that these values represent the production that is transferred up trophic levels. They do not represent the standing stock of biomass at each trophic level. Knowing the net primary production of the phytoplankton allows researchers to estimate the proportion of this production that is taken by the fishery.

It has been estimated that 8% of the world's aquatic primary production is required to sustain global fisheries. Considering continental shelf and upwelling areas specifically, these ecosystems provide one-fourth to one-third of the primary production required for fisheries. This high fraction leaves little margin for error in maintaining resilient ecosystems and sustainable fisheries.

Large-Scale Shifts in Ecosystems

A growing body of empirical evidence suggests that ecosystems may shift abruptly among alternative states. In fact, large-scale shifts in ecosystems have been observed in lakes, coral reefs, woodlands, desserts, and oceans. For example, a distinct shift occurred in the Pacific Ocean ecosystem around 1977 and 1989. Abrupt changes in the time series of fish catches, zooplankton abundance, oyster condition, and other marine ecosystem properties signified conspicuous shifts from one relatively stable condition to another (**Figure 6**). Also termed 'regime shifts', the implications of these abrupt transitions for fisheries and oceanic CO_2 uptake are profound, yet the mechanisms driving these shifts remain poorly understood. It appears that changes in oceanic circulation driven by weather patterns can be evoked as the dominant causes of this state shift. However, competition and predation are becoming increasingly recognized as important drivers of change altering oceanic community dynamics. In fact, fisheries are well known to affect entire food webs and the trophic organization of ecosystems. Therefore, one could imagine that the sensitivity of a single keystone species to subtle environmental change could cause major shifts in community composition. Given this interplay between and within the biotic and abiotic components of an ecosystem, resolving the causes of regime shifts in oceanic ecosystems will likely require an understanding of the interactions between the effects of fisheries and the effects of physical climate change.

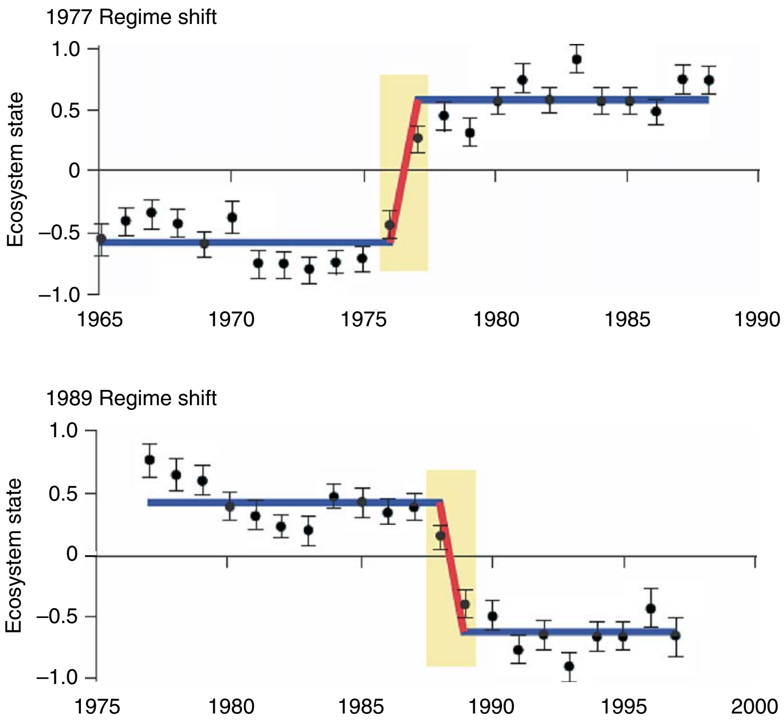

Figure 6 Distinct shifts in ecosystem states, also referred to as 'regime shifts', occurred in the Pacific Ocean ecosystem around 1977 and 1989. The ecosystem state index shown here was calculated based on the average of climatic and biological time series. From Scheffer M, Carpenter S, Foley JA, Folke C, and Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413: 591–596.

Studying Ecosystem Dynamics

Stable Isotopes

Important insights into ecosystem dynamics can be revealed through the use of naturally occurring 'stable isotopes'. These alternate forms of elements can reveal both the source of material flowing through an ecosystem and its consumer's trophic position. This is because different sources of organic matter can have unique isotopic signatures which are altered in a consistent manner as materials are transferred throughout an ecosystem, from trophic level to trophic level. Consequently, stable isotopes provide powerful tools for estimating material flux and trophic positions.

The elements C, N, S, H, and O all have more than one isotope. For example, carbon has several isotopes, two of which are ^{13}C and ^{12}C. In nature, only 1% of carbon is ^{13}C. Isotopic composition is typically expressed in δ values, which are parts per thousand differences from a standard. For carbon,

$$\delta^{13}\mathrm{C} = \left[\left(\frac{^{13}\mathrm{C}/^{12}\mathrm{C}_{\mathrm{sample}}}{^{13}\mathrm{C}/^{12}\mathrm{C}_{\mathrm{standard}}}\right) - 1\right] \times 10^3$$

Consequently, δ values express the ratio of heavy to light isotope in a sample. Increases in these values denote increases in the amount of the heavy isotope component. The standard reference material for carbon is PeeDee limestone, while the standard for nitrogen is nitrogen gas in the atmosphere. Natural variation in stable isotopic composition can be detected with great precision with a mass spectrometer.

Stable isotopes record two kinds of information. Process information is revealed by physical and chemical reactions which alter stable isotope ratios, while source information is revealed by the isotopic signatures of source materials. When organisms take up carbon and nitrogen, chemical reactions occur which discriminate among isotopes, thereby altering the ratio of heavy to light isotope. This is known as 'fractionation'. Although carbon fractionates very little (0.4‰, 1 SD = 1‰), the mean trophic fractionation of δ^{15}N is 3.4‰ (1 SD = 1‰), meaning that δ^{15}N increases on average by 3.4‰ with every trophic transfer. Because the δ^{15}N of a consumer is typically enriched by 3.4‰ relative to its diet, nitrogen isotopes can be used to estimate trophic position. Stable isotopes can provide a continuous measure of trophic position that integrates the assimilation of energy or material flow through all the different trophic pathways leading to an organism. In contrast, δ^{13}C can be used to evaluate the ultimate sources of carbon for an organism when the isotopic signatures of the sources are different.

Stable isotopes can track the fate of different sources of carbon through an ecosystem, because a consumer's isotopic signature reflects those of the key primary producers it consumes. For example, in both lake and coastal marine ecosystems, δ^{13}C is useful for differentiating between two major sources of available energy, benthic (nearshore) production from attached macroalgae, and pelagic (open water) production from phytoplankton. This is because macroalgae and macroalgal detritus (specifically kelp of the order Laminariales) is typically more enriched in δ^{13}C (less negative δ^{13}C) relative to phytoplankton due to boundary layer effects. Researchers have exploited this difference to answer many important ecosystem-level questions. Below are two examples.

During the late 1970s and early 1980s, in the western Aleutian Islands of Alaska, where sea otters had recovered from overexploitation and suppressed their herbivorous urchin prey, productive kelp beds dominated. There, transplanted filter feeders, barnacles and mussels, grew up to 5 times faster compared to islands devoid of kelp where sea otters were scarce and urchin densities high. Stable isotope analysis revealed that the fast-growing filter feeders were enriched in carbon suggesting that macroalgae was the carbon source responsible for this magnification of secondary production.

In four Wisconsin lakes, experimental manipulations of fish communities and nutrient loading rates were conducted to test the interactive effects of food web structure and nutrient availability on lake productivity and carbon exchange with the atmosphere. The presence of top predators determined whether the experimentally enriched lakes operated as net sinks or net sources of atmospheric carbon. Specifically, the removal of piscivorous fishes caused an increase in planktivorous fishes, a decrease in large-bodied zooplankton grazers, and enhanced primary production, thereby increasing influx rates of atmospheric carbon into the lake. Atmospheric carbon was traced to upper trophic levels with δ^{13}C. Here, naturally occurring stable isotopes and experimental manipulations conducted at the scale of whole ecosystems illustrated that top predators fundamentally alter biogeochemical processes that control a lake's ecosystem dynamics and interactions with the atmosphere.

Whole Ecosystem Experiments

Large-scale, whole ecosystem experiments have contributed considerably to our understanding of ecosystem dynamics. With its beginnings in wholesale watershed experiments in the 1960s, ecosystems are now being studied experimentally and analyzed as system of interacting species processing nutrients and energy within the context of changing abiotic conditions. This is particularly relevant these days given the effects of anthropogenic climate forcing and pollution in both terrestrial and oceanic ecosystems.

A classic series of whole-lake nutrient addition experiments conducted in northwestern Ontario by David Schindler and his research group illustrated the role of phosphorus in temperate lake eutrophication. To separate the effects of phosphorus and nitrate, the researchers split a lake with a curtain and fertilized one side with carbon and nitrogen and the other with phosphorus, carbon, and nitrogen. Within 2 months, a highly visible algal bloom had developed in the basin in which phosphorus had been added providing experimental evidence that phosphorus is the limiting nutrient for phytoplankton production in freshwater lakes. Certainly, algae may show signs of nitrogen or carbon limitation when phosphorus is added to a lake; however, other processes often compensate for these deficiencies. For instance, CO_2 is rarely limiting because physical factors such as water turbulence and gas exchange regulate its availiblity. Further, nitrogen can be fixed by blue-green algae. These species, which are favored when nitrogen is in short supply, increases the availability of nitrogen to algae, and the lake eventually returns to a state of phosphorus limitation. The practical significance of these results is that lake europhication can be prevented with management policies that control phosphorus input into lake and rivers.

Using Management Policies as Ecosystem Experiments

It has become increasingly common to use management policies as experiments and test their effects on ecosystem dynamics. An excellent example of this approach is the use of marine reserves to investigate the ecosystem-level consequences of fishing. Essentially, well-enforced marine reserves constitute large-scale human-exclusion experiments and provide controls by which to test the ecosystem effects of reducing consumer biomass via fishing at an ecologically relevant scale. Dramatic shifts in nearshore community structure have been documented in well-established and well-protected marine reserves in both Chile and New Zealand. In northeastern New Zealand's two oldest marine reserves, the Leigh Marine Reserve and Tawharanui Marine Park, previously fished predators, snapper (*Pagrus auratus*) and rock lobster (*Jasus edwardsii*), have increased in abundance by 14- and 3.8-fold, respectively, compared to adjacent fished waters. Increased predation leading to reduced survivorship and cryptic behavior of their herbivorous prey, the sea urchin (*Evechinus chloroticus*), has allowed the macroalga (*Ecklonia radiata*) to increase significantly within the reserves, a trend that has been developing in the Leigh reserve for the past 25 years (Figure 7). Although this provides evidence that fishing can indirectly reduce ecosystem productivity, the trophic dynamics described above are context dependent and vary as a function of depth, wave exposure, and oceanographic circulation (Figure 8). For example, both in the presence and absence of fishing, urchin densities decline

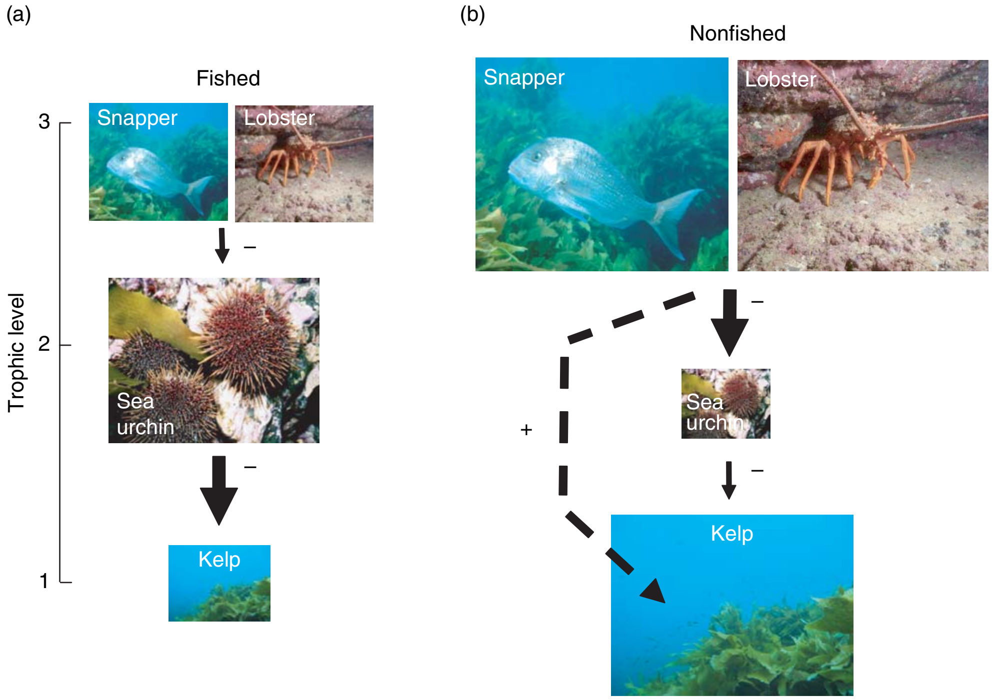

Figure 7 (a) In nearshore fished ecosystems in northeastern New Zealand, snapper and lobster densities have been reduced due to fishing pressure resulting in high sea urchin densities, urchin barrens, and reduced kelp production. (b) In marine reserves, where previously fished snapper and lobster have recovered, sea urchins that have not been consumed by these predators behave cryptically, hiding in crevices. Consequently, kelp forests of *Ecklonia radiata* dominate. Photos by Nick Shears, Hernando Acosta, and Timothy Langlois.

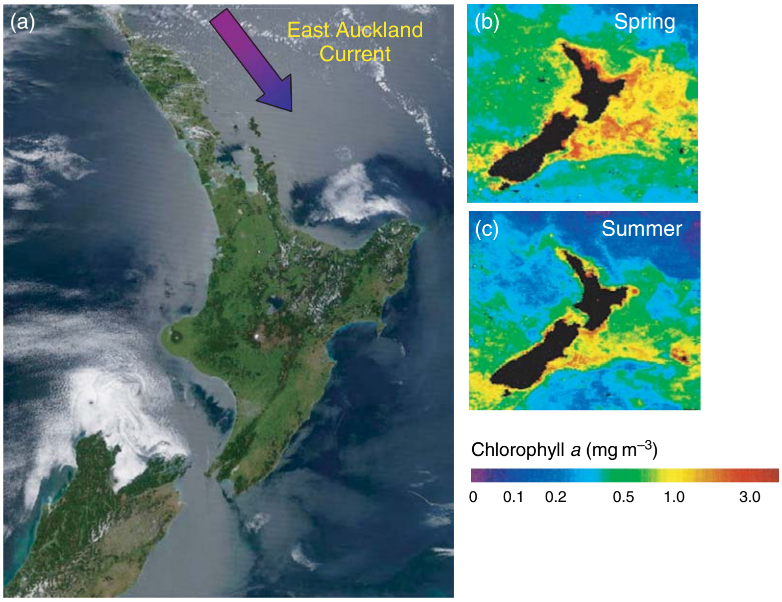

Figure 8 The effects of fishing on nearshore ecosystems are influenced locally by wave exposure and regionally by oceanographic circulation. (a) In northeastern New Zealand, ocean circulation patterns influence nutrient delivery and thus (b) spring and (c) summer pelagic primary production. Satellite images: SeaWiFs Project, Ocean Color Web.

to nearly 0 individuals per m^2 below depths greater than 10 m due to unfavorable conditions for recruitment, despite the presence or absence of snapper and lobster, while at depths above 3 m, wave surge can preclude urchin grazing both inside and outside the reserves. Furthermore, where oceanic conditions hinder urchin recruitment, the effects of fishing on macroalgae become less clear-cut. These physical constraints highlight the importance of abiotic context on biotic interactions. Ultimately, one can gain a lot of information by using management policies as experiments.

Although policy experiments have played an important role in elucidating ecosystem dynamics, in many cases, it is politically intractable or logistically impossible to experiment with whole ecosystems. Under such circumstances, researchers have used alternative techniques to explore ecosystem dynamics. Models in ecology have a venerable tradition for both teaching and understanding complex processes. Ecosystem models are now being used to gain insight into the ecosystem-level consequences of management policies, from fisheries to carbon emissions. For more information on ecosystem models and using management policies as experiments, see the section entitled ‘Social–ecological systems, Humans as key ecosystem components’.

Ecosystem Function and Biodiversity

Accelerating rates of species extinction have prompted researchers to formally investigate the role of biodiversity in providing, maintaining, and even promoting ‘ecosystem function’. Typically, studies experimentally modify species diversity and examine how this influences the fluxes of energy and matter that are fundamental to all ecological processes. In many cases, studies are designed to document the effects of species richness on the efficiency by which communities produce biomass, although the effects of species diversity on other ecosystem functions such as decomposition rates, nutrient retention, and CO_2 uptake rates have also been examined. Several seminal studies report a positive relationship between biodiversity and ecosystem function. Yet, the generality of the results, and the mechanisms driving them, have provoked considerable debate and several counterexamples exist.

At the crux of the debate lies a question with deep historical roots: do some species exert stronger control over ecosystem processes than others? Imagine two distinct positive relationships between biodiversity and ecosystem function (Figure 9). In type A communities, every single species contributes to the ecosystem function measured, even the rare species. By contrast, in type B communities, almost all of the ecosystem function measured can be provided by relatively few species, suggesting that many species are in fact redundant. Few empirical studies support type A relationships, rather, empirical evidence points to the prevalence of type B relationships. In fact, a recent meta-analysis of 111 such studies conducted in multiple ecosystems on numerous trophic groups found that the average effect of decreasing species richness is to decrease the biomass of

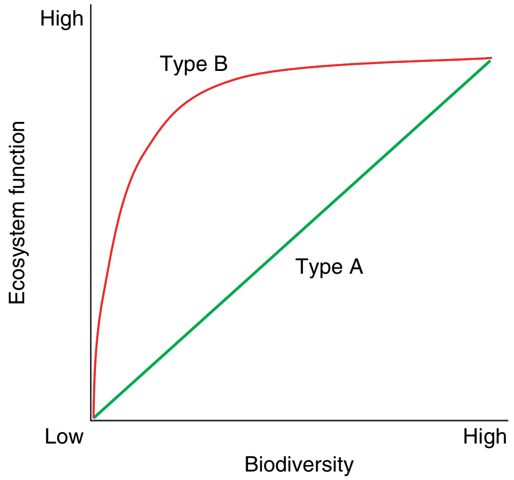

Figure 9 Type A communities: every single species contributes equally to ecosystem functioning. Type B communities: ecosystem function is provided by only a few species.

the focal trophic group, leading to less complete depletion of resources used by that group. Further, the most species-rich polycultures performed no differently than the single most productive species used in the experiment. Consequently, these average effects of species diversity on ecosystem production are best explained by the loss of the most productive species from a diverse community. These results could be considered consistent with what has become known as the 'sampling effect'.

Critics argue that a positive relationship between species diversity and ecosystem function is a sampling artifact rather than a result of experimentally manipulated biodiversity *per se*. Such a 'sampling effect' can arise because communities comprising more species have a greater chance of being dominated by the most productive taxa. Yet, controversy surrounding the 'sampling effect' itself exists given the duality in its possible interpretation: is this a real biological mechanism that operates in nature or is it an experimental artifact of using random draws of species to assemble experimental communities? To add to the ecosystem function–biodiversity debate is the critical issue that many of these studies focus on a single trophic level and neglect or dismiss multiple trophic-level interactions, such as herbivory and other disturbances well known to alter ecosystem processes, calling into question the generality of these results.

Despite the controversy, these studies generally reinforce the notion that certain species exert much stronger control over ecological processes than others. However, identifying which species these are in advance of extinction remains a challenge. Nonetheless, identifying the mechanisms driving ecosystem functioning is an important conservation priority given that human well-being relies on a multitude of these functions.

Ecosystem Perspectives in Conservation Science

Ecosystem Services

Humans have always relied on nature for environmental assets like clean water and soil formation. Today, these assets are receiving global attention as 'ecosystem services', the conditions and processes by which natural ecosystems sustain and fulfill human life. Natural ecosystems perform a diversity of ecosystem services on which human civilization depends:

1. regulating services – purification of air and water, detoxification and decomposition of wastes, moderation of weather extremes, climate regulation, erosion control, flood control, mitigation of drought and floods, regulation of disease carrying organisms and agricultural pests;
2. provisioning services – provision of food, fuel, fiber, and freshwater;
3. supporting services – formation and preservation of soils, protection from ultraviolet rays, pollination of natural vegetation and agricultural crops, cycling of nutrients, seed dispersal, maintenance of biodiversity, primary production; and
4. cultural services – spiritual, esthetic, recreational.

Although critical to human existence, ecosystem services are often taken for granted or at best, greatly undervalued. This is ironic given that many ecosystem services are very difficult and expensive to duplicate, if they can be duplicated at all. Normally, ecosystem services are considered 'free' despite their obvious economic value. For example, over 100 000 species of animals provide free pollination services, including bats, bees, flies, moths, beetles, birds, and butterflies (Figure 10). Based on the estimate that one-third of human food comes from plants pollinated by wild pollinators, pollination has been valued at US$4–6 billion per year in the US alone. Globally, the world's ecosystem services have been valued at US$33 trillion a year, nearly twice as much as the gross national product of all of the world's countries.

The idea of paying for ecosystem services has been gaining momentum. Yet, because ecosystem services are typically not sold in markets, they usually lack a market value. Given the value of natural capital, nonmarket valuation approaches are being developed by economists and ecologists to account for ecosystem services in decision-making processes. The notion being that economic valuation gives decision makers a common currency to assess the relative importance of ecosystem processes and other forms of capital.

Yet, assigning value to ecosystem services is tricky and some analysts object to nonmarket valuation, because it is a strictly anthropogenic measure and does not account for

Figure 10 Pollination services, provided by bees, bats, butterflies, and birds to name a few, have been valued at US$4–6 billion per year in the US alone. Consider the global value of this important ecosystem service. Photos by Steve Gaines, Heather Tallis.

nonhuman values and needs. Yet, in democratic countries, environmental policy outcomes are determined by the desires of the majority of citizens, and voting on a preferred policy alternative is ultimately an anthropogenic activity. A second objection to nonmarket valuation is a disagreement with pricing the natural world and dissatisfaction with the capitalistic premise that everything is thought of in terms of commodities and money. The point of valuation, however, is to frame choices and clarify the tradeoffs between alternative outcomes (i.e., draining a wetland may increase the supply of developable land for housing but does so at the cost of decreased habitat and potential water quality degradation). Finally, a third objection to nonmarket valuation stems from the uncertainty in identifying and quantifying all ecosystem services. Advocates argue that economic valuation need not cover all values and that progress is made by capturing values that are presently overlooked.

Despite the uncertainties, valuing ecosystem services can sometimes pay off. When New York City compared the coast of an artificial water filtration plant valued at US$6–8 billion, plus an annual operating cost of US$300 million, the city chose to restore the natural capital of the Catskill Mountains for this watershed's inherent water filtration services and for a fraction of the cost (US$660 million). Ultimately, the valuation of ecosystem services, even if flawed, may get ecosystem processes on the decision-making table and lead to more sustainable policies in light of ever-expanding human populations.

Ecosystem services are threatened by growth in the scale of human enterprise (population size, per-capita consumption rates) and a mismatch between short-term needs and long-term societal well-being. With a global population soon to number 9 billion people, ecosystem services are becoming so degraded, some regions in the world risk ecological collapse. Many human activities alter, disrupt, impair, or reengineer ecosystem services such as overfishing, deforestation, introduction of invasive species, destruction of wetlands, erosion of soils, runoff of pesticides, fertilizers, and animal wastes, pollution of land, water, and air resources. The consequences of degrading ecosystem services on human well-being were examined in the Millennium Ecosystem Assessment (MA) 2005, which concluded that well over half of the world's ecosystems services are being degraded or used unsustainably. The MA developed global ecological scenarios as a process to inform future policy options. These scenarios were based on a suite of models that were designed to forecast future change. The MA based its scenario analyses on ecosystem services. Specifically, scenarios were developed to anticipate responses of ecosystem services to alternative futures driven by different sets of policy decisions. Following the completion of this ambitious ecological study, there is now a growing movement to make the value of ecosystem services an integral part of current policy initiatives.

Social–Ecological Systems, Humans as Key Ecosystem Components

Humans are a major force in global change and drive ecosystem dynamics, from local environments to the entire biosphere. At the same time, human societies and global economies rely on ecosystem services. As such, human and natural systems can no longer be treated independently because natural and social systems are strongly linked. Accumulating evidence suggests that effective environmental management and conservation strategies must take an integrated approach, one that considers the interactions and feedbacks between and within social, economic, and ecological systems. As a result, the concept of coupled 'social–ecological systems' has become an emerging focus in environmental and social science and ecosystem management. Social–ecological systems are considered as evolving, integrated systems that typically behave in nonlinear ways. The concept of resilience – the capacity to buffer change – has been increasingly used as an approach for understanding the dynamics of social–ecological systems. Two useful tools for building resilience in social–ecological systems are structured scenario modeling and active adaptive management.

Models of linked social–ecological systems have been developed to inform management conflicts over water quality, fisheries, and rangelands. These models represent ecosystems coupled to socioeconomic drivers and are explored with stakeholders to probe the management decision-making processes. Alternative scenarios force participants to be absolutely explicit about their assumptions and biases, thereby improving communication between stakeholders and exposing the ecological consequences of various management policies.

Adaptive management is an approach where management policies themselves are deliberately used as experimental treatments. As information is gained, policies are modified accordingly. This approach helps isolate anthropogenic effects from sources of natural variation and, most importantly, considers the consequences of a human perturbation on the whole ecosystem. In contrast, basic research on various parts of an ecosystem leads to the challenge of assembling all the data into a practical framework. Yet, biotic and abiotic ecosystem components are not additive, they interact. Due to these interactions, the dynamics of an ecosystem cannot be extrapolated from the simple addition of an ecosystem's components. Adaptive management examines the response of the system as a whole rather than a sum of its parts. Furthermore, this approach involves adaptive learning and adaptive institutions that acknowledge uncertainties and can respond to nonlinearities. In sum, structured scenario modeling and policy experimentation are tools that can be used to examine the resilience of social–ecological systems to alternative management policies and conservation strategies.

Ecosystem-Based Management

Recognizing the need to sustain the integrity and resilience of social–ecological systems has led to calls for 'ecosystem-based management', a management approach that considers all ecosystem components, including humans and the physical environment. With the overall goal of sustaining ecosystem structure and function, this management approach:

- focuses on key ecosystem processes and their responses to perturbations;
- integrates ecological, social, and economic goals and recognizes humans as key components of the ecosystem;
- defines management based on ecological boundaries rather than political ones;
- addresses the complexity of natural processes and social systems by identifying and confronting uncertainty;
- uses adaptive management where policies are used as experiments and are modified as information is gained;
- engages multiple stakeholders in a collaborative process to identify problems, understand the mechanisms driving them, and create and test solutions; and
- considers the interactions among ecosystems (terrestrial, freshwater, and marine).

Ecosystem-based management is driven by explicit goals, executed by policies and protocols, and made adaptable by using policies as experiments, monitoring their outcomes and altering them as knowledge is gained.

Traditionally, management practices have focused on maximizing short-term yield and economic gain over long-term sustainability. These practices were driven by inadequate information on ecosystem dynamics, ignorance of the space and timescales on which ecosystem processes operate, and a prevailing public perception that immediate economic and social value outweighed the risk of alternative management. Seeking to overcome these obstacles, ecosystem-based management relies on research at all levels of ecological organization, explicitly recognizes the dynamic character of ecosystems, acknowledge that ecological processes operate over a wide range of temporal and spatial scales and are context dependent, and presupposes that our current knowledge of ecosystem function is provisional and subject to change. Ultimately, ecosystem-based management recognizes the importance of human needs while addressing the reality that the capacity of our world to meet those needs in perpetuity has limits and depends on the functioning of resilient ecosystems.

See also: Ecophysiology; Ecosystem Ecology.

Further Reading

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Ecotoxicological Model of Populations, Ecosystems, and Landscapes

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Introduction

Ecological risk assessment has developed over approximately the last 25 years as a scientific practice for assessing risks of toxic chemicals in the environment. Important issues addressed by ecological risk assessment approaches include chemical contamination at industrial facilities or hazardous waste sites; the potential for chemical contamination of fish and wildlife from production and release of new chemicals; possible effects of toxic chemicals on endangered species; and biomagnification of chemicals in food chains. Ecological risk assessment has become an important tool for government agencies throughout the world in evaluating and regulating toxic chemicals.

Ecological risk assessment often deals with the potential effects of toxic chemicals in the environment by extrapolating toxicity data from laboratory experiments on test species to organisms, populations, and higher-level ecological systems in nature. Traditionally, ecotoxicology has used laboratory toxicity testing with single species to develop response thresholds indicative of no-effects or effects doses (or concentrations). Current methods for ecological risk assessment still focus on the endpoints of survival, growth, and reproduction of individual organisms because those endpoints are easily evaluated in laboratory tests. However, this focus has been questioned by ecotoxicologists who recognize the need to address higher levels of biological organization, such as populations, food webs, and ecosystems.

Need for Ecological Relevance in Risk Assessments

Most toxicity data are developed for biological endpoints at the level of the individual organism, such as mortality, fecundity, or physiological responses. Suborganismal endpoints such as alterations in enzymatic expression are becoming more common with increased research into biomarkers that can measure changes in these pathways. Typical risk assessments ignore effects above the level of the organism, or only qualitatively discuss risks to populations and higher levels of organization. Ecotoxicological models are important tools for addressing these higher levels of organization in an ecological risk assessment.

Ignoring population-level or higher-level effects and focusing only on organism-level endpoints may over- or underestimate risks, leading to possible errors in environmental management decisions. Thus, ecological risk assessments should address ecologically relevant endpoints, such as population growth, population age/size structure, recruitment, biodiversity, ecosystem productivity, and indices of landscape pattern. Ecological relevance