

Some may confound recombination and synthesis. A synthesis brings a new interpretation, a personal or stylistic achievement. The difference is most clear in history. Arnold J. Toynbee's theory of history and Hobsbawm's *The Age of Empire* are syntheses. Fernand Braudel's *The Mediterranean World* is a recombination of segments of social sciences, largely history and geography. Perry Anderson's *Lineages of the Absolutist State* is largely synthesis, whereas Karl Wittfogel's *Oriental Despotism* is largely recombination. The recombinations are varied. Child development includes developmental physiology, language acquisition, and socialization. Indo-European studies encompass segments of historical linguistics, archeology, prehistory, and botany. Scholars in criminology come from subfields in law, sociology of deviance, social psychology, endocrinology, urban studies, social economics, and ethnopolitics. The study of artificial intelligence encompasses formal logic from philosophy, grammar and syntax from linguistics, and computer programming from computer science. Folklore studies includes sectors from historical linguistics, cultural anthropology, social history, and comparative literature.

In one generation the number of social scientists has increased 10-fold. Their status in the profession depends mostly on their contribution to knowledge, and much less on their performance as teachers. As teachers they are generalists, as researchers, specialists. A strong feeling of diminishing marginal returns is perceived among the mass of social scientists. This phenomenon of saturation and overcrowding has been called the 'paradox of density': the tendency of densely populated disciplines to produce less innovation per head in spite of the greater effort applied in these overcrowded domains (Dogan and Pahre 1990, p. 32). What is perceived by some scholars as 'dispersion' and 'disintegration' should be considered as manifestations of the growth of specialties, resulting in the weakening of the saturated disciplinary core, a process engendered by centrifugal and autonomous tendencies of the specialties across disciplines. The recombination of specialties across disciplines requires a remodeling of the intellectual map of the behavioral social sciences.

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Species and Speciation

At first glance, 'species' should be a relatively easy term to define: a group of organisms sharing a common biological lineage. Yet biologists have argued over the details of the definition since around 1900. This is in large part because the definition inevitably reflects concepts about processes resulting in the formation of species (or speciation), which lie at the heart of Darwinian evolution. Those speciation processes also underlie observed patterns of biodiversity in both space and time.

1. Species Concepts

Species concepts proposed since around 1950 may be broadly grouped into three categories: typological (based on shared traits), biological (based on breeding habits), and evolutionary (based on lineage) concepts. In the first case, the goal is usually a definition that follows taxonomic practice in species descriptions. The second and third categories reflect ideas about the speciation process.

1.1 Typological Species Concepts

Typological species concepts are based on the premise that a group of individuals of one 'type,' sharing a list of traits, constitute a species. This set of species concepts includes the phenetic species concept (Sokal and Crovello 1970) and the genotypic cluster definition (Mallet 1995). In these cases, species are individuals sharing well-defined clusters of traits, with few to no individuals with intermediate traits. Some versions of what are usually referred to as phylogenetic species concepts (e.g., Cracraft 1983) also fall into the typological category, as species are defined by clusters of shared traits, although individuals are also grouped by population or lineage (for asexual organisms).

Traits may be genotypes or phenotypes; that is, the genes possessed by an organism or the characters resulting from the expression of those genes. However, as its name implies, the genotypic cluster definition focuses on genotypes. Phenotypic traits are commonly measured as length, width, etc., of some body part, or as proteins separated and visualized on a gel. Genotypic traits tend to be quantified as DNA or RNA base sequences. For example, bacterial species that cannot be grown in the laboratory are often described based on their DNA differences and similarities.

Taxonomists routinely use these typological species concepts when they identify individual organisms to species. The definitions have the advantage that they can be applied to almost any organism, dead or alive, fossil or recent. All one needs to be able to do is to make measurements of the phenotype and/or the genotype of the organism in question. However, this is also the disadvantage: one has to choose appropriate traits to measure, which will highlight the differences and similarities among individuals.

1.2 The Biological Species Concept and Its Relatives

The biological species concept states that species are populations of interbreeding organisms. This concept, strongly espoused by Mayr (1942), was dominant until the 1980s. It continues to be widely cited.

The initial formulation of the biological species concept focused on reproductive isolation and hence restriction of gene exchange between species. The inverse of inter-specific reproductive isolation, use of

shared mate recognition and fertilization systems within a species, was later put forward by Paterson (1985). For example, two species of frogs could be discriminated upon based on their inability to produce viable offspring, or alternatively by shared mating calls and ability to produce viable offspring within each species.

Some relatively obvious difficulties arise in applying this species definition to individual cases. First, the requirement for interbreeding makes the application to asexual or clonal organisms impossible. Second, many populations are geographically separated and it is not known whether they could interbreed or not if they were brought together in the same place. Third, application to the fossil record is nearly impossible, as the probability of finding two fossil organisms interbreeding is exceedingly low, and even if that were to occur, the question of viable offspring remains. Nonetheless, the concept is useful as an embodiment of the necessity for restricted gene exchange between species.

1.3 The Evolutionary Species Concept and Its Relatives

Evolutionary species concepts place weight on defining species based on organisms' historical or evolutionary lineage. These concepts arose initially out of the recognition that species do occasionally interbreed. Interbreeding results in movement of genes from individuals of one species into the gene pool of another (introgression), but in some cases, species maintain their morphological and ecological distinctness even in the face of gene introgression. Definitions by Simpson (1951) and Wiley (1978) focused on species as lineages that have their own evolutionary histories and fates.

Most phylogenetic species concepts also fall under this heading. A species is defined as those organisms within a lineage between the initial splitting off of the species (cladogenesis) and either extinction of the lineage or further cladogenesis (e.g., Hennig 1966). The idea has been refined further to assert that such lineages must be monophyletic (derived from one common ancestor). However, the observation of gene introgression suggests that while individual traits in a species may be monophyletic, it is unlikely that all traits will be.

In practice, application of these species concepts requires knowledge of evolutionary history, which at present is obtained through comparisons of traits and constructions of cladograms (or genealogical trees) representing phylogenetic hypotheses. The data used are thus similar to that described in Sect. 1.1.

1.4 Pluralistic Views of the Species Concept

While broader conceptualizations of species may be unwieldy in terms of the data required to define a set of

individuals as a species, such concepts have been put forward as more realistic and defensible. Templeton (1989) offered a cohesion species concept, which defines species based on a combination of factors promoting genetic divergence between populations along with those promoting genetic similarity within populations, and includes factors that limit the spread of variation through genetic drift or natural selection. This concept combines biological species and recognition concepts outlined above with a more explicit incorporation of evolutionary processes. Identification of species starts with identification of an evolutionary lineage (as in evolutionary species concepts), followed by tests of reproductive isolation or mate recognition systems, and culminating with examination of the uniformity of selection regimes or ecological adaptations within groups.

1.5 Remaining Problems with Species Concepts

Most of these discussions of species assume that species are now formed as well-defined entities. This is clearly not the case for any of the definitions or concepts presented in Sects. 1.1–1.4. We can identify races and sub-species, which eventually may form species, using the typological approach; hybrid zones between species challenge the biological species approach; and gene introgression poses problems for monophyly. As a result, further refinement of the species concept is likely in the future.

2. Speciation Mechanisms

In practice, speciation occurs through formation of barriers to gene exchange between groups of organisms, concurrent with or followed by genetic differentiation of the groups.

2.1 Pre- and Post-zygotic Barriers to Gene Exchange

The barriers to gene flow are often lumped into two classes: pre-zygotic and post-zygotic mechanisms, named depending on whether they occur before or after the uniting of the gametes to form a zygote. Pre-zygotic mechanisms include all the factors associated with mate location, courtship, and mating, either behavioral or morphological. They also include the process of gamete union to form a zygote. Post-zygotic mechanisms include hybrid inviability or sterility. In general it is believed that even though post-zygotic mechanisms may initially isolate two species, selection should favor the development of pre-zygotic mechanisms whenever variation allowing that development occurs. This is because the investment by individuals in a hybrid offspring is higher if only post-zygotic mechanisms are in place.

2.2 Specific Barriers to Gene Exchange

Specific barriers to gene exchange include morphology, behavior, and genetic and cytoplasmic incompatibility. The first, morphology, has been well documented in a number of insect-pollinated plants. The location of the anthers (pollen bearing structures) relative to the nectaries combined with the body size and shape of the insects determines whether visiting insects actually brush against the anthers and hence transport pollen to other flowers.

Speciation may also involve behavioral divergence between two groups. Behavioral changes involved in speciation are usually associated with courtship and mating rituals. For example, species' differences in mating calls occur in frogs and crickets. Pheromones, or chemicals used to communicate between individuals, may also change. Moths, butterflies, and flies, for instance, use pheromones as integral parts of mate attraction or courtship. The chemical composition of the pheromone mix is generally species-specific. Species may also be isolated by differences in the timing of courtship and mating either within the year or within the day. Seventeen year and 13 year cicadas are an extreme example of such temporal isolation. These cicadas develop underground, emerging as adults to mate at the end of a 17 or 13 year lifespan, depending on the species. Each of three species of 17 year cicadas in the USA has a corresponding very similar 13 year cicada species. Yet, 17 and 13 year cicadas will only overlap as adults once every 221 years. Finally, species may be effectively isolated if they have different courtship or mating locations. The fruit fly, *Rhagoletis pomonella*, is a classic example. Courtship and mating occur on the fruit tree species where the female will later lay eggs. Initially in USA, hawthorn fruits were used; a new race of the fly moved onto apple in the nineteenth century, and then onto sour cherry in the mid-twentieth century. *Rhagoletis* races on each of these hosts respond to specific odors and color, shape and size cues, effectively isolating them (summarized in Bush 1998).

Genetic incompatibility between species arises in several ways. For example, egg and sperm, or pollen and stigma can possess surface proteins that prevent either fusion of the egg and sperm into a zygote, or pollen tube growth allowing fertilization of the plant ovum. A modification of these incompatibilities is seen in patterns of sperm or pollen precedence within a species, which limit gene exchange and could precede speciation (Howard 1999). Alternatively, once a hybrid zygote is formed, it may have low viability or be sterile. Mating between a horse and a donkey, for example, produces mules, which are sterile. Thus genes from the hybrid mating are not transferred beyond one generation. Empirically, the sex for which survival or fertility is more affected by hybridization tends to be the heterogametic sex (or the sex possessing dissimilar sex chromosomes, commonly called 'x' and

'y' chromosomes), in a phenomenon labeled 'Haldane's Rule' (Haldane 1922). This suggests that genes affecting hybrid sterility might be localized to the sex chromosomes. However, the genetics underlying hybrid sterility have been explored in *Drosophila*, which does show stronger male than female sterility in hybrid crosses. Genes affecting either male or female sterility are spread throughout the genome, and the number involved in male sterility alone sometimes exceeds 100 genes (summarized by Wu and Hollocher 1998).

Genetic barriers may also arise through changes in the number of chromosomes in new species (Ramsey and Schemske 1998). This is particularly common in plants. Gametes (in this case, pollen and ova) generally have a single copy of each chromosome (termed haploid), uniting to give a zygote with two copies of each chromosome (termed diploid). In the case of hybrids between two species, each of the two copies will come from different species, and gamete formation may be impeded because the cells cannot properly divide. Occasionally, however, errors in cell division occur, and diploid gametes are produced. If these form within hybrid individuals, then the resulting tetraploid zygote is completely fertile, as it now contains a complete set of the chromosomes from each of the original parent species. Subsequent gamete formation can proceed normally and the offspring are interfertile, but cannot mate successfully with the parental species. Such polyploidy has been demonstrated for example in the history of both agricultural tobacco and wheat. Other sorts of errors can produce individuals with other chromosome copy numbers; anything greater than diploid is generally called polyploid. No matter what their origin, if polyploid individuals are viable, the gametes they produce cannot usually produce viable offspring by uniting with gametes from their diploid parents.

Cytoplasmic incompatibility occurs when factors in the cytoplasm of the two gametes are not compatible, resulting in the death of the zygote. *Wolbachia* bacteria in insects, which are passed with the cytoplasm from mother to offspring, are one example. Currently, it is believed that males infected with *Wolbachia* produce sperm which must be 'rescued' by a factor in eggs produced by females that are also infected, before viable zygotes are produced. Whether this mechanism has been involved in speciation in the past, or is 'simply' a factor enhancing reproductive isolation at present is not yet established (see Werren 1998 for a review).

2.3 Differentiation: Selection and Chance

Both the development of reproductive isolation and the differentiation of other characters identifying organisms as members of a species could be influenced by selection or by genetic drift. In the former case, adaptation to a particular set of environmental conditions drives speciation. In the latter case, chance

events, such as the genetic diversity present in individuals that become geographically isolated, or that happens to be included when a polyploid individual is formed, influence the results of speciation. The relative influence of these two forces has been the subject of debate; like many polarized debates in biology, most cases probably fall along the continuum between the two ends.

3. Biogeography of the Speciation Process

Evolutionary biologists have historically categorized speciation based on the geographic relationship of the newly evolved species. This classification reflects differences of opinion as to the relative role of geography in reducing gene exchange between putative species. Nonetheless, the actual evolutionary processes underlying speciation may be the same in each of these types of speciation.

3.1 Allopatric Speciation

'Allopatric' derives from 'allo' meaning 'separate' and 'patria' meaning 'country.' Allopatric speciation is thus speciation that occurs through geographic isolation of two populations or groups of populations. In this scenario, a population is split by some geographic barrier, such as a mountain range or river for terrestrial organisms, or a land mass for aquatic organisms. Over time, individuals in populations on each side of the barrier differentiate. This may be due to a founder effect, in which only part of the genetic variability originally present is represented in a new population; to chance loss of genetic variation through accidents of who happens to reproduce or not; or to adaptation to environmental differences on each side of the barrier. This differentiation between the divided populations is extensive enough to include the evolution of differences in reproductive biology, such that when the two populations are re-united by the removal of the barrier, they are no longer able to inter-breed and are viewed as separate species.

Support for the allopatric speciation model increased with the discovery of continental drift and plate tectonics, and the subsequent increased understanding of geologic history. Such continental rearrangement at a deep time level, and geographic changes associated with Pleistocene ice ages in more recent times, provide the geographic variation needed for allopatric speciation. Enhanced understanding of geologic events also provided the opportunity to test expected distributions of species under allopatric speciation through the study of vicariance biogeography, or the geographic distribution of species as a result of subdivision of ancestral species' ranges.

Allopatric speciation has been the dominant geographic model for speciation processes since around 1950, although other models are currently gaining support. This dominance derived from the argument

that development of genetic isolation would most likely occur if incipient species were physically isolated from each other for a time period, allowing the evolution of reproductive isolating mechanisms.

3.2 Parapatric Speciation

'Parapatric' derives from 'para' meaning 'near' and 'patria' meaning 'country.' Parapatric speciation thus occurs when a smaller population is isolated, usually at the periphery of a larger group, and becomes differentiated to the point of becoming a new species. Gene flow may remain possible between the two populations during the speciation process, and hybrid zones may be observed at the interface between the two populations as a result.

The best-known example of incipient parapatric speciation occurs in populations of the grass *Agrostis tenuis* which span mine tailings and normal soils. Individuals that are tolerant to heavy metals, a heritable trait, survive well on contaminated soil, but poorly on non-contaminated soil. The reverse occurs for intolerant populations. Gene flow occurs between sub-populations on and off mine tailings, but hybridization is inhibited by slight differences in flowering time between the two locations (McNeilly and Antonovics 1968, McNeilly and Bradshaw 1968).

3.3 Sympatric Speciation

'Sympatric' derives from 'sym' meaning 'together with' and 'patria' meaning 'country.' Sympatric speciation thus refers to speciation occurring within a single population. Because of the lack of geographic isolation, sympatric speciation was historically regarded by many biologists as being impossible. However, evidence is accumulating that sympatric speciation does indeed occur.

The most obvious mechanism that can result in sympatric speciation is speciation through polyploidy (Ramsey and Schemske 1998). A chance doubling of the chromosome number can lead to reproductive isolation through zygote inviability, without a preceding need for geographic isolation. Given that about half of all flowering plants are polyploid, this form of speciation may have played a large role in their formation.

Hybridization between two species, followed by rapid changes in the hybrid to enhance reproductive isolation from the parents has been held up as a form of sympatric speciation, particularly in plants. While the number of solid examples of this speciation mechanism are few, it does occur (Dowling and Secor 1997, Rieseberg 1997).

Genetic introgression through mechanisms other than hybridization, or genetic rearrangements ('jumping genes') are a potential source of variability

within a population that could lead to speciation, but are essentially unexplored at present.

Small shifts in the ecological niche of individuals within a population are also argued to result in a form of sympatric speciation. The host races of *Rhagoletis* described above are a case in point. Another example is the radiation of species of cichlid fish within small crater lakes in Cameroon (Schliewen et al. 1994). Genetic analysis indicates that the species in each lake derive from a single ancestor. Although species differ slightly in habitat preference, the lakes are small enough that the different fish species are sympatric. In order for this mechanism to be effective, natural and sexual selection would need to act in the same direction. For example, if individuals diverge in resource use, and individuals with similar resource use prefer each other as mates, resource use races will evolve, which may eventually become full species. Note that this form of speciation has conceptual affinities both to the biological species concept (reproductive isolation) and to the recognition species concept (species cohesion).

4. Space: Patterns of Biodiversity Resulting From Speciation

The different modes of speciation outlined above each result in a different spatial pattern of biodiversity. Hybrid zones between newly formed species are the predicted outcome of allopatric speciation, if the geographically isolated populations have not developed full reproductive isolation prior to removal of the geographic barrier. Further, the establishment of a geographic barrier is expected to divide ancestral populations of many species within the flora and fauna of a region. Removal of that barrier and recontact of newly divergent flora and fauna can result in multiple individual hybrid zones that overlap, or suture zones. Such suture zones mark boundaries between regional floral and faunal assemblages. Remington (1968) outlined six major suture zones and a number of minor suture zones in the Nearctic region, including a compendium of known hybridizing pairs of species within each suture zone and an analysis of the likely geographic barriers whose removal resulted in the now-observable suture zone pattern.

Ring species also result from the interaction of speciation with a geographic barrier, but with a twist. As populations of a species expand into new areas, moving around a geographic barrier, they can form a ring around that barrier. While the immediately adjacent populations at each point around the ring interbreed, the terminal populations are reproductively isolated and cannot interbreed. Ring species thus can be thought of as a result of geographically extended parapatric speciation. Irwin et al. (2001) present an outstanding example of a ring species in the case of the greenish warbler (*Phylloscopus trochi-*

loides), whose six sub-species circle the Tibetan Plateau. The sub-species that are sympatric at the ends of the ring in central Siberia do not interbreed. The structure of songs involved in mate choice have diverged due to selection pressures favoring increased song complexity as the species expanded from the southwest around on the eastern and western sides of the plateau, eventually contacting again north of the plateau. Interestingly, there is now a gap in the ring in central China, which is probably due to habitat destruction by humans. The recentness of this gap has not allowed time for song divergence across the gap, but one could predict speciation across the gap in the future.

Sympatric speciation can generate a different pattern of biodiversity, hot spots of endemic species. Endemic species have very localized distributions, being found in one (usually small) area. Such species are not necessarily rare; the localized populations may be quite large. The cichlid fish species assemblages found in the crater lakes of Cameroon and cited above, along with the much richer cichlid diversity in the rift lakes of east Africa, are classic examples of hot spots of endemic species. In Lake Victoria, for example, over 300 species are found, of which very few are found anywhere else.

Overall biogeographic patterns of diversity within a region should therefore reflect the relative dominance of allopatric, parapatric, and sympatric speciation in shaping the flora and fauna. However, these biogeographic patterns are all too easily disturbed by human activities, which include habitat destruction resulting in species extinction and species transport resulting in new mixing of floras and faunas. This disturbance lends urgency to attempts to understand the causes of biogeographic patterns at the beginning of the twenty-first century, before the evidence is muddied by human activity.

5. Time: Speciation Speed

Based on the mechanisms of speciation outlined in Sects. 2 and 3, it is clear that speciation takes variable amounts of time to occur. Speciation via polyploidy, for example, can be nearly instantaneous. Speciation via changes in sexual signals involved in mate choice may be a much more gradual event.

From a lineage perspective, there are two models of speciation rates. First, speciation may occur through gradual change within the lineage, such that over time species 'a' is transformed into species 'b.' Second, lineages may split by either budding off a new lineage while the ancestral lineage remains unchanged, or by branching into two new lineages with the loss of the ancestral lineage. Thus, in the first model, change is slow; in the second, speciation events are rapid and interspersed among periods of no change or stasis. The first model has been dubbed 'gradualism' and the

second, 'punctuated equilibrium' (Eldridge and Gould 1972). Large debates about the relative importance of gradualism and punctuated equilibrium raged among paleontologists throughout the 1970s and 1980s. The debate had a bearing on the role of natural selection and adaptation in speciation, as contrasted with genetic drift or chance founder effects. Supporters of the gradualist position usually argued that natural selection is of overwhelming importance, while supporters of punctuated equilibrium, initially at least, postulated a strong role for founder effects resulting in sub-sampling of the variation present in an ancestral species in a newly geographically isolated population, enhancing the speed of evolution of new species in those isolated populations. Support for both gradualism and punctuation exists in the fossil record, making resolution of the debate difficult. In addition, the time scale of the fossil record is very coarse, making it difficult to determine exactly how saltatorial a lineage might be.

See also: Adaptation, Fitness, and Evolution; Evolution, History of; Evolutionary Selection, Levels of: Group versus Individual; Evolutionary Theory, Structure of; Extinction of Species; Natural Selection; Primates, Evolution of

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Spectral Analysis

Spectral analysis is one of several statistical techniques necessary for characterizing and analyzing sequenced data. Sequenced data are observations that have been taken in one, two, or three dimensional space, and/or time. Examples might be observations of population density along a road, or of rainfall over an area, or of daily births at a hospital. One important limitation is that the observations be equally spaced in order that the analysis proceed efficiently. Spectral analysis refers to the decomposition of a sequence into oscillations of different lengths or scales. By this process, the observations in what is called the data domain are converted into the spectral domain. The reasons for doing this are that: (a) some forms of manipulation are easier in the spectral domain; and (b) the revealed scales are necessary statistical descriptors of the data and may suggest important factors that affect or produce such data. The following will provide brief descriptions of: (a) Fourier analysis and its use in manipulating data that are assumed to be periodic; (b) relevant statistics; and (c) one approach to spectral analysis of nonperiodic data including an example.

1. Fourier or Harmonic Analysis

Here data are represented by y where the position in the sequence is labeled by j , i.e., $y[j]$, where j varies from 0 to $(n-1)$. Because trigonometric functions require radians for their calculation the label j is converted to radians with $2\pi j/n$. What Fourier showed in 1822 was that almost any equally spaced sequence $y[j]$ could be fitted exactly by a set of cosine and sine curves. In addition, since no information was lost, these could be returned to the original data. There was one important assumption, that the data were periodic, i.e., that they repeated themselves both forwards from $(n-1)$ and backwards from 0 indefinitely.

A sinusoidal curve,

$$y[j] = A[k] \cos\{(2\pi k j)/n - \Phi[k]\},$$

as displayed by curve (a) in Fig. 1 is characterized by its frequency label, k , its amplitude, $A[k]$, and phase, $\Phi[k]$. The frequency, k , is the number of complete oscillations that occur over the total observations, n . For curve (a) this is 2. For n observations k may have integer values of 0 to $+n/2$ (n even). Frequency may also be expressed in observational units as $f = k/n\Delta t$ where Δt is the interval between observations. In the example, if y is observed daily for a year, the oscillation at $k = 2$ has a frequency of $f = 2/(365 \times 1 \text{ day}) = 1/182.5$ th of a cycle per day = 2 cycles per year. It also has a wavelength (peak to peak distance) of $1/f = 182.5$ days = $1/2$ year. The highest frequency that may be calculated is $f_{\max} = 1/(2\Delta t)$. The amplitude, $A[2]$, of curve (a) is 0.5. This also provides the variance of the curve, which is half the square of its amplitude, $A^2[2]/2 = 0.125$. The phase $\Phi[k]$, when it is divided by k to give the phase shift, gives the distance of the first peak from the origin. In this case $\Phi[2]/2 = 0.46$. Curve (a) can also be represented by the sum of a simple cosine curve ($y[j] = a[k] \cos(2\pi k j)/n$) as displayed as curve (b) and a simple sine curve ($y[j] = b[k] \sin(2\pi k j)/n$) given by curve (c). From trigonometry we can show that $A[k] = (a^2[k] + b^2[k])^{1/2}$, and $\Phi[k] =$

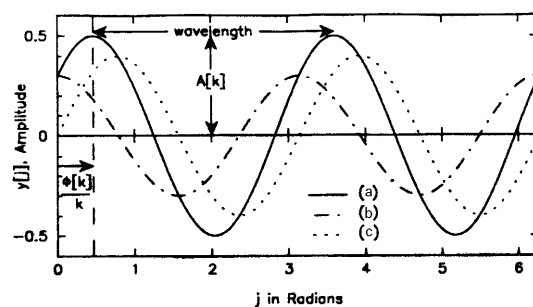


Figure 1

Examples of (a) sinusoidal, (b) simple cosine, and (c) simple sine curves for periodic data

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