POPULATIONS, SPECIES AND COMMUNITIES

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Summary

Biologists deal with a dynamic rather than a static system. Thus, they are not only interested in describing the status quo of organisms (specific cases) but are eager to understand and to describe the processes governing evolution (general principles). This dual ambition requires that, when interpreting biological data, the questions asked should always be framed in a specific context. For this purpose, a precise terminology of entities in which evolutionary changes can occur is desirable. This is certainly true for concepts of populations, species and communities. A pure phenetic description of organisms might be sufficient to describe the status quo but will not allow us to understand the dynamics of a population, a species or a community. Populations are the reproductive units of a species in which intraspecific selection processes take place.

Populations of a species are temporarily and spatially varying heterogeneous subgroups, and some can even be the origin of new speciation processes. A species is the more inclusive unit of inheritance within which the species-specific information transmitted from one generation to the next is fairly stable. Communities build the frame for the evolution of a species. Together with abiotic environmental factors, the interactions among species determine the fate of each species but also that of the entire community. However, the enormous diversity of organisms makes it impossible to deduce definitions for the units of evolution that will apply for any particular case in nature. In this contribution, various concepts of populations, species and species community are reviewed. In addition, basic mathematical models that describe evolutionary mechanisms and principles influencing natural societies are presented. The shortcomings of general concepts are highlighted. Several examples will illustrate the constant need to adjust such general concepts to the specific requirements of a particular investigation and the need to always specify the underlying assumptions.

1. Introduction

> *"The natural laws by which the number of species in the natural kingdoms is preserved, undestroyed, and their relative proportions kept in proper bounds are objects extremely worthy of our attentive pursuit and researches"*
>
> (Carl Linnaeus).

Biological systems can be described at different hierarchical levels of complexity from molecules to ecosystems. Biological structures are usually grouped into categories that are defined by a certain degree of similarity. To analyze the evolutionary processes that shape such structures, it is necessary to systematically describe their variety in nature.

The Swedish naturalist Carl Linnaeus (1707-1778) is considered the founder of modern systematic botany and of scientific nomenclature. He began to group the plant kingdom systematically on the basis of the character and number of reproductive structures. In the same century, the natural principles responsible for biological diversity also evoked increasing interest. It was recognized that characters giving individuals a selective advantage over others were more likely to be transferred from one generation to the next. In 1809, Chevalier de Lamarck (1744-1829) proposed an evolutionary theory that assumed the inheritance of characters. However, Lamarck was criticized because, in his fourth evolutionary law, he postulated that the use or disuse of traits during the lifespan of individuals has an impact on their inheritance. Today, most biologists refer to this idea as *Lamarckism*. In 1859, Charles Darwin published *The Origin of Species by Natural Selection*. Darwin's evolutionary theory, the so-called *Darwinism*, is based on inheritable characters of individuals that favour or disfavour the survival and reproduction of their carriers. It took another seventy years before Sergej S. Chetvernikov, in 1926, suggested that, in order to understand evolutionary mechanisms, the genetics of individuals had to be considered in the light of the population in which they were living. Indeed, between 1900 and 1940 many of the most important theoretical fundamentals, that have been decisive for our understanding of ecological and evolutionary processes, were discovered. The introduction of simple mathematical models that describe the dynamics of genes in populations and ecological interactions among individuals within populations, as well as among species, into evolutionary theories led to the so-called Modern Synthesis.

What is the basic unit of ecological and evolutionary processes? This question concerns biologists even today. Is it an individual, a group of individuals, a population, a species, or a community of species? Some authors have taken radical views and challenged the traditional opinion that evolutionary processes can be explained at the group or population level. In 1989, for example, Richard Dawkins suggested that DNA is a selfish molecule and as such its only reason to exist is its most efficient replication. In such a scenario, individuals would be merely the containers of DNA required for replication.

Regardless of such points of view, one has to define precisely the functional units that are considered in ecology and evolution. Beyond the scientific interest itself, this is most important in order to develop optimal strategies in species' conservation and understand our own impact on natural systems. This chapter summarises the various concepts of populations, species and communities applying examples from plant and animal species. The last section will focus on interactions among species such as food webs, predator-prey interactions, and host-parasite interactions.

2. Populations and Species

> *"And no such study (of species) will be constructive unless based on a sound species concept. This is the reason why a deep understanding of the nature of species is of such utmost importance"*
>
> (Ernst Mayr).

2.1 The Species Concept

Numerous approaches have been taken to define the term ‘species’. Some attempts intended to find the most inclusive species definition while others focused on the applicability of the term. The following list will point out some major concepts but is far from being complete (see *Evolution and the Species Concept*).

1. The **Phenetic Species Concept** groups organisms together on the basis of their resemblance with one another.
2. The **Biological Species Concept** defines a species as a group of individuals on the basis of reproductive isolation. Individuals of a certain species can reproduce and have fertile progeny but are reproductively isolated from other species.
3. The **Recognition Species Concept** considers sexual organisms as does the Biological Species Concept. It defines a species as *“the most inclusive population of individual biparental organisms which share a common fertilization system”*.
4. The **Ecological Species Concept** assumes that organisms are adapted to the resources they exploit and the habitats they occupy. Clusters of phenetically similar organisms are expected to result from ecological processes controlling the division of resources.
5. The **Cohesion Species Concept** that defines a species as *“the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability”*. Individuals may have the ability for sexual reproduction and/or *“all individuals in a*

population display exactly the same ranges and abilities of tolerance to all relevant ecological variables".

6. The **Phylogenetic Species Concept** considers the evolutionary history of species and defines a species as *"an irreducible (basal) cluster of organisms, diagnostably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent"*.

Obviously, some species definitions listed above differ only slightly but all of them have some disadvantages. They are either very general or do not apply to all organisms. Thus, one has to specify which of these species concepts is referring to before interpreting scientific results. The Biological Species Concept and Recognition Species Concept, for example, cannot be applied to organisms that do not reproduce sexually but certainly offer a solid basis for hypotheses when studying biparental organisms. Other concepts, such as the Phylogenetic Species Concept, are more relevant to clonal organisms because they help avoiding the pitfall of defining each clonal lineage as a separate species. Accordingly, the criteria of the Biological Species Concept are too strict for closely related species that hybridise frequently in nature and produce fertile progeny.

The European weevil species *Otiorhynchus scaber* for example, consists of different groups of individuals that reproduce either sexually or asexually. The latter can be divided into different chromosomal lines. In this case, the Phylogenetic Species Concept is the concept of choice. Despite all differences, the clonal lineages are most likely to have evolved through hybridisation between related sexually reproducing species and, therefore, form a single evolutionary unit.

To overcome difficulties in differentiating between 'similarity among individuals' and 'similarity among groups of individuals', the "subspecies" is sometimes introduced into a classification system as an intermediate taxonomic rank. Ernst Mayr refers to a subspecies as a "*geographically defined aggregate of local populations which differ taxonomically from other such subdivisions of the species*".

The taxonomic status of Neanderthals, for example, is still controversially discussed but may serve as an excellent example. It is still unclear whether Neanderthals represent a separate species within the genus *Homo*, *H. neanderthalensis*, or rather a subspecies of *Homo sapiens*, *Homo sapiens neanderthalensis*, or even a geographical variant of *Homo sapiens*. Skeletal remains found in Kebara (Israel) and Jebel-Qafzeh (Israel) indicate that both taxa coexisted for several ten thousands of years.

However, these finds only indicate the coexistence of different individuals. A critical issue in this context is the question whether Neanderthals had the ability to interbreed with *Homo sapiens* individuals. Recent molecular genetic studies provided new evidence in support of the hypothesis that both (sub-) species were reproductively isolated and did not hybridise. It was possible to recover authentic DNA from some Neanderthal fossils and retrieve the nucleotide sequences of parts of mitochondrial DNA. The data indicate that the mitochondrial DNA lineages of Neanderthals and anatomically modern man separated roughly 500 000 years ago.

Pitfalls in conservation programmes of Tatra Mountain ibex (*Capra ibex ibex*) in the former Czechoslovakia, illustrate the problems in defining species, subspecies or local populations from a more applied point of view. The native ibex population became extinct through extensive hunting. Later, some specimens from Austria could successfully be introduced and subsequently gave rise to a new population. Some years later, this small population was mixed with individuals introduced from Turkey (*C. ibex aegagrus*) and from Sinai (*C. ibex nubiana*).

The fertile hybrids, however, had offspring in February, the coldest month of the year in the northern hemisphere. The new-borns did not survive these conditions and, consequently, the population became extinct. In their conservation efforts, biologists had focused exclusively on the reproductive ability of *Tatra ibex* and had neglected the local adaptation of the (sub-) species, acquired during its evolution.

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Biographical Sketches

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