AN IDIOSYNCRATIC SUBSET OF ECOLOGICAL THEORY ACCORDING TO AYRES
Each line represents a theory; those with asterisks are elaborated with postulates at end; indents imply increasing specificity; criticism is encouraged.

Physiological ecology
  Climatic affects on physiology
    Global patterns in air currents and precipitation
  Primary metabolism and respiration
    Linkage between energy supply and population size
      Laws of thermodynamics
    Fick’s law of diffusion
      Counter-current exchange systems
  Water balance and osmoregulation
  Effects of temperature
    Biochemical kinetics
    Jack-of-all-trades is a master of none
    Switches in species interactions
      Phenological race hypothesis
    Homeostasis vs. conformation
      Effects of body size on overwintering strategies of homeotherms

Animal nutritional ecology
  Tradeoffs between food quality and food availability
  Flow of energy and matter through organisms
  Strategies of digestion
    Microbial fermentation
  Coping with plant secondary metabolites
    Detoxification systems
      Tannin detoxification
      Nutrient acquisition vs. toxin management
  Costs and benefits of dietary specialization
  Multiple nutritional requirements
  Phylogenetic and ecological constraints

Energy acquisition in autotrophs
  Nutrient acquisition in autotrophs
    Patterns among elements in uptake kinetics and ecological limitations
    Mycorrhizal symbioses

Plant responses to variable resource supply
  Tradeoffs between resource requirements and growth potential
    Liebig’s law of the minimum
    Dynamic investment optimization

Plant defense theory
  Carbon: nutrient balance hypothesis
  Growth: differentiation balance hypothesis
  Optimal allocation
  Inducible vs constitutive defenses
Population ecology
  Dispersal
    Costs and benefits of dispersal of in time or space
  Habitat selection
    Ideal free distribution
  Population demography
  Life-history theory
    r vs K selection
    Evolution of semelparity
    Evolution of senescence
    Evolution of clutch size
  Population regulation
  Complex dynamics
  Metapopulations
  Source-sink dynamics

Evolution
  Particulate inheritance
  Hardy-Weinberg equilibrium
  Evolution by natural selection
    Circumstances under which genetic variance can be maintained in heritable traits linked to fitness
    Shifting balance model
    Evolution by common descent

Community ecology
  Interspecific competition
  Plant-herbivore interactions
  Predator-prey interactions

Ecosystem ecology
  Energy flux in ecosystems
    Effects of species diversity
    Laws of thermodynamics
  Nutrient flux in ecosystems
  Water flux in ecosystems
  Anthropogenic climate change
A few examples of theories (according to Matt Ayres)
Notice that all have the general structure of having a modest number of postulates (often about 5), which, if true, permit some statements about nature that are more general than any of the postulates by themselves (“Therefore, ...”). Theories do not have to be true, just logical.

**Phenological Race Hypothesis**

Postulates

- P₁: Mature leaves are of lower nutritional quality for insect herbivores than immature leaves.
- P₂: Insects have lower survival and fecundity when they eat leaves of lower nutritional quality.
- P₃: Insect development rate is temperature-dependent.
- P₄: Leaf maturation rate is temperature-dependent.
- P₅: Insect development and leaf maturation have different temperature responses.

Therefore, insect herbivores that feed in the spring are engaged in a developmental race with their host plants. Depending on the temperatures, the insects or the leaves might complete development first. Insect abundance tends to increase when they win the developmental race.

**Liebig’s Law of the Minimum**

Postulates

- P₁: Plant growth requires many different resources (e.g., H₂O, sunlight, N, P, K, CO₂)
- P₂: The relative availability of different essential resources may vary dramatically from site to site and year to year
- P₃: Each resource fills unique physiological needs of the plant
- P₄: One resource cannot be substituted for another.

Therefore, plant growth is limited by the one resource that is least available relative to physiological needs of the plant. However, the limiting resource can vary depending upon the environment.


Postulates

- P₁: Plants will allocate resources towards growth until water, nutrients, or carbohydrates limit further growth
- P₂: Tissue growth is negatively associated with tissue differentiation because:
  1. They compete for the same pool of carbohydrates
  2. Differentiation processes require mature intracellular architecture
- P₃: Sink-limited plants tend to be differentiation-dominated; source-limited plants tend to be growth-dominated
- P₄: Differentiation dominated plants have relatively high allocation to secondary metabolism

Therefore, plant growth tends to be inversely related to defense. Water or nutrient limitations tend to increase plant defenses, even as they constrain plant growth.
**Fick’s Law of Diffusion**

\[ R = D \cdot A \cdot \frac{\Delta p}{d} \]

Where:
- \( R \) = Rate of diffusion (moles / sec)
- \( D \) = Diffusion constant; value depends upon material through which diffusion is occurring (cm\(^2\) / sec)
- \( A \) = Area across which diffusion is occurring (cm\(^2\))
- \( \Delta p \) = Difference in partial pressures or concentration across diffusion surface (mm Hg or moles / cm\(^3\))
- \( d \) = Distance a molecule must travel to reach the area of lower concentration; e.g., membrane thickness (\( \mu m \))

Therefore, the effect of \( D, A, \Delta p, \) and \( d \) on diffusion of \( O_2 \) is as described by the equation, which permits understanding of the adaptations of organisms for oxygen acquisition.

**A Theory of Global Precipitation Patterns**

1. Air warms at the equator - from surface up
   - Shortwave radiation (sunlight) passes through atmosphere
   - Longwave radiation (heat) is absorbed and reflected back to earth by the atmosphere (especially water vapor and carbon dioxide)
2. Warm air rises; cold air drops
3. Warm air holds more moisture than cold air
4. Rising air cools; dropping air warms (adiabatic)
5. Coriolis force: in the northern hemisphere, air moving north is deflected west to east (relative to an observer on earth)

These processes produce broad global patterns in precipitation (e.g., deserts at about 23-33° latitude) that have predictable effects on the physiological ecology of resident organisms.

**A Theory of Anthropogenic Climate Change**

Postulates
- \( P_1 \): Atmospheric concentrations of CO2 are increasing.
- \( P_2 \): Anthropogenic combustion of fossil fuels account for the increases in CO2.
- \( P_3 \): CO2 is permeable to shortwave radiation (e.g., incoming sunlight) but tends to reflect longwave radiation (e.g., radiant heat from the surface of the earth). That is, CO2 is a greenhouse gas.
- \( P_4 \): Realistic simulations of atmospheric dynamics, ocean current systems, and global energy flux indicate that the increases in CO2 will lead to meaningful climate warming and significant alterations of precipitation patterns.
- \( P_5 \): The attributes of individuals, populations, communities, and ecosystems will change as a result of projected alterations in temperature, precipitation, CO2, and cloud cover.

Therefore, human combustion of fossil fuels is altering the planetary ecosystem, and a continuation of current patterns in human energy use will have global impacts (probably some of them deleterious) on biodiversity, agriculture, forestry, recreation, water supplies, ocean levels, disease, economics, urban geography, and other aspects of human society.
THEORY OF EVOLUTION BY NATURAL SELECTION (DARWIN 1859)

Postulates
P₁: All populations have potential for exponential growth
P₂: Resources are limited therefore not all individuals survive and reproduce
P₃: Individuals within a population vary
P₄: Some variable traits have a heritable basis
P₅: Some heritable traits are linked to fitness

Therefore natural selection occurs and the fit of organisms to their environment tends to improve.

THEORY OF EVOLUTION BY COMMON DESCENT

• Life on earth has originated only once
• New species are derived by splitting from existing species (through reproductive isolation with subsequent modification)
• Extinction is forever

Therefore, all species are related to all other species but in varying degrees

THEORY OF HARDY-WEINBERG EQUILIBRIUM (1908)

Genotype frequencies in a population are a constant and predictable function of allele frequencies if:
1. Species is diploid and sexual.
2. The trait of interest is not sex-linked.
3. Generations are nonoverlapping.
4. Mating is panmictic (i.e., every individual has the same probability of mating with every other individual.
5. Population size is very large (infinite)
6. There are no mutations in the trait of interest.
7. There is gene flow into or out of the population
8. No natural selection occurs

e.g., For the case of a 2 allele system (A and a), genotype proportions in the population can be predicted by
\[ p^2 + 2pq + q^2 = 1 \]
where:  
\[ p = \text{proportion of allele A in the population} \]
\[ q = \text{the proportion of allele a in the population} \]

THEORY OF PARTICULATE INHERITANCE

• Each character is represented in a fertilized egg by two alleles, one derived from the mother and one from the father.
• The combination of these two alleles determines the phenotype
• The alleles do not blend, but remain discrete from generation to generation
• When gametes are formed in heterozygous diploid individuals, the two alternative alleles segregate from one another
• Each gamete has an equal probability of possessing either member of an allele pair
• Genes that are located on different chromosomes assort themselves independently
A GENERAL THEORY OF PHYSIOLOGICAL ECOLOGY

Characteristics of the physical environment can limit the distribution and abundance of populations.

P₁: In many areas, organisms of a particular species cannot tolerate the abiotic environment. Any individuals that disperse to such an inhospitable area will soon die.

P₂: In other areas, the abiotic environment may allow individuals to survive, but preclude them from reproducing at a replacement rate. Such populations can only be sustained by continual immigration from more suitable habitats and are known as sink populations (which occur within sink habitats).

P₃: Many physical factors can prevent a particular species from inhabiting a given area (e.g., temperature, moisture, light intensity, relative humidity, pH, salinity, soil mineral concentrations, etc.)

P₄: Species vary in their responses to the physical environment, and therefore in the habitats where they can maintain viable populations. Natural selection continues to act on this variation to produce a match between the physiological adaptations of organisms and the physical environment where they occur.

P₅: Physiological adaptation to one abiotic environment frequently entails tradeoffs that limit survival and reproduction in other environments.

A THEORY OF GLOBAL PRECIPITATION PATTERNS

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EFFECTS OF BODY SIZE ON OVERWINTERING STRATEGIES OF HOMEOTHERMS

- Large animals require more total food but less food / kg.
- Fat reserves accumulated during the summer can contribute appreciably to the winter energy budgets of large mammals but not small mammals
- Thermoregulation during winter requires less energy for large mammals than small mammals
- Thick fur is chiefly an adaptation of medium sized mammals because large mammals do not need it and small mammals cannot afford it.

Postulates

P₁: Metabolic rate increases with body size as about MetRate = a • Mass^{0.70}

P₂: Food requirements are proportional to metabolic rate

P₃: Maximum fat reserves increase with body size as about MaxFat = a • Mass^{1.0}

P₄: Heat loss is proportional to surface area, but heat production is proportional to mass.

P₅: Surface: volume ratio decreases with increasing body size

P₆: The insulative value of fur is a function of fur length and is independent of body mass.

- Plants have been selected to be plastic in their use of resources such that growth is maximized across a range of environmental conditions.
- Optimal resource allocation strategies can be predicted by analogy with economic models for profit maximizing firms that produce products from multiple resources.
- Optimizing plants adjust resource acquisition strategies such that their growth is equally limited by all resources.

\[ P_1 \] Plants acquire resources when they are least expensive and use them when they are most valuable. Storage enables plants to acquire resources at minimal cost and to use them at times of maximal benefit.

\[ P_2 \] Plants tend to produce tissues (e.g., leaves or fine roots) at the output level for which marginal cost equals marginal revenue.

\[ P_3 \] Plants tend to harvest resources such that the ratio of marginal product to cost is equalized for all resources required by the plant. Similar benefit to cost ratio for each necessary resource.

\[ P_4 \] Internal resources (e.g., sugar, water, and nutrients) tend to be allocated among competing processes (e.g., photosynthesis and nutrient acquisition) such that each resource limits all processes to the same degree (i.e., when the marginal rate of technical substitution is the same for all processes).

\[ P_5 \] Plants adjust in the short term (acclimatization) and long term (adaptation) to minimize differences in exchange ratios across space and time. Exchange ratios = relative quantity of two resources acquired per expenditure of a resource (e.g., g Carbon / g Water acquired per expenditure of a unit of Nitrogen)

**A General Theory of Population Demography**

Given age-specific mortality rates and age-specific natality rates, it is possible to predict:

1. Potential rate of population increase \((R_0, r, \lambda)\) under a stable age distribution or any specified age distribution;
2. Generation time;
3. Reproductive value of each age class;
4. The stable age distribution;
5. The expectation for future life of individuals in each age class.
6. The rate at which a perturbed population will return to its characteristic age structure and growth rate.
A GENERAL THEORY OF PREDATOR-PREY INTERACTIONS

- Predation can have important evolutionary and ecological consequences for both predator and prey.
- Predation can have far reaching effects on the structure and function of communities and ecosystems.

Postulates

P_1: The physiological condition of individual predators and prey are influenced by the presence of the other species.

P_2: The behavior of individual predators and prey are each influenced by the presence of the other species.

P_3: The dispersion of predator and prey populations are each influenced by the presence of the other species.

P_4: Predator-prey interactions influence the evolution of many attributes of many species, including behavior, morphology, and life history.

P_5: The population dynamics of predator and prey populations are each influenced by the presence of the other species. Frequently, these effects are reciprocal so that their population dynamics are coupled. Outcomes of these demographic interactions can include extinction of one or both species, stable coexistence of both species, and coupled oscillations; some specific attributes of predators, prey, and their environment permit specific predictions regarding which of these outcomes is most probable (e.g., predator efficiency in converting prey into offspring, the availability and use of alternative prey species, the relative generation times of predators and prey, and the availability prey refuges within the environment).

P_6: The structure of broader biological community within which the predator and prey exist can be altered as a result of predator-prey interactions (e.g., maintenance of species diversity by keystone predators).

P_7: The structure and function of ecosystems can be altered as a result of predator-prey interactions (e.g., trophic cascades and changes in conditions for primary producers).
**Energy Flux in Ecosystems**

- Net primary productivity (NPP) is a function of energy input, water availability, temperature, and nutrient availability. However, the relative importance of these factors varies among ecosystems. For example, terrestrial systems tend to be most productive in the tropics, where temperature and radiation are greatest, while marine systems tend to be most productive in regions of nutrient upwelling (frequently at high latitudes).

- Energy is dissipated and lost as it flows through ecosystems. It is an open system that requires sustained energy input.

- Given constant NPP and energy flux rates, ecosystems tend to converge on a steady state in which respiration = NPP.

- Ecosystems have ergodic properties. That is, with constant flux rates, the eventual equilibrium condition (total respiration rate and pool sizes of trophic compartments) is independent of initial pool sizes.

- Increases in NPP tend to increase energy flux and energy pool sizes throughout the ecosystem.

- Increases in consumer respiration rates tend to reduce the pool size of DOM but not the pool size of plants.

- Cool temperatures tend to reduce the ratio of live biomass to DOM. Thus the energy pools of high latitude ecosystems tend to be dominated by DOM, while those of tropical ecosystems tend to be dominated by live biomass.

- At equilibrium, the detritus based system accounts for more productivity and energy flux than the grazing system.

- Because flux rates can vary greatly among trophic levels, standing biomass (g/m\(^2\)) is not always an accurate predictor of productivity (g/m\(^2\)•year\(^{-1}\)).

**Postulates**

\(P_1\): NPP is a function of photosynthesis, which requires solar energy to drive the endothermic reaction; mineral nutrients for construction of enzymes, cofactors, and membranes; and water, as part of the reaction, and to replace that lost in transpiration during acquisition of CO\(_2\). Photosynthesis rates tend to be higher at warmer temperatures (to about 30°C) than at cooler temperatures.

\(P_2\): Energy flow in ecosystems obeys the laws of thermodynamics.

\(P_3\): Ecosystems can be conceptualized as compartments of energy, with energy flux between them. One simple abstraction includes four compartments (plants, grazers of the plants and their predators, dead organic matter, and detritivores and their predators) and seven fluxes (representing consumption, death and defecation, and respiration).

\(P_4\): Respiration rates tend to increase exponentially with temperature, while productivity increases at a lesser rate and even tends to decline at high temperatures.

\(P_5\): Carbon flux, biomass flux, and energy flux, are so highly correlated that they are usually interchangeable.
Ecosystem productivity tends to increase with species diversity due to niche complementarity.

- **P₁**: Species differ in their resource requirements.

- **P₂**: Increased species diversity results in more complete use of limiting resources. (Each limiting resource tends to be drawn to a level determined by the species with the most efficient resource use ability. Thus, the addition of species can increase efficiency of resource use within the community, but not decrease it).

- **P₃**: More complete use of limiting resources leads to increased productivity.

- **P₄**: Species within diverse communities are more likely to experience the benefits of facilitation or mutualism.

- **P₅**: Increased species diversity buffers against productivity losses from spatial and temporal variability in resource supply rates. This is because (1) diverse communities are more likely to contain one or more species with high growth rates under any combination of resource supply rates (“portfolio effect”), and (2) reduced growth of species experiencing suboptimal resource supplies eases competitive inhibition of other species.

**Broad consequences if true**
The current rapid rates of species losses from ecosystems may have significant deleterious effects on ecosystem productivity, sustainability, and carbon storage.

Even carefully selected monocultures cannot match the sustainable productivity of diverse species assemblages.

**Related theories**
Ecosystems with high species diversity are more stable and predictable in their productivity and pool sizes.

Ecosystems with high species diversity are more efficient at retaining nutrients.

The stability of individual populations is reduced by increased species diversity.