

On the co-evolution of life and its environment

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Abstract

Life interacted with climate and geochemical cycles during the evolution of system earth. The only way to understand this interaction and appreciate its strength is by modelling it. Models, however, are only useful if their construction satisfies a number of basic requirements, which are briefly discussed in the context of the empirical cycle; many models do not satisfy these requirements. Modelling the interaction is only in its childhood; the biology in existing models for climate and geochemical cycles is generally weak. The main interaction mechanisms are briefly reviewed. The Dynamic Energy Budget theory offers a useful framework for modelling the interactions; this theory specifies the uptake and use of substrates (including nutrients and light) by organisms and imply body-size scaling relationships for parameter values that quantify the processes of uptake and use of substrates. Current developments of the DEB theory are indicated, emphasising the syntrophic interactions between species of organism, which are characteristic for life. The theory of adaptive dynamics is currently applied to DEB-structured theoretical ecosystems to understand the process of self-organisation at an evolutionary time scale. The hope is that this will

lead to insight into the structural and functional aspects of ecosystems, which can be used to model the evolution of life and its environment.

1 Introduction

The subject of coevolution of life on earth and its environment is fundamental to biology, and essential for understanding the global consequences of human actions. The idea that life has had, and still has, a substantial impact on geochemical cycles and climate is the essence of the Gaia hypothesis. Many varieties of this idea exist, but most of the ideas are rather qualitative.

An increasing number of global climate models are appearing in the literature, where life plays some role. Most of these models are difficult to judge, because they do not result from a set of mechanistic assumptions, but are constructed to describe particular phenomena and observed patterns. Some experienced modellers seem to think that this is the main task of models, see e.g. (Harte, 1991); I disagree with this point of view.

Models have a lot in common with a story about quantities, phrased in the language of mathematics; they can have (and frequently do have) errors in grammar, they can tell non-sense and be uninteresting. However, they can also be exiting, depending on they way they are put together.

After identification of the scientific problem, the empirical cycle should start with a set of assumptions, a *derivation* of a mathematical model from these assumptions, a sequence of tests on consistency, coherence, parameter sensitivity, and relevance with respect to the problem (Figure 6.1).

[Figure 1 about here.]

The second part of the empirical cycle then consists of auxiliary theory for how variables in the model relate to things that can be measured, the setup of adequate experiments and/or sampling and measurement protocols to test model predictions, the collection of the measurements, and statistical tests of model predictions against measurements. These tests could reveal that the protocols have been less than adequate, and should be redesigned and executed; possible inadequacies should be detected in the auxiliary theory. So inconsistencies between data and model predictions not necessarily point to inadequacies in the model itself.

If anywhere in this two-segment cycle the need appears to improve the model, it should not be changed directly, but the list of assumptions should be adapted, and the whole process should be repeated. It is a long and painstaking process, but sloppy procedures easily lead to useless results. Advocates of beginning the empirical cycle with observations, rather than with assumptions, are frequently unaware of the implicit assumptions that need to be made to give observations a meaning. The most important aspect of modelling is to make all assumptions explicit. If modelling procedures are followed in a sloppy way, by adapting models to fit data directly, it is likely that the result will be sloppy too; one easily falls in the trap of curve-fitting. If it comes to fitting curves to data, the use of a pencil, rather than a model, is so much easier.

A lot more can be said about constraints on useful models, but a fair observation is that most existing climate and geochemical models are still weak in the role of biota and that geochemical cycling models are not well-integrated with climate models. Reasons are in the lack of training in biology of modellers, who frequently have a background in physics and/or chemistry, the lack of training in modelling and mathematics of biologists and geologists, and the complexity of life. The subject obviously calls for a multidisciplinary approach, for which we still need to find effective organizational structures.

The next section briefly recompiles the main interactions between life and its environment that need consideration to reach a basic understanding of coevolution.

2 Effects of life on climate

Climate modelling mainly deals with energy (temperature) and water balances. Heat and water transport and redistribution, including radiation and convection in atmospheres and oceans, depends on many chemical aspects which means that climate modelling cannot be uncoupled from modelling biogeochemical cycling. I here focus on radiation, as affected via albedo and absorption by greenhouse gases.

Water

Because of its abundance, water is by far the most important greenhouse gas. Its origin is still unclear; some think it originates from degassing of the hot young planet

(Krauskopf and Bird, 1995), others think from meteoric contributions in the form of carbonaceous chondrites (Berner, 1996), which possibly continues today.

Plants modify water transport in several ways. Although plants can extract foggy water from the atmosphere particularly in arid environments (by condensation at their surface as well as via the emission of condensation kernels), they generally pump water from the soil into the atmosphere, and increase the water capacity of terrestrial environments by promoting soil formation in bare environments (chemically, with help of bacteria (Berthelin, 1983)) thereby reducing water runoff to the oceans. This became painfully clear during the flooding disasters in Bangladesh, that followed the removal of Himalayan forests in India. On a short time scale, plants greatly reduce erosion; their roots prevent or reduce soil transport by common mild physical forces. In combination with rare strong and usually very temporal physical forces that remove vegetation (fires in combination with hurricanes or floods, for instance), however, plants increase erosion on a longer time scale, because plants enhance soil-formation in rocky environments. Because such ‘catastrophes’ are rare, they have little impact on short time scales. The effects of plants on climate and geochemistry were perhaps most dramatic during their conquest of dry environments in the middle Devonian. It came with a massive discharge of nutrients and organic matter into the seas, that lead to anoxia and massive extinctions in the oceans (Algeo et al., 2001).

Plants, therefore, affect the nutrient (nitrate, phosphate, silica, carbonates) supply to the oceans in complex ways, and thus the role of life in the oceans in the carbon cycle. Plants pump water from the soil into the atmosphere much faster in the tropics than in the temperate regions because of temperature (high temperature comes with large evaporation), seasonal torpor (seasons become more pronounced towards the poles, so plants are active during a shorter period in the year towards the poles) and nutrients in the soil (plants pump to get nutrients, which are rare in tropical soils).

Plants substantially influence their local environment, and facilitate colonization by other forms of life, which follows a sequence of ecosystem succession. As holds for most forms of life, plants, and especially the flowering plants, need other organisms (fungi, animals) for survival and propagation. Their massive appearance in the Carboniferous greatly affected global climate, via effects on the carbon cycle (Berner, 2001). Most climate models keep the mean global relative humidity constant at 50%,

e.g. (Crowley and North, 1991), but this assumption can be questioned.

Carbon dioxide

Carbon dioxide is the second most important greenhouse gas. Its dynamics involves the global carbon cycle, which is still poorly known quantitatively. This is partly due to the coupling with other cycles.

Carbon dioxide is removed from the atmosphere by chemical weathering of silicate rocks, which couples the carbon and silica cycles. This weathering occurs via wet deposition, and gives a coupling between the carbon and the water cycle. When ocean down-washed calcium carbonate and silica oxide precipitate and become deeply buried by plate tectonics in earth's mantle, segregation occurs into calcium silicate and carbon dioxide; volcanic activity puts carbon dioxide back into the atmosphere. Geochemists generally hold this rock cycle to be the main long-term control of the climate system.

Westbroek (Westbroek, 1991) argued that the role of life in the precipitation processes of carbonates and silica oxide became gradually more important during evolution. Mucus formers (by preventing spontaneous precipitation of super-saturated carbonates) and calcifiers have controlled carbonates since the Cretaceous. Diatoms (and radiolarians) have controlled silicates since the Jurassic (Krumbein and Werner, 1983). Corals and calcifying plankton (coccolithophores and foraminiferans) have an almost equal share in calcification. In freshwater, charophytes are in this guild. For every pair of bicarbonate ions, one is transformed into carbon dioxide for metabolism, and one into carbonate. Planktonic derived carbonate partly dissolves, and contributes to the build up of a concentration gradient of inorganic carbon in the ocean. This promotes the absorption of carbon dioxide from the atmosphere by seawater.

The dry deposition of carbon dioxide in the ocean is further enhanced by the organic carbon pump, where inorganic carbon is fixed into organic carbon, which travels down to deep layers by gravity. This process is accelerated by predation where unicellular algae are compacted into faecal pellets, and partial microbial decomposition recycles nutrients to the euphotic zone, boosting primary production. The secondary production also finds its way to the deep layers.

Most of the organic matter is decomposed in the deep ocean. The net effect is a depletion of inorganic carbon from the euphotic zone, which promotes the transport

of carbon from the atmosphere into the oceans. This process is of importance on a time scale in the order of millenia (the cycle time for ocean's deep water), and so is relevant for assessing effects of an increase of atmospheric carbon by humans. It is less important on much longer time scales.

In nutrient-rich shallow water, organic matter can accumulate fast enough to form anaerobic sediments, where decomposition is slow and incomplete and fossilization into mineral oil occurs. Although textbooks on marine biogeochemistry do not always fully recognize the role of plants in the global carbon cycle, cf (Libes, 1992, p 139), coal deposits in freshwater marshes are substantial enough to affect global climate. Oil formed by plankton and coal by plants mainly occurs on continental edges, and affects climate on the multi-million time scale.

Methane

Methane is the third most important greenhouse gas; 85 % of all emitted methane is (presently) produced by methanogens (in syntrophic relationships with other organisms, sometimes endosymbiotic) in anaerobic environments (sediments, guts) (Mah et al., 1977; Ferry, 1993). The flux is presently enhanced by large scale deforestation by humans via termites. Apart from accumulation in the atmosphere, and in fossilized gas, big pools ($2 \cdot 10^3$ – $5 \cdot 10^6$ Pg) of methane hydrates rest on near shore ocean sediments. Since methane can capture infrared radiation 25 times better than carbon dioxide, on a molar basis, a release of the methane hydrates can potentially destabilize the climate system (Lashof, 1991). Oxydation of methane is a chief source of water in the stratosphere (Butcher et al., 1992), where it interferes with radiation.

Like carbon dioxide, the methane balance is part of the global carbon cycle. Since most of life's activity is limited by nutrients, the carbon cycle cannot be studied without involving other cycles. Nitrogen (nitrate, ammonia) is the primary limiting nutrient, but iron might be limiting as well in parts of the oceans (Baar and Boyd, 2000; Chai et al., 2000). After assuming that dinitrogen fixing cyanobacteria could eventually relieve nitrogen limitation, Tyrell (Tyrell, 1999) came to the conclusion that nitrogen was proximately limiting primary production, and phosphate was ultimately doing so. The question remains, however, are cyanobacteria active enough? Many important questions about the nitrogen cycle are still open, even if oceans represent a sink or a source of ammonia, nitrates and nitrous oxide (Jaffe, 1992). The

latter is after methane, the next most important greenhouse gas, which can intercept infrared radiation 200 times better than carbon dioxide.

Most nutrients enter the oceans via rivers from terrestrial habitats, which couples both systems and makes coastal zones very productive. The surface area of this habitat has obviously been under control by plate tectonics and seawater level changes, and therefore with ice formation and temperature. These remarks serve to show the link between climate and biochemical cycles.

Dioxygen

Complex relationships exist between the carbon and oxygen cycles. Dioxygen results from photosynthesis, so there is a direct relationship between dioxygen in the atmosphere and buried fossil carbon. The latter probably exceeds dioxygen on a molar basis, because of e.g. the oxidation of iron and other reduced pools in the early history of the earth. Photorespiration links dioxygen to carbon dioxide levels; both gases bind competitively to rubisco and drive carbohydrate synthesis in opposite directions. This effect of dioxygen is possibly an evolutionary accident that resulted from the anoxic origins of rubisco. Spontaneous fires require at least 75 % of present day dioxygen levels, and oxygen probably now sets an upper boundary to the accumulation of organic matter in terrestrial environments, and so partly controls the burial of fossilized carbon (Worsley et al., 1991). The extensive coal fires in China at 1 km depth, that occur since human memory, illustrate the importance of this process. Model calculations by Berner (Berner, 1991) suggest, however, that dioxygen was twice the present value during the Carboniferous. If true, this points to the control of fossil carbon accumulation by oxygen being weak. The big question is, of course, to what extent humans are perturbing the climate system by enhancing the burning of biomass and fossil carbon. The massive burning of the worlds' rain forests after the latest el Niño event makes it clear that their rate of disappearance is accelerating, despite the world-wide concern.

Albedo

Apart from greenhouse gases, the radiation balance is affected by albedo. Ice and clouds are the main controlling components. Cloud formation is induced by micro-aerosols, which result from combustion processes, volcanos and ocean spray derived salt particles. Phytoplankton (diatoms, coccolithophorans) affects albedo via the

production of dimethyl sulfide (DMS), which becomes transformed to sulphuric acid in the atmosphere, acting as condensation nuclei. The production is associated with cell death, because the precursor of DMS is mainly used in cell's osmo-regulation. Plants, and especially conifers, which dominate in taiga and on mountain slopes, produce isoprenes and terpenes (Brasseur et al., 1999), which, after some oxidation transformations, also result in condensation nuclei. Since plants cover a main part of the continents, plants change the colour, and so the albedo of the earth, in a direct way. Condensation nuclei derived from human-mediated sulfate emissions now seem to dominate natural sources, and possibly counterbalance the enhanced carbon dioxide emissions (Charlson, 1995).

Ice affects the climate system via the albedo and ocean level. If temperature drops, ice grows and increases the albedo, which makes it even colder. It also lowers the ocean level, however, which enhances weathering of fossil carbon and increases atmospheric carbon dioxide. This affects temperature in the opposite direction, and illustrates a coupling between albedo, and the carbon and water cycles.

3 Effects of climate on life

Climate affects life mainly through temperature, and in terrestrial environments, by precipitation and humidity. Nutrient supply and drain is usually directly coupled to water transport. The transport of organisms themselves in water and in air can also be coupled to climate. The effects are in determining both geographical distribution patterns, abundance and activity rates.

The effects of body temperature of physiological rates are well described by the Arrhenius relationship within a species-specific range of temperatures, which approximately results in a two-to-three-fold increase in rate (respiration, feeding, reproduction, growth, etc) for a 10 degrees increase in body temperature. At the lower temperature boundary, most organisms can switch to a torpor state, while instantaneous death results when temperature exceeds the upper boundary. Many species of organism that do not switch to the torpor state, escape bad seasons by migration, some of them travelling on a global scale. Endotherms (birds and mammals) are well known examples of spectacular migrations; their energy budgets are tightly linked to the water balance. The capacity to survive periods of starvation has close links with

body size; these periods tend to be proportional to volumetric body length.

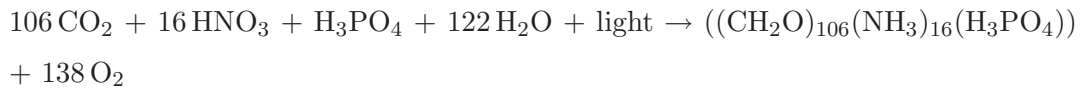
Plant production increases in an approximately linear way with annual precipitation, which illustrates the importance of water availability in terrestrial environments. Plants use water for several purposes, one of them being the transport of nutrients from the soil to their roots. This is why the ratio of the surface areas of shoots and roots enters in the saturation constants for nutrient uptake by plants. Precipitation also affects nutrient availability via leakage.

Extensive pampa and savannah ecosystems require regular fires for existence. Many plant species require fire to trigger germination.

Local differences between seasons in temperate and polar areas are large with respect to global climate changes during the evolution of the earth, which complicates the construction of simple models that aim to be realistic.

4 Synthesis: metabolic organization

The above-mentioned interactions between life and its environment serve as a kind of shopping list for models with a minimum complexity. When it comes to kinetics, we have to insert a minimum level of biological detail. The popular ‘RKR’ model (Redfield et al., 1963) for plankton reads



In the eyes of a biologist, however, a lot more needs to be done to understand life’s activities at a global scale. More realistic modelling is still far away, however, but some progress has been made towards a basic understanding of the organization of metabolism at ecosystem scale. This understanding is essential for making a healthy start with incorporating the mentioned interactions.

I here focus on some recent developments in the Dynamic Energy Budget (DEB) theory (Kooijman, 2000; Kooijman, 2001; Nisbet et al., 2000), which aims to identify the rules organisms follow for the uptake of nutrients, substrate, food, and their use for the purposes of maintenance, growth, development and reproduction. It appears that all organisms (micro-organisms, plants, animals) basically follow the same rules. The theory shows how organisms gradually reached an almost perfect state of homeostasis in evolutionary history, especially in animals, and how this poses stoi-

chiometric constraints on life's activities, which organisms partially escape through the use of intracellular metabolic pools, combined with movements in spatially heterogeneous environments.

One of the difficulties in modelling life is that many factors determine its propagation, which easily leads to complex models that observe the conservation of mass and the second law of thermodynamics. Take, for instance, phytoplankton. The Ocean's top layers are rich in light, but poor in nutrients. The reverse applies at the bottom of the mixed layer. By making use of intracellular pools of carbohydrates and nutrients, cells manage to grow and divide if they are moved through the water column by wind action, even if the local nutrient/light environment does not support growth. Apart from nutrients and light, this involves wind as a growth-controlling factor. Model details have been worked out (Kooijman et al., 2002), and will soon be applied as module in ocean circulation models in an attempt to quantify ocean's primary production more realistically.

The metabolic organization of organisms has been captured within a single framework by the DEB theory, which can be used to understand evolutionary aspects of metabolism. Different species of organism, using different substrates for growth, reproduction and maintenance, can become engaged in a symbiotic relationship with each other when they start using each others' products to supplement their substrates. This relationship can become obligatory when they actually require those products. It turns out to be possible to merge these initially independent populations by incremental changes of some parameter values such that the new endosymbiotic single population again follows the DEB rules (Kooijman et al., 2003b), including the various forms of homeostasis. The parameter changes may be under evolutionary control (see below). This helps to understand the quantitative aspects of the evolution of eukaryotes (Margulis, 1970; Margulis, 1993), and the intracellular dynamics of plastids. The process of self-organization can be studied at ecosystem level as follows.

Take, for instance, a homogeneous body of water that is closed for mass, but open for energy. It contains certain amounts of inorganic carbon, and nutrients; we here follow ammonia and inorganic carbon only. When we inoculate this with a single mixotroph, it will start to grow autotrophically, and detritus will appear as a result of the aging process (which is also specified by the DEB theory). Let us assume, for

simplicity's sake, that the mixotroph can fully mineralize this detritus. Its appetite for detritus relative to autotrophic activity is set by parameter values, the 'binding probabilities', which are coupled to the specific maximum uptake capacities and the costs for growth (due to the costs for the assimilation machineries).

All we have to do to study self-organization is to allow the binding probabilities follow a random walk across the generations, keeping the parameters constant for each individual. One daughter inherits the parameter value of the mother, the other can deviate by small amounts with certain (small) probabilities. Depending on the ratio of total carbon and total nitrogen, the mixotroph community can segregate into populations of auto- and heterotrophs, and the latter can specialize of different compounds, and/or the community continues to exist as mixotrophs (Kooijman et al., 2002). The segregation process can be stimulated by allowing the binding probabilities to drop independently to zero with a small probability. The DEB theory takes care of all aspects of mineral recycling, stoichiometric couplings and energy dissipation; no additional rules are required for selection or definitions for fitness measures. The system is self-selecting and self-organizing, just as Darwin meant it to be.

If exposed to suitable conditions, symbiotic relationships can develop between auto- and heterotrophs, that exchange carbohydrates against nutrients directly; the DEB model for plants has basically the structure of a symbiosis between root and shoot, the model for mixotrophs can be viewed as a further integration of the metabolism of both partners. The formation of symbiotic relationships, and the dynamics of prebiotic evolution that leads to the DEB-kinetics are subjects of present theoretical research.

We can extend this thought-experiment in several ways. One is allowing carnivory to occur, by including another binding probability. The mixotroph community can then develop into a canonical community, i.e. a community that consists of producers, consumers and decomposers (Kooijman and Nisbet, 2000). A next step is to allow for body-size segregation. The basic processes are already covered by the DEB theory, which shows why the primary parameters can be grouped into intensive parameters, which are independent of ultimate body size, and extensive ones, which tend to covary across species; if expressed in the proper units, they are all proportional to ultimate volumetric length. This covariation couples many traits, such as respiration, feeding, growth, and reproduction rates, life span, etc. By inserting this coupling into the

random walk of parameter values across generations, food webs can develop. Other steps towards realism is to include spatial structure (a one-dimensional axis can allow for light and redox gradients and gravitation), and to open the environment for leakage and nutrient inputs. (Opening a closed environment is simple theoretically; most existing models do not allow application in a closed environment, because they do not fully respect conservation of mass, and energy dissipation).

Most of the existing population dynamical models suffer from mayor deficiencies in the context of the DEB theory, because they do not relate the properties of individuals to that of populations and they are not based on energy and mass (nutrient) balances at the various levels of organization. Individual-based population dynamical theory only started in the 1980's (Metz and Diekmann, 1986), but is developing fast (Cushing, 1998; Diekmann et al., 1998; Diekmann et al., 2001). The incorporation of balances is more problematic. Most population dynamical models describe grazing, for instance, on the basis of simple assumptions about the growth of vegetation (or phytoplankton), in order to analyse the population dynamics of herbivores. Although primary production is usually nutrient limited, these models do not account for the release of nutrients during grazing, and at death of the herbivores. Herbivores do stimulate primary production, as do carnivores. The nutrient release that is associated with predation, and its indirect stimulatory effects on primary and secondary production is usually not taken into account. Moreover, carnivores have a preference for the weak, which compete with the productive individuals for food. So, predation comes with an increase of food availability and a reduction of the probability of attracting contagious diseases for the healthy ones (Kooijman et al., 2003a). The mutualistic aspects of the herbivore-carnivore symbiosis have been underestimated so far; this also applies to other metabolic relationships between organisms. Insight into the dynamics of foodwebs and the stabilizing role of omnivory and cannibalism is still in its childhood.

The indicated lines of thought can be used to understand how an ecosystem develops and interacts in a given physico-chemical environment. It will not be easy to extract mathematical properties from this type of simulation, but the task is not hopeless given the rather simple and straightforward principles on which the DEB theory is based. I expect that surface area/volume relationships, in combination with mass and energy balances and stoichiometric constraints will turn out to be the major

organization principles that operate on all space-time scales. Life is mainly restricted to a thin skin around the globe, which receives light and nutrients across its surface, while maintenance requirements involve biomass, so a measure of volume. This not only holds for living systems as a whole, but also for each individual; observations confirm that substrate (food, nutrients) uptake is proportional to individuals' surface area, and maintenance to individuals' structural mass; surface area/volume relationships explain the main differences in metabolic rates between bacteria and whales. Cellular metabolism can be understood in terms of interactions between surface-bound transport and transformation (membranes), and volume-based intracellular accumulation of compounds. The interplay between surface areas and volumes is felt at all levels of biological organization. One only has to think about the weathering of rocks (which involves surface areas), for instance, to realize that the surface area/volume interplay is a major organizing factor for many aspects of earth systems science.

5 Discussion

Plate tectonics seems to dominate long-term transport of energy and water, and thus climate. This applies not only to ocean circulation patterns, but also to rainfall patterns as modified by mountains. Rainfall relates to weathering and nutrient cycling, so it seems fair to state that plate tectonics also dominates the long-term development of life. Atmospheric dynamics operates at a spatial scale that is 2–3 orders of magnitude larger, and a temporal scale that is 2–3 order of magnitude smaller than ocean dynamics, which complicates their incorporation into a single model. Life dynamics operates at many scales simultaneously, implying that realistic modelling of the activities of life will not be easy.

The understanding of the role of life requires a deeper insight into ecosystem functioning. The systematic study of the development of community structure, as simulated along the lines sketched above, will be a huge amount of work. The hope is that aggregation methods will allow us to simplify the main features of the process, and that invariants will show up, between ecosystem structure and function that can be used to study the intriguing process of coevolution of life and its environment. No guarantee can be given for solving all problems that need to be solved, but partial

results of the exercise will be helpful for many less far reaching applications of the theory.

Being free of empirical assumptions, and respecting chemical and physical constraints of metabolic organization, the DEB theory offers a rigorous framework for understanding context-specific selection mechanisms, which seem to be linked to the development of this planet. The strength of the approach is that core concepts, such as selection, optimization and self-regulation, appear as emergent properties from low-level mechanisms. Although the application in global modelling is not easy, nor straightforward, a systematic approach is required for a deeper understanding of the underlying principles. This point of view seems well accepted for purely physical aspects, but less so for biological ones. The sensible incorporation these processes into biogeochemical modelling of earth's development requires a well-coordinated interdisciplinary research program.

More information about the research program on the DEB theory and its results is given at

<http://www.bio.vu.nl/thb/deb>

You can freely download software packages from the electronic DEB laboratory to understand relationships between many variables in the context of this theory.

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List of Figures

- 1 The empirical cycle as conceived by a theoretician; follow white arrows for “yes”, black ones for “no”. In the knowledge that nonsense models can easily fit any given set of data well, given enough flexibility in the parameters, realism is not the first and not the most important criterion for useful models. Lack of fit (so lack of realism) just indicates that the modelling job is not completed yet. This discrepancy between prediction and observation can be used to guide further research, which is perhaps the most useful application of models. This application to improve understanding only works if the model meets the criteria indicated in the figure; few models meet these criteria, however. 20

Empirical cycle

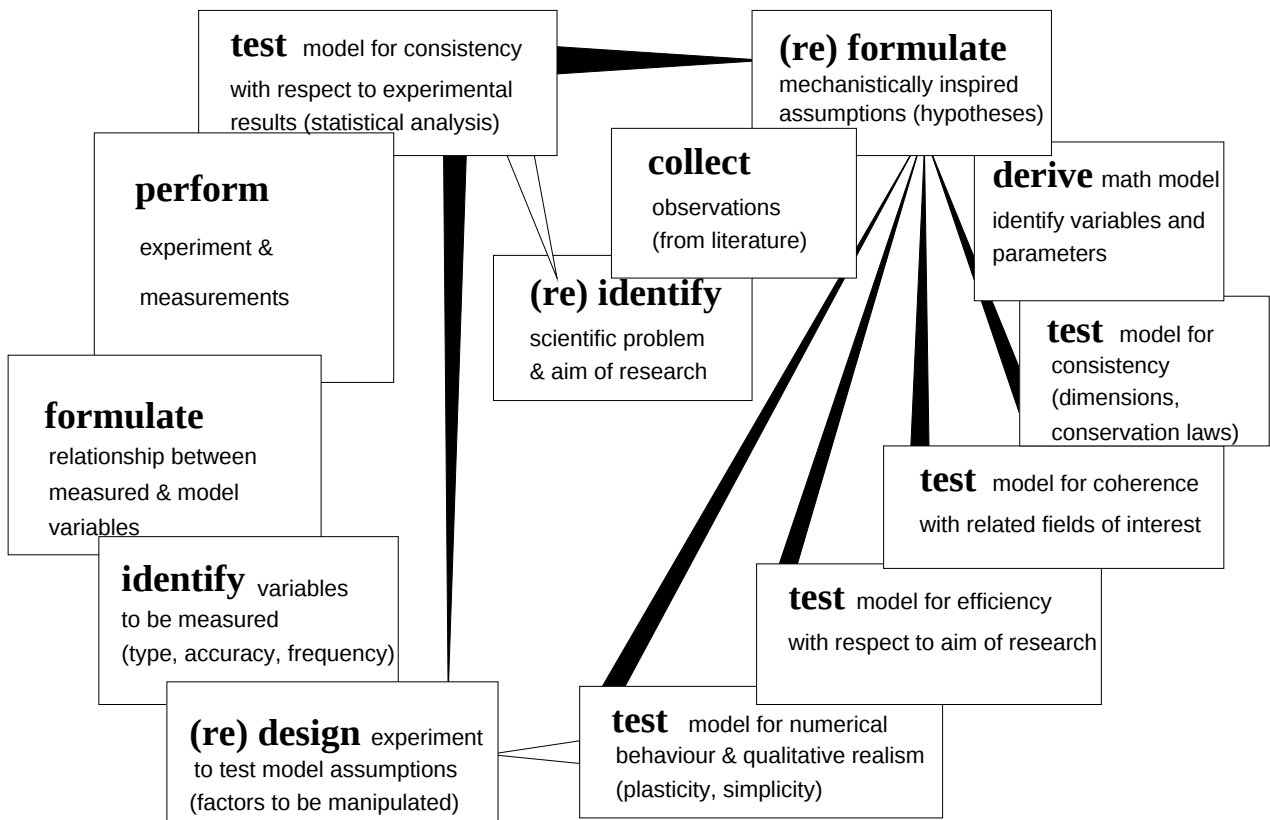


Figure 1: The empirical cycle as conceived by a theoretician; follow white arrows for “yes”, black ones for “no”. In the knowledge that nonsense models can easily fit any given set of data well, given enough flexibility in the parameters, realism is not the first and not the most important criterion for useful models. Lack of fit (so lack of realism) just indicates that the modelling job is not completed yet. This discrepancy between prediction and observation can be used to guide further research, which is perhaps the most useful application of models. This application to improve understanding only works if the model meets the criteria indicated in the figure; few models meet these criteria, however.