

# Conclusions

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What can we conclude from this set of chapter about limits to knowledge in evolutionary genetics? The very question requires that we look into the future and imagine those areas that will be forever refractory to future innovation. This is a daunting task, because we are participants in an era of unparalleled technical innovation in biology. We have seen biology answer questions that seemed beyond the bounds of knowledge a decade or two decades ago. We are confident that the future will replicate the recent past and produce answers to today's seemingly intractable problems. Many of the chapters in this volume reflect this view and reflect the problem of separating the merely difficult from the set of biologically interesting questions that lie beyond the bounds of knowledge.

There are two big questions in biology: How does the organism work and how did it get to be the way it is? The first question is the province of cell, developmental, and physiological biology (and all their specialized descendants), but it is also fundamental to understanding biological adaptation. The second question is the major concern of evolutionary biology. (I include the problem of prediction within this second category.) I think it is fair to say that the larger community of biologists is confident that we will understand how the organism works in exquisite detail. To illustrate how our grasp of this question has changed, I recall as an undergraduate student more than 35 years ago taking introductory biology and finding that the text included a section entitled "what is life." This section included a serious discussion of *elan vital* and the notion that understanding life might involve extraphysical explanations. It is difficult to imagine such a discussion today. We are absolutely committed to the notion that physically based and mechanistic explanations of how the organism works will be obtained. Certainly the recent progress of biology provides a strong basis for such confidence.

The second question of how did life get to its present state is more

problematic (as is the corollary of how do we use our understanding in the prediction and management of biological systems). Our understanding of the past is rooted in the theory of evolution by natural selection. This is a statistical theory, but as noted in different ways by several authors, we have just one realization of the stochastic process of earthbound biological evolution to study, and it is not very informative to apply statistical means to the understanding of a single realization. It seems clear that our understanding of the past and our ability to predict the future will remain hazy and weakly defined. That is not to say that we cannot understand the broad outlines of biological history, but rather that we are unlikely to know the precise historical scenario.

Because of the statistical nature of genetic transmission and natural selection, our theories of the past and future are broad generalizations that do not provide a detailed explanation for the particular outcomes that we study as biologists. A place where this theme of the particular is especially apparent concerns the issue of biological interaction. Biological organisms clearly exhibit strong interactions at the molecular, developmental, and metabolic levels, so there is good reason to believe that interaction also is manifest at the statistical level, but our theoretical tools for studying biological systems are based on the minimization of interaction in the interests of generality and tractability. Several authors discuss the problem of biological interaction in different contexts. Because the biological system is complex, with thousands of actually or potentially interacting components across both the genetic and environmental dimensions, the ability to understand and predict the statistical behavior of these systems is limited.

Let me conclude with one final thought. The triumph of the physical sciences was to deduce a set of laws that govern the behavior of physical systems. This law-bound framework defines the possible. Rosenberg (Chapter 3) argued that evolution, and hence, all of biology, is governed by the law of natural selection and that this is the only law in biology. Despite the fact that the theory of evolution by natural selection is the major unifying law of biology, over the past 25 years, evolutionary genetics has focused a great deal of attention on nonselective causes for molecular evolution. This focus on neutrality has been of value because it has presented a clear and well-defined null hypothesis for statistical analysis, but it also has directed attention away from the central problem of biological adaptation. What a curious detour to have so much attention to be devoted to non-adaptive explanations for molecular diversity. Perhaps this detour reflected the social environment of the times. The notion of subjectivity in science appeared in several chapters in terms of Bayesian priors or in terms of our collective judgment on what constitutes an interesting question. A limit to knowledge may simply be our belief systems and their role in determining the directions that our search for knowledge takes.

# Index

- Adaptation, 2, 74, 81–84, 90, 138–139, 188, 204, 233, 249  
  strategies in study of, 88–90
- Adaptationism, 81–82, 84
- Adaptationist, 78
- Adaptative evolution, 42–48, 205, 230, 235
- Adaptive fixation, 140
- Adaptive haplotype, 114
- Adaptive value of variants, 77
- Adaptive variation, 81
- Additive model of gene action, 203
- Additivity, 211–212, 215
- African–non-African split, 199
- Allele, 183, 186, 196–197, 199, 208, 216, 218–219, 225, 230
- Allelic substitution, 207, 244
- Allozymes, 135–136
- Amechanistic paradigm, 54, 74, 76–81, 91
- Amino acid replacement, 245–246
- Amino acid sequence, 155–160
- Amino acid substitution, 45, 171, 173
- Amino acid variation, 103
- Ancestral character states, 117–134, 144  
  analysis of, 119–133  
  distributions, 120–131  
  modeling, 119–120  
  probability issues, 122–133
- Ancestral disease mutation, 197
- Anthropogenic fragmentation, 188
- Anthropomorphism, 63
- Asexual lineage, 181
- Ateles chamek*, 174
- Ateles geoffroyi*, 174
- Atropy, 83
- Australopithecus afarensis*, 15
- Background effect, 219
- Background selection, 139–140  
  model, 105, 107
- Bacterial chemostats, 144
- Base pair substitution, 142
- Bayesian framework, 113, 117
- Bayes' rule, 119, 121
- Behavioral ecologists, 23
- Behe, Michael, 11  
  antievolutionary argument of, 11
- Best linear unbiased prediction (BLUP), 226
- Beyond reasonable doubt, 11
- Big Bang theory, 13
- Binary character state, 120
- Biogenetic law, 14
- Biological diversity, 35
- Biological generalization, 63, 70  
  use of models, 64–66
- Biological laws, 58, 60–61, 64–65, 68, 85–86
- Biological organization, 2, 49
- Biological understanding, 68  
  historical discipline, 58, 66, 69–71  
  laws of, 58–68  
  limitations to, 53–55  
  paradigm concepts on, 53, 75–76  
  perspectives of, 53, 57–59  
  role of generalization in, 63–70  
  world views on, 75–76
- Biological variation, 20
- Biology as historical discipline, 58, 66, 69–71, 113
- Biotic invasion, 180
- Birds, 7
- Blind variation, 71
- Blood-clotting process, 11
- Breast cancer, 208–209
- Breeders' equation, 229
- Breeding population, 2
- Breeding program, 190
- Breeding value, 226–227
- Bush baby, 154

- Cambrian period, 8, 21  
 Canalization, 90  
 Carboniferous period, 7–8  
 Causality, 58–59, 62, 67–68, 70, 208–209  
 Cenozoic era, 7–8  
*Ceteris paribus* laws, 61–62, 84  
 Chalcone synthase, 43  
 Cholesterol, 208, 220  
 Chronic disease, 205  
 Churchill, Gary, 113  
 Circadian rhythm, 155  
 Circumstantial evidence, 5  
 Clades, 170  
 Cladism, 15  
 Climatic change, 180  
 Coalescence theory, 38–41  
 Coalescent method, 183  
 Coalescent time, 144  
 Coancestry, 199, 201  
 Coancestry coefficient, 199  
 Coding sequence, 164  
 Codon bias, 54, 87  
 Cognitive agent, 59  
 Cognitive particularism, 76  
 Color phenotype, 47–48  
 Color vision, 114, 151
  - evolutionary genetics of primate, 151–175
    - natural selection, 152
    - role of gene conversion, 152
  - evolutionary mechanisms in, 171–172, 175
  - origin in higher primates, 165–171
  - prosimians, 154
- Community ecology, 219  
 Comparative anatomy, 15  
 Comparative genomics, 114  
 Complex reality, 207  
 Conditional probability, 199, 201  
 Congenital deafness, 207  
 Conservation biology, 115, 180, 227, 233  
 Conservation genetics
  - genetic planning in, 181–183
  - goal of, 181
  - modeling in, 185–188
  - movement among reserves, 188–190
  - value of effective population size in, 183–185
- Conservation plan, 184–186, 191  
 Conserved species, 190  
 Covariations, concept of, 246  
 Cretaceous period, 7–8  
 Crossing over, 105  
 Cuvier, Georges, 14
- Daphnia*, 231  
 Darwin, Charles, 3–5, 17–18, 35  
 Demes, 187  
 Demographic plan, 180  
 Devonian period, 7–8  
 Dichromacy, 173  
 Diploid epistasis, 216  
 Diploidy, 215  
 Direct sequence analysis, 136  
 Directional selection, 138  
 Disease liability, 207  
 Disease model, 197  
 Disease resistance, 190  
 Disease risk, 206–208  
 Disease transmission, 190  
 Divergence, 44, 98, 161–163, 165–166, 171, 174–175, 191, 239, 244  
 Diversity enhancement, 138  
 DNA divergence, 245  
 DNA sequence, 39, 97, 102–103, 108, 137, 141, 144, 183, 210  
 Dominance, 211, 227  
 Doolittle, Russell, 11  
 Drift-mutation balance, 186  
 Drift-mutation process, 40  
*Drosophila*, 90, 103–106, 135, 139, 144, 211, 228, 231, 240–242, 244–246
- Ecological method, 184  
 Ediacaran period, 8  
 Einstein, Albert, 100  
 Electromorph frequency, 136  
 Embryology, 14–15  
 Empirical anomaly, 80  
 Empirical exploration, 1  
 Empirical generalization, 64, 66  
 Empirical reality, 53  
 Empiricism, 65–66  
 Endothermy, 86  
 Environmental variability, 84, 207  
 Eocene epoch, 7–8  
 Epidemiological methods, 207  
 Epistasis, 83, 90, 210–211, 217, 219–221, 227  
 Epistatic interaction, 207, 210–212  
 Epoch-limited generalization, 70  
 Equilibrium-neutral model, 143  
*Escherichia coli*, 87  
 European butterfly, 181  
 Evolution
  - adaptation perspectives in, 2, 74, 81–84, 90, 138–139, 188, 204, 233, 249

Evolution (*cont.*)

- alternative theories on, 24–28
- biological laws on, 58, 60–61, 64–65, 68, 85–86
- causes of, 17–20
- critics on, 11–14, 75–77, 80
- culture changes on, 26–27
- effect of sample size on, 114, 125, 143, 209
- embryo comparison—human vs. canine, 10
- experimental study of, 137–138
- fact of, 3–13
  - structure of Darwin's argument on, 5
- genetics on, 100–110, 114, 225, 229; *see also*
  - Conservation genetics; Genetic variance
- human, 22–24, 195–201
- inferring ancestral character states in, 117–134
- limitation of knowledge on, 27–28, 98, 201
- limitations to historical inference on, 113
- macrolevel understanding of, 20–22
- major events of multicellular life, 8
- Markov modeling in, 119–123, 134
- mechanisms of change, 1
- modeling of, 89, 201
- molecular genetic variation on, 19
- moral limitation of, 23
- natural selection perspectives on: *see* Natural selection
- paradigmatic limitations to knowledge on, 73–92
  - amechanistic view on, 76–81
- path of, 14–17
- philosophical limitations to knowledge on, 84–86
- population genetics on: *see* Population genetics
- prospects for knowledge extension on, 86–91
- random external forces on, 25
- role of divergence: *see* Divergence
- role of generalizations in, 239–242, 250
- role of prediction in, 113; *see also* Prediction
- role of time scales on, 90–91
- scientific revolutions on, 97–110
- shifting balance theory of, 18–19
- social behavior on, 18
- social constructivist argument on, 27–28
- societal changes on, 26–27
- stochastic nature of, 138, 201
- study of genetics in: *see* Evolutionary genetics

Evolution (*cont.*)

- theory of, 195
- use of generalities in, 91–92
- use of molecular data in, 135–145
- vertebrate homology, 9
- Evolutionary cooperation, 27
- Evolutionary equilibrium, 196–198
- Evolutionary genetics, 114, 225, 229; *see also*
  - Evolution
    - impact of scientific revolutions on, 100–110
- Evolutionary psychologists, 23
- Evolutionism, 12
- Evolutionist, 12, 19, 24, 77–79, 81, 113
- Exceptionless generalization, 60, 65, 70, 86
- Exon, 47
- Extinction, 180, 188–190
  - risk, 181
- Extinction–recolonization cycle, 187–191
  
- Familial cluster, 205
- Familial disorders, 208
- Familial hypercholesterolemia, 208
- Fecundity, 187, 231
- Fisher's fundamental theorem of natural selection, 77
- Fisher's microvariationism, 77, 80
- Fisher's model, 64
- Fisher–Wright population model, 103
- Fishes, 7
- Fitness difference, 78–79, 81
- Fitness, 82, 86, 104, 107, 183, 189, 215, 217–219, 244–245
- Flavonoid biosynthesis, 43–44, 74
- Flowering plant, 45
- Fluctuating neutral space, 245–246
- Fossil record, 4–5, 7, 11, 14–15, 17
  - table of strata, 7
- Founder effect, 190
- Fragmentation, 185
- Functional biologist, 78
- Functional equivalence, 59
- Functional individuation, 62–63, 71, 85
  
- Galago garnetti*, 154
- Galago senegalensis*, 155
- Galapagos islands, 6
- Game theory, 26
- Gametic disequilibrium, 83
- Gene conversion, 114, 152–153, 161–165, 167, 170, 174–175
- Gene conversion–recombination, 47

- Gene duplication, 44, 165, 171  
 Gene expression, 210, 212  
 Gene flow, 188  
 Gene frequency, 183  
 Gene genealogy, 38  
 Gene mapping, 74, 196  
   human disease, 196–198  
 Gene markers, 197, 209  
 Gene relationships, 46  
 Genealogy, 138  
 Gene–ecological interaction, 48  
 Generalization, 239–242, 250  
 Genesis, story of Creation, 13  
 Genetic bias, 55  
 Genetic defects, 207–208  
 Genetic distance, 45  
 Genetic diversity, 114, 180  
 Genetic drift, 18, 36, 38, 108–109, 181–183,  
   187, 232, 246  
 Genetic fingerprinting, 18  
 Genetic heterogeneity, 207–209  
 Genetic method, 183  
 Genetic planning, parameters of, 181–183  
 Genetic reality, 205  
 Genetic similarity, 38  
 Genetic trait, 206  
 Genetic transmission, 53, 113, 195, 205, 250  
 Genetic variance, 36, 77, 181–190, 205, 217,  
   227, 230–231, 234, 243  
 Genetic–ontogenetic complexity, 38  
 Genome, 106, 136, 139, 142  
 Genomic incompatibility, 233  
 Genomics enterprise, 1  
 Genotype, 54, 74, 78, 82, 143, 180–181, 203,  
   211, 215, 219  
 Genotype–environment interactions, 220–221  
 Genotype–phenotype prediction, 207, 216,  
   220–221  
 Genotype–phenotype–environment interactions,  
   77–78  
  
 Haeckel, Ernst, 14  
 Haldane's rule, 234, 241–242, 247  
 Haplotype diversity, 161  
 Hardy–Weinberg distribution, 83  
 Heat-shock protein, 90  
 Hereditary transmission, 35  
 Heritability, 217, 227, 229–230  
 Heterozygosity, 182, 184  
 Hierarchical model, 199–201  
 Hill–Robertson effect, 103–109  
  
 Historical inference, 1–2, 36–37, 49, 53, 67,  
   114, 135  
 History of life, 21  
   models, 22  
 Hitchhiking model, 104  
*Homo sapiens*, 15  
 Homozygosity, 186  
*Hordeum vulgare*, 41  
 Hudson Kreitman Aguadé test, 103  
 Human cognition, 75  
 Human disease gene mapping, 196  
 Human evolution, 22–24  
   genetic methods in, 209  
 Human identification, 198–201  
   hierarchical model of, 199–201  
 Human nature, evolutionary perspectives of,  
   23–24  
 Human population  
   idealized evolutionary history, 200  
   structure of, 195–201  
 Hybrid incompatibility, 242  
 Hybridization, 233–234, 240  
  
 Identity-by-descent, 38–39  
 Implicit law, 68  
 Inbreeding, 180–181  
   depression, 181, 183, 186  
 Indel, 167  
 Independent interferer, 61–62  
 Inorganic–organic transition, 4, 13  
 Interdemic model, 187  
 Interfering factor, 61–62  
 Invertebrates, 7  
*Ipomoea purpurea*, 43, 47, 74  
 Island model, 185–186  
 Isozyme state, 38  
  
 Johnson, Phillip, critic of evolution, 12  
 Jurassic period, 8  
  
 Kauffman NK model, 204, 214–216  
 Kuhn's paradigm, 75–76  
  
 Land–sea transition, 15  
*Lemur catta*, 154  
 Lineage, 137, 163  
 Linear models, 210–211  
 Linkage disequilibrium, 104, 184, 196–197,  
   227  
 Linkage effects, 104

- Linkage equilibrium, 142  
 Linnaean hierarchy, 4  
 Lipid metabolism, 208
- MacArthur–Wilson theory, 21  
 Macroevolution, 1, 20–22, 145, 229  
 Major histocompatibility complex, 242  
 Male sterility, 241–242  
 Mammals, 7  
 Markov process, 119–123, 134  
 Mathematical truth, 64  
 Mating design, 203  
 Maxwell, James Clerk, 100  
 McDonald–Kreitman test, 103  
 Medical genetics, 203, 205, 228  
 Mendel's laws, 65  
 Mendelian cross, 144  
 Mendelian disorders, 205  
 Mendelian genetics, 17–18  
 Mesozoic era, 7–8  
 Metabolic pathways, 89  
 Metapopulation, 181, 185–191  
 Michelson–Morley experiment, 100  
 Micromutationism, 77  
 Microsatellite sequence, 114  
 Microvariationism, 80, 88  
 Miocene epoch, 7–8  
 Mississippian period, 8  
 Model system, 89  
 Modern Synthesis, 73, 75–77, 91, 100, 226  
 Molecular clock assumption, 113, 124, 126, 129  
 Molecular data, 137
  - evolutionary history from, 135, 138–139
  - inferring selection from, 135
 Molecular drift, 15  
 Molecular evolution, 104  
 Molecular genetic variation, 19  
 Molecular homology, 90  
 Molecular markers, 182, 227  
 Molecular organization, 59  
 Molecular variation, 139  
 Monophyly, 167–168  
 Morning glory, 43, 47, 74  
 Muller's mechanism, 241–242  
 Multicolinearity, 209  
 Multilocus traits, 226  
 Multinomial theory, 198  
 Mutation, 104–107, 114, 135, 137, 139–142, 145, 155, 157, 182, 186, 208, 228, 232–233, 245
- Mutational meltdown, 183, 232  
 Mutation–selection balance, 204
- Natural selection, 17, 22, 24–25, 35–36, 53–54, 58–59, 62–63, 66, 68–69, 71, 73–74, 77–79, 82, 85, 92, 99, 103–105, 108–109, 141–142, 170, 181, 183, 205, 231, 250  
 Naturalism, 12–13  
 Naturalist, 12, 75  
*Naturphilosophie*, 25  
 Neighbor-joining method, 163, 168–170  
 Neighbor-joining tree, 46  
 Neo-Darwinism, 18  
 Neutral assumption, 74, 83  
 Neutral drift, 68  
 Neutral infinite sites mutation model, 103  
 Neutral model, 102, 107, 109, 138  
 Neutralism, 246  
 Neutralist–selectionist controversy, 81, 87, 136  
 Neutrality, 40–41, 54, 74, 83, 87, 104, 107, 136, 140–141, 250  
 Neutral-selective paradigm, 103–104  
 New World monkeys, 152  
 Newtonian mechanics, 101  
 Nomological force, 85  
 Nomological generalization, 62, 64  
 Nonadditive interaction, 227  
 Nonequilibrium thermodynamical system, 24  
 Nonfunctional theory, 66  
 Nonrandom association, 142  
 Nonstrict laws, 61–62  
 Nontrivial risk, 189  
 Normal science, 80  
 Nucleotide
  - diversity, 143
  - sequence, 136, 139–140
  - substitution, 142, 161–162
 Null hypothesis, 41, 83  
 Null model, 103
- Old World monkeys, 152  
 Oligocene epoch, 8  
 Oligogeny, 88  
 Ontogeny, 14  
 Oolite period, 7  
 Ordovician period, 8  
 Organic complexity, 24  
 Organismal phenotype, 82, 91  
 Organism–environment interaction, 90

- Origin of life, 13  
 philosophical perspectives, 26  
 scientific perspectives, 24–26
- Origin of Universe, 13
- Otolemur crassicaudatus*, 154–155
- Otolemur garnetti*, 155
- Outbreeding depression, 190, 233
- Overlapping generations, 184
- Paleocene epoch, 8
- Paleozoic era, 7–8
- Panglossian paradigm, 82
- Paradox of false correlation, 213, 220
- Parametric uncertainty, 115
- Parent–offspring regression, 217
- Particulate system of inheritance, 35
- Pedigree, 196
- Pennsylvanian period, 8
- Permian period, 7–8
- Phage evolution, 144
- Phenotype mapping, 143
- Phenotype, 42–43, 54, 74, 77–78, 82, 136–137, 145, 155, 203, 206–207, 209–210, 221, 227–228
- Phenotype–environment interactions, 74
- Phenotype–genotype dichotomy, 204
- Phenotypic diversity, 226  
 links to adaptation, 48
- Phenotypic plasticity, 84
- Phenotypic variation, 205, 229
- Phylogeny, 14, 36, 113, 117, 119–120, 126  
 ant, 118  
 molecular clock assumption in, 113, 124, 126, 129  
 primate, 152, 170–172, 175  
 schematic representation of, 152  
 star model of, 119, 124, 126
- Platt's strategy, 87
- Pleistocene epoch, 7–8
- Pliocene epoch, 7–8
- Polygenicity, 78
- Polygeny, 88
- Polymorphic frequency, 141
- Polymorphism, 41–42, 104–108, 135, 139–143, 175, 242, 245
- Population biologist, 80
- Population bottleneck, 40
- Population dynamics, 232–233
- Population expansion, 138–139
- Population extinction, 232
- Population fragmentation, 185–188
- Population genetics, 2, 35, 54, 74, 81–82, 88, 104, 179  
 adaptive evolution in complex systems 42–48  
 divergence, 44  
 gene conversion–recombination, 47  
 gene duplication, 44  
 studies with morning glory, 47  
 analysis of gene genealogy, 38–42  
 future prospects, 144–145  
 limitations to knowledge, 35–50  
 classification, 37–38  
 models for, 36, 64–66, 115  
 new insights in, 139–140  
 overview of, 35–37, 136–138, 145, 180  
 theory of, 73–74, 84, 197, 201  
 inferences from coalescence theory, 40–41
- Population neutral mutation parameter, 107
- Population size, 104–106, 108, 115, 137, 179, 182, 187, 190, 196, 232–233, 246  
 measuring effective, 183–185
- Population subdivision, 41–42
- Population viability, 185
- Precambrian era, 8
- Prediction, 1, 86, 113–115, 179–180, 191, 195, 203, 207, 210, 215–216, 218, 249
- Prediction in biology, 53, 57–58
- Primary period, 7
- Primates, 152  
 color vision systems in, 153–155  
 comparison of opsin sequences, 157  
 origin in higher primates, 165–171
- Probability, 122–133, 195, 198, 201
- Prosimians, 152
- Protein synthesis, 87
- Punctuated equilibria, 24
- Quantitative genetics, 225  
 limits to knowledge in, 225–235  
 meaning of variation in, 229–232  
 nature of variation in, 227–229  
 outbreeding depression on, 233–234  
 phenotypic vs. genetic values in, 226–227  
 population dynamics/size on, 232–233  
 prediction of phenotype from genotype, 203–222  
 limitations of, 205  
 overview of, 203–204  
 species incompatibilities on, 233–234
- Quantitative trait loci, 209, 227



- Quantitative variation  
 meaning of, 229–232  
 nature of, 227–229
- Quantum mechanics, 101
- Quaternary period, 8
- Random drift, 104, 183, 232
- Random mating, 182, 184, 199, 226
- Realization, 38
- Recalcitrant trait, 205
- Recolonization, 190
- Recombination, 1, 40, 104, 114, 136, 139–141, 143, 145, 153, 171, 189, 191, 196–197, 201, 209, 215, 218, 227, 231
- Reproductive generation, 59
- Reproductive incompatibility, 234
- Reproductive success, 82, 104, 184, 188
- Reptiles, 7
- Repulsion disequilibrium, 230–231
- Restriction mapping, 136
- Retrodiction, 58, 69
- Risk, 208  
 disease, 206–208  
 extinction, 181  
 nontrivial, 189
- Russian evolutionism, 27
- Sample size, 114, 125, 143, 209
- Secondary period, 7
- Segregating variants, 105–106
- Selection, 135, 140–141  
 model, 245–246
- Selection coefficient, 106–107
- Selection–drift dichotomy, 54
- Selective breeding, 226–227
- Selective sweep, 40–41, 105, 107, 139, 141
- Self-replicating RNA, 13
- Sequence exchange, 161
- Sexual dynamics, 138
- Sexual selection, 1, 17
- Sexuality, 19  
 evolution of, 19
- Shifting balance theory, 18–19
- Silurian period, 7–8
- Simians, 152
- Similarity, 161
- Simpson's paradox, 212–214, 219
- Simulation-based methods, 143
- Single-locus marginal effects, 211
- Social behavior, 1
- Social construction, 26
- Social text, 2
- Sociobiologist, 18, 23
- Spatial sequence homogeneity, 141
- Speciation, 203–204, 234, 240, 243
- Species, 99
- Species differentiation, 233, 239, 243–244  
 divergence, 245  
 Haldane's rule on, 241  
 impact of generalization on, 241–242  
 overview of, 239–241  
 uncertainty in extrapolation on, 243–246
- Species incompatibility, 233
- Species survival, 115
- Spectral sensitivity, 114, 151, 155–157, 160, 175
- Spectral shifts, 158–159
- Spectral tuning, 156, 159, 160, 170  
 amino acid residues for, 155–160
- Spermatogenesis, 242, 244
- Star model, 130
- Statistical model, 179, 206–207, 210–211, 217–218, 226
- Stochastic process, 195
- Structural diversity, 59
- Tajima's test, 140
- Tarsiers, 152
- Taxonomy, 15
- Technological innovation, 1
- Temporal method, 183
- Temporal sequence, 113
- Tertiary period, 7–8
- Theoretical construct, 1, 36, 54
- Thermal adaptation, 84
- Thermal stress, 90
- Thermodynamics, 86
- Thesis–antithesis–synthesis cycle, 76
- Tight linkage, 105–106, 161
- Time scale, 90–91, 114, 137, 179, 245
- Tortoises, 6
- Trait locus analysis, 204
- Trait mapping, 136
- Transcription factors, 211–212
- Transcriptional regulation, 242
- Transmembrane model, 156
- Triallelic system, 154, 165, 167, 171, 173–174
- Trias period, 7
- Triassic period, 8
- Trichromacy, 114, 165, 171, 173
- Two-locus model, 65

Uncertainty, 98–99, 115, 117, 134, 181, 195,  
198, 240, 243–244

Variability, 142

Viable population size, 2

Wealden period, 7

Western European evolutionism, 27

Whale, stages in evolution of, 16

Wild barley, 41

Wright, Sewall, 18

Wright's hierarchical inbreeding coefficient, 185

X-linked color vision, 153, 161, 615, 170, 174

Zhivotovsky–Gavrilets model, 216–219