Glossary

Abaptation The process by which the present match between organisms and their environment, and the constraints on this match, have been determined by evolutionary forces acting on ancestors. The prefix 'ab-' emphasizes that the heritable characteristics of an organism are consequences of the past and *not* anticipation of the present or future.

Abiotic Nonliving; usually applied to the physical and chemical aspects of an organism's environment.

Abundance The number of organisms in a population, combining 'intensity' (density within inhabited areas) and 'prevalence' (number and size of inhabited areas).

Acclimation The habituation of an organism's physiological response to environmental conditions (usually applied to laboratory environments).

Acclimatization The habituation of an organism's physiological response to environmental conditions (usually applied to natural environments).

'Acid rain' Rain with a very low pH (often below 4.0) resulting from emissions to the atmosphere of oxides of sulfur and nitrogen.

Adaptation A confusing word used to mean quite different things. (i) Characteristics of organisms evolved as a consequence of natural selection in its evolutionary past and which result in a close match with features of the environment and/or constrain the organism to life in a narrow range of environments. The prefix 'ad-' is unfortunate as it implies that the process anticipates the present or the future (*see* **Abaptation**). (ii) Changes in the form or behavior of an organism *during its life* as a response to environmental stimuli, e.g. the formation of sun and shade leaves on the same tree and the acquisition of cold tolerance as a result of prior experience of low temperatures. (iii) Changes in the excitability of a sense organ as a result of continuous stimulation.

Adenosine triphosphate (ATP) Molecule composed of adenine, ribose and three phosphate groups bound by high-energy linkages and associated with energy transfer in living cells.

Adiabatic expansion Expansion taking place without heat entering or leaving the system.

Adventitious roots Roots that arise in 'abnormal' positions, e.g. from a stem or leaf. The contrast is with the primary roots that develop from the axis of a seedling and roots that arise from other roots.

Aerobic decomposition The process of breakdown of organic molecules to simple inorganic constituents when oxygen is in free supply.

Aesthetic injury level The level of pest abundance above which aesthetic or sociological considerations suggest control measures should be taken against the pest.

Aestivation A state of dormancy during the summer or dry season. (The word is also used by botanists to describe the arrangement of the parts in a flower bud.)

Aggregated distribution The distribution of organisms in which individuals are closer together than they would be if they were randomly or evenly distributed.

Aggregation of risk A pattern in which prey vary, from prey patch to prey patch, more than would be expected by chance alone in their risk of being attacked by a predator (especially applied to hosts varying in their risk of being attacked by parasitoids).

Aggregative response The response of a predator through which it spends more time either in habitat patches with higher densities of prey, leading to higher densities of predators in patches with higher densities of prey, or in habitat patches with lower densities of prey, leading to higher densities of predators in patches with lower densities of prey. (*See also* **Aggregation of risk**.)

Alcohol dehydrogenase (ADH) An enzyme catalyzing the conversion of alcohols into aldehydes and ketones, and the reverse.

Allee effect A disproportionately low rate of recruitment when density is low.

Allelochemical A substance produced by one organism that is toxic or inhibitory to the growth of another.

Allelopathy The production and release into the environment of chemicals that are toxic to other species but not to the producer.

Allochthonous material Organic matter entering a stream, lake or ocean but derived from an adjacent terrestrial system.

Allogenic succession A temporal succession of species at a location that is driven by external influences which alter conditions.

Allometry The study of the changing proportions of the parts of an organism as size changes, either in individual growth (ontogenetic) or comparing related organisms of different sizes (phylogenetic).

Allopatry Occurring in different places; usually refers to geographical separation of species.

Amensalism An interaction in which one organism (or species) adversely affects a second organism (or species), but the second has no effect (good or bad) on the first.

Anadromous A species of fish that spends part of its life cycle in fresh water and another part in the ocean.

Anaerobic decomposition A process of breakdown of organic molecules to simpler inorganic constituents, that occurs in the absence of oxygen.

Analogous structures Organs of different evolutionary origin which perform the same role in different organisms.

Angiosperms Flowering plants. Strictly, those seed-bearing plants that develop their seeds from ovules *within* a closed cavity, the ovary (*cf*. gymnosperms, in which the ovules are naked).

Annual A species with a life cycle which takes approximately 12 months or rather less to complete, whose life cycle is therefore directly related to the annual cycle of weather, and whose generations are therefore discrete.

Anoxic Without oxygen.

Antagonistic resources A pair of resources for which increased consumption by an organism of one resource leads to an increased requirement by that organism for the other.

Anthropocentric Regarding humans as the central fact of the universe and interpreting everything in relation to them.

Aposematism Conspicuous appearance of organism that is noxious or distasteful.

Apparency theory A theory seeking to explain, in evolutionary terms, the variation in chemical defenses produced by different plants as a result of how 'apparent' they are (how large, how long-lived, how numerous, etc.) to the herbivores that attack them.

Apparent competition An interaction in which the organisms (or species) have adverse effects on one another by virtue of the beneficial effects that each has on a predatory organism (or species) which they share.

Arthropod A member of the animal phylum Arthropoda, which includes the insects, crustaceans (e.g. crabs, shrimps, barnacles), spiders, scorpions, mites, millipedes and centipedes.

Assimilation efficiency The percentage of energy ingested by an animal that is absorbed across the gut wall.

Asymmetric competition Competition between two organisms (or species) in which one is much more severely affected than the other.

Autochthonous material Organic matter produced within a community (to contrast with **allochthonous material** that is produced outside it).

Autocidal control A type of pest control in which the pest is manipulated so that it contributes significantly to its own control, or literally 'kills itself'.

Autocoprophagy The reingestion of one's own feces.

Autogenic succession A temporal succession of species at a location that is driven by processes operating within the community (in contrast with **allogenic succession**).

Autotroph An organism that is independent of outside sources for *organic* food materials and manufactures its own organic material from inorganic sources.

Autotrophic succession A temporal succession of species at a location principally involving plants.

Awn A stiff bristle, especially on the grains of cereals and grasses.

Axillary bud A bud produced in the angle between a leaf and the stem that bears it, i.e. the normal position of a lateral bud.

Bacteroids In legume nodules the symbiotic *Rhizobium* bacteria that have entered an active nitrogen-fixing state and have usually ceased to divide and commonly become banded and branched.

Balanced preference A preference by a consumer for food items based on the need of the consumers to obtain a balanced diet of complementary food items.

Basic reproductive rate (R_0) The average number of offspring produced by individuals in a population over the course of their life.

Benthic communities The plants, microorganisms and animals that inhabit the bed of aquatic environments.

Bicentric distribution The presence of a species (or other taxonomic class) in two widely separated geographical areas.

Biodiversity In its most general sense, biodiversity refers to all aspects of variety in the living world. Specifically, the term may be used to describe the number of species, the amount of genetic variation or the number of community types present in an area.

Biogeochemical cycling The movement of chemical elements between organisms and nonliving compartments of atmosphere, lithosphere and hydrosphere.

Biogeography The study of the geographical distribution of organisms.

Biological control The use of a pest's natural enemies in order to control that pest.

Biological oxygen demand The rate at which oxygen disappears from a sample of water — a measure of deoxygenating ability commonly used as an index of the quality of sewage effluent.

Biological pesticides A preparation used to provide immediate control of a pest, and which consists of biological as opposed to chemical material.

Biomagnification The increasing concentration of a compound in the tissues of organisms as the compound passes along a food chain, resulting from the accumulation of the compound at each trophic level prior to its consumption by organisms at the next trophic level.

Biomass The weight of living material. Most commonly used as a measure per unit area of land or per volume of water. Commonly includes the dead parts of living organisms, e.g. the bark and heart wood of trees and the hair, claws, etc. of animals which are strictly 'necromass'.

Biome One of the major categories of the world's distinctive plant assemblages, e.g. the tundra biome, the tropical rainforest biome.

Biorational insecticides Insecticides which have no, or relatively limited, adverse effects on other, non-pest organisms in the pest's environment.

Biosecurity Policies and practices to prevent the invasion of an area by alien species.

Biospecies A species for which it has been established (or at least generally agreed) that members of the species can interbreed with one another and produce fertile offspring but cannot do so with individuals that do not belong to that biospecies.

Biota The fauna and flora together; all the living organisms at a location.

Biotic Living; usually applied to the biological aspects of an organism's environment, i.e. the influences of other organisms.

Biotrophic A word used of parasites that can complete their development on only a living host (*cf.* **Necroparasite**).

Biotype A physiological race or a group of individuals having distinctive genetic characters in common.

Boreal Northern.

Botanical insecticides Chemicals extracted from plants for the control of insect pests.

Boundary layer The relatively still layer of water just above the bed of a river.

Brackish Saline water with a concentration between fresh water and seawater.

Breeding dispersal Movement between two successive breeding areas.

Brood parasitism The act of leaving eggs or progeny to be reared by an individual that is not the parent — usually a member of another species.

Browsers Vertebrate herbivores that feed from trees or shrubs.

Calcareous Composed of, or containing, lime or limestone.

Capture–recapture A method for estimating the size of populations of mobile organisms (usually animals), in which one or more samples are captured, marked and released, and one or more samples examined for the proportion of recaptured marks (broadly speaking, high in small populations and low in large).

Carbohydrase An enzyme that acts on carbohydrate.

Carbon (C) 3 plants Those in which the assimilation of atmospheric carbon dioxide is directly via the enzyme ribulose-1,5-bisphosphate carboxylase in the cells of the leaf mesophyll.

Carbon (C) 4 plants Species of higher plants in which the assimilation of atmospheric carbon dioxide in the photosynthetic process is indirect, via the enzyme phosphoenol pyruvate carboxylase in the sheaths surrounding the veins of the leaves.

Carboniferous period Geological period from *c.* 270 to 220 million years ago.

Carnivory The consumption by an organism of living animals or parts of living animals.

Carrying capacity The maximum population size that can be supported indefinitely by a given environment, at which intraspecific competition has reduced the *per capita* net rate of increase to zero. An idealized concept not to be taken literally in practice.

Catabolism The decomposition by living organisms of complex organic molecules to simpler forms, with the release of energy.

Catastrophe A major change in the environment that causes extensive damage and usually widespread death, and occurs so infrequently that the effects of natural selection by similar events in the past (if they have ever occurred) do not remain in the 'genetic memory' of the species. The Mt St Helens volcanic eruption was in this sense a catastrophe (*cf.* the recurrent hurricanes in eastern USA which may be defined as 'disasters').

Catch per unit effort Usually applied to the harvesting of a natural resource (e.g. marine fish), the total catch (in terms of numbers or biomass) divided by the total harvesting effort (e.g. a product of the total number and size of ships and the number of days that they fished).

Cecum A blindly ending sac at the junction between the small and large intestines.

Cellulase An enzyme capable of mobilizing cellulose.

Cellulolytic enzymes Enzymes that act on cellulose.

Cellulose A complex polymer of glucose molecules. The fundamental cell wall constituent in all green plants.

Census In ecology, an attempt to count every member of a population.

Chaos Applied to a time series of population abundance or density, a pattern in which elements of the pattern are never repeated exactly, and where two very similar abundances in the time series follow trajectories subsequently which diverge from one another exponentially. None the less, the series is not random and fluctuates within definable limits.

Chaparral A thicket of low evergreen oaks or dense tangled brushwood.

Character displacement A measurable physical difference between two species that has arisen by natural selection as a result of the selection pressures on one or both from competition with the other.

Chemosynthesis The synthesis of organic molecules by certain bacteria that use the energy released by specific inorganic molecules.

Chlorophyll Green pigment(s) found in almost all plants and playing a crucial role in the capture of radiant energy in the process of photosynthesis.

Chloroplast The inclusions (plastids) within plant cells which contain chlorophyll.

Classical biological control (or importation) The introduction of a natural enemy from a pest's native habitat to maintain that pest below its economic threshold.

Classification A mathematical procedure for categorizing communities in which communities with similar species compositions are grouped together in subsets.

Climax The presumed endpoint of a successional sequence; a community that has reached a steady state.

Cline A chain of different forms of species.

Clonal dispersal The movement or growth away from each other of the parts of a modular organism (commonly, but not necessarily, becoming detached from each other).

Clone The whole product of growth from a single zygote, in organisms that grow by the repeated iteration of units of structure (modular organisms) and in which the units have, at least potentially, the capacity for physiological independence. The parts of a clone are genetically identical except for what are probably rare somatic mutations.

Clumped distribution The distribution of organisms in which individuals are closer together than if they were distributed at random or equidistant from each other. (= Aggregated distribution.)

Coefficient of interference A measure of the extent to which interference amongst consumers increasingly depresses individual consumption rates as consumer density increases.

Coefficient of variation A statistical term, referring to the standard deviation of a distribution divided by the distribution's mean, and hence providing a standardized measure of the variation in a distribution, which does not increase simply because the mean itself increases or because the units of measurement change.

Coevolution The process by which members of two (or more) species contribute reciprocally to the forces of natural selection that they exert on each other, e.g. parasites and their hosts.

Coexistence The living together of two species (or organisms) in the same habitat, such that neither tends to be eliminated by the other. This begs lots of questions about the meaning of 'living together' and the 'same habitat'.

Cohort generation time (T_c) An approximation to the true generation length, which takes no account of the fact that some offspring may themselves develop and give birth during the reproductive life of the parent; hence, simply the average time between the birth of a parent and the birth of its offspring.

Cohort life table A life table constructed by monitoring a group of individuals all born during the same short period, from this time of birth through to the death of the last surviving individual.

Collector–filterers Aquatic animals that filter small particles of organic matter from the water flowing over them.

Collector–gatherers Aquatic animals that gather small particles of organic matter from the sediment.

Colonization The entry and spread of a species (or genes) into an area, habitat or population from which it was absent.

Commensalism An interaction in which one organism (or species) beneficially affects a second organism (or species), but the second has no effect (good or bad) on the first.

Community The species that occur together in space and time.

Community stability The tendency of a community to return to its original state after a disturbance.

Community structure The list of species and their relative abundances in a community.

Compartmentalization in communities A tendency in communities to be organized into subunits within which interactions are strong but between which interactions are weak.

Compensation point The intensity of radiation at which photosynthesis equals and balances respiration.

Competition An interaction between two (or more) organisms (or species), in which, for each, the birth and/or growth rates are depressed and/or the death rate increased by the other organisms (or species).

Competition coefficient In interspecific competition, a measure of the competitive effect of one species on another relative to the competitive effect of the second species on itself.

Competitive exclusion The elimination from an area or habitat of one species by another through interspecific competition.

Competitive Exclusion Principle *see* **Gause's Principle**.

Competitive release The expansion of the niche of a species associated with the lack of competition with other species; for instance, because it occurs on an island where competitors are absent.

Complementarity A condition of two resources of which less is required when they are taken together than when consumed separately.

Complementary resources A pair of resources for which consumption by the consumer of one resource reduces the consumer's requirements for the other.

Conservation The principles and practice of the science of preventing species extinctions.

Conservation biological control Manipulation that augments the density or persistence of populations of generalist natural enemies that are native to the pest's new area.

Conspecific Belonging to the same species.

Constant escapement A maximum sustainable yield strategy whereby a fixed number of breeding individuals are left at the end of each hunting season.

Consumption efficiency The percentage of energy available that is actually consumed at a trophic level. In the case of herbivores it is the percentage of net primary productivity that is ingested.

Contest competition Intraspecific competition in which mortality compensates exactly for increases in density, so that there are a constant (or approximately constant) number of survivors irrespective of initial density.

Continental drift The separation and movement of land masses in geological time.

Continentality Climatic conditions associated with locations in the middle of large continents.

Control action threshold (**CAT**) The combination of pest density and the densities of the pest's natural enemies beyond which it is necessary to intervene and take control measures against the pest, to prevent its population rising to a level at which it will cause economic damage.

Convergent evolution The process by which organisms of different evolutionary lineages come to have similar form or behavior.

Coprophagy The consumption of feces.

Correlogram A statistical procedure for the analysis of time-series data and to test for the presence of cyclic phenomena.

Coupled oscillations Linked fluctuation in the abundance of two species, broadly speaking a 'predator' and a 'prey', in which low prey abundance leads to low predator abundance which leads to high prey abundance, which leads to high predator abundance which leads to low prey abundance, and so on.

Crassulacean acid metabolism (**CAM**) A pathway for the assimilation of carbon dioxide by plants, in which carbon dioxide is fixed into organic acids during the night and released during the day for photosynthesis. Characteristic of succulent desert plants.

Cretaceous period A geological era; the final part of the Mesozoic, from approximately 140 to 170 million years ago.

Critical population size (S_t) The abundance of susceptible hosts in a population necessary to just sustain a parasite of that host; below

S_T the parasite will decline to extinction, above S_T its abundance will increase.

Crypsis Form or behavior of an organism that makes it difficult to detect, e.g. camouflage from a predator.

Cuticle In plants, a layer of waxy substance on the outer surface of epidermal cell walls. In animals, the outermost layer of many invertebrates.

Cyanogenic Releasing hydrogen cyanide.

Cytoplasm The living matter within a cell, excluding the genetic material.

Decomposition The breakdown of complex, energy-rich organic molecules to simple inorganic constituents.

Degradative succession A temporal succession of species that occurs on a degradable resource.

Demographic process A process capable of changing the size of a population, viz. birth, death or migration.

Density dependence The tendency for the death rate in a population to increase, or the birth or growth rate to decrease, as the density of the population increases.

Density independence The tendency for the death, birth or growth rate in a population neither to rise nor fall as the density increases.

Deoxyribonucleic acid (DNA) The carrier of genetic information in cells; capable of self-replication as well as coding for RNA synthesis.

Depensation A pattern of particularly low recruitment rate in a population at low density.

Desert A desolate and barren region, usually deficient in available water, and with scant vegetation.

Deterministic forces Forces which can be characterized exactly with no element of chance or probability (*cf.* **Stochastic forces**).

Detritivory Consumption of dead organic matter (detritus) usually together with associated microorganisms.

Developmental threshold The body temperature of an organism below which no development occurs.

Devonian period A geological era lasting from approximately 400 to 360 million years ago.

Diapause A state of arrested development or growth, accompanied by greatly decreased metabolism, often correlated with the seasons, usually applied only to insects.

Dicotyledon A member of one of the two classes of flowering plants, distinguished by having seedlings with usually a pair of seedling leaves (cotyledons) and commonly with floral parts in fours or fives, leaves with net venation and ability to form wood by secondary (cambial) cell division within the tissues.

Differential resource utilization Normally used only in the context of interspecific competition, the use of different resources by two different species, or the use of the same resource at a different time, in a different place, or generally in a different manner.

Diffusion coefficient A measure of the rate of movement of solutes or gases in response to a concentration gradient in the medium in which they are dissolved.

Dimorphism The existence of two distinct forms of an organism or organ, e.g. winged and wingless generations in the life of aphids, winged and wingless seeds produced from the same flower.

Disaster Major disturbances in the life of a community or population which occur sufficiently often to leave their record in the 'genetic memory' of the population (*cf.* **Catastrophe**).

Discounting An important economic consideration where each bird in the hand now (or fish in the hold) is worth more than an equivalent bird or fish some time in the future. The value of the current catch can be placed in the bank to accrue interest, so that its total value increases. Hence, the value of the resource (bird or fish) in the future must be discounted by loss of possible interest earned.

Discrete generations A series of generations in which, strictly, each one finishes before the next begins. Commonly, however, the early life cycle stages of the succeeding generation overlap with the end of the final stages of the preceding generation.

Disease The disturbed or altered condition of an organism (malfunctioning) caused by the presence of an antagonist (toxin or pathogen) or the absence of some essential (e.g. micronutrient or vitamin).

Disjunct distribution The geographical distribution of a species or other taxonomic class of which parts are widely separated.

Dispersal The spreading of individuals away from each other, e.g. of offspring from their parents and from regions of high density to regions of lower density.

Dispersal polymorphism Two or more types of dispersal structures found within a species or among the progeny of an individual.

Distribution The spatial range of a species, usually on a geographical but sometimes on a smaller scale, or the arrangement or spatial pattern of a species over its habitat.

Disturbance In community ecology, an event that removes organisms and opens up space which can be colonized by individuals of the same or different species.

Diversity *see* **Species diversity**.

Diversity index A mathematical index of species diversity in a community.

Dominance-controlled community A community where some species are competitively superior to others so that an initial colonizer of an opening left by a disturbance cannot necessarily maintain its presence there.

Dominant species Species which make up a large proportion of community biomass or numbers.

Donor-controlled models Mathematical models of predator–prey interactions in which the donor (prey) controls the density of the recipient (predator) but not the reverse.

Dormancy An extended period of suspended or greatly reduced activity, e.g. aestivation and hibernation.

Dynamic equilibrium The state of a system when it remains unchanged because two opposing forces are proceeding at the same rate.

Dynamic pool models Models of harvesting that take into account population structure.

Dynamically fragile Describes a community which is stable only within a narrow range of environmental conditions.

Dynamically robust Describes a community which is stable within a wide range of environmental conditions.

Ecological energetics The branch of ecology in which communities are studied from the point of view of the energy flowing through them.

Ecological niche A term with alternative definitions, not all of them synonymous. To state two: (i) the 'occupation' or 'profession' of an organism or species; or (ii) the range of conditions, resource levels and densities of other species allowing the survival, growth and reproduction of an organism or species. Hence, if each condition, resource or other species is seen as a dimension, the niche is an *n*-dimensional hypervolume.

Ecological speciation Speciation driven by divergent natural selection in distinct subpopulations.

Ecological stoichiometry The analysis of constraints and consequences in ecological interactions of the mass balance of multiple chemical elements.

Ecomorph Species within which individuals fall into classes that are distinct in morphology, ecology and/or behavior.

Economic injury level (**EIL**) The level of pest abundance above which it costs less to control the pest than is saved by pest control, but below which it costs more than is saved.

Economic threshold The density of a pest at which action should be taken to prevent it reaching the economic injury level.

Economically optimum yield The yield from a harvesting operation at which the value of a harvest set against the costs of obtaining that harvest is maximized.

Ecophysiology The study of physiology and tolerance limits of species that enhances understanding of their distribution in relation to abiotic conditions.

Ecosystem A holistic concept of the plants, the animals habitually associated with them and all the physical and chemical components of the immediate environment or habitat which together form a recognizable self-contained entity. The concept is due to Tansley (1935).

Ecotype A subset of individuals within a species with a characteristic ecology.

Ectomycorrhiza An association of a fungus and the root of a plant (usually a tree) in which the fungus forms a sheath around the root and penetrates *between* the cells of the host.

Ectoparasite A parasite that lives on the surface of its host.

Ectotherm An organism in which the body temperature relies on sources of heat outside itself.

Effective population size (N_e) The size of a genetically idealized population with which an actual population can be equated genetically.

Elasticity analysis A means, using population projection matrices, of identifying phases and processes in a species' life cycle that are important in determining abundance.

Electivity A measure of the preference, or lack of it, shown by a consumer species for its range of prey.

Emergent properties Properties not possessed by individuals or populations that become apparent only when the community is the focus of attention.

Emigration The movement of individuals out of a population or from one area to another.

Endemic Having their habitat in a specified district or area, or the presence of a disease at relatively low levels, all the time.

Endobiont (**endosymbiont**) An organism which lives *within the cells* of a host organism in a mutualistic relationship or doing no apparent harm.

Endogenous rhythm A metabolic or behavioral rhythm that originates within the organism and persists even when external conditions are kept constant.

Endotherm An organism which is able to generate heat within itself to raise its body temperature significantly.

Enemy release hypothesis The proposition that species may become pests simply because, by colonization of a new area, they escape the control of their natural enemies.

Environmental 'grain' The scale of spatial patchiness of an environment from the point of view of a particular, specified species.

Environmental 'noise' Extraneous background signals that tend to mask biotic processes.

Enzyme denaturation Structural change in an enzyme, involving an unfolding of peptide chains and rendering the enzyme less soluble, produced by mild heat or various chemicals.

Ephemerals Organisms with a short life cycle, especially plants whose seeds germinate, grow to produce new seeds and then die all in a short period within a year.

Epidemic The outbreak of a disease which affects a large number and/or proportion of individuals in a population at the same time.

Epidemiology The study of the occurrence of infectious diseases, their origins and pattern of spread through a population.

Equilibrium theory A theory of community organization that focuses attention on the properties of the system at an equilibrium point, to which the community tends to return after a disturbance.

Equitability The evenness with which individuals are distributed among species in a community.

Essential resources A pair (or more) of resources, where neither resource can substitute for the other.

Eukaryote Organism with cells possessing a membrane-bound nucleus in which the DNA is complexed with histones and organized into chromosome, i.e. protozoans, algae, fungi, plants and animals.

Euphotic zone The surface zone of a lake or ocean within which net primary productivity occurs.

Eutrophication Enrichment of a water body with plant nutrients; usually resulting in a community dominated by phytoplankton.

Evapotranspiration The water loss to the atmosphere from soil and vegetation. The *potential* evapotranspiration may be calculated from physical features of the environment such as incident radiation, wind speed and temperature. The *actual* evapotranspiration will commonly fall below the potential depending on the availability of water from precipitation and soil storage.

Even distribution The distribution of organisms in which the average distance between them is greater than would occur if they were distributed at random.

Evolutionarily stable strategy (**ESS**) A strategy which, if adopted by most of a population, cannot be bettered by any other

strategy, and will therefore tend to become established by natural selection.

Evolutionary trees Lineages designed to show the evolutionary history of relationships between groups of organisms.

Exact compensation Density dependence in which increases in initial density are exactly counterbalanced by increases in death rate and/or decreases in birth rate and/or growth rate, such that the outcome is the same irrespective of initial density.

Exogenous Originating outside an organism.

Exploitation competition Competition in which any adverse effects on an organism are brought about by reductions in resource levels caused by other, competing organisms.

Exploiter-mediated coexistence A situation where predation promotes the coexistence of species amongst which there would otherwise be competitive exclusion.

Exponential growth Growth in the size of a population (or other entity) in which the rate of growth increases as the size of the population increases.

Extinction The condition that arises from the death of the last surviving individual of a species, group or gene, globally or locally.

Extrafloral nectaries Nectar-secreting glands found on the leaves and other vegetative parts of plants.

Extrinsic factors Literally, factors acting from outside. In ecology, physical and chemical features of the environment, and other organisms, are all extrinsic factors acting on an organism.

Facilitation (**successional**) In which the influence of early species in a community succession is to facilitate establishment of later ones by changing the conditions encountered.

Facultative annual An organism (the phrase is usually used of plants) which may in some circumstances complete its life cycle within 12 months.

Facultative mutualism The condition in which one or both species in a mutualistic association may survive and maintain populations in the absence of the other partner.

Fecundity The number of eggs, or seeds, or generally offspring in the first stage of the life cycle, produced by an individual.

Fecundity schedule A table of data displaying the lifetime pattern of birth amongst individuals of different ages within a population.

Field capacity The condition of a soil when it contains all the water retained after draining freely under gravity.

Fitness The contribution made to a population of descendants by an individual *relative* to the contribution made by others in its present population. The relative contribution that an individual makes to the gene pool of the next generation.

Floristic equilibrium The species composition of a flora when there is no further internally or externally generated change.

Folivores Animals that eat leaves.

Food chain An abstract representation of the links between consumers and consumed populations, e.g. plant–herbivore–carnivore.

Food web Representation of feeding relationships in a community that includes all the links revealed by dietary analysis.

Founder-controlled community A community where a large number of species are approximately equivalent in their ability to colonize an opening left by a disturbance, are equally well fitted to the abiotic environment and can hold the location until they die.

Frequency dependence Of a predator, describes the tendency to take disproportionately more of the commoner prey species.

Fugitive A species that is good (and hence amongst the first) in colonizing gaps.

Functional response The relationship between a predator's consumption rate of prey and the density of those prey.

Fundamental net reproductive rate (***R***) The average number of individuals that each existing individual in a population gives rise to one time interval later; hence, the multiplication rate relating size of a population to its size one time interval earlier.

Fundamental niche The largest ecological niche that an organism or species can occupy in the absence of interspecific competition and predation.

Gamete A reproductive cell (haploid) which unites with another in fertilization to produce a zygote from which a new individual (genet) arises.

Gause's Principle The idea that if two competing species coexist in a stable environment, then they do so as a result of differentiation of their realized niches; but if there is no such differentiation, or if it is precluded by the habitat, then one competing species will eliminate or exclude the other.

Gene A unit of inherited material—a hereditary factor.

Gene flow The consequence of cross-fertilization between members of a species across boundaries between populations, or within populations, which results in the spread of genes across and between populations.

Generation length (***T***) Not quite the average length of time between the birth of a parent and the birth of its offspring (the 'cohort generation time'): the production by offspring of their own offspring during the life of the original parent makes the average, computed over many generations, less than the cohort generation time.

Genet The organism developed from a zygote. The term is used especially for modular organisms and members of a clone to define the *genetic individual* and to contrast with 'ramet' the potentially physiologically independent part that may arise from the iterative process by which modular organisms grow.

Genetic drift Random changes in gene frequency within a population resulting from sampling effects rather than natural selection, and hence of greatest importance in small populations.

Genetic engineering Any change in the genetic constitution of an organism brought about by artificial means other than simple artificial selection and which would not usually occur in nature, such as the introduction of a gene from one species to another.

Genotype All the genetic characteristics that determine the structure and functioning of an organism.

Gentes Applied to cuckoos: separate lines laying their eggs in the nests of different host species.

Geometric series A series of numbers in which each is obtained by multiplying the preceding term by a constant factor, e.g. 1, 3, 9, 27, etc.

'Ghost of competition past' A term coined by J.H. Connell to stress that interspecific competition, acting as an evolutionary force in the past, has often left its mark on the behavior, distribution or morphology of species, even when there is no present-day competition between them.

Global stability The tendency of a community to return to its original state even when subjected to a large perturbation.

Global warming The predicted warming of the planet resulting from increasing atmospheric concentrations of radiative gases such as carbon dioxide, methane, nitrous oxide and chlorofluorocarbons.

Glycoside A derivative of glucose (or another sugar) in which one hydrogen atom is replaced by an organic radical.

Gonad Organs of animals which produce gametes.

Gradient analysis The analysis of species composition along a gradient of environmental conditions.

Granivores Animals that eat seeds.

Grazer A consumer which attacks large numbers of large prey during its lifetime, but removes only a part of each prey individual, so that the effect, although often harmful, is rarely lethal in the short term, and never predictably lethal.

Grazer–scrapers Aquatic animals that graze the organic layer of algae, microorganisms and dead organic matter on stones and other substrates.

Greenhouse effect Warming of the earth's atmosphere as a result of increases in carbon dioxide and other gases.

Gross primary production (GPP) The total fixation of energy by photosynthesis in a region.

Group selection The evolutionary process which is supposed to act through the different numbers of descendants left by groups rather than by individuals.

Guild A group of species that exploit the same class of environmental resources in a similar way.

Habitat Place where a microorganism, plant or animal lives.

Habitat diversity The range of habitats present in a region.

Halophyte A plant that tolerates very salty soil.

Handling time The length of time a predator spends in pursuing, subduing and consuming a prey item and then preparing itself for further prey searching.

Hardening A process by which the tolerance of extreme conditions, e.g. cold or drought, is increased by prior exposure to the same but less extreme conditions.

Haustoria Branches of parasitic plants or fungi which enter the tissues or cells of the host.

Hemiparasite Plants that are photosynthetic but form connections with the roots or stems of other plant species, drawing most or all of their water and mineral nutrient resources from their host.

Herbicide A chemical or biological preparation that kills plants.

Herbivory The consumption of living plant material.

Herd immunity A level of immunity in a population ('herd') of hosts such that the number of susceptibles is held below the critical population size, S_T, and R_0 therefore remains less than 1. Often the ultimate aim of a vaccination program.

Heritable variation The proportion of variation in a trait due to the effects of genetic factors.

Heterotroph An organism with a requirement for energy-rich organic molecules (animals, fungi and most bacteria).

Heterotrophic succession A temporal succession of species at a location, principally involving animals.

Heterozygote An organism carrying different alleles at the corresponding sites on homologous chromosomes.

Hibernate To remain dormant during the winter period.

Holoparasite Parasitic plants which lack chlorophyll and are therefore wholly dependent on their host plant for the supply of water, nutrients and fixed carbon.

Homeostasis Maintenance of relatively constant internal conditions in the face of a varying external environment.

Homeotherm An organism which maintains an approximately constant body temperature, usually above that of the surrounding medium.

Homing To return accurately to the place of origin, e.g. the return of salmon, after migration to the sea, to the same river in which they originally hatched.

Homologous structures Similarity in structure assumed to result from a common ancestry, e.g. the wing of a bird and the foreleg of a mammal.

Homozygote An organism carrying identical alleles at the corresponding sites on homologous chromosomes.

Host An organism which is parasitized by a parasite.

Host density dependence Applied to the aggregation of risk to hosts from parasitoid attacks: hosts in either higher or lower host density patches tend to be at a greater risk of attack (direct and inverse host density dependence, respectively). Could also be applied to other predator–prey interactions. (*See also* **Aggregation of risk** and *cf.* **Host density independence**.)

Host density independence Applied to the aggregation of risk to hosts from parasitoid attacks: risk varies from patch to patch but is not related to host density in a patch. Could also be applied to other predator–prey interactions. (*See also* **Aggregation of risk** and *cf.* **Host density dependence**.)

Host races Sympatric subpopulations exchanging genes at a rate of more than around 1% per generation.

Hydrological cycle The movement of water from ocean, by evaporation, to atmosphere, to land and back, via river flow, to ocean.

Hydrophilia An overwhelming desire for water.

Hydrospheric Pertaining to the water in soil, river, lake and ocean.

Immigration Entry of organisms to a population from elsewhere.

Immune response A response mounted by an animal in which specific antibodies (vertebrates only) and/or cytotoxic cells are produced against invading microorganisms, parasites, transplanted tissue, and many other substances which are recognized as foreign by the body.

Inbreeding depression A loss of vigor amongst offspring occurring when closely related individuals mate, resulting from the expression of numbers of deleterious genes in a homozygous state and from a generally low level of heterozygosity.

Incidence function The relationship between island size and the proportion of islands of that size occupied by the species in question.

Incubation period The period during which the embryo in an egg develops before hatching. Also, in epidemiology, the period between infection and the appearance of symptoms of disease.

Individualistic concept Concept of the community as an association of species that occur together simply because of similarities in requirements and not as a result of a long coevolutionary history.

Industrial melanism A phenomenon in which black or blackish forms of species have come to dominate populations in industrial areas.

Inflorescence The organ bearing an aggregation of flowers in a flowering plant.

Inhibition (**successional**) The tendency of early successional species to resist the invasion of later species.

Inoculation The introduction of a disease organism or vaccine, usually through a deliberately made wound.

'Inoculation' biological control The periodic release of a control agent where it is unable to persist throughout the year, with the aim of providing control for only one or perhaps a few generations.

Insecticide A chemical or biological preparation that kills insects.

Intensity of abundance The number of individuals per habitable site in a community (*cf.* **Prevalence** (**of abundance**)).

Intensity of infection The number of parasites per host in a population (*cf.* **Prevalence of infection**).

Interference coefficient *see* **Coefficient of interference** and **Mutual interference**.

Interference competition Competition between two organisms in which one physically excludes the other from a portion of habitat and hence from the resources that could be exploited there.

Interglacial period Period between glaciations, during which species begin to recolonize locations occupied previously.

Interspecific competition Competition between individuals of different species.

Intraspecific competition Competition between individuals of the same species.

Intrinsic rate of natural increase (***r***) The per capita rate of increase of a population which has reached a stable age structure without competitive or other restraints.

Inundation biological control The release of large numbers of a natural enemy, with the aim of killing those pests present at the time, but with no expectation of providing long-term control as a result of the control agent's population increasing or maintaining itself.

Inverse cube law A law which states that the intensity of an effect at a point B due to a source at A varies inversely as the cube of their distance apart.

Inverse square law A law which states that the intensity of an effect at a point B due to a source at A varies inversely as the square of their distance apart.

Irreplaceability An index of the potential contribution that a site will make to a defined conservation goal and the extent to which the options for conservation are lost if the site is lost.

Island biogeography The study of distribution of species and community composition on islands.

Island disharmony Where the relative proportions of different taxa are not the same on islands as they are on the mainland.

Isocline A line linking points, each of which gives rise to the same rate of population increase for the species being considered. The points may represent combinations of species densities or combinations of resource levels.

Isotherm A line on a map that joins places having the same mean temperature.

Isotonic Having the same osmotic pressure.

Isotopes Atoms of the same element having the same chemical properties but differing in mass and in the physical properties that depend on their mass.

Iteroparity Where organisms produce offspring in a series of separate events during and after each of which the organisms maintain themselves in a condition that favours survival to reproduce again subsequently (though the 'separate events' may merge into continuous reproduction).

***K* selection** Selection of life history traits that promote an ability to make a large proportionate contribution to a population which stays close to its carrying capacity — the traits being, broadly, large size, delayed reproduction, iteroparity, a small reproductive allocation, much parental care, and the production of few but large offspring.

***k* value** The loss of individuals from a given stage of a life cycle when the numbers at the beginning and end of the stage are both expressed as common logarithms, i.e. $\log_{10}$ (before) − $\log_{10}$ (after).

Key factor analysis A statistical treatment of population data designed to identify factors most responsible for change in population size.

Keystone species A species whose removal would produce a significant effect in the community of which it is part, changing its fundamental nature.

Killing power Synonymous with ***k* value**.

Lack clutch size Where natural selection favors not the largest clutch size but a compromise clutch size, which, by balancing the number produced against their subsequent survival, leads to the maximum number surviving to maturity.

Lacunarity An index of aggregation derived from fractal geometry that quantifies the variability in the distribution of gap sizes.

Leaf area index The area of leaves exposed over a unit area of land surface.

Leptokurtic A symmetric frequency distribution which differs from a normal distribution by deficiency in the shoulders compared to the tails and the top.

Life cycle The sequence of stages through which an organism passes in development from a zygote to the production of progeny zygotes.

Life form Characteristic structure of a plant or animal.

Life history An organism's lifetime pattern of growth, differentiation, storage and reproduction.

Life table A summary of the age- or stage-related survivorship of individuals in a population.

Light compensation point *see* **Compensation point**.

Lignin Complex organic material deposited within the cell walls of plants associated with cellulose, especially in wood and fibers.

Limiting similarity The level of similarity between two competing species which cannot be exceeded if the species are to coexist.

Lipase Enzyme(s) that split true fats into alcohols and acids.

Lithospheric Pertaining to rocks and sediments.

Littoral zone The zone at the edge of a lake or ocean which is periodically exposed to the air and periodically immersed.

Local stability The tendency of a community to return to its original state when subjected to a small perturbation.

Logistic equation A much-used equation for the growth of a single-species population without discrete generations under the influence of competition, which is simple and captures the essence of actual examples but very few of the details of actual examples.

Longevity Length of life.

Macroecology The study of distribution and abundance at large spatial and temporal scales.

Macrofauna Large animals in a community within an arbitrary size range, e.g. between 2 mm and 20 mm body width, in soil invertebrates.

Macroinvertebrate An invertebrate with a body length greater than 2 mm.

Macroparasite A parasite which grows in its host but multiplies by producing infective stages that are released from the host to infect new hosts. They are often intercellular or live in body cavities, rather than within the host cells.

Marginal value theorem A proposed decision-rule (derived from theoretical exploration) for a predator foraging from patches of prey which it depletes, that states that the predator should leave all patches at the same rate of prey extraction, namely the maximum average overall rate for that environment as a whole.

Marsupial mammal A mammal in which the young are born in a very immature state and migrate to a pouch where they are suckled until relatively mature.

Masting The production, in some years, of especially large crops of seeds by trees and shrubs.

Maturation The process of becoming fully differentiated, fully functional and hence fully reproductive.

Maximal food chain A sequence of species running from a basal species (plant) to another species that feeds on it and so on to a top predator (fed on by no other).

Maximum sustainable yield (MSY) The maximum crop or yield that can be removed repeatedly from a population without driving it towards extinction.

Mean intensity of infection The mean number of parasites per host in a population (including those hosts that are not infected).

Megafauna The largest arbitrary size categorization of animals in a community, e.g. > 20 mm body width in soil invertebrates.

Megaherbivore A term referring to very large terrestrial grazing animals (> 1000 kg), such as elephants, also including the many species that went extinct in the last 30,000 years or so.

Megaphyte Plants with normally unbranched stems or trunks and bearing a crown of very large leaves. The inflorescence is commonly also massive.

Meristem A part of a plant in which cell division is concentrated (especially the shoot apices, lateral buds and a zone near the tips of roots and rootlets).

Mesocosm An enclosed artificial ecosystem, at an intermediate scale, designed to mimic natural ecological processes.

Mesofauna Animals in the size range 100 mm to 2 mm body length.

Mesophyll The internal nonvascular tissue of a leaf. In green plants it is in these cells that most chloroplasts are found and in which most photosynthesis occurs.

Metabolism The sum of all chemical reactions occurring within a cell or an organism.

Metamorphosis Abrupt transition between life stages; for example from larval to adult form.

Metapopulation A population perceived to exist as a series of subpopulations, linked by migration between them. However, the rate of migration is limited, such that the dynamics of the metapopulation should be seen as the sum of the dynamics of the individual subpopulations.

Microbes Microorganisms: any microscopic organism, including bacteria, viruses, unicellular algae and protozoans, and microscopic fungi such as yeasts.

Microbivores Animals that feed on microorganisms.

Microclimate The climate within a very small area or in a particular, often tightly defined, habitat.

Microcosm An enclosed artificial ecosystem, at a very small scale, designed to mimic natural ecological processes.

Microfauna The smallest arbitrary size categorization of animals in a community.

Microflora Bacteria, fungi and microscopic algae.

Microparasite A parasite which multiplies directly within its host, usually within host cells.

Microsite The small subset of environments within a habitat that provide the specialized resources and conditions required for a phase in the life of an organism, e.g. the cracks or crevices which provide conditions suitable for germination of the seed of a particular species.

Microtopography Very small scale (roughly, 'organism-sized') variations in the height and roughness of the ground surface.

Migration The movement of individuals, and commonly whole populations, from one region to another.

Mimicry The resemblance of an organism (the mimic) either to another organism or to a nonliving object (the model), presumably conferring a benefit on the mimic in natural selection.

Miocene A geological era lasting from approximately 25 to 5 million years ago.

Modular organisms Those that grow by the repeated iteration of parts, e.g. the leaves, shoots and branches of a plant, the polyps of a coral or bryozoan. Modular organisms are almost always branched, though the connections between branches may separate or decay and the separated parts may in many cases then become physiologically independent, e.g. *Hydra* spp. and duckweeds (*Lemna* spp.). (*See also* **Ramet** and *cf.* **Unitary organisms**.)

Moisture gradient A spatial gradient in the availability of water in soil.

Monoclimax theory The concept that all successional sequences lead to a single characteristic climax in a given region.

Monocotyledons One of the two main groups of flowering plants (*see* **Angiosperms**). Characterized normally by the presence of just a single seedling leaf (cotyledon) and commonly by floral parts arranged in threes, parallel leaf veins and the inability to form secondary tissues, e.g. wood, from cell division within the tissues.

Monoculture A large area covered by a single species (or, for crops, a single variety) of plant; or, in experiments, plants of the same species grown alone without any other species.

Monogenean An ectoparasitic trematode flatworm, parasitic on fish or amphibia, and having only one host in its life cycle.

Monomorphic Occurring in only one form.

Monophagy Where an organism consumes only a single type of food item.

Monotreme mammal A primitive mammal belonging to one of only three genera, laying eggs but having hair and secreting milk.

Morphogenesis The development of size, form and other structural features of organisms.

Morphology The form and structure of an organism.

Motile organism An organism capable of spontaneous movement.

Multiple resistance (to pesticides) Resistance of an organism to a number of pesticides requiring different mechanisms to counteract their effects.

Mutual antagonism Describes two species with reciprocal negative effects on each other (either interspecific competition or mutual predation).

Mutual interference Interference amongst predators leading to a reduction in the consumption rate of individual predators which increases with predator density.

Mutualism An interaction between the individuals of two (or more) species in which the growth, growth rate and/or population size of both are increased in a reciprocal association. (*See also* **Facultative mutualism** and **Obligate mutualism**.)

Mycorrhiza A commonly mutualistic and intimate association between the roots of a plant and a fungus. (*See also* **Ectomycorrhiza** and **Vesicular arbuscular mycorrhiza**.)

***n*-dimensional hypervolume** *see* **Ecological niche**.

'n'-shaped curve More correctly, 'unimodal': a curve with a single maximum.

Natal dispersal Movement between where the individual was born and where breeding first takes place.

Natural selection The force that causes some individuals in a population to contribute more descendants (and genes) than others to subsequent generations and so leads to changes in the genetic composition of populations over time (evolution). (*See also* **Fitness**.)

Necromass The weight of dead organisms, usually expressed per unit of land or volume of water. The term is sometimes used to include the dead parts of living organisms, e.g. the bark and heartwood of trees, the hair and claws of animals.

Necroparasite A parasite that kills its host (or a part of it) and continues growth on the dead resource.

Net primary production (NPP) The total energy accumulated by plants during photosynthesis (gross primary production minus respiration).

Neutral models Models of communities that retain certain features of their real counterparts but exclude the consequences of biotic interactions; they are used to evaluate whether real communities are structured by biotic forces.

Neutralism The lack of an interaction between two organisms (or species): neither has any effect on the other.

Niche The limits, for all important environmental features, within which individuals of a species can survive, grow and reproduce.

Niche complementarity The tendency for coexisting species that occupy a similar position along one niche dimension, e.g. altitude, to differ along another, e.g. diet.

Niche differentiation The tendency for coexisting species to differ in their niche requirements.

Niche divergence An evolutionary process whereby the niches of two species become less similar.

Niche opportunity The potential provided in a given region for invaders to succeed—in terms of a high availability of resources and appropriate physicochemical conditions (coupled with a lack or scarcity of natural enemies).

Niche packing The tendency for coexisting species between them to fill the available 'space' along important niche dimensions.

Nitrification The conversion of nitrites to nitrates, usually by microorganisms. The term is commonly used to describe the process of conversion of ammonium ions via nitrites to nitrates.

Nitrogen fixation The conversion of gaseous nitrogen (N_2) into more complex molecules. The process is used industrially to produce nitrogen fertilizers. Biological nitrogen fixation is accomplished by both free-living and symbiotic microorganisms (prokaryotes). The process is more properly called 'dinitrogen fixation'.

Node The place on a stem where one or more leaves arise.

Nonequilibrium theory In community ecology, concerned with the transient behavior of a system away from any equilibrium point, it specifically focuses attention on time and variation.

Null hypothesis The hypothesis that an observed pattern of data and an expected pattern are effectively the same, differing only by chance, not because they are truly different. A statistical significance test is then generally applied to the data to test whether the hypothesis can be rejected. If so, the observed and expected patterns are said to be significantly different. Tests do not establish that the null hypothesis is true. 'Expected' patterns may be derived from theory or from other, related data sets.

Nunatak Islands standing out in a 'sea of ice' during periods of glaciation and in which species may have persisted.

Nutrient cycling The transformation of chemical elements from inorganic form in the environment to organic form in organisms and, via decomposition, back to inorganic form.

Obligate mutualism A condition in which a mutualistic relationship with other species is essential for a species to survive.

Oligophagous Consuming a small range of types of food items.

Omnivory Feeding on prey from more than one trophic level.

Ontogenetic Occurring during the course of an organism's development.

Opportunistic species One that is capable of exploiting spasmodically occurring environments.

Optimal diet model Mathematical formulation of prey selection that would, in theory, provide the best energy returns to the consumer: used as a yardstick to assess actual performance.

Optimal defense theory An evolutionary theory that predicts that the more important an organ or tissue is for an organism's fitness, the better protected it will be.

Optimal foraging theory An evolutionary theory that predicts the details of foraging behavior based on mathematical models.

Optimum similarity The level of similarity between competing species, which, if either exceeded or reduced, would lead to a lowering of fitness for individuals in at least one of the species.

Ordination Mathematical system for categorizing communities on a graph so that those that are most similar in species composition appear closest together.

Osmoregulation Regulation of the salt concentration in cells and body fluids.

Osmosis Diffusion of water across a semipermeable membrane.

Osmotic pressure The tendency of water to move across a semipermeable membrane into a solution.

Outbreeding In which genetically dissimilar organisms mate with each other.

Overcompensating density dependence Density dependence that is so intense that increases in initial density lead to reductions in final density.

Overexploitation Exploitation of (removal of individuals or biomass from) a natural population at a rate greater than the population is able to match with its own recruitment, thus tending to drive the population towards extinction.

Overgrowth competition Competition amongst sessile organisms where the mechanism is the growth of one individual over another, preventing the efficient capture of light, suspended food or some other resource.

Palaeoarctic The biogeographical region comprising the landmass of Europe and Asia from its northern border to the Sahara and Himalayas.

Pampa(s) The treeless plains of South America, south of the Amazon.

Parallel evolution The evolution along similar lines of systematic groups that had been separated geographically at an earlier stage in their history.

Parasite An organism that obtains its nutrients from one or a very few host individuals causing harm but not causing death immediately.

Parasitoid Insects (mostly wasps and flies) in which the adults are free-living, but eggs are laid in, on or near an insect host (or rarely, a spider or isopod), after which the parasitoid larva develops in the host (itself usually a pre-adult), initially doing little apparent harm, but eventually consuming and killing the host before or during the pupal stage.

Partial refuges Areas of prey habitat in which their consumption rate by predators is less than the average for the habitat as a whole, as a result of the predators' behavioral responses to the prey's spatial distribution.

Passive dispersal Movement of seeds, spores or dispersive stages of animals caused by external agents such as wind current.

Patch dynamics The concept of communities as consisting of a mosaic of patches within which abiotic disturbances and biotic interactions proceed.

Patchiness Where populations of species are patchily distributed.

Patchy habitat A habitat within which there are significant spatial variations in suitability for the species under consideration.

Pathogen A microorganism or virus that causes disease.

Perfectly substitutable resources A pair (or more) of resources, where either resource can wholly replace the other.

Permafrost Layer of permanently frozen soil.

Permanent wilting point The condition of a soil in which water is sufficiently unavailable to cause plants growing in it to wilt irrecoverably.

Perturbation approach In community ecology, an experimental approach in which artificial disturbances are used to unravel species interactions.

Pest species Simply: any species which we, as humans, consider undesirable. More explicitly: a species which competes with humans for food, fiber or shelter, transmits pathogens, feeds on people, or otherwise threatens human health, comfort or welfare.

Petiole The stalk of a leaf.

pH A scale of acidity (1–7) or alkalinity (7–14) derived from the logarithm of the concentration of hydrogen ions (10^{-1} to 10^{-14}).

Phagocyte White blood corpuscle capable of destroying harmful bacteria.

Phenology Strictly the study of periodic biological events; in practice often applied to periodic phenomena themselves, such as the lifetime pattern in an organism of growth, development and reproduction in relation to the seasons.

Phenotype A visible, or otherwise measurable, physical or biochemical characteristic of an organism, resulting from the interaction between the genotype and the environment.

Phenotypic plasticity The ability of a single genotype to express itself in different ways in different environments.

Pheromones Chemicals released, usually in minute amounts, by one animal, that are detected by, and act as a signal to other members of the same species.

Philopatry 'Home-loving' behavior, i.e. a tendency not to disperse from the natal environment (where the organism was born).

Phloem A plant tissue in the veins (vascular bundles) of plants that is responsible for most of the transport of organic solutes.

Photon flux density A measure of incoming solar radiation.

Photoperiod Length of the period of daylight each day.

Photosynthate The energy-rich organic molecules produced during photosynthesis.

Photosynthesis Utilization of the energy of sunlight to combine carbon dioxide and water into sugars.

Photosynthetic capacity The rate of photosynthesis when incident radiation is saturating, temperature is optimal, relative humidity is high, and carbon dioxide and oxygen concentrations are normal.

Photosynthetically active radiation (PAR) Those wavelengths in the spectrum of radiation that are effective in photosynthesis.

Phyletic lines Links drawn between present and past groups of organisms which imply their evolutionary relationships and derivation.

Phyllosphere The microenvironment on or in the immediate neighborhood of a leaf.

Phylogeny Evolutionary history of a taxonomic group.

Physiological time A measure combining time and temperature and applied to ectothermic and poikilothermic organisms, reflecting the fact that growth and development in particular are dependent on environmental temperature and therefore require a period of time temperature rather than simply time for their completion.

Physiology Study of the internal processes and activities of organisms.

Phytoaccumulation Where a contaminant is taken up by particular plants, which are then harvested to reduce contaminant concentrations in soil.

Phytoalexins Complex organic compounds produced by plants in response to infection and that are inhibitors of further growth by the pathogen.

Phytophagous Feeding on plant material.

Phytoremediation The placement of certain specialist plants in contaminated soil to reduce the concentrations of heavy metals and other toxic chemicals.

Phytostabilization Where root exudates of particular plants precipitate heavy metals and thus reduce the ecological damage they might otherwise cause.

Phytotransformation The elimination of a contaminant by the action of plant enzymes.

Placental mammal Mammals that develop a persistent placenta, i.e. all mammals other than marsupials and monotremes.

Pleistocene A geological era lasting from approximately 2 million to 10,000 years ago.

Pliocene A geological era lasting from approximately 5 to 2 million years ago.

Pogonophoran A marine invertebrate of the phylum Pogonophora.

Poikilotherm An organism whose body temperature is strongly correlated with that of its external environment.

Polycentric distribution The presence of a population, species or other taxonomic group in several widely separated places.

Polyclimax theory The idea that succession leads to one of a variety of climaxes, depending on local environmental conditions.

Polymorphism The existence within a species or population of different forms of individuals, beyond those that are the result simply of recurrent mutation.

Polyphagous Consuming a wide range of types of food items.

Polysaccharide A carbohydrate polymer made up of a chain of monosaccharides, e.g. starch, cellulose.

Population A group of individuals of one species in an area, though the size and nature of the area is defined, often arbitrarily, for the purposes of the study being undertaken.

Population cycle Changes in the numbers of individuals in a population which repeatedly oscillate between periods of high and low density.

Population density The numbers in a population per unit area, or sometimes 'per unit volume', 'per leaf' or whatever seems appropriate.

Population dynamics The variations in time and space in the sizes and densities of populations.

Population ecology The study of the variations in time and space in the sizes and densities of populations, and of the factors causing those variations.

Population fluctuations Variations over time in the size of a population.

Population projection matrix A matrix of values, each one of which represents, for each time step, either the probability of individuals in a population passing from one class to another (e.g. from juvenile to adult), or of surviving and remaining in the same class, or the expected number of individuals contributed (usually by birth) from one class to a 'younger' class.

Population pyramid A means of illustrating the age structure of a population diagrammatically, by placing the youngest age class at the base and stacking successive age classes above it.

Population regulation A tendency in a population for some factor to cause density to increase when it is low and to decrease when it is high.

Population viability analysis (PVA) An analysis, generally applied to populations or species in danger of extinction, of the population's chances of extinction.

Potential evapotranspiration *see* **Evapotranspiration**.

Prairie grassland A local, North American, name for the temperate grassland biome.

Precocity Reproduction occurring early in the life and growth of an organism relative to other organisms of the same or related species that, relatively, delay reproduction.

Predation The consumption of one organism, in whole or in part, by another, where the consumed organism is alive when the consumer first attacks it.

Predator An organism that consumes other organisms, divisible into true predators, grazers, parasites and parasitoids.

Prevalence (of abundance) The proportion or percentage of habitable sites or areas in which a particular species is present.

Prevalence of infection The proportion, or percentage, of a population that is infected with a specific parasite.

Prey An individual liable to be, or actually, consumed (and hence killed) by a predator.

Primary productivity The rate at which biomass is produced per unit area by plants.

Production efficiency The percentage of energy assimilated by an organism that becomes incorporated into new biomass.

Productivity The rate at which biomass is produced per unit area by any class of organisms.

Prokaryote A cell lacking a membrane-bound nucleus; a bacterium or cyanobacterium.

Propagule A term used for a structure in a plant (occasionally used for invertebrates) from which a new individual may arise, e.g. seed, corm, bulb, cyst, and which may often also be a unit of dispersal.

Protoplasm Living matter.

Protozoan Single-celled animal.

Pseudo-interference A pattern of declining predator consumption rate with increasing predator density, reminiscent of the effects of mutual interference, but resulting from the aggregative response of the predator.

Pteridophytes A division of the plant kingdom comprising ferns, horsetails, clubmosses and their allies. Plants with true stems, leaves and roots (diploid) reproducing by spores and alternating with a free-living inconspicuous sexual (haploid) generation (prothalli).

Q_{10} The quotient of two reaction rates at temperatures differing by 10°C.

Quadrat A sampling unit used to assess density of organisms.

***r* selection** Selection of life history traits that promote an ability to multiply rapidly in numbers — the traits being, broadly, small size, precocious reproduction, semelparity, a large reproductive allocation and the production of many but small offspring.

Races/subspecies Subdivisions of a species, with clear morphological distinctions and/or limited interbreeding between them, but between which interbreeding is still possible such that they are not separate biospecies.

Radiative evolution An evolutionary process that involves the branching of an evolutionary lineage and so leads to greater systematic diversity.

Ramet An offshoot or module formed by vegetative growth in some plants and modular invertebrates that is actually or potentially independent physiologically, e.g. the runners of the strawberry, the tubers of the potato, the polyps on a colonial hydroid.

Random distribution Lacking pattern or order. The result of (or indistinguishable from the consequence of) chance events.

Rank–abundance diagram A graphic plot of differential abundances of species in a community.

Ranked preference A preference exhibited by a consumer between food items all of which can be classified on the same simple scale (usually energy value).

Rarity *see* **Prevalence (of abundance)** and **Intensity of abundance**.

Realized niche That portion of its potential (fundamental) niche occupied by a species when competitors or predators are present.

Reciprocal predation An interaction between two species (or individuals) in which each preys upon the other, so that the interaction is, in essence, competitive.

Recombination The formation in offspring of combinations of genes not present in either parent. This results from the assortment of chromosomes and their genes during the production of gametes and the subsequent union of different sorts of gametes at fertilization.

Recruitment Additions to a population, either through birth or immigration, or, in the case of net recruitment, the differences between such additions and the losses resulting from death or emigration.

Regression analysis Analysis of the mathematical relationship between two variables.

Regular distribution The arrangement of individuals with respect to each other which has some pattern or order that ensures that they are more widely separated from each other than would be expected by chance.

Regulation *see* **Population regulation**.

Relative humidity Very roughly, the dampness of the air; more correctly, the percentage saturation of the air with water vapor; better still, the mass of water vapor per unit volume of air as a percentage of the same measure for saturated air at the same temperature.

Relict population An often very locally distributed residue from a large population that has declined.

Remoteness In island biogeography, the distance an island is from a mainland source of colonizing organisms.

Reproduction The production of new individuals, usually by sexual means, through the production of a zygote from which the new individual grows; though organisms that fall apart as they grow are often misleadingly said to undergo asexual reproduction.

Reproductive allocation Strictly, the proportion of an organism's available resource input that is allocated to reproduction over a defined period of time; often in practice, the proportion of an organism's mass or volume that is reproductive tissue.

Reproductive cost The decrease in survivorship and/or rate of growth, and hence the decrease in the potential for future reproduction, suffered by an individual as a result of increasing its current allocation to reproduction.

Reproductive isolation The isolation from each other, in space or time, of two parts of a population of which the individuals would be capable of interbreeding were this not prevented by their isolation. Such isolation is believed to be normal precondition for the evolution of new species to occur, especially in animals.

Reproductive output The production of offspring by an individual or population.

Reproductive rate The number of offspring produced by an organism per unit time or over a defined period of time.

Reproductive value The expected relative contribution of an individual to the population of its descendants, by reproduction, now and in the future.

Residual reproductive value (RRV) The expected relative contribution of an individual to its population, by reproduction, for all stages of its life cycle subsequent to the present.

Resilience The speed with which a community returns to its former state after it has been disturbed.

Resistance The ability of a community to avoid displacement from its present state by a disturbance.

Resource That which may be consumed by an organism and, as a result, becomes unavailable to another, e.g. food, water, nesting sites, etc.

Resource depletion zone The region around a consumer in which the availability of a resource is reduced, e.g. the zone around the absorbing surface of a root from which nutrients and water are absorbed.

Resource inhibition Where essential resources become damaging when in excess.

Resource partitioning The differential use by organisms of resources such as food and space.

Resource–ratio hypothesis The proposition that species' dominance at any point in a terrestrial succession is strongly influenced by the relative availability of two resources: often light and a limiting soil nutrient (often nitrogen).

Respiration Any or all of the processes used by organisms to generate metabolically usable energy.

Restoration ecology The science concerned with the deliberate colonization and revegetation of derelict land, especially after major damage from activities such as mining and waste disposal and after land has been released from agricultural use.

Resurgence in pests A rapid increase in pest number, after the immediate impact of a control measure has passed, resulting from adverse effects on the natural enemies of the pest.

Rhizosphere The surface and immediate neighborhood of a root which provides a specialized environment for microorganisms. The term is also used to define the microflora that lives in this region.

Ring-barking The removal of bark and the immediately underlying living tissues from a ring around the stem or trunk of a tree or shrub. This severs the route of transport of leaf products down to the roots.

Ruderal A plant of waste places, usually associated with human disturbance. The word distinguishes this group of plants from 'weeds' which are plants that are a nuisance to human activities — the ruderal is not necessarily a nuisance.

Ruminant Herbivorous mammals such as cows that chew the cud and have complex stomachs containing microorganisms that break down the cellulose in plant material.

Salt pan A basin or pool containing an accumulation of salty water or salt.

Saprophyte An organism that carries out external digestion of nonliving organic matter and absorbs the products across the plasma membrane of its cells (e.g. fungi).

Savanna The tropical grassland biome.

Scramble competition The most extreme form of overcompensating density dependence in the effect of intraspecific competition on survivorship where all competing individuals are so adversely affected that none of them survive.

Searching efficiency The instantaneous probability that a given predator will consume a given prey (also called 'the attack rate').

Secondary pest outbreaks When natural enemies of potential pests are strongly affected (typically by chemical pesticides), allowing potential pests to become actual pests.

Secondary productivity The rate at which biomass is produced per unit area by heterotrophic organisms.

Seed bank The population of viable dormant seeds that accumulates in and on soil and in sediments under water.

Selective pressure A force acting on populations that determines that some individuals leave more descendants (or genes) than others to subsequent generations (and so gives direction to the process of evolution).

Self-limitation A process where intraspecific competition leads to a reduction in reproduction and/or survival at higher densities.

Self-thinning The progressive decline in density which accompanies and interacts with the increasing size of individuals in a population of growing individuals.

Semelparity Where organisms produce all of their offspring in a single reproductive event over one relatively short period.

Senescence The gradual and ininevitable deterioration, with age, in the condition of an organism until it is demonstrably less fecund and able to survive than it was earlier in its life.

Serotiny The retention by a plant (usually by trees) of seeds in hard enclosing structures, e.g. ovaries or cones so that they are not dispersed and free to germinate until after some disaster, especially forest fire.

Serpentine soil Soil formed by the weathering of serpentine rock that contains high concentrations of various heavy metals. Serpentine soils are commonly localized and bear a specialized flora of species tolerant of these metals and of locally specialized 'ecotypes' of species that are also found elsewhere.

Sessile organism Literally a 'seated' organism. One whose position is fixed in space except during a dispersal phase, e.g. a rooted plant, barnacles, mussels (*Mytilus*), corals.

Sexual recombination The process by which DNA is exchanged between homologous chromosomes by chromosome pairing and crossing-over at meiosis during gamete formation.

Shredders Aquatic animals that feed on coarse particles of organic matter.

Sigmoid curve An 'S-shaped' curve in which there is an initial acceleration phase followed by a subsequent deceleration phase leading to a plateau.

Silurian A geological era lasting from approximately 438 to 408 million years ago.

Skewness A frequency distribution that is not symmetric, i.e. the peak is notably displaced towards either the left or the right.

Social facilitation An increase in consumption rate with increasing consumer density, resulting, for instance, from an increased time available for feeding when less time is required for vigilance against predators.

Somatic polymorphism The presence on the same genetic individual (genet) of organs of two or more different forms, e.g. several different leaf shapes on the same plant, two distinct types of seed produced on the same flower or inflorescence, modules of very different form in the body of a salp.

Speciation The process by which two or more new species are formed from one original species.

Species–area relationship A common pattern in which the number of species on islands decreases as island area decreases.

Species-deletion stability Tendency in a model community for the remaining species to remain at locally stable equilibria after a species is made extinct.

Species diversity An index of community diversity that takes into account both species richness and the relative abundance of species.

Species richness The number of species present in a community.

Species turnover When new species continually colonize (usually an island) whilst others become extinct, such that the total number of species remains roughly constant.

Spiracle A hole in the sides of insects through which the tracheal respiratory system connects with the exterior, and which can be opened and closed.

Stable equilibrium In an ecological context, a level of a population, or populations, or of resources, which is returned to after slight displacements from that level.

Stable limit cycles A regular fluctuation in abundance, the path of which is returned to after slight displacements from the path.

Standing crop The biomass of living organisms within a unit area.

Static life table A life table constructed from the age structure of a population at a single moment in time.

Steppe Treeless plains of southeastern Europe and Siberia.

Stochastic forces Random processes that affect community structure.

Stock assessment Quantitative predictions about the response of a harvested population to alternative management choices.

Stoichiometry The science concerned with mass balance of chemical elements as they move through food webs.

Stoloniferous Bearing stolons.

Stolons Horizontally growing, short-lived, stems that root at the nodes. Usually at or on the surface of the soil.

Stoma (***pl.* stomata**) Pore in the epidermis of plants through which gas exchange takes places; especially abundant on leaves.

Stress Physics has a strict definition of 'a force per unit area' and producing 'strain' in the body to which the force is applied. Biology has a wide variety of meanings, e.g. any condition that results in reduced growth, any condition that prevents an organism from realizing its 'genetic potential'. The word is often redundant, e.g. the effects of drought stress/the effects of drought. The word is also often used confusingly in two senses, both to describe force and the condition induced in the organism by the force — a confusion of stimulus and response. We have tried not to use the word.

Structural diversity Range of types of physical structure in a community that may provide habitats for species.

Stylet Slender, elongated mouth part, usually of an insect, used for stinging or piercing prey or sucking sap.

Subpopulation Spatially separate portions of a species' population, between which there is only limited dispersal compared to the rate of dispersal within them. A group of subpopulations is often referred to as a metapopulation.

Succession The nonseasonal, directional and continuous pattern of colonization and extinction on a site by populations.

Succulents Plants with fleshy or juicy tissues with high water content characteristic of desert and saline environments.

Superorganism concept The view of communities as consisting of member species that are tightly bound together both now and in their common evolutionary history.

'Supertramp species' Species with good colonizing ability that arrive earliest in a new habitat.

Surplus yield model A simple model of the impact of harvesting on a population, in which the population is represented by its size or biomass, undifferentiated into any internal structure.

Surplus yield models Simple models of harvesting from which all complications of population structure are omitted.

Surrogate resource A resource, not in itself in limited supply, which is competed for because of the access it provides to some other resource, which is or may become limited in supply.

Survivorship The probability of a representative newly born individual surviving to various ages.

Survivorship curve A plot of the declining size of a cohort, or presumed cohort, as the individuals die, usually with time on the horizontal axis and $\log_{10} l_x$ on the vertical axis (where l_x is the proportion of the original cohort still alive).

Sustainability Where an activity can be continued or repeated for the foreseeable future.

Switching Of a predator, the tendency to switch between prey categories according to their relative abundance in the environment.

Symbiosis A close association between the individuals of pairs of species. The term 'mutualism' is reserved for symbioses for which there is evidence that the association brings mutual gains.

Sympatry The presence of two or more species living in such proximity that breeding between them should be possible, though their continued existence as separate species indicates that it does not normally happen. This contrasts with allopatry in which regional or geographical isolation normally denies the possibility of interbreeding.

Synergism The situation in which the combined effect of two forces, e.g. treatment with two drugs, is greater than the sum of their separate effects.

Taiga The coniferous forest that extends across much of North America and Eurasia bounded by tundra to the North and by steppe to the south.

Tannins Complex astringent substances containing phenolic compounds found in plants and usually making the plant material less readily digested. Especially common in bark, unripe fruits and galls on woody plants.

Target pest resurgence When treatment (typically with a chemical pesticide) affects a pest's natural enemies such that on removal of the treatment, and in the continued absence of the natural enemies, the pest reaches even higher abundances than those before the treatment.

Taxonomy The study of the rules, principles and practice of classifying living organisms.

Tectonic plate An area of the earth's crust which moves during geological time resulting in continental drift and other major changes in the topography of the surface of the globe.

Temperature coefficient *see* Q_{10}.

Temperature–size rule The observation that the final size of an organism tends to decrease with rearing temperature.

Temporal variation Variability in conditions, such as temperature, on an hourly, daily or seasonal basis.

Terpenoids Aromatic hydrocarbons formed by many plants and responsible for many of the plant scents.

Territoriality The establishment by an animal or animals of an area from which other individuals are partially or totally excluded.

Tertiary A geological era lasting from approximately 65 to 2 million years ago.

Thermoneutral zone The range of environmental temperatures for an endotherm over which it has to exert the minimum metabolic effort in order to maintain a constant body temperature.

Thinning line The line on a plot of log mean individual weight against log density along which self-thinning populations of a sufficiently high biomass tend to progress, and beyond which they cannot pass.

Third generation insecticides Synthesized, usually organic insecticides, which are nevertheless produced with the aim of minimizing the impact on non-pest, non-target species.

Tiller A branch formed at or near ground level by grasses and sedges.

Time-delay population model A model of population growth in which the net reproductive rate of individuals currently is determined by the population size some time previously.

Time series analysis The statistical analysis of a series of equivalent observations taken at a succession of points in time. In ecology, these are usually repeated observations of the abundance of a population, and the analysis seeks to shed light on the pattern of abundances.

Tolerance (successional) Where modification of the environment by early occupants has little or no effect on subsequent performance of late-successional species.

Topography Representation of the physical structure of an environment.

Traits Life history characteristics of species such as body size, fecundity, growth rate and niche breadth.

Transfer efficiency Efficiency with which energy is passed through various steps in the trophic structure of a community.

Transgenic An organism containing a gene which has been artificially transferred from a member of another species.

Transient polymorphism The occurrence of two (or more) forms of a species or of genes (alleles) within a population while one form is being replaced by another.

Transmission threshold The basic reproductive rate of a parasite that is a necessary condition for a disease to spread.

Transpiration The evaporation of water from a plant surface.

Triassic A geological era lasting from approximately 250 to 213 million years ago.

Trichome Single- or many-celled outgrowth from the epidermis of a plant. A plant hair.

Trophic cascades Food web interactions where the effects of top predators on their prey cascade down to lower trophic levels.

Trophic level Position in the food chain assessed by the number of energy-transfer steps to reach that level.

Trophic structure The organization of a community described in terms of energy flow through its various trophic levels.

True predator A predator that kills other organisms (their prey) more or less immediately after attacking them, killing several or many over the course of its lifetime.

Tundra The biome that occurs around the Arctic circle, characterized by lichens, mosses, sedges and dwarf trees.

Turbulence Fluid flow in which the motion at any point varies rapidly in direction and magnitude.

Turgor The distention of living tissue due to internal pressures.

Undercompensating density dependence Density dependence in which death rate increases, or birth or growth rate decreases, less than initial density increases, so that increases in initial density still lead to (smaller) increases in final density.

Unit leaf rate The dry weight increment made by a plant over a period of time expressed as a function of the plant's leaf area.

Unitary organisms Those that proceed by a determinate pathway of development of a tightly canalized adult form, e.g. all arthropods and vertebrates. The contrast is with **modular organisms** in which growth occurs by the indeterminate iteration of repeated units of structure (modules).

Unstable equilibrium In an ecological context, a level of a population, or populations, or of resources, from which slight displacements lead to larger displacements.

Vacuole Membrane-bound, fluid-filled sac within the cytoplasm of a cell.

Vector (i) Any agent (living or otherwise) that acts as a carrier for a pathogenic organism and transmits it to a susceptible host. (ii) A physical quantity with a direction as well as a strength.

Veldt Open pastureland in South Africa.

Vesicular arbuscular mycorrhiza (VAM) An intimate and perhaps usually mutualistic association between a fungus and a plant root in which the fungus enters the host cells and also usually extends widely into the surrounding soil (*cf*. **Ectomycorrhiza**).

Vital attributes (species) Properties of species that determine their place in a succession.

Weed species Plants that threaten human welfare by competing with other plants that have food, timber or amenity value.

Zero isocline or **zero net growth isocline (ZNGI)** An isocline along which the rate of population growth is zero.

Zonation The characteristic distributions of species along environmental gradients.

Zygote Diploid cell resulting from the fusion of female and male gametes.