UNIVERSITY OF THE ARCTIC

Module 6
Ecological Principles

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Key Terms and Concepts

Following are the key principles that you will encounter in this module. They are applicable to both terrestrial and aquatic systems.

Biomes, communities, and ecosystems. How do we define systems? Similar climate, topography, and geology interact to generate similar vegetation and fauna in different parts of the Arctic. Within these major biomes, distinct plant communities form the basis of dynamic ecosystems.

Biodiversity. The number of species tends to be low in the Arctic because the ecosystems are young and the environment is severe. This allows important genetic variation within species, and different ecosystems add to biodiversity.

Adaptation and selection. The flora and fauna use many physical, physiological, reproductive, and behavioural strategies to survive.

Population dynamics and control. The numbers of plants and animals vary greatly over time. Climate can have positive or negative effects on numbers, but it acts independent of the population size. Other factors, such as predation, are density dependent.

Productivity, nutrient cycling, and food webs. Plant production through photosynthesis supports food chains and webs. At each step, energy is lost in respiration as well as converted to new biomass. This is consumed by the next trophic level or passes into decomposition. Each step has distinct transfer efficiencies that determine redistribution of C and nutrients.

Succession. How do communities change? As glaciers melt or new surfaces are exposed on ocean floors, primary succession begins with plant growth. Accumulation and recycling of nutrients encourage ecosystem development. Disturbance through storms or freeze-thaw activity promotes secondary succession.

Resource utilization, management, and sustainability. We exploit natural resources directly (e.g., hunting, fishing) or indirectly through land and water management and indirectly through pollution and habitat disruption. The Driver-Pressure-State-Impact-Response model provides a comprehensive general framework for analysis of human impacts.

Learning Objectives

This module you should help you to

1. be aware that, like the physical sciences, ecology has principles or rules that help us to understand the structure and function of ecological systems in the Arctic.
2. recognize these key challenges in Arctic ecology:
   – identifying the hierarchy of scales in space and time
   – recognizing environmental gradients
   – understanding interactions and feedback effects
3. understand how the main ecological principles listed under Key Terms and Concepts apply to the terrestrial and aquatic systems in the Arctic.

Reading Assignments

AMAP (1997), *Arctic Pollution Issues: A State of the Environment Report*.

CAFF (2001), *Arctic Flora and Fauna: Status and Conservation*.

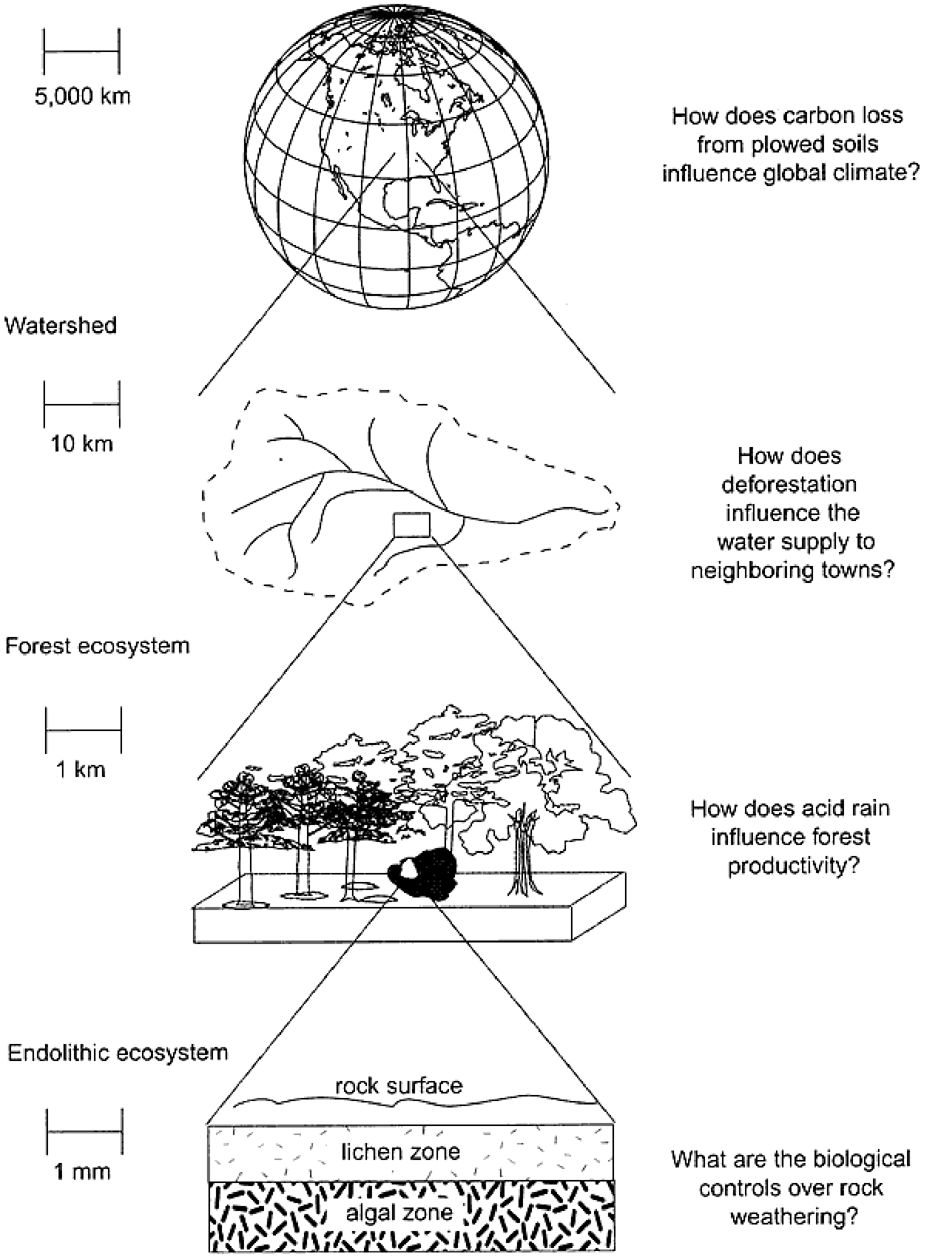
Overview

There are many different ways to consider the tundra, its lakes and rivers, the coast, the seas, and the ocean. You can describe them in your own way, but it is important to remember that there are general scientific rules or principles that apply to ecological systems and that help you to explore them systematically. In this module, a series of basic principles are outlined as a framework for the contents of other modules. Three practical approaches are widely applicable: (1) Always consider how patterns or processes change as they move up or down the *scales in space and time*, from local to regional to global or from minutes to years to decades. (2) Environmental conditions change along *small or large gradients*, from the air, through the vegetation and into the soil, or up mountains. (3) *Interactions and feedback* are a normal part of ecology. Changes in one part of the system affect other parts, often causing a chain of effects, with positive or negative feedback to the original part.

Lecture

Introduction

The northern landscapes and seascapes have been carved by ice, snow, and water acting on the underlying geology. These landscapes and seascapes, within the severe climate, provide the environment within which the flora and fauna of the Arctic survive and thrive. It is also the environment in which people interact with the natural resources. It is the physical environment, plus the biota and people, that combine to generate the distinctive Arctic habitats and ecosystems that range from polar deserts to boreal forests, from streams and lakes to great rivers, and from the rich continental shelf to the productive oceans. These systems and the participating organisms are still evolving because the region is very young in geological and evolutionary time scales. It is only a few thousand years since the last ice age ended; the climate is continually changing and other factors (*globalization*) are increasingly important. We have a good understanding of the ecology of the present Arctic flora and fauna and some knowledge of past changes, but there is increasing concern over future sustainability and an increasing recognition of the complex interactions within the systems. Therefore, we need to use all our knowledge, including application of principles of ecology, to improve our understanding of both current and future changes. The general principles also provide an essential framework to help us organize the wealth of information and ideas concerning Arctic ecology and its future that will be presented in Modules 7 to 13.



Source: Chapin et al. (2002)

Fig. 6.1 A hierarchy of ecosystems ranging in size by 10 orders of magnitude and examples of questions to be addressed. Global (4 x 10^7 m in circumference); Watershed (1 x 10^5 m in length); Forest (1 x 10^3 m in diameter); Endolithic (Arctic internal rock surface) ecosystem (1 x 10^{-3} m in height).

Three basic features should be recognized when considering any species, sites, processes, or systems, particularly in the Arctic. These are hierarchy of scales, environmental gradients, and interactions and feedback effects.

Hierarchy of Scales

Most ecological information is based on studies in a small area—often a few metres or hectares—and over a short time, often with repeated observations over a few years. The challenge is how to apply this information to larger areas and longer times. Upscaling or extrapolating in space is difficult but can be done by stratified sampling or survey, and by use of different tools, for example, remote sensing. Alternatively, ecological studies can begin at large scales and work downwards (see fig. 6.1). Whichever approach is used, it is critical to understand the physical as well as the ecological changes that occur at different spatial scales. The same principle applies when considering time scale: Will the trends observed over a few years show gradual continuation, or are there thresholds that give a large change after a long time? Or are changes cyclical? In order to discover, understand, and predict trends over decades, centuries, or millennia, information is accumulated from a wide variety of sources, for example, historical documents and analyses of sediments and ice cores.

Environmental Gradients

A particularly important feature of Arctic ecology is the influence of environmental gradients. The climatic regime has a strong influence on Arctic species and systems and the microclimate that is so important in ecology is strongly influenced by both small and large changes in the shape or topography of the land or sea. At a large scale, ecological changes are often expressed in relation to latitude or altitude. These are convenient surrogate measures that represent the temperature, moisture, and wind and radiation regimes that actually affect the terrestrial ecology and represent continuous changes in environmental factors; that is, they are gradients. Similarly, the distance from the sea represents an oceanic-continental gradient on land, while the water depth is a key variable in freshwater and marine environments reflecting temperature, salinity, light, and, often, nutrient concentration.

Within the Arctic, micro-scale gradients are of particular importance. For example, although the climate is usually defined in standard meteorological observations, it is not that which is experienced by the vegetation, small animals, and soil organisms on land. The temperature and moisture regimes change dramatically at the leaf surface, within the vegetation, and within the soil profile. The microclimatic regimes also change over short lateral distances as a result of small topographic variations caused by the cover of ice and snow, or by stones and rocks. Thus, ideas of “the length of the season” have to be adjusted for particular groups of organisms, for particular topography, and for different types of soil. Once again, the same principle applies within aquatic systems, in which the physical location related to topography and orientation influences the water temperature, light, and current, with the added influence of ice. However, as always, the physical environment shows a series of gradients, sometimes with a distinct step function. The more extreme the overall climatic conditions, the more the flora and fauna exploit these gradients and steps, often in subtle ways.

Interactions and Feedback Effects

A consistent feature of Arctic ecology is that a change in the species composition or structure of a habitat can result in important secondary, indirect, or cumulative effects and potentially positive or negative feedback effects. This is illustrated by some examples related to climate change. A small decrease in the cover of snow or ice resulting from climate warming, for example, can cause exposure of the darker soil or water surface. This increases absorption of solar radiation and reduces the amount of radiation that is reflected back to the atmosphere (reduced albedo)—this is a positive feedback to climate warming. In contrast, an increase in plant cover and biomass through climate warming can absorb more atmospheric carbon and, hence, reduce the climate warming—this is a negative feedback effect.

Student Activity

1. What determines ecological changes on a large scale on land?
2. What does the gradient of water depth determine?
3. What determines ecological changes on a micro scale?

Biomes, Communities, and Ecosystems

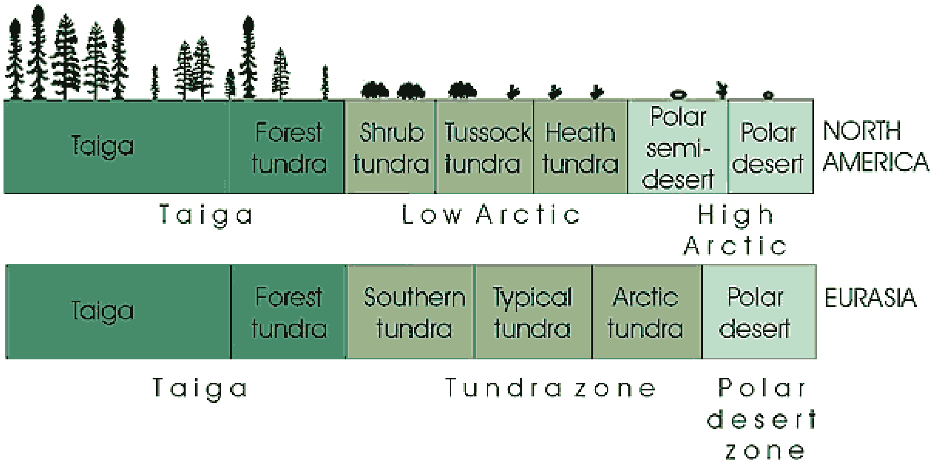
A biome or biogeographic region is a major ecological community that stretches over a vast area and is usually characterized by a dominant vegetation. In the Arctic, the Tundra biome covers many thousands of square kilometres and is related to the general climate and topography that determines the particular conditions for plant growth and the associated animals. Although local conditions result in small-scale patches (m^2) of different types of vegetation, these patches are repeated and provide the pattern characteristic of the landscape or biome.

The general patterns are particularly well described by Bliss and Peterson (1992) as follows:

> In the Low Arctic, riparian zones along rivers and streams are occupied by herbaceous and tall shrub vegetation. Rolling uplands north of the tree line

> generally contain low shrubs of Salix and Betula along with dwarf shrubs of the various heath species that fit within a matrix of upland sedges, including cottongrass tussocks and forbs. Beyond these landscapes are large areas dominated by sedges, dwarf shrub species (mainly heaths), and scattered low shrubs of Salix and Betula. Lowlands that are imperfectly drained and the more expansive coastal plain lowlands are dominated by wetland sedges, grasses, and mosses forming extensive mires. Elevated habitats generally contain low or dwarf shrubs, cushion plants, lichens and graminoids; species adapted to well-drained or intermediately drained soil. These are the major vegetation types within the Low Arctic of Alaska, mainland Canada and much of mainland Siberia.
>
> In the High Arctic of the Canadian Archipelago, the northern portion of the Taimyr Peninsula and the Soviet Archipelagos, the vegetation is shorter and sparser. There are few areas of mire, but much of the landscape is covered with cushion plants, lichens, and mosses or with scattered vascular plants in a substrate of mosses and lichens. These are the polar semi-deserts. Other vast areas—the polar deserts—have almost no plant cover. Here, vascular plants form the major biomass, with lichens and mosses very limited.

The composition of biomes, defined mainly by their plant communities, shows some variation between continents—and, as always, is a matter of considerable debate amongst academic ecologists! However, there is general agreement in the main pattern, as arranged in figure 6.2, and in the "real world" as shown in figures 6.3.a–d.



Source: CAFF (2001)

Fig. 6.2 A comparative classification of North American and Eurasian Arctic vegetation

Source: CAFF (2001, 27), Ecology, in *Arctic Flora and Fauna: Status and Conservation* (Helsinki: Edita), http://www.caff.is/sidur/uploads/OSA_02.PDF

Fig. 6.3.a. Polar desert (Cornwallis Island, Canada)

Source: CAFF (2001, 27), Ecology, in *Arctic Flora and Fauna: Status and Conservation* (Helsinki: Edita), http://www.caff.is/sidur/uploads/OSA_02.PDF

Fig. 6.3.b. Semi-desert (Northeast Greenland)

Source: CAFF (2001, 27), Ecology, in *Arctic Flora and Fauna: Status and Conservation* (Helsinki: Edita), http://www.caff.is/sidur/uploads/OSA_02.PDF

Fig. 6.3.c. Tussock tundra (Northeast Greenland)

Source: CAFF (2001, 27), Ecology, in *Arctic Flora and Fauna: Status and Conservation* (Helsinki: Edita), http://www.caff.is/sidur/uploads/OSA_02.PDF

Fig. 6.3.d. Forest tundra (Finnish Lapland)

Each of the plant communities is associated with distinctive invertebrate and vertebrate faunas and communities of soil organisms. It is the interaction of the combined flora, fauna, and the associated physical environment that generates the processes that constitute the terrestrial ecosystems of the Arctic. These include the many important processes on which we depend, for example, productivity, organic matter decomposition and accumulation, and hydrology. Some of the richest areas occur at the interface between communities and ecosystems, such as the forest and tundra readily identified by the treeline or at the interface between land and water. It is these transition zones, or ecotones, that tend to have high biodiversity through the combination of species from both biomes, but also with species that utilize resources from both communities.

In freshwater and marine systems, physical conditions are arguably more dominant and more stable than on land. Less emphasis is given to vegetation classification and more to the basic physical environment. Thus, we recognize the major river systems, including their vast catchments, lakes, and distinctive ecologies. Community characteristics in both standing and flowing water are determined by water depth and movement, seasonal ice, sediment load, nutrient content, and acidity. The great rivers of Siberia drain vast areas of wetlands and relatively flat tundra, generating high solute and sediment loads, and supporting high biodiversity both in the water and on adjacent land. The ecological boundaries are, like their physical environment, fluid. These rivers form the extensive stuaries and deltas so important for migratory birds and fish feeding on the rich bottom fauna (see fig. 6.4).

Source: CAFF (2001)

Fig. 6.4 The Lena Delta

The coastal and tidal zones contain distinct communities determined by substrate stability—rock, gravel, sand, and mud. Each substrate harbours a distinctive combination of resident and transitory micro-organisms, flora, and fauna. Beyond low tide, and with increasing depth, the extensive continental shelf contains distinctive but interacting bottom (benthic), open-water (pelagic), and surface (planktonic) communities. The open ocean shows communities that are least spatially defined and most dynamic. There is strong vertical zonation of organisms, related to a combination of ice cover, light, salinity, and temperature—key environmental factors that are also distributed latitudinally (see Modules 3 and 8). The Arctic Ocean is distinguished as a "mediterranean sea"—it is a sea surrounded by land, relatively self-contained and with very restricted access to the south.

Throughout the Arctic, whether in terrestrial, freshwater, or marine ecosystems, we can identify and classify communities, habitats, and ecosystems with similar or different characteristics. This is a convenient way to describe and compare systems and to quickly communicate their features. However, although all of these systems can be described as though they are discrete, self-contained units, repeated in different parts of the Arctic, all of them show the same general characteristics:

- recurrent micro-, meso-, and macro-scale patterns in space
- dynamic micro-, meso-, and macro-scale changes in pattern over time
- connection to and interaction with both adjacent and distant systems—they are not isolated units
- distribution along environmental gradients, rather than existing as discrete units
- enhanced ecological activity where there are step changes in the systems, that is, in the ecotones

There are certainly recognizable recurrent patterns, but it is the integrity of the Arctic system that emerges as a dominant feature. The ecological interactions between the ocean and freshwater and terrestrial systems are particularly strong in the Arctic. The ice edge is an ecological interface between sea and land through predation; ocean-feeding birds nest on and fertilize the land; fish migrate between the seas and freshwater systems; insect larvae grow in freshwater areas but emerge to feed, mate, and migrate on and over land. Thus,

- the Arctic is a single, integrated system in terms of its ecological functioning.
- the Arctic interacts ecologically with the rest of the world through the migration of terrestrial, freshwater, and marine fauna.

Student Activity

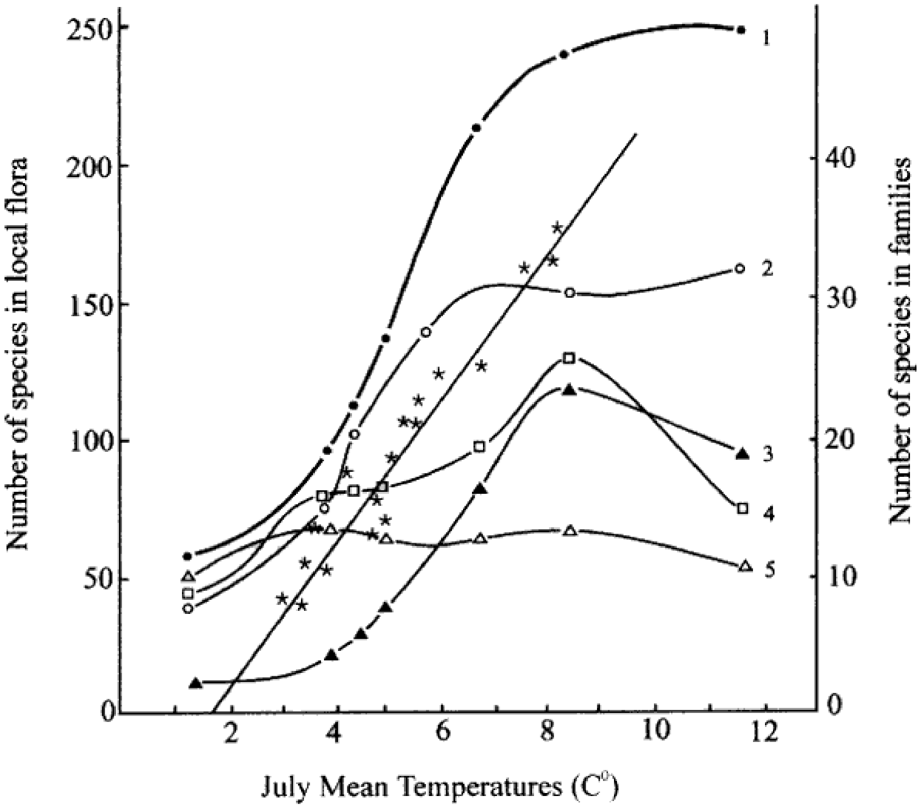
1. Do biome patterns in North America correspond to those in northern Europe and Asia?
2. What constitutes the terrestrial ecosystems of the Arctic?
3. What are common characteristics of the ecosystems of the Arctic?

Biodiversity

The Arctic is widely considered to be a region with low biodiversity—that is, poor in number of species. Yet, three broad types of biodiversity are recognized, representing different taxonomic scales:

- **Genetic diversity.** This is an expression of the range of genotypes within a species (intra-specific variation), but morphological and behavioural variations within a species may also occur, as in phenotypic variation, where the genotype interacts with the environment. In the Arctic, heterogeneity within species may reflect the relatively young state of the regions, as the last major disturbance (i.e., the last ice age was only about 15,000 years BP) combined with geographic separation of widely distributed species, allowing genetic divergence. At a finer scale, species variation can occur within a few metres where micro-topography provides large microclimatic variation, which selects for variants within a population.
- **Species richness.** This is expressed by the number of species in a standard area (e.g., 10,000 km^2) or in a designated habitat. It is the simplest and most widely used expression of *biodiversity*. Species *evenness*, describing the uniformity of the distribution of species, can be calculated from the repetition of individual species in different sampling units.
- **Habitat or ecosystem diversity.** The number of distinct units within a landscape or seascape is a useful but infrequently expressed indication of the regional heterogeneity.

The basic principle is that the number of species decreases with increasing climate severity. This applies when going north or with increasing altitude. The gradient principle applies to most taxonomic groups but, like most principles, there are exceptions (see fig. 6.5). For example, the species diversity of wading birds (Charadriformes) increases in the northern coastlines because of large areas of suitable habitat. Similarly, the diversity of marine species is particularly high just south of Iceland where the Greenland-Scotland Ridge generates a strong thermal gradient separating the distinct faunas of the Arctic and the boreal North Atlantic bioregions.



Source: Matveyeva and Chernov (2000)

Fig. 6.5 The relationship between July mean temperature and the number of vascular plant species in local floras on the Taymyr Peninsula. Note that although there is a general rule for the whole flora (1), some plant taxa, for example saxifrages (5), do not conform. Legend: 1. The whole flora; 2. Poaceae; 3. Cyperaceae; 4. Brassicaceae; 5. Saxifragaceae. The regression line is for vascular plants in the Canadian Arctic Archipelago.

Interest in biodiversity is often focused on areas of high diversity—the "hot spots"—and on species extinctions. On both criteria, the Arctic does not appear to rate highly, but it does contain species that are uniquely adapted to thrive in severe cold conditions (*psychrophiles*). There are very good principles on which to ensure the understanding of diversity and its function in the Arctic flora and fauna:

- Moral and ethical principles focus on our responsibilities as humans to protect all species.
- The evolutionary potential of the Arctic flora and fauna is high, given its relative youth. This argues for conservation of varieties, genotypes, and subpopulations as well as species. It is this variety that is likely to provide the capacity to buffer responses to environmental change.

- Biodiversity influences many ecosystem functions and can provide resistance to change. Arctic biodiversity is relatively low and the function of individual species is generally broad. Thus, loss of individual species can have widespread consequences. This is a key principle, but one that needs more evidence to test it.
- An economic and commercial principle is that the future value of individual species is unknown and we therefore have a responsibility to sustain all species. It is argued that Arctic species may be of particular importance—for example, through their physiological capacity to resist extreme environments (*extremophiles*)—and many species are still virtually unknown, such as those associated with recently discovered deep ocean vents supporting *chemosynthetic* life forms.

Adaptation and Selection

For plants and animals to survive, grow, and reproduce in the severe climates of the North requires that they adopt particular strategies. Some species achieve this by changing their existing characteristics to suit the environmental conditions (*adaptation*); others have particulat characteristics that make them well suited to the Arctic conditions (*selection*). Terrestrial plants that adopt particular strategies to suit particular environmental conditions fall into three categories:

- **Ruderal species (R).** These species have rapid growth rates and a short life span. They produce large numbers of widely dispersed propagules. This gives them the ability to rapidly colonize disturbed ground, especially if it is fertile. They have a short, vigorous life and disperse widely.
- **Competitive species (C).** These species grow more slowly and are long lived. They convert their photosynthate into large biomass and also into defence chemicals that protect against herbivores and parasites. They tend to occur in mature stages of succession and resist competition.
- **Stress-tolerant species (S).** These species tend to grow in habitats subject to extreme climatic or nutrient-poor environments. They can survive these conditions by adopting a “wait and see” strategy, storing reserves and resisting periods of severe environmental conditions, then growing rapidly when the conditions are right. Propagation is often vegetative.

Table 6.1 Traits of plant competitors, ruderals, and stress-tolerators and some of their effects on ecosystem functioning. (Based on Grime 2001)

Traits	Competitors	Ruderals	Stress-tolerators
Life history	Long	Very short	Very long
Life span of leaves and roots	Short	Short	Long
Potential growth rate	Rapid	Very rapid	Slow
Concentration of mineral nutrients in leaves	High	High	Low
Concentration of carbon in leaves	Low	Low	High
Leaf toughness	Low	Low	High
Palatability	High	High	Low
Decomposition rate	Rapid	Very rapid	Slow
Seed or spore production	Delayed	Very rapid	Very delayed
Some Effects on Ecosystems			
Primary production	High	Moderate	Low
Carbon concentration in vegetation and soil	Moderate	Low	High
Retention of mineral nutrients and pollutants	Weak	Very weak	Strong
Resistance to physical damage	Low	Low	High
Recovery from damage	Rapid	Very rapid	Very slow

There are many species that are intermediate between these three strategies (see table 6.1). Clearly, the Arctic climate, with its very short growing season, favours plant species adopting stress-tolerant strategies. Where there is ground disturbance owing to glacial retreat or freeze-thaw cycles, ruderal strategies are generally inappropriate because of low soil fertility. In the Low Arctic and tundra-boreal habitats, species tend to show strategies that are intermediate between stress tolerance and competitive. Although these characteristics are defined for plants, the general principles tend to apply to animals—it is the combination of attributes that enables species to survive, grow, and reproduce in these extreme environments.

Some examples from different species illustrate how these very general strategies are translated into action by individual Arctic species. Survival under extreme cold conditions in mammals is often achieved by **physical** insulation with fur or fat and reduced extremities to minimize heat loss. In plants, the cushion growth form efficiently captures solar radiation. **Physiological** adaptations include winter dormancy in mammals; antifreeze chemical defence in arthropods; maintaining metabolic activity at sub-zero temperatures in bacteria; and resistance to high salinity in ice algae. **Feeding behaviour** is maintained at low temperatures in Arctic char through a specific gene that is absent in other fish. **Reproductive** adaptations include maximum fertility for predatory birds and mammals in years with lemming abundance, as well as vegetative propagation in plants, which reduces the uncertainty of seed dispersal.

Summer abundance of food attracts migratory fish, mammals, and birds to breed in summer and then to overwinter in temperate or tropical regions. Physiological adaptations are needed to store adequate energy reserves for migration and behavioural adaptations to navigate over thousands of miles. Given the scarcity of nutrients in the juvenile Arctic soils, many plants have established intimate relationships (*symbiosis*) with fungi to form fungal roots (*mycorhizas*). The fungus takes up nutrients, particularly phosphorus, from the soil and transfers them to the host plant which, in return, provides carbohydrates to the fungus. Another symbiotic adaptation is the widespread association of nitrogen-fixing algae with higher plants.

In summary, the great diversity and often multiple adaptations to the young and extreme environment is a marked characteristic of Arctic flora and fauna. These combine to generate the predominantly stress-tolerant strategy. In the more temperate boreal forest and relatively rich lowlands where the climate is warmer and soil more mature, competitive strategies and some ruderal strategies are increasingly obvious. It is possible that the stress-tolerant adaptations that have evolved in Arctic flora and fauna in response to past and present climatic variability and extremes may hold the key to the future. Thus, Arctic species are *pre-adapted* to cope with climate change. They have evolved strategies to cope with the stress of extreme and highly variable climates. Current and expected future changes in climate must take account of the existing ecological flexibility and genetic variability that characterize the Arctic flora and fauna.

Student Activity

1. What are the three types of biodiversity?
2. What are the four principles useful for ensuring diversity?
3. What are the three strategies adopted by plants for particular environmental conditions?
4. What are some physiological and behavioural adaptations of mammals?
5. How are some plants interdependent with fungus or algae?

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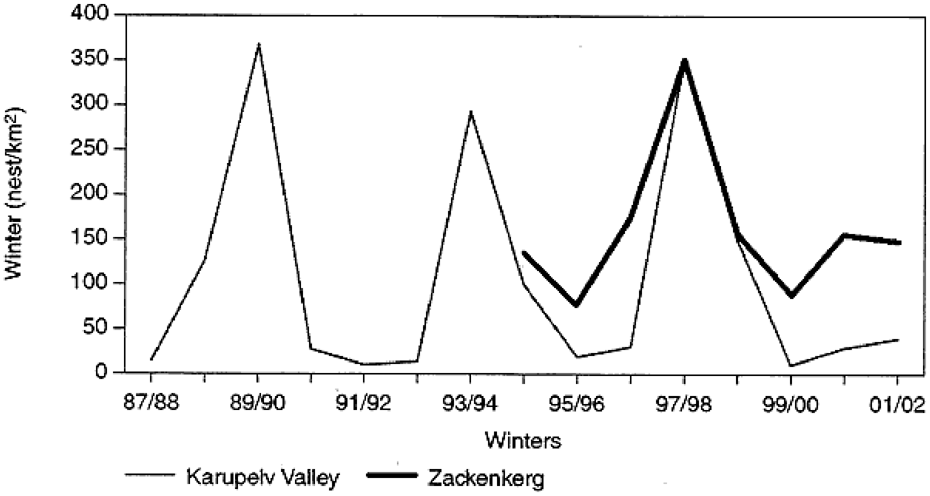
Population Dynamics and Environmental Control

The diversity of species may be low in the Arctic but the size of the populations is often large and highly variable. What are the general principles that govern population dynamics? Basically, two broad types of regulation are recognized: *density dependent* and *density independent*. Density dependence is where mortality is high when populations are high and low when the populations are low, thus, tending to generate cyclical populations often related to food availability or predation. Density independent dynamics occur in populations when external, often environmental, factors cause populations to crash or thrive, independent of the size of the population. Although these principles have been largely developed for fauna, there are significant parallels within the flora.

Both density dependent and density independent dynamics are widespread in the Arctic. Which one applies to a particular species is partly determined by the position in the range of the species concerned. At the northern edge of the range, a species is usually limited by the climate, and it is here that density independent factors dominate. In the middle of the range of the same species, where it is better adapted to the physical environment, there is a much greater degree of density dependence. At the southern edge of its range, a species will usually be limited by competition with species that thrive in milder climates. The following two examples illustrate the type of dynamics and the interaction of factors that are frequent in the North.

Lemmings (species of the genera *Lemus* and *Dicrostonyx*) are a widely distributed and important component of the Arctic fauna: their grazing influences plant composition and distribution, and lemmings are a major food source for many predators. They are well known for the cyclic population patterns (see fig. 6.6) and for the mass migrations of some species that can occur when populations are high. The factors determining lemming cycles are a complex combination of climate, food availability and quality, and predators, often acting concurrently and varying in importance in different areas. But the pattern is reasonably consistent. After a crash in numbers, the population gradually recovers in the absence of low numbers of predators; rising lemming numbers gradually attract predators (foxes, ermine, skuas, snowy owls) that breed but lag behind lemming densities. At peak lemming populations, predation rates increase, vegetation is overgrazed, and high densities cause behavioural changes amongst the lemmings. The combination of circumstances then causes a population crash and migration. The five-to-ten-year cycle then begins again. The predators migrate or, if they are resident, their breeding slows or stops and their populations decline until the lemming population begins to recover. Although this is not a simple predator-prey control of the lemming and predator populations, it does illustrate the general principle of density dependent population regulation. Similar dynamics are apparent in many populations of seabirds synchronized to the population changes in prey fish stocks.



Source: Berg (2003)

Fig. 6.6 Fluctuations of two collared lemming (*Dicrostonyx groenlandicus*) populations in northeast Greenland, separated by 260 km of coastline

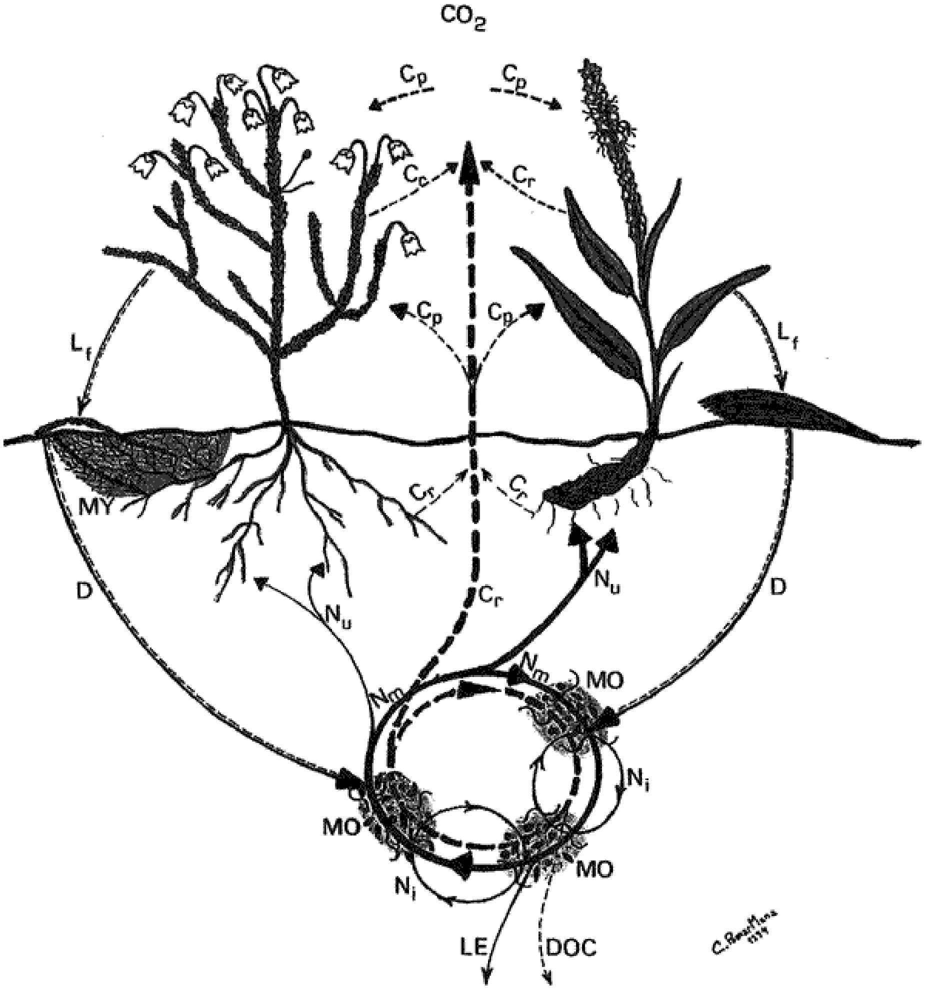
Climate plays an important role in determining population density of many animal species and often has further consequences for other organisms. For example, the autumnal moth (*Epirrita autumnalis*) and winter moth (*Operophtera brumata*) feed on birch and the sawfly *Neodiprion sertifer* on Scots pine, which cover vast areas of northern Fennoscandia. Populations tend to show cycles of about nine years, but a major factor controlling densities is the winter temperature. Temperatures below –35°C kill the eggs that have been laid in the bark of the trees, causing populations to crash. Warmer winters, as expected with climate change, may increase the frequency and intensity of outbreaks of the defoliators that overwinter as eggs. The forest defoliation takes decades to recover and can have feedback effects to climate change by changing the snow cover and thus the albedo (Neuvonen et al. 1999). The forest defoliation takes decades to recover and can have feedback effects to climate change.

As always, the general principles must be applied with care and understanding. In this case, the density dependent and density independent principles have general application, but populations respond to a complex of interacting factors and to different factors at different times and in different places. The principles are useful guidelines to help thinking and analysis—they are not dogmatic rules.

Productivity, Nutrient Cycling, and Food Webs

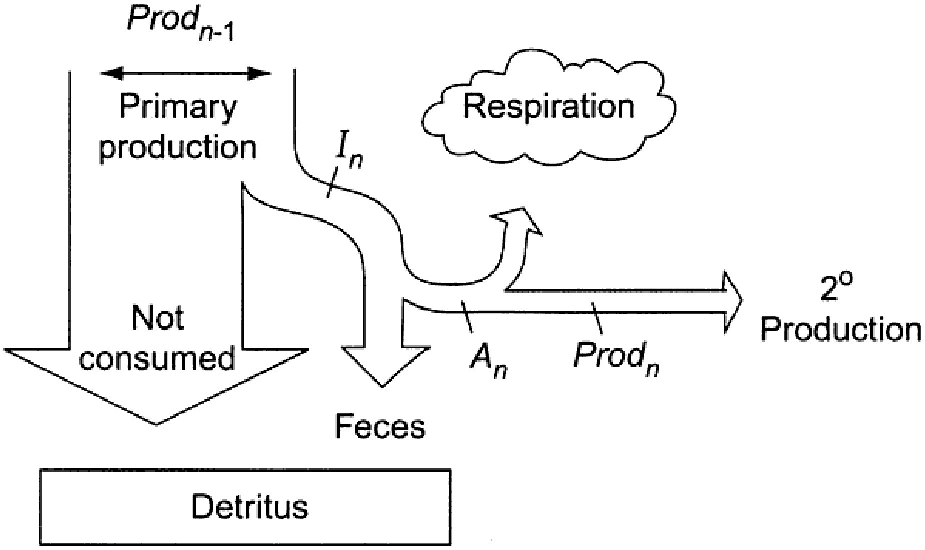
The basis of life in the Arctic is the process of photosynthesis: the fixation of carbon by plants, mainly by vascular plants and mosses in terrestrial systems but also by algae in marine systems. The short summer as well as the low temperatures limit photosynthesis, but plants have various adaptations to enhance photosynthesis and growth (e.g., low temperature optima and cushion or prostrate growth habit to capture and retain heat). The long daylight and low light saturation are partial compensations for the short season, but the highest light intensities occur early in the season when growth is still limited by temperature. A further limitation is that the high density of mitochondria and high protein turnover needed to enhance photosynthesis and respiration demand nitrogen. Thus, the availability of nutrients is a limitation to photosynthesis in terrestrial systems but less so in the coastal or upwelling marine environments.

Photosynthesis is the initial step in determining productivity of the system. The fixed carbon (*gross primary production*) on land may be respired to support metabolic activities, leaving the remainder for conversion to growth (*net primary production*). The next stage is in *secondary production* along one of two routes: consumption by herbivores, or death and decomposition of parts or the whole plant. Much of the plant production ingested by invertebrate or vertebrate herbivores is undigested and deposited as faeces, so it joins the *decomposer subsystem*. The digested and assimilated food is converted into growth or respired to support metabolism. This fractionation of the original photosynthate is repeated when a herbivore is eaten by a carnivore—and so on. The amount of carbon or nutrient passing along each pathway diminishes with each step and also depends on the *conversion efficiency*, which varies with the type of food and with different types of consumer—mammals have a low efficiency of conversion to growth because they use much of the assimilated food to maintain their body temperature (*homeothermic*) compared to invertebrates, which are cold-blooded (*poikilothermic*). Dead plant material, faeces, and dead animals all pass into the decomposer subsystem where they are decomposed by bacteria, fungi, or fauna. Once again, the fractionation process generates new growth, which is consumed by fauna—and so on (see fig. 6.7 and fig. 6.8).



Source: Jonasson et al. (2000)

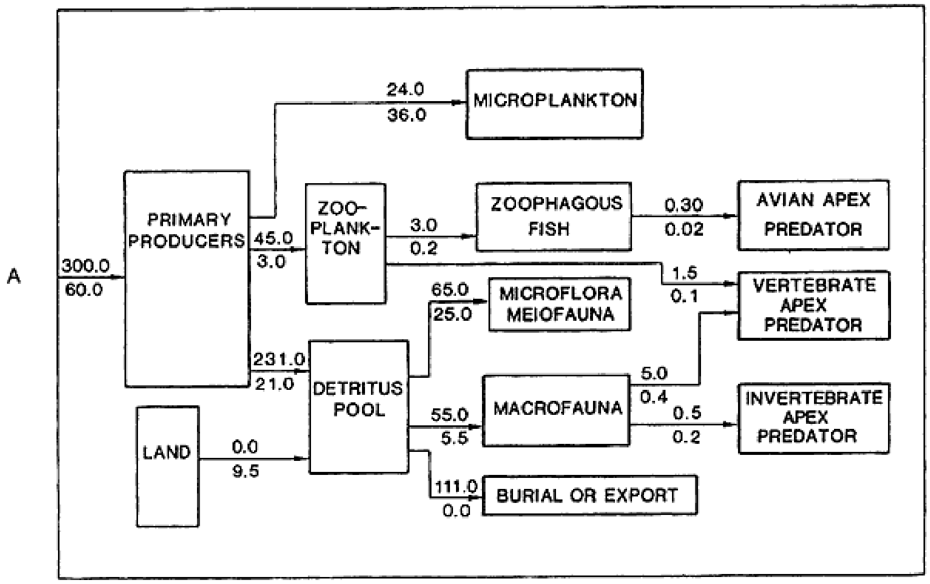
Fig. 6.7 Generalized picture of the exchange of carbon (C; dashed lines) between the atmosphere, plants, and soils and the cycle of nutrients (full lines) between plants and soils. The plants fix atmospheric carbon through photosynthesis (Cp). The C enters the soil through litter fall (Lf). The litter is decomposed (D), and C is returned to the atmosphere through plant and soil microbial (MO) respiration (Cr). Nutrients in litter and soil organic matter are mineralized (Nm) by soil microbes, after which they are available for plant or microbial uptake. Some nutrients are transferred from the soil to the plants through mycorrhizas, while part of the nutrients and dissolved organic carbon (DOC) are leached (LE) out of the soil and disappear from the terrestrial ecosystem.



Source: Chapin et al. (2002)

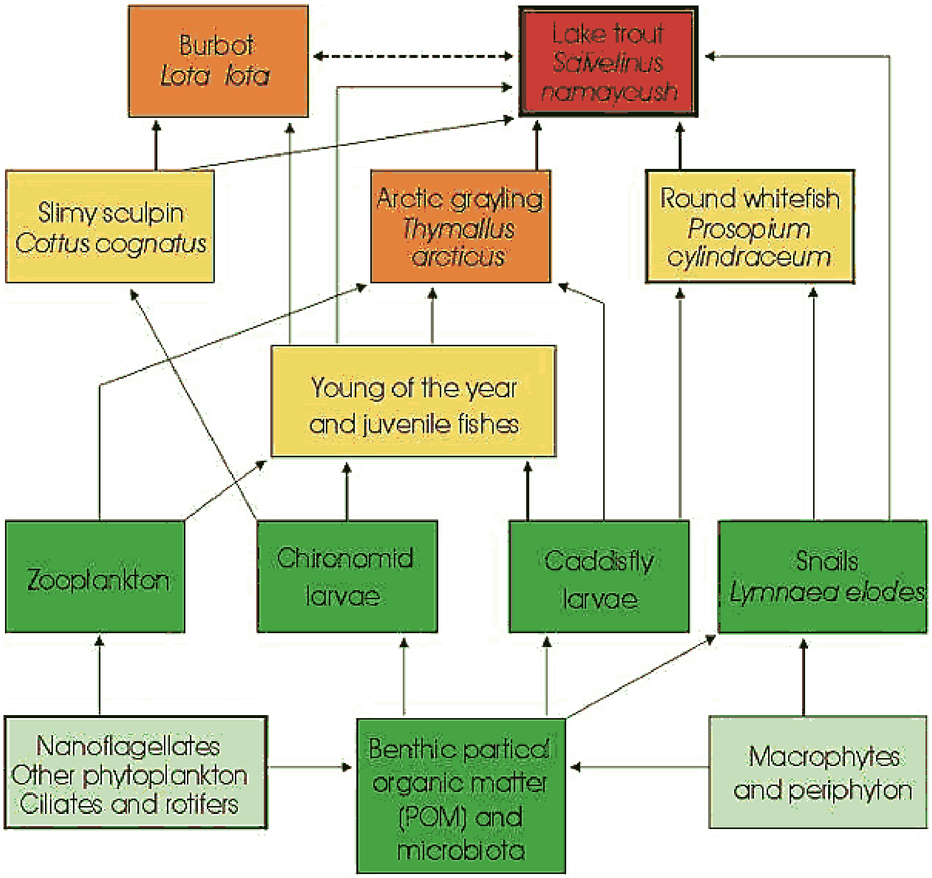
Fig. 6.8 Generalized diagram showing the fractionation of organic matter, carbon, or energy as it moves through the food chain. A small part of primary production is ingested by herbivores (I_n), but most is not consumed and passes into the litter and soil as detritus. Much of the ingested plant material is undigested and is deposited as faeces. The assimilated material (A_n) is used mainly for metabolism and is returned to the atmosphere in respiration, leaving a small fraction that is converted into growth, that is, secondary production.

Net primary production (photosynthesis minus respiration) in the Arctic decreases with latitude but broadly ranges between 50 and 500 g (dry weight) m^{-2} $year^{-1}$ in terrestrial habitats, with higher rates in very sheltered warm areas. Similar rates are found in freshwater lakes and in the seas, with some exceptionally high rates up to 600g m^{-2} $year^{-1}$ on the western Bering and Chukchi shelves. But there is a dramatic difference in that terrestrial production is through long-lived higher plants with large biomass contrasting with the aquatic systems where primary production is generated by small, short-lived algae and cyanobacteria with a low total biomass in the plankton. It is generally considered that the relatively large plant biomass on land tends to directly sustain large vertebrate herbivores, and hence large carnivores (e.g., reindeer or caribou and muskox, plus polar bears, wolves, and foxes in the High Arctic). In contrast, the microscopic planktonic algae of marine and freshwater systems tends to support large numbers of small invertebrate herbivores (e.g., protozoa, crustacea, and fish larvae), which then support larger organisms in the food chain (see fig. 6.9 and fig. 6.10). The contrast is between the terrestrial system with large primary biomass with slow turnover versus the aquatic system with small primary biomass with rapid turnover. This is a broad generalization based mainly on the visible herbivores and carnivores. But, once again, there are some contradictions. The decomposition subsystem, both on land in the soil and in the bottom sediments of aquatic systems, tend to build up the food chains through a sequence of increasing size and longevity from micro-organisms through larger invertebrates to vertebrates.



Source: Sakshaug and Walsh (2000)

Fig. 6.9 Generalized quantities of carbon flowing through the food web of the coastal shelf region of the Bering Sea. Upper figures are for the Siberian side; lower ones for the Alaskan side. For simplification, not all transfers are shown and the principles illustrated in figure 6.8 apply.



Source: CAFF (2001)

Fig. 6.10 The food web of Toolik Lake in northern Alaska, showing the keystone position of lake trout. The diagram omits the microbial food web and the important input of carbon from external sources such as terrestrial vegetation to the lake.

The processes involved at each step in the food chains result in some material, whether plant, microbial, or animal being recycled through the decomposer subsystem. As that material is decomposed, the nutrients are released back into the environment and are available for plant uptake. This nutrient recycling is important in the Arctic, where many land habitats in particular are poor in available minerals because of the young state of the systems—a capital of nutrients has not yet been built. The cold soils of the Arctic, especially in permafrost areas also tend to retard the rate of decomposition and nutrient cycling. Further, one of the adaptations of plants to resist herbivory is to produce defence compounds that are distasteful or even toxic to herbivores. These defence compounds also tend to inhibit decomposers, slowing the process of decomposition, reducing availability back to the plants and thus enhancing accumulation of soil organic matter. Fundamentally, the rate of decomposition of organic residues is determined by three types of factors, known as the decomposition triangle:

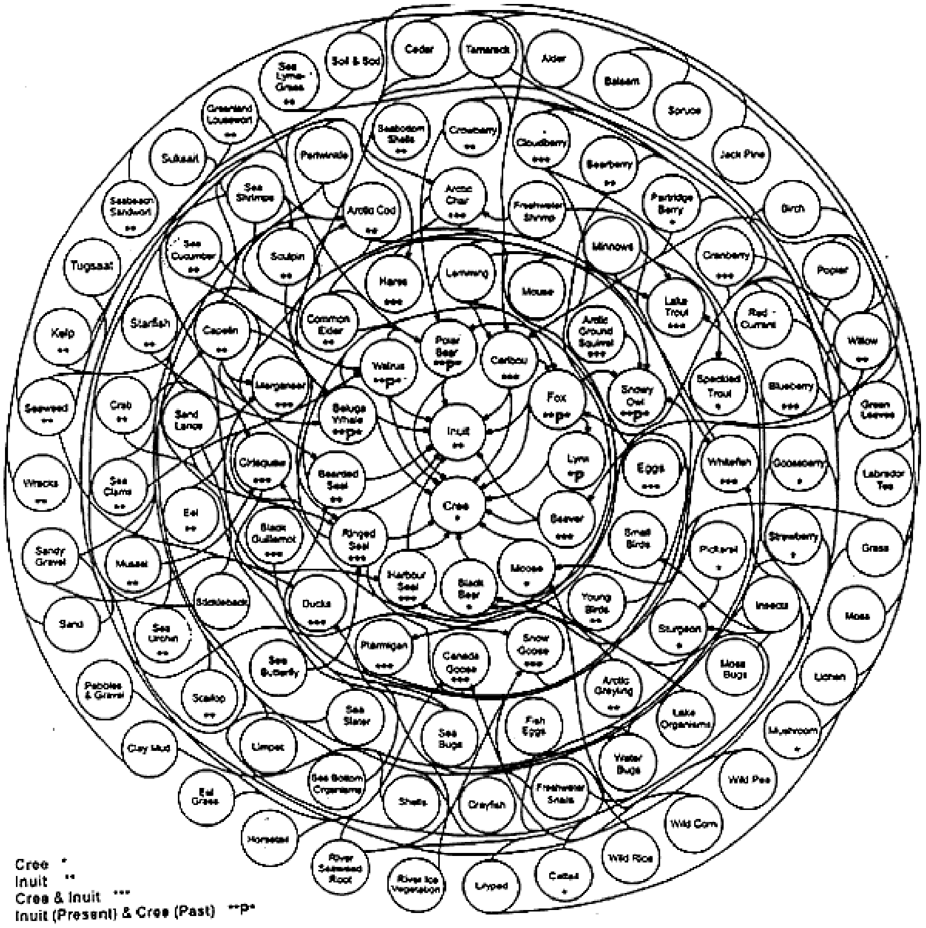
O, the decomposer *o*rganisms present. In the case of the Arctic, earthworms that dominate decomposition in temperate regions are virtually absent.

P, the *p*hysico-chemical environment to which the organisms respond. In the Arctic, P is a combination of low soil temperatures and the moisture content, with decomposition inhibited by low moisture in polar deserts and semi-deserts, but by anaerobic conditions caused by waterlogging.

Q, the *q*uality of the organic matter. The quality of litter in the Arctic is poor because of the high content of ligno-cellulose in long-lived woody plants, plus mosses that are resistant to decomposition and the influence of resistant defence compounds (often polyphenols) generated by the plants to inhibit herbivores.

The relative influence of this triangle of factors varies between different habitats; but the overall effect is that although primary production is low in the Arctic, the rate of decomposition is particularly low and there are large accumulations of soil organic matter, including extensive areas of peat where there is waterlogging. It has been estimated that the Arctic contains about 20% of the world's soil carbon, and this has been accumulating since the last ice age. One critical question is, will the process of accumulation continue, or will the changing climate result in a change in the balance between production and decomposition, causing the tundra to become a source rather than a sink of atmospheric carbon.

A hierarchy of organisms form the food webs that characterize the terrestrial, freshwater, and marine environments, linking both the primary production and decomposition subsystems. Theoretical analysis indicates that stability of food webs is influenced by both the diversity of species at each level (there are replacement species if one is lost) and the number of levels or links in the chain (long chains tend to be unstable). (See Moore and de Ruiter 2000 or Moore and Hunt 1988). This indicates that northern food webs may be unstable because of the relatively few species involved. This may be compensated by the ability of some species to feed on a wide range of both plants and animals—they are omnivores and generalist rather than specialist feeders. The complexity of the food webs and the exceptional linkages between land and water is beautifully illustrated by the Hudson Bay food web, which describes the network of feeding relationships that determine the food of Inuit and Cree peoples (see fig. 6.11).



Source: McDonald, Arragutainaq, and Novalinga (1997)

Fig. 6.11 Hudson Bay food web, drawn from information on seasonal foods in Cree and Inuit diets and the foods eaten by the animals in these diets

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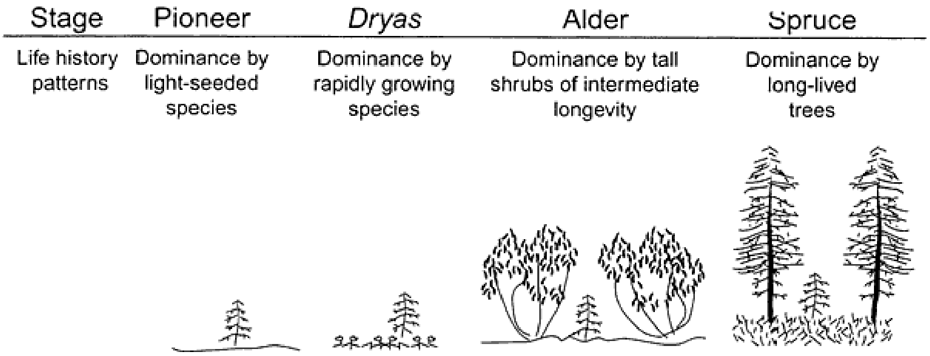
Student Activity

1. What types of regulators cause crashes in the population of lemmings and foxes?
2. What regulates the population of moths in the North?
3. What affects the net primary production in aquatic systems and terrestrial systems?
4. What are the three factors in the decomposition triangle?
5. What determines the stability of a food web?

Succession

As the ice sheets and glaciers retreat during periods of warming, fresh ground is exposed and is slowly colonized by cyanobacteria, algae, lichens, mosses, or higher plants. The type and rate of initial colonization depends on the physical and chemical properties of the exposed substrate. Species from the early stages in succession are often short-lived and have the capacity to fix nitrogen. They are gradually replaced by larger, slower-growing and longer-lived shrubs and trees (*Alnus, Betula*, *Picea*, or *Pinus*). Soil organic matter accumulates, and gradually the ecosystem is established, tending to move through a succession of ruderal (R) to competitive (C) species. The general changes during succession are reasonably predictable, with similar sequences of organisms occurring throughout the region. Over decades and centuries, changes in species composition slow down; they are increasingly determined by biological rather than physical factors, and the system becomes more stable, approximating to a stable climax. The early studies in Glacier Bay, Alaska (see fig. 6.12), follow this classical view of *primary succession*, where a new site is exposed by glacial retreat, or by a buildup of sandbanks in rivers, or by raised beaches through isostatic rebound or ice sour in coastal waters, exposing new substrates.



Source: Chapin et al. (2002)

Fig. 6.12 Glacier Bay succession. The main features of plant life history patterns following glacial retreat at Glacier Bay, Alaska.

Where a site that is already vegetated is severely disturbed by erosion, burning, or defoliation, much of the accumulated organic matter can remain, providing an initial capital of nutrients and a bank of seed in the soil. These conditions initiate *secondary succession*, which tends to be more rapid than the primary succession. A feature of the Arctic is the role of the environment in causing secondary succession through disturbance by freeze-thaw cycles (*cryoturbation*), which exposes fresh substrate, for example, through frost boils or downslope movement of material (*solifluction*). Tundra lake systems are also regenerated through the thaw-lake cycle, where accumulation of organic matter raises the lake bed above the water level, but later the changing depth of permafrost causes depression and slumping to regenerate the lake.

The type of primary and secondary succession differs between the Low and High Arctic, influenced by the severity of the climate. In the Low Arctic, the pattern over time is for replacement of species—*directional succession*—determined mainly by biological interactions. In the High Arctic, where conditions are much more severe, the succession is much more restricted and is determined mainly by the ability of species to colonize and survive. These environments particularly favour stress-tolerant (S) species: vegetation is patchy and replacement of species is not apparent in many places; the species present are determined by chance rather than by biological interactions and directional replacement.

Although succession has been very largely defined in botanical terms, the fauna, particularly soil microflora and invertebrates, follow similar patterns for similar reasons. This is succession on a micro scale, but it is critical in determining the more obvious plant succession. In the early stages of plant succession, where nitrogen and other nutrients are not readily available, cyanobacteria and other micro-organisms are critical in fixing atmospheric nitrogen or mineralizing phosphorus from parent material. Symbiotic relationships between plants and N-fixing bacteria, or between plants and mycorrhizal fungi, are critical in early successional stages. Similarly, bacteria and fungi colonize plant debris, followed by a succession of invertebrates, mainly microarthropods and insect larvae, which decompose the litter, generate humus, and recycle nutrients.

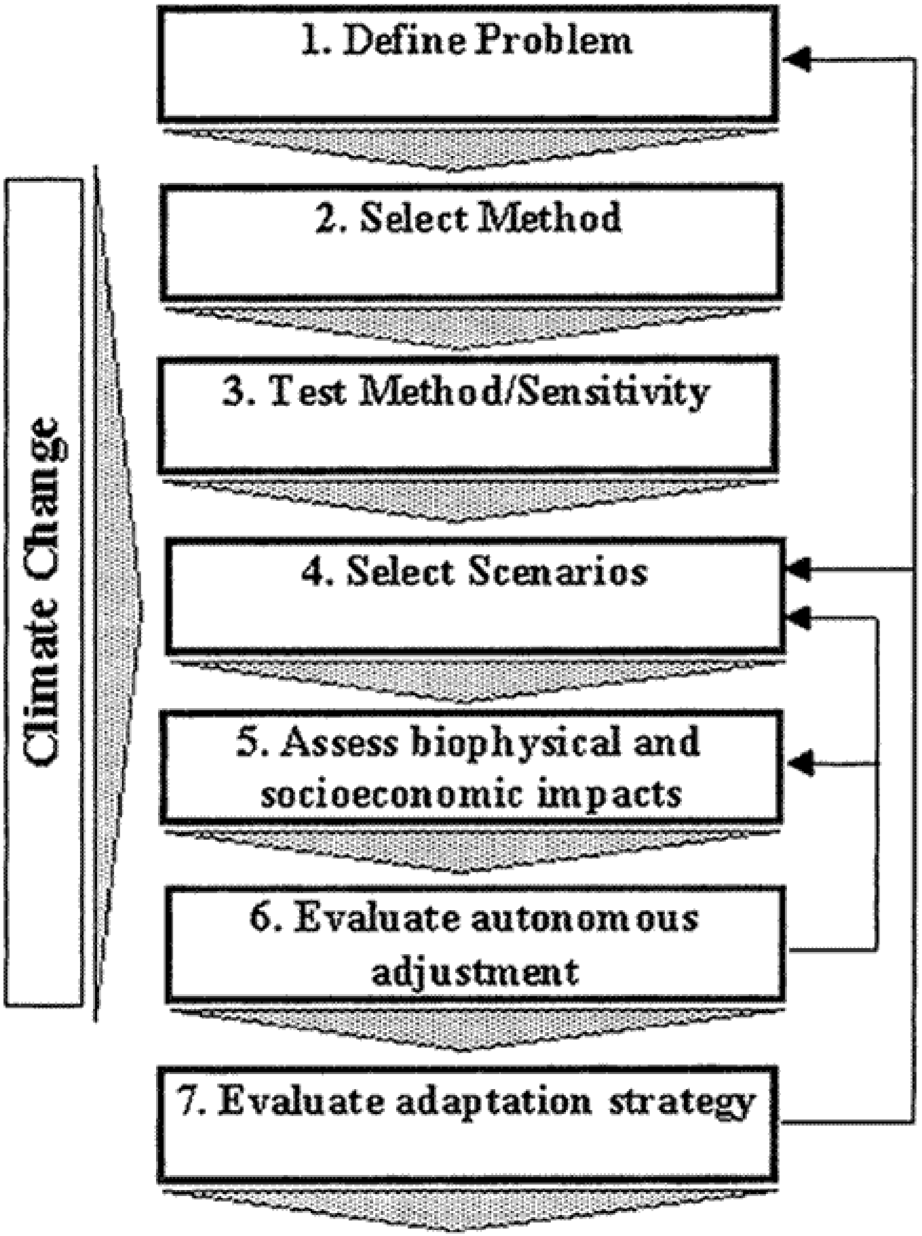
Resource Utilization, Management, and Sustainability

Arctic environments, species, and ecosystems are, and always have been, in a state of flux. This is one of the most dynamic regions of the world. Change is normal. Daily, seasonal, annual, and millenial variations in climate form the basis of change, but many other factors are superimposed on climate dynamics. Changes in one factor or in one area effect other factors or areas. During the twentieth century, the human influence has increased dramatically, although the effects in the Arctic have been less than in many other regions of the world. What are the general principles that can help us to understand current impacts of human activity and can assist us in planning for the future?

Our understanding of the general principles that govern the spatial and temporal dynamics of biodiversity, of populations, of productivity and food webs, and of primary and secondary succession are all reflected in our understanding of human participation in Arctic ecology. We are direct and indirect participants in Arctic ecology. It is here that human participation in the ecology of other species is most intimate, especially amongst the indigenous peoples of the North. Participation can be grouped into four general categories, reflecting the mode of action:

- **Direct influence in the cropping of natural resources**—whether hunting for caribou, eider duck, cod, seals, or whales, or in the cropping of berries, wood, or bark—occurs throughout the Arctic. Cropping by humans functions in a manner similar to other predators, with a degree of density dependent regulation of the amount of crop taken. Human cropping tended to respond to availability, taking large crops when populations were high and vice versa, but technology and commercial interests have tended to result in excess harvesting, depressing populations excessively, in some cases nearing extinction. Excessive cropping of particular species usually has negative effects on the rest of the food web.
- **Direct influence through habitat management** is practised mainly in the Low Arctic; for example, the herding of reindeer is particularly well established and requires a detailed understanding of land management, animal husbandry, and animal behaviour. Less clearly understood are the effects of the damming of streams, rivers, and lakes as a means of managing fish stocks, especially when this action is associated with the introduction of new varieties or species. Aquaculture is not, as yet, practised within the Arctic, but that may change as alternative fish stocks are investigated, or when environmental conditions change.
- **The indirect effects of habitat change** through grazing management, wood harvest, and particularly urban infrastructure are recent developments. They tend to result in fragmentation, with increased patchiness and less connectivity between natural habitats, thus influencing species movement between habitats and causing isolation of populations. Patch dynamics is a particular branch of ecology that has developed and applies the principles of *island biogeography*. For many species that breed in the Arctic, critical habitat change may occur when they are overwintering at lower latitudes outside the Arctic.
- **Indirect influence of contaminants**. Chemical contaminants result from local intensive industry and waste disposal, as well as long-distance transport from within or outside the circumpolar region (AMAP 1997). The contaminants are mainly distributed by atmospheric or ocean circulation in various forms. The impact of local industrial contamination can be very obvious in the loss of vegetation and fauna, but the mechanisms of long-distance transport of contaminants and their effects tend to be much more subtle. For example, *bioaccumulation* is now recognized as a mechanism by which persistent organic pollutants (POPs) are absorbed in fatty tissues of marine organisms; these increase in concentration up through marine food chains and into human populations that selectively consume fatty tissues. Unacceptably high concentrations are now found in young children of some indigenous peoples.

The human influences are clearly varied and can influence many different aspects of Arctic ecology. It is in Environmental Impact Assessment (EIA) that the ecological principles must be applied. A seven-step process, developed in relation to climate change, has general application in EIA (see fig. 6.13). A key step is in the selection of scenarios. A scenario is a coherent, internally consistent and plausible description of a possible future state of the world or of a smaller defined biogeographical unit. The scenarios must have scientific credibility with a basis in theory as well as data. A critical and challenging feature of the scenario is that it must provide a description of the likely future state of the system. This predictive aspect, with the current state as a baseline, often takes the form of the expected outcome from a number of different actions, thus providing decision makers with information on which to assess options.



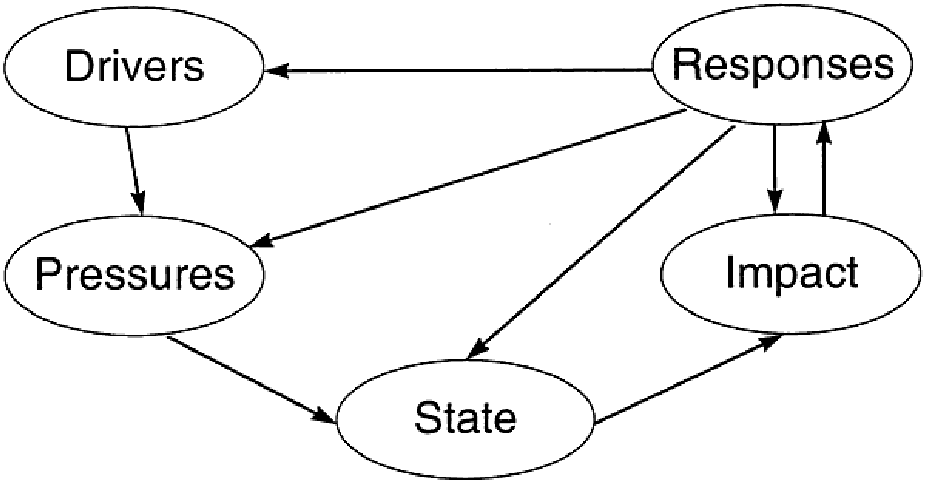
Source: Lange (2000)

Fig. 6.13 Basic steps in Environmental Impact Assessment

Probably the best-known scenarios are those on global climate change in response to carbon emissions developed by the International Panel on Climate Change (IPCC). These have predicted warmer and wetter winter climates in the North and enhanced frequency and intensity of extreme climatic events. Recent climatic evidence from the Arctic is consistent with the scenario predictions. Specific climate change scenarios for the Arctic are being used to assess the likely impacts on terrestrial, freshwater, and marine ecosystems in the Arctic Climate Impact Assessment (ACIA). Policy decisions are the natural outcome of such assessments, and the Montreal Protocol on Substances that Deplete the Ozone Layer (Montreal Protocol), limiting emission of chlorofluorocarbons (CFCs), is an excellent example of the combination of scientific observations and the application of scientific principles to policy formation. In this case, the main observations were on the reduction of the Antarctic and Arctic stratospheric ozone layer, combined with some evidence on increased ultraviolet radiation (UV-B) and associated increases in skin cancer and eye damage. The combination of these discrete observations, linked with good theoretical evidence, provided a credible scenario on which emissions of CFCs were ended, and now a gradual decline in UV is evident.

The climate impact assessment and the actions taken to control CFCs are good examples of a general framework for analysis of environmental impacts—the **DPSIR model** (see fig. 6.14). Taking UV-B as an example,

- **Driver** of change. The basic driver is increased demand for efficient refrigeration systems.
- **Pressure** on the environment. The immediate causal agent is chlorofluorocarbons (CFCs).
- **State** of the environment. Change in the state variable (stratospheric ozone and UV-B radiation).
- **Impact**. Enhanced skin cancer, suppression of immune system, and damage to eyes in humans.
- **Response**. International agreement to end CFC production and find alternatives (Montreal Protocol).



Source: Smeets and Weterings (1999)

Fig. 6.14 The DPSIR model: a framework for consideration and reporting on environmental issues; a systems-analysis approach.

Although the impact on human health was the most influential evidence in establishing the Montreal Protocol, enhanced UV-B also has significant impacts on other organisms: plants, animals, and micro-organisms. The causal links between CFCs, ozone, UV-B, and environmental health also illustrates the need to consider the combination of economic, social, and environmental issues. This is the central principle of *sustainable development*—"development that meets the needs of the present without compromising the ability of future generations to meet their own needs" (Brundtland Commission 1987). The main elements of the concept were outlined in 1972 at the United Nations Conference on the Environment in Sweden and were established in 1987 at the World Commission on the Environment and Development. The Declaration on the Establishment of the Arctic Council in 1996 highlights the "commitment to sustainable development in the Arctic region."

There is no single goal of sustainable development or variable to measure it. "Rather, it is an analytic framework intended to provide structure and coherence to thinking about human/environment relations" (Young 1998). Thus, the scientific principles outlined in this module represent some of the main elements that contribute ecological structure and coherence to the analytical framework of sustainable development. They also provide a theoretical framework for Modules 7 to 14.

Summary

Ecological principles? They may seem a bit academic and theoretical, but ecology is much more than simply identifying and listing plants, knowing where birds nest, or putting up fences to protect some rare species. It is about understanding how the landscape—or the lake, or coast, or ocean—has changed, is changing, and is likely to change. It is about how different species interact with each other and with the environment; how it all fits together in time and space; what the system's important dynamics and controls are.

This module describes some of the main ecological principles, or guidelines, to help you to look at animals, plants, habitats, landscapes, or regions, and think about the dynamics that shape them and their futures. The principles are the basic tools—or concepts—with which to analyze and describe the system and understand the factors that have shaped it. The term "biodiversity" means much more than simply the number of species that you can count. The physical and physiological characteristics of individual species can tell you much about how they survive—or do not survive—in particular environments. It tells how individual populations vary with time, what controls them, and how they are linked in food webs with varying productivity. Communities change with time and follow repeatable successions. We may try to manage these communities or populations. Our understanding of the ecological principles, will, to a large extent, determine our success.

These principles are actually models. They are simplifications of the complex "real world." They are not hard and fast rules. They can guide your thinking, but you have to apply them sensibly and scientifically.

Student Activity

1. What is succession?
2. Is there an example of primary succession in your area?
3. Where does secondary succession occur nearest you?
4. What happens to succession in the High Arctic?
5. What direct and indirect influences do humans have on the environment in your area?
6. What are the seven steps in the Environmental Impact Assessment (EIA) process?
7. What does DPSIR stand for?
8. What might sustainable development mean for your community?

Study Questions

1. How many ecosystems can you identify in your area, and what are their distinguishing characteristics? Are there any important environmental gradients, and how do they affect the ecosystems?

2. How have these ecosystems changed in living memory, and what has caused these changes? Can you identify key sources of information about changes?

3. Draw a model to show the food webs of one of the ecosystems in your area. Which are the main pathways of carbon transfer? Can you identify any transfers into or out of the ecosystems?

4. For a common plant or animal in your area, can you identify the stages in its life history and the factors that influence its survival? What are its main strategies for survival?

5. What do you think will be the factors causing ecological change in your area in the next 50 years? What will be their main effects on the ecology, and what actions should be taken? See if you can represent these changes as a DPSIR model.

Glossary of Terms

albedo	the proportion of light reflected by a surface (e.g., snow, ice, water, vegetation) back to the atmosphere.
biomass	**1** the total quantity or weight of organisms in a given area or of a given species. **2** non-fossilized organic matter (esp. regarded as fuel).
biome	**1** a large, naturally occurring community of flora and fauna adapted to the particular conditions in which they occur, e.g. tundra. **2** the geographical region containing such a community.
biota	the animal and plant life of a region.
catchment	**1** the act or process of collecting water. **2** a place where water is collected; a reservoir.
Charadriformes	wading birds.
cryoturbation	environmental disturbance caused by freeze-thaw cycles, which exposes fresh substrate.
defoliation	the act of removing leaves from plants.
delta	a triangular tract of deposited earth, alluvium, etc., at

	the mouth of a river, formed by its diverging outlets.
extrapolate in space	predict on the basis of known facts or observed events; generalize from a small-scale space sampling to a larger scale.
fauna	the animal life of a particular region, geological period, or environment.
Fennoscandia	the land mass in NW Europe comprising Scandinavia, Finland, and the adjacent area of NE Russia.
flora	the plants of a particular region, geological period, or environment.
forb	any herbaceous plant other than a grass.
gradient	the rate of rise or fall of temperature, pressure, etc., in passing from one region to another.
mire	**1** a stretch of swampy or boggy ground. **2** wet or soft mud; muck.
psychrophiles	species able to thrive in severe cold conditions.
remote sensing	the scanning of the Earth by satellite or high-flying aircraft in order to obtain information about it.
riparian zones	areas along rivers and streams.
solifluction	movement of substrate material upward (e.g., by frost expansion) or downslope.
succession	the process by which a plant or animal community successively gives way to another until a stable climax community is reached.
surrogate	a substitute.
upscaling	generalizing from a small-scale space or population sampling to a larger scale.
vascular plant	a plant with conducting tissue.

One of the best dictionaries for this area of study is the *Oxford Concise Dictionary of Ecology*, edited by Michael Allaby (Oxford University Press, 1996).

There is also a good short glossary at the back of Chapin, Matson, and Mooney (2002), *Principles of Terrestrial Ecosystem Ecology* (New York: Springer-Verlag), 375–392.

References

Allaby, Michael. 1996. *Oxford Concise Dictionary of Ecology*. Oxford University Press.

Arctic Council. 1996. *Declaration on the Establishment of the Arctic Council* [online]. http://www.arctic-council.org/establ.asp. Ottawa: Arctic Council.

Arctic Monitoring and Assessment Programme (AMAP). 1997. *Arctic Pollution Issues: A State of the Environment Report* [online]. http://maps.grida.no/uarctic/. Oslo: Norway.

Barber, K., ed. 2001. *The Canadian Oxford Dictionary*. Don Mills, ON: Oxford University Press.

Berg, T. B. G. 2003. The Collared Lemming (Dicrostonyx groenlandicus) in Greenland: Population Dynamics and Habitat Selection in Relation to Food Quality. PhD diss., Natural Environment Research Institute, Roskilde, Denmark.

Bliss, L. C., and K. M. Peterson. 1992. Plant Succession, Competition, and the Physiological Constraints of Species in the Arctic. In *Arctic Ecosystems in a Changing Climate*, edited by F. S. Chapin, R. L. Jefferies, J. F. Reynolds, G. R. Shaver, and J. Svoboda, 111–136. San Diego: Academic Press.

Brundtland Commission. 1987. *Brundtland Report: Our Common Future*. World Commission on Environment and Development. Oxford: Oxford University Press.

Chapin, F. Stuart, Pamela A. Matson, and Harold A. Mooney. 2002. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag.

Conservation of Arctic Flora and Fauna (CAFF). 2001. *Arctic Flora and Fauna: Status and Conservation* [online]. http://www.caff.is/sidur/sidur.asp?id=18&menu=docs. Akuryeri, Iceland.

Grime, J. P. 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties*. Second edition. Chichester: Wiley.

Jonasson, S., T. V. Callaghan, G. R. Shaver, and L. A. Nielsen. 2000. Arctic Terretrial Ecosystems and Ecosystem Function. In *The Arctic: Environment, People, Policy*, edited by M. Nuttall and T. V. Callaghan, 275–313. Australia: Harwood Academic Publishers.

Lange, M. A. 2000. Integrated Global Impact Assessment. In *The Arctic: Environment, People, Policy*, edited by M. Nuttall and T. V. Callaghan, 517–553. Australia: Harwood Academic Publishers.

Matveyeva, N., and Y. Chernov. 2000. Biodiversity of Terrestrial Ecosystems. In *The Arctic: Environment, People, Policy*, edited by M. Nuttall and T. V. Callaghan, 233–273. Australia: Harwood Academic Publishers.

McDonald, M., L. Arragutainaq, and Z. Novalinga, eds. 1997. *Voices from the Bay: Traditional Ecological Knowledge of Inuit and Cree in the Hudson Bay Bioregion*. Ottawa: Canadian Arctic Resources Committee.

Moore, J. C., and H. W. Hunt. 1988. Resource Compartmentalisation and the Stability of Real Ecosystems. *Nature* 333:261–263.

Moore, J. C., and P. C. de Ruiter. 2000. Invertebrates in Detrital Food Webs along Gradients of Productivity. In *Invertebrates as Webmasters in Ecosystems*, edited by D. C.Coleman and P. F.Hendrix, 161–183. Oxford: CABI.

Neuvonen, S., P. Niemela, and T. Virtanen. 1999. Climate Change and Insect Outbreaks in Boreal Forests: The Role of Winter Temperatures. In *Animal Responses to Global Change in the North*, edited by A. Hofgaard, J. P. Ball, K. Danell, and T. V. Callaghan. Ecological Bulletins 47:63–67.

Sakshaug, E., and J. Walsh. 2000. Marine Biology: Biomass, Productivity Distributions and Their Variability in the Barents and Bering Seas. In *The Arctic: Environment, People, Policy*, edited by M. Nuttall and T. V. Callaghan, 161–196. Australia: Harwood Academic Publishers.

Smeets, E., and R. Weterings. 1999. *Environmental Indicators: Typology and Overview*. Technical Report 25. Copenhagen: European Environment Agency.

Vincent, W. F., and J. E. Hobbie. 2000. Ecology of Arctic Lakes and Rivers. In *The Arctic: Environment, People, Policy*, edited by M. Nuttall and T. V. Callaghan, 197–232. Australia: Harwood Academic Publishers.

Young, Oran R. 1998. Emerging Priorities for Sustainable Development in the Circumpolar North. *The Northern Review* 18:38–46. Special issue. Proceedings of the Circumpolar Conference, “Sustainable Development in the Arctic: Lessons Learned and the Way Ahead,” held May 12–14, 1998, Whitehorse, YT, Canada. [Also online]. http://www.dartmouth.edu/~arctic/articles/whitehorse.html.