## Evolutionary synthesis

In his recent *TREE* article, Ernst Mayr[1] claims that the evolutionary synthesis outlined about 60 years ago, though incomplete (because of some residual controversies between naturalists and geneticists), was 'more than a synthesis' for, in effect, all the antidarwinian paradigms were successfully refuted. He envisages the unified biology of the future as a unanimous adherence to a holistic concept of the individual as the target of evolution. Mayr's purpose might have been to defend organismic biology from too zealous reductionists among molecular biologists. However, both individual genes and individual organisms are systems (holistic targets) as well as components (reductionist targets) of more-complex systems – genomes, populations, biotic communities and the biosphere as a whole (holistic targets again). Is it not in the spirit of a synthesis to have various targets rather than a single target?

Mayr admits that the architects of the synthesis were 'busy enough straightening out their own differences and refuting the antidarwinians to have time for such a far-reaching objective' as the unification of biology. Indeed, for a rising paradigm, refutation of competing paradigms is an achievement in itself, while a successful synthesis would incorporate rather than refute competing ideas.

Darwin left open the crucial evolutionary questions of progress, morphological elaboration, origin of the higher taxa and their meaning, community evolution, geological crises, etc. He was not totally successful in placing man in the context of the evolutionary paradigm. In effect, his theory severed the natural sciences from traditional ethics, stirring up humanistic criticism while inspiring both Marx and Nietzsche. Did his successors strive to fill the major gaps or were they too busy refuting their rivals?

Was Julian Huxley's synthetic volume practically ignored because he (the only English native of the greater anglophone 'architects') 'lacked the ability to organize his thought', or because the synthesis was not actually at stake? Did developmental biologists resist the synthesis because, for some mysterious reason, they 'did not want to join' or was the synthesis too narrow for them to join?

Pre-darwinian developmental biology discovered an amazing parallelism of morphological succession from simple to complex organisms, the palaeontological record and individual development[2]. Through this, biology was transformed from haphazard observations to a science capable of analytical approaches to diverse but orderly phenomena of life, to unique but essentially repetitious historical processes running in parallel in various evolving systems – a predictive science with a perspective of unification.

These incipient developments were swept out by the advent of selectionism. For selectionists, though writing casually of parallelism, they failed to recognize its fundamental significance, nor were they interested in directional processes airily assigned to the realm of theology.

Thermodynamics, a physical discipline describing directional change in natural systems, is contemporaneous with Darwinian theory but, while Ludwig Boltzmann borrowed extensively from evolutionary biology, there was no feedback. Population growth was taken as an evidence of fitness – a pivotal idea of the selectionist synthesis – though populations, as a system, evolve from growth controlled by negative environmental feedbacks to equilibrium supported by intrinsic growth regulations. In all biological systems, their components evolve from broad to narrow functional overlaps (niche overlap in ecology) and respectively from intense to relaxed natural selection, a major entropy-producing factor, which is further relaxed in humans. Optimal human strategies in both natural and artificial systems are guided by the minimal entropy production-rate principle, in full agreement with intuitive ethics[3].

An evolutionary synthesis based on these ideas will be very different from the neo-darwinian one and hopefully more consistent with the modern Weltanschauung.

We are repeatedly told that, before 1930, biology was in a 'chaotic state' and there was no viable alternative to the selectionist synthesis. Actually, it infringed upon the earlier and perhaps more productive attempt which is still not too late to retrieve.

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**References**

1 Mayr, E. (1993) *Trends Ecol. Evol.* 8, 31–34
2 Agassiz, L. (1849) *Twelve Lectures in Comparative Embryology*, Boston Society of Natural History
3 Krassilov, V.A. (1986) *Unsolved Problems of Evolutionary Theory*, Far-Eastern Academy Press (in Russian)

## Aerobic denitrification

In his review of aerobic denitrification in soils and sediments[1], David Lloyd states that the use of nitrate as a terminal electron acceptor when oxygen is available is of no known advantage.

This generalization may not be correct when the available carbon and energy source is an alkane or an aromatic hydrocarbon such as benzene. The metabolic attack on these compounds is initiated by an oxygenase or dioxygenase enzyme that uses molecular oxygen as a cosubstrate. When oxygen is present in excess there is no problem. However, when oxygen is available in limiting quantities there would be a distinct advantage for a cell to use the oxygen for substrate activation and an alternate electron acceptor as an electron sink for respiration.

This is not an entirely hypothetical problem. Benzene and other aromatic hydrocarbons, as well as alkanes of various chain lengths, are frequent and serious pollutants of soils, sediments and aquifers. In these environments, oxygen is present in very limited quantities. Aeration of these environments is difficult and can cause extensive volatilization of the hydrocarbons. This phenomenon, often termed 'air stripping', creates the illusion of bioremediation, when in fact a soil or water pollution problem is simply converted to an air pollution problem. Under these circumstances, a hydrocarbon-degrading organism that can continue to denitrify in the presence of low levels of oxygen would be of great interest for use in bioremediation processes. By allocating the available oxygen to substrate activation, rather than respiration, the organism would benefit by being able to grow at the expense of an otherwise metabolically unavailable compound and the microbiologist would have a potentially useful tool for bioremediation.

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**References**

1 Lloyd, D. (1993) *Trends Ecol. Evol.* 8, 352–356

## Reply from D. Lloyd

The richness of biological variety makes generalization hazardous! Kafkewitz and Su have pointed out an excellent example of an exception to my statement that, 'the use of nitrate as terminal electron acceptor when oxygen is available is of no known advantage', and I am grateful. There may well be others. Recently, Hentschel and Felbeck[1] described the energetics of intracellular bacterial chemoautotrophic symbionts of the vestimentiferan tubeworm *Riftia pachyptila* found around the 'black smokers' (hydrothermal vents) in the deep oceans. In these bacteria, nitrate respiration allows oxygen around the symbionts to be maintained at extremely low concentrations, yet energy can still be obtained via respiratory pathways. The maintenance of low oxygen is thought to be necessary, in this case, in order to minimize the alternative oxygenase reaction of the symbionts' ribulose 1,5-bisphosphate carboxylase (rubisco), the key enzyme of the Calvin–Benson cycle of $CO_2$ fixation.

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**References**

1 Hentschel, U. and Felbeck, H. (1993) *Nature* 366, 338–340

## Cladistics and convergence

Trueman[1] attempts to refute the suggestion of Foley[2] that the widespread occurrence of convergence might make it impossible to construct unambiguous cladograms. However, the facts invalidate his arguments. One must distinguish between homoplasy due to convergence and homoplasy due to parallelophyly. Convergence will never cause any trouble; parallelophyly, however,