EVOLUTIONARY DIRECTION II

Brian Tunstall
2008

Key words: Evolution, natural selection, competition, species, ecosystems, communities

Abstract

Factors associated with changes in species and biological populations are considered in relation to the direction of change over time. Conclusions are drawn as to the processes and outcomes and these are presented as postulates.

PREFACE

The initial work that forms the foundation of this paper was prepared in 1978. This is attached essentially unchanged. Reconsideration of the material in 2004 extended the developments to include non-genetic biological evolution. A development in 2008 added the mechanism for speciation.

If circumstances allow the work is expected to be extended to all matter and not just biological organisms. This would entail consideration of some basic precepts relating to matter and thermodynamics. However, given the circumstances it is released now while identifying that it is incomplete.

A large section on the social aspects of evolution has been removed to provide a focus on the biology. The social aspects of evolution will likely be presented elsewhere.

Reference is made to a book *The Politics of Science* which has been written but not released. The plan is to release it following updates that include further consideration of global warming and the incorporation of religion. Science and religion have been combined throughout most of the last few thousand years. The constraints imposed in addressing religion will be identical to those applied to science.

SUMMARY

Evolution arises because of the finite life span of individuals and depends on differences between individuals and variations / fluctuations in the environment. With genetic evolution the information needed to build life is transferred across generations through reproduction. With non-genetic evolution the information is transferred across generations through education. The environment determines what information survives.

Evolutionary development arises from differences between individuals, and is directed towards increasing the benefit to individuals. The benefit occurs through selection eliminating or reducing competition. Competition can be reduced by eliminating or suppressing others or by avoiding competition. Competition can be avoided by utilising different resources or by collaboration. With effective collaboration the combined capability increases the availability of resources compared to the individuals acting alone.

While evolutionary direction is set by individuals its implementation depends on populations. A change does not survive unless adopted by a population and can be rejected even where it could provide benefit. The essential link between direction and implementation means that benefit to individuals tends to be associated with benefit to populations.

Competition is the primary means of increasing efficiencies but increasing efficiency alone ultimately leads to extinction. Developments arise through the utilisation of new resources and hence involve the avoidance of competition. Direction in evolution is set by the avoidance of competition.

As organisms develop through the utilisation of new resources evolutionary development does not necessarily involve the elimination of others. Indeed, developments build upon what previously existed and often involve interdependencies. The full spectrum of forms produced through evolutionary development therefore tends to be maintained over time.

Organisms can be eliminated by changes to the physical environment as well as through competition, and this effectively makes resource available to others. Extinction is an important part of evolution as it increases opportunities for new forms to develop. The number of different organisms present depends on resource constraints rather than limitations in the number of different organisms that can potentially develop.

The general directions of evolutionary development involve the following changes in the characteristics of individuals:

- Small to big
- Short to long lived
- Simple to complex
- Increased use of resources
- High to low reproductive rate
- Increased parental care for progeny
- Increased collaboration within populations
- Development of non-genetic information transfer
- Decreased dependence on environmental conditions

These developments usually involve interdependencies. Increased longevity is generally associated with increased size and complexity, decreased reproductive rate, increased parental care and increased collaboration within populations.

Theoretically the ultimate goal for evolution would be the use or control of all resource by a single individual but, given the finite life span of biota, this situation is not sustainable. The finite life span of individuals results in the occurrence of one organism providing opportunities for others. This functional characteristic of ecosystems results in a characteristic structural forms.

The future

Future outcomes cannot be predicted as they depend on unknown events and circumstances. The best that can be done is to extrapolate generalisations or apparent principles derived from past events. Human development will involve increased efficiencies of resource use as well as the increased use of resources. Known forms of resource will be further exploited and new forms of resource developed. Reproduction will further be controlled, mainly through individual decisions, with an associated high importance assigned to progeny. Collaboration will increase largely through improvements in information transfer (communication).

The key uncertainties with such projections relate to the occurrence of catastrophic changes in the environment, such as a glacial period. The associated dramatic decline in food, and hence ability to support existing populations, typically results in wars. Conflict now has the potential to eliminate most life on the planet along with the information used by humans for non-genetic evolutionary development.

The catastrophic change currently facing the human population is global warming. This represents desertification caused mainly by agriculture. It is a direct consequence of efforts to feed the expanding population. It is a classic example of a species degrading the environment on which it depends and has occurred on a global scale. It likely has precedence in the dinosaurs.

So what's new?

In one way nothing new has been presented but in another everything is new except for the fundamentals provided by Darwin. The reason for this apparent paradox is that everything presented has likely been said before, albeit usually in another context, but the conclusions are largely contrary to the prevailing views on evolution.

There does not appear to be any conflict with the suggestions here and those of Darwin. There are, however, many conflicts with suggestions ascribed to Darwinian theory, as with the suggestion that selection involves survival of the fittest. While an ability to compete is usually essential for survival evolutionary development has depended on the avoidance of competition largely through collaboration.

The developments here depend on the application of logic to derive generalisations from a large amount of diverse information. While the logic may sometimes appear tortuous the conclusions are sometimes simple, even to the point of being self evident. The need to rely on logic, and the associated difficulties, arise from the interdependencies. The issues are not unresolvable as appears to arise with the question which comes first, the chicken or the egg (for evolution the chicken is the egg so they occur together), but the interdependencies make it difficult to separate cause and effect. This has resulted in many considerations on evolution elsewhere incorporating tautology.

The key differences between this and common views on evolution are:

a. The focus on the individual rather than population.
b. The importance of avoiding competition.
c. The importance of non-genetic transfer of information.

Viable populations tend to increase but not maximise their resource use. Development is conservative to reduce the risk of elimination.

INTRODUCTION

Evolution has become the keystone of biology in representing the one general theory that applies in all biological disciplines such as ecology, taxonomy, and genetics. This contrasts with physics where there are numerous laws having general applicability. Biology has only contributed one unifying theory to science and that is usually not assigned the status of a law.

The theory given by Darwin in '*On the origin of species by means of natural selection'* (Darwin, 1959) effectively remains unchanged as the reference despite the subsequent advances in genetics. The large increase in knowledge has not resulted in a significant development of the original work Darwin's theory has mainly been used to 'explain' results from studies rather than studies being used to develop the concept.

Several reasons can be advanced for this situation. The most obvious, as addressed in *The Politics of Science*, is that studies that conform to a generally accepted view are promoted while non-conforming studies tend to be rejected. A situation develops whereby the design and interpretation of scientific studies are directed to supporting the theory they are meant to test, hence there is strong tendency for the maintenance of the status quo. Acceptance of an existing situation provides certainty that the efforts spent on the research will be rewarded with publication.

The inertia associated with the strong tendency to retain existing views and reject alternatives is evidenced by the situation with Galileo, Darwin and many others. While the achievements of Darwin in developing the theory were remarkable so too were his achievements in getting the theory accepted. His efforts included becoming an expert in an accepted discipline, being part of the organisation used to justify the alternate views, surreptitiously testing responses, and gaining support from influential people. The barriers to gaining acceptance were immense and such barriers remain today when proposals are contrary to the established orthodoxy.

Another aspect that promoted the theory gaining acceptance was the focus on the positive aspects of evolution. The book was an excellent marketing exercise whereby positive aspects of evolution were highlighted and negative aspects seldom mentioned. The theory was later incorrectly presented and popularised as involving the survival of the fittest rather than elimination of the unfit as the latter would have been socially unacceptable. The focus on social acceptability may help explain why such a fundamental issue as extinction has effectively been ignored as for science such a lack of rigour is untenable. Most biologists identify extinction as being bad and to suggest otherwise is heresy.

This focus on the positives was appropriate for what Darwin addressed, the origin of species. However, extension of his work to evolution contains major deficiencies, the most obvious being that evolution involves extinction by way of loss of species as well as the generation of new species. The work of Darwin is explicit for what it addressed but inevitably contains limitations when addressing evolution. Its extension to evolution generally without due consideration of the constraints has produced a number of significant misconceptions.

The validity or applicability of common views that genes are selfish, organisms are adapted to their environment, selection is determined by the survival of the fittest, direction in evolution is random, and natural selection reinforces the norm are examined below. Such questioning of established positions generates antagonism. A dilemma therefore arises as addressing such issues generates opposition while failure to address them leaves one open to accusations of bias. This situation is compounded as suggesting direction in evolution is an anathema for some and considered by to be 'anti science'.

Another dilemma when addressing prior perceptions is that the considerations then tend to revolve around the prior views. This constraint is often necessary to achieve communication as new ideas are most readily communicated by reference to existing paradigms. However, it produces a bias that has the potential to prevent or limit the identification of alternatives. For Darwin this was not an issue as his work was diametrically opposed to the prevailing views and he astutely separated science and religion.

The appended paper on *Evolutionary Direction* written in the 1970s logically addresses direction in evolution. These considerations arose from questioning how simple plant competition models for pasture species involving component replacement could give realistic results. It thereby provided new insights. However, the development and presentation of the work were constrained by the science training and the orthodoxy in presenting a scientific paper. While some considerations start from basic principles most of the work is woven around considerations presented by others. The outcome is that the considerations are unduly constrained and so provide an incomplete picture. The occurrence of constraints arising from context is illustrated by a thermodynamic based analysis being incomplete because of the inadequate consideration of biology.

The development of the material here has been evolutionary. It was commenced to provide a more user friendly version of principles given in the 1970s paper but was developed by exploring concepts rather than by simply changing the form of the earlier presentation. The consideration that led to most development was the questioning of the difference between a realist and a skeptic as this led to an examination of non-genetic biological evolution. The occurrence of such evolution was inferred in the 1970s work but its full significance was not then appreciated.

The consideration of non-genetic biological evolution identified discrepancies with the considerations of natural selection given in the paper *Evolutionary Direction*. Selection was generalised as involving elimination of the unfit which, while an improvement on survival of the fittest, is still deficient. The detailed postulates given in the 1970s paper still appear to be sound but the generalisation on selection has limited validity. This deficiency, which arose from constraints associated with using prior work as basis for development, is corrected here.

One question that arises is does this contain anything new? Applying the scientific method no claim can be made that information presented here has not been previously presented. Indeed, personal experience is that identifying something completely new is extremely rare. Ideas thought to be new have usually previously been identified by others. The difference is how the ideas and information have been pieced together. The differences between conclusions reached here and those presented previously arise from context and the structure of the analysis rather than the material used.

The analysis is based on the scientific method. The work may be of interest to those linking evolution and religion but it has no direct relevance to such considerations. The most relevant point to religion is likely the identification of the limitations to what can be concluded when applying the scientific method.

The use of the scientific method relates to its efficiency and reliability in resolving issues. That is why science is assigned value by the community. However, it turns out that science has a direct role in human evolution. The issues addressed in the book *The Politics of Science* are integral to human evolution as they address how science is managed and practised. With hindsight the link between the two pieces of work is not surprising but it was not appreciated until both had largely been completed.

CONTEXT

The context involves analysis using the scientific method but, as noted in *The Politics of Science*, there is no unambiguous or generally accepted definition of what constitutes science. The general approach taken is that science involves logical argument based around observations but this does not provide a unique solution as forms of logic can differ, observations are not necessarily fact, and the analysis conducted depends on the range of observations.

Aspects of the scientific method

Popper regarded prediction as being an essential part of any scientific law. As knowledge that biological evolution occurs through a process of natural selection does not translate into an ability to predict the future Popper would not assign the status of a law to Darwin's theory of species evolving through a process of natural selection. This is despite the inordinate number of tests of the theory that demonstrate that such change occurs naturally and through human intervention.

Popper also considered that with complex systems testing could only be conducted on parts of the system: that it is not possible to apply scientific tests to large and complex systems[1]. Darwin's theory has passed all such tests but has been relegated to a theory because of the complexity of the system being addressed rather than the general validity of his findings. Passing the tests does not allow for prediction.

That organisms evolve is now well accepted. How they evolve has become the study of genetics. Why they evolve, while starting as the study of evolution, has become engulfed in and is now scarcely separate from genetics. This is reflected in replies to the question `what is evolution directed towards?' The usual reply is that the question is anthropomorphic, that evolution can only be considered in retrospect. This has the corollary that evolution is best studied in terms of mechanism in that while the endpoint may not be capable of prediction the means by which it is reached may be. The focus has been on the process rather than outcomes despite the summary explanation of the process as an outcome, namely the survival of the fittest.

The above constraints have resulted in much of the current evolutionary theory being developed around specific examples where parts of a system have been studied in isolation. The conclusions reached can be relevant to the system studied but be difficult to relate to the overall process of evolution. In evolution, as in ecology, the total is rarely if ever the sum of the component parts. Many mutations and recombinations of genes can occur without new species evolving. Many species can evolve without there being a net course to evolution.

The inductive approach usually applied in science is inherently unreliable with ecology, and hence evolution, as it attempts to extrapolate to new situations from localised detailed observations. Where change occurs through interaction the need is to analyse the system as a whole rather than to attempt to synthesise the net response from studies of the individual components. This arises because interactions that determine outcomes cannot be evaluated from observations of individual components. Predictions derived by projecting results from localised observations cannot be expected to be correct in ecology or evolution. Indeed, they can be expected to be misleading

---

[1] This is not an effective test where the systems function through interaction as is standard in biology. Popper's approach is unreliable to the extent of being misleading when addressing ecology.

The approach used in ecology is deductive and this interpolates within a broad range of observations. This can lack precision but interpolation is inherently reliable because it takes account of the interactions. The discrete, part system studies cannot be ignored for they provide the bulk of the available factual information, but to allow for a synthesis of this information the interpretations placed on the results must often be revised in the light of our knowledge of the system as a whole. In complex systems deduction is more reliable than induction if only because of the reliance on interpolation rather than extrapolation.

Logical constraints adopted in the analyses here are:

- Science is based on the analysis of observations.
- Theory cannot refute observations as observations are used to test theories.
- Science depends on testing with any failure resulting in rejection.
- There is no absolute truth or correct answer as, even if correct answer exists, there is no means for it to be recognised.
- Knowledge of process does not necessarily allow prediction.
- Studies on parts of a system cannot reliably identify how the total system functions.
- Analysis of a total system does not validate any component models of the system.
- Where two explanations are equally applicable the simplest prevails.
- The best explanation now will not be the best in the future.
- If something can occur then, given sufficient time, it likely will occur.

The last point does not mean that all potential life forms must exist at the same time as for this to arise there is an additional need for persistence.

The issue of sceptics versus realists is addressed in *The Politics of Science.* Sceptics reject a hypothesis when it cannot be shown to be correct[2] while realists accept a hypothesis until it is negated. Failure to negate a hypothesis does not make it correct, it is simply accepted until disproved. The test identifies that, within particular bounds set by current knowledge, the hypothesis is consistent with observations and can be used in developing science until it is negated. Sceptics change the normal onus of responsibility whereby scientists have to disprove something to achieve rejection to others having to prove their point to gain acceptance.

Science cannot provide the truth but this does not necessarily mean there is no truth. It simply takes account of the fact that we have no way of identifying what the truth is and therefore no way of testing whether science is providing it. Science currently cannot definitively identify the truth as, even if it finds it, there is no way of identifying that it has been found.

Proposals that can be tested and be shown to be invalid are rejected. Those that cannot be tested remain as proposals unrelated to science. Science cannot be used to make any valid comment on views that cannot be tested other than they have unknown validity.

An inability to test a proposition does not make it incorrect. It simply identifies that it does not accord with the existing constructs used in science. Such propositions are noted but not used in developing science until they can be tested. The ability to test depends on developments in science hence the limitations can relate to scientific capabilities rather than the proposition.

---

[2] Sceptics typically assume the right to decide what is correct.

Issues with some common perceptions of evolution

The above considerations can be used to examine the applicability of some common perceptions regarding evolution. These perceptions are considered here so as to limit their impact on subsequent considerations. Their existence is noted but they are addressed in a manner that prevents their adversely impacting on subsequent considerations.

Genes are selfish

Realistically no gene can survive on its own so they cannot afford to be selfish. Genes gang together to form organisms wherein the selfless contribution of each gene contributes to the growth and reproduction of the organism essential for the genes to survive. Genes are intrinsically cooperative as it is essential for their survival.

Organisms are adapted to their environment

That which lives is adapted to live. The existence of an organism axiomatically identifies that the organism is adapted to the environment in which it occurs so reference to organisms being adapted is tautological. Application of this proposition usually results in circular arguments

Selection in evolution is directed towards the survival of the fittest

The fittest is determined by the numbers that survive to produce new generations so the situation arises by definition. Those that breed more are said to be the fittest and the 'science' simply identifies associated traits. While survival of the fittest is used to 'explain' many results the considerations are axiomatic or circular. The proposal is tautological.

Direction in evolution is random

Well founded analyses have shown that evolutionary change can effectively be random. However, taken over the history of life there has been a pronounced change in the form of organisms. Life did not begin with humans and it is unlikely that is where it will end.

Natural selection reinforces the norm

Well documented studies have shown that natural selection tends to reinforce the norm by eliminating the extremes. It therefore tends to maintain the status quo. However, the time scale for such observations is short thus the results are not applicable for evaluating long term change.

Summary conclusions

Some of these perceptions are logically invalid while others are only valid within limited circumstances and so are not generally applicable. The limitations mean that generalisations based on the precepts will likely be invalid. For example, the survival of the fittest is given as an explanation for a wide range of observed occurrences when at best it describes the obvious but usually explains nothing.

Denial of Evolution

Some continue to believe that man was created independently of other organisms. This position is most simply addressed by identifying that a wide range of organisms contain common genes. Moreover, genes can be transferred between very different forms of organisms thereby illustrating the commonality of the genetic base. The probability of this situation arising by chance is zero. Absence of a complete evolutionary record is trivial given the detailed knowledge of the relationships between the genetic blue print of organisms.

Another perception is that all organisms were created independently by the same maker according to a plan. Intelligent design is given as an alternate theory said to address a proposed deficiency in Darwin’s theory that observed large rapid changes in the fossil record could not have occurred through a series of small incremental changes. This issue of incremental or evolutionary change versus suggested revolutionary change is addressed later, but the concept of intelligent design is addressed here.

Intelligent design represents an engineering approach to biology whereby the design is meant to efficiently achieve a particular outcome. Without knowing what that outcome is meant to be there is no means of determining if there has been intelligent design or accidental discovery. The theory is not testable in any way and therefore does not incorporate a basic requirement of the scientific method. It is an assertion rather than a scientific hypothesis or theory. In the jargon, it is not science.

An issue with evolution is whether the benefits arise with individuals, species, communities, or the entire system. With intelligent design directed at improving the system there would be no predators on plants as they reduce the primary production in several ways, one being the expenditure of energy by plants on chemical warfare and protective thorns. Application of intelligent design to biology would exclude the existence of predators and pathogens except where animals are being produced according to a wide diversity of design criteria. For intelligent design to be applicable it would have to be applied to each organism independently which, given the suggested global overview of intelligent design, hardly seems intelligent.

The main intelligent design argument is based around one form of a flagellum. The key factual error is the suggestion that a flagellum could not work without all of the components they identify when different organisms exhibit an array of designs of differing complexity. The key logical error is that the development of part of an organism is evaluated independently of the remainder of the organism. An organism is not simply the sum of its component parts and evaluations of components outside the context of the total system of the organism and its environment are inherently unreliable.

A flagellum serves to provide mobility but with single celled organisms mobility is achieved in several ways. Cilia are one mechanism while an amoeba simply moves the location of part of the cell wall and the other parts eventually follow. Bacteria can also move again without there being obvious motile structures. With intelligent design the question arises of why the different designs to achieve the same objective? The suggested intelligent design looks much more like trial and error. Organisms take advantage of opportunities where they have the capability to do so and develop without regard to performance criteria other than their success.

In science where there are two valid explanations the simplest explanation prevails, hence even if intelligent design was considered to be ‘scientific’ it must be rejected in favour of the simpler explanation of trial and error. Evolution through natural selection involves trial and error.

WHAT IS LIFE?

Thermodynamics has everything degrading to a very level playing field. The progression is inexorably towards what could be termed a completely degraded state. Theoretically a completely degraded state is the only system that is fully sustainable without continuing inputs from external sources.

Life, by way of biological organisms, builds self-reproducing systems that increase the level of organisation and concentration of energy. The development of life therefore opposes the degradation. The development and growth of organisms is diametrically opposed to the general decline of physical systems that is inevitably occurring.

Life can only exist as part of the general physical system, and it improves its lot at the expense of the remainder of the system. The more life develops the greater the overall physical decline. The faster life develops the faster the rate of decline in the overall system.

While from a global perspective sustainability is not achievable local situations exist were the gains balance or exceed the losses, as evidenced by the existence of life. Development of one part or section of the system at the expense of the remainder is the basic mode of operation of life. A dynamic sustainability by way of maintaining equality between inputs and outputs can therefore be achieved locally but not globally.

Life is not the only material that can grow and become more organised. With existing knowledge it is, however, the only material that harnesses external energy sources to replicate itself such that the replicates split from the parent and invade new territories. Reproduction and the invasion of new territories are central to life.

Another characteristic of life not shared by purely physical systems is the highly transient nature of individuals. Death is common to all life and the only guarantee in life is death. While physical systems usually degrade slowly the end of the life for an individual organism is abrupt.

Important aspects of life that derive from these basic considerations are:

- Exploitation of external energy sources
- Invasion of new territories
- Finite life span of individuals
- Reproduction

The need for reproduction is a direct consequence of the finite life span as without reproduction life would cease to exist.

Energy and matter are physically interchangeable and the energy source for many organisms derives from matter. There apparently is, however, a need for matter for organisms to exist as no organisms composed purely of energy or developed directly from energy have as yet been identified. Even if matter is viewed as representing different configurations of energy these configurations are essential to the existence of life and the configurations are identified as being matter.

Life as we know it is based around a carbon backbone. The structure of the matter determines the function whereby the arrangement of the matter allows organisms to grow and reproduce. The DNA provides the blueprint for the structure and addresses all life requirements including replication.

How does it Work?

Most simply life is a genetic strand gaining energy and matter from its surrounds but being sufficiently buffered from the physical environment to allow its use of the energy and matter for growth and replication. The buffering is necessary to provide appropriate conditions for the chemical reactions involved in growth and reproduction. Organisms represent localised chemical factories built around a genetic blueprint that obtain their energy and materials from their surrounds.

The complexity of the chemical reactions depends on the level of control of the biological environment. This is minimal with the simple viral structure described above but increases greatly with the development of membranes. Even single celled organisms have a well developed structure with organelles that allow for different chemical reactions in different parts of the cell. The complexity of chemical reactions is greatest in highly evolved organisms such as mammals and this is achieved by having organs that address specific functions.

Organisms survive by exploiting their environment and so must have contact with it. However, their ability to exploit the environment depends on the complexity of chemical reactions where this depends on the level of isolation from the environment. The occurrence of chemical reactions depends on providing an appropriate environment. A basic design consideration for organisms therefore includes the trade off between the contact with the external environment needed to gain resource and isolation from that environment needed to process and utilise the resource. The resource is energy and matter.

Some Definitions

The above identifies life as being a self reproducing aggregation of chemicals that can invade new territories. The term organism acknowledges the organisation of chemicals based around the carbon atom and refers to particular life forms or expressions of life.

An individual organism is logically a single entity that satisfies the criteria for life. Recognising an individual can be simple but there are ambiguities. Most individuals in colonies of insects for example, cannot reproduce. For evolution the colony equates with an individual.

Apart from the lack of direct connectivity the organisational arrangement of colonies is no different to other organisms composed of diverse but spatially coherent units such as cells that serve different functions but interact to work to a common cause. For evolution the individual is the assemblage of life components needed to achieve growth and reproduction and invade new territories. Communication between the components is needed for coordination but physical interconnectivity is not essential for communication. Members of insect colonies use chemicals for communication as well as sound and electromagnetic signals.

Ambiguity also arises when addressing the situation where one organism divides into two that may or may not remain attached. Each new organism is self contained and capable of independent functioning and reproduction. The fundamental question is whether the division of a single celled organism produces one or two new individuals. If only one is produced then individuals can potentially have an infinite life span.

Observations that demonstrate drift in the characteristics of microbial populations indicate that the division likely results in two new individuals. This test is not definitive in resolving the question as drift can arise through the parent organism dieing earlier than the progeny.

However, it is definitive in identifying that the life span of an individual is finite as the original parent form of the organism is lost.

A functional difference exists between definitions of individuals for ecological and evolutionary purposes. For ecology an individual is a self sustaining but not necessarily self perpetuating organism but for evolution the self perpetuation is essential. A tree is significant in the functioning of a plant community whether it produces progeny or not. It only contributes to the evolution of the species where it has progeny that survive to reproduce.

Definitions for organisms and associated terms are:

- Organism: a spatially coherent assemblage of organic molecules obtaining energy and matter from its surrounds for use in growth and replication
- Colony: a group of organisms relying on the combined organisms for growth and replication
- Population: a group of interactively reproducing similar individuals
- Species: a group similar individuals capable of interactively reproducing
- Community: a group of interacting organisms, like and/or unlike

While these define distinct forms of occurrence of life they need not be completely definitive. The term species is likely of most consequence. The definition does not encompass situations where groups of similar organisms are maintained through asexual reproduction, although this requirement could be accommodated by deleting the word interactively from the definition. It does not identify the level of similarity or difference between the individuals but this is normal as there is no set level of difference between species.

For animals the issue of similarity is usually addressed by a requirement for the progeny to be capable of reproduction. Where dissimilar animals can interbreed their progeny are generally sterile. However, this circumstance need not apply with plants as where different species interbreed their progeny are often fertile. The differentiation between species appears to be determined as much by the environment as by the genetic complement. There is no apparent unambiguous definition of a species.

Summary definitions for different approaches to studying relationships between these units are:

- Genetics: the blue print for organisms
- Evolution: the change in the capability and form of organisms over time
- Ecology: the relationship between organisms and their environment.
- Taxonomy: a systematic approach to classification.

With evolution occurring through natural selection operating on the genetic variability between individuals, evolution is a combination of genetics and ecology. Genes provide the variable organisms while ecology examines the drivers for change by way of the interactions between the organisms and their environment.

Classifications need only be systematic but for plants and animals (biota) the classifications are designed to be natural in reflecting the patterns of evolutionary development. Classifications are used to infer the patterns of evolution as well as providing a system for labelling (naming) biota.

A significant limitation of biological classifications was previously the need to infer genetic links from morphological characteristics. This constraint technically no longer applies but the consequences are still embedded in the existing classifications. There is an intrinsic incompatibility in the historic Linnean classification, which is agglomerative, and the genetic approach which is divisive in producing the family tree.

Even with good genetic information the issue arises as to the level of similarity/dissimilarity needed to identify a species. An inability to resolve this issue means that classifications depend strongly on the view of the beholder with the desire to recognise more species producing an ever expanding classification that encompasses refinements such as sub-species, varieties and cultivars.

The considerations here initially address evolution in terms of change in the genetic complement of organisms over time and this is the traditional approach. However, this is later expanded to identify that biological evolution has also involved the development and transfer of information that is not genetically encoded. Evolution in biology does not depend solely on genetics.

Gangs of Genes

The concept that genes are selfish is either anthropomorphic or embodies the concept that nothing happens without intent. It requires that the ability to form intent extends beyond organisms to their components. There is an experiment that indicates this may occur for genetic material but there is nothing that relates to an individual gene.

Organisms represent operational units formed on the blue print of their component genes. They are the functional manifestations without which genes would not survive. Genes combine to form self perpetuating organisms essential to their survival.

The cooperation of genes extends beyond individuals and species as genes can move between species. Genetic material can be exchanged between individuals of different species with the earliest forms of life. More recently evolved forms of organisms have greater restriction on such exchange but that does not prevent genetic change occurring through contact with very dissimilar organisms.

A characteristic of life is that organisms have increased their gene complement by building upon what previously existed. Some genes are common to a very wide range of organisms while groups of genes are similarly common to many species. The difference in genetic complement between species can be very small compared to the genes that they share.

While genes provide the blueprint it is generally the interaction between organisms with their environment that determines which combinations survive. Lethal genes that prevent organisms living or breeding can arise but these produce extinction. Such genes are naturally eliminated where they are expressed.

This need for expression for natural selection to have effect identifies a significant characteristic of genes: the effect of a gene depends on the other genes present. Genes do operate as gangs.

As genes do not operate on their own but depend on the interaction with other genes there can be genes present that have no apparent role in the functioning of an organism. While this lack of an apparent role can reflect deficiencies in knowledge it can also reflect the historic accumulation of genetic material. Natural selection does not operate on something that does not affect the interaction between the organism and its environment.

Environment Interactions (Natural Selection)

Darwin suggested that selection improves organisms in relation to their conditions. Those considering that natural selection arises through competition have interpreted this as representing the survival of the fittest.

Selection determines which combinations of genes survive and those unsuited to the environment cease to exist. Unfavourable combinations of genes are eliminated while those suited to the conditions persist through reproduction. The main issue for evolution is the elimination of the gene combinations as these cannot contribute to the future. The promotion of particular gene combinations can also be important but only insofar as they provide a new capability. The promotion of variations on a theme is of no consequence.

The proposition given in the *context* is that organisms take advantage of opportunities where they have the capability to do so, and they develop without regard to performance criteria other than their own success. Organisms function to increase the benefits to them. This is compatible with the views of Darwin, the survival of the fittest, and with the proposition in the appended *Evolutionary Direction* that natural selection is directed towards elimination of the unfit even though the last two proposals are diametrically opposed.

As noted earlier, discussions on survival of the fittest become circular while elimination of the unfit is definitive. Evolution builds on what already exists and discards gene combinations that do not work. However, the viability of gene combinations depends on the environment thus elimination can occur through an individual being in the wrong place at the wrong time. Evolution can contain a large element of chance.

Examples used to illustrate survival of the fittest are usually based on observations of populations of particular species in particular environments. Interactions with other species and the environment are usually intentionally limited, and it is assumed that observed changes are internal to the population being studied. However, there is abundant evidence that external factors such as climate change have provided opportunities for some by eliminating others. Evolutionary development does not solely depend on the internal characteristics of populations and the elimination of some by external factors can be to the benefit of others.

Significant aspects of the interaction between organisms and their environment are:

- It is effected through groups or combinations of genes (individual organisms) rather than individual genes.
- Gene combinations unsuited to the environment are eliminated rather than individual genes.
- The gene combinations that survive are suited to the environment but are not necessarily best suited.
- The gene combinations that survive can include genes that are irrelevant to the particular environment.

This has evolution occurring through natural selection eliminating the unsuited.

The term unsuited is used in preference to unfit as it identifies there is no single correct solution. The assessment of performance is made relative to particular conditions and hence changes with those conditions. Something eliminated in one environment may perform well in another. The assessment of suitability is therefore relative rather than absolute as inferred by the use of the term fittest.

The issue this raises is how can elimination result in evolution being directed towards increasing the benefit for the individual. If selection only involves elimination then the benefit derives indirectly through the elimination of competition. Organisms must avoid elimination to have any chance of developing but the development is generally interpreted as depending on positive reinforcement.

There may be a positive aspect to selection whereby those that breed most increase their numbers more than others. However, while the gene combinations with greater numbers may have the greatest chance of evolving into something new this is by no means necessary. Changes in the environment could lead to the extinction of those that have been strongly promoted, particularly since exploitation of the environment can render it unsuitable to the organism dependent on it. As the promotion of some need not eliminate the others any positive aspect of evolution is therefore promotion of the fittest and not survival of the fittest.

This promotion of the fittest could be regarded as being equivalent to survival of the most suited. However, neither of these explanations resolves the tautological issue raised in the *context*. The fittest and most suited are determined by the greatest increase in numbers hence the argument is circular. There is no measure of fitness that is independent of the measure of promotion and therefore no rational basis for an evaluation of evolutionary performance. All that can be done is to describe the attributes or traits thought to be associated with fitness.

The difference between elimination and promotion is functionally significant. Promotion only places value on that which is beneficial under the prevailing conditions which, if only promoted individuals survive, means that neutral as well as detrimental attributes are lost. Elimination allows neutral attributes to persist. Elimination maintains a greater number of gene combinations where this is beneficial in addressing the changes in environmental conditions that inevitably occur. Elimination minimises losses and hence maximises the chances of being able to take advantage of future opportunities.

The practical difference between promotion and elimination can be illustrated by Darwin’s dogs where humans have positively selected to produce a great diversity of forms. Many of these forms would be identified as subspecies if they occurred naturally. As humans represent a natural part of the system the different forms can logically represent subspecies, if not species, where the assigned level depends on the significance assigned to characteristics such as the capacity to interbreed. Humans are identified as being accountable for evolutionary changes associated with increased extinctions due to human activity and so logically they can also be linked with developments.

The main differences in the forms selected by humans compared with the wild populations relates to survivability in different environments, and the potential for change. The selected forms depend on humans for their persistence whereas wild populations do not. The selected forms have lost many capabilities because the positive selection for particular traits. None of the selected forms have the potential to return to the original wild form.

Several factors are involved in the inability to reverse evolution, a key one being that the chances of redeveloping lost capabilities are remote. The inadvertent loss of capabilities associated with positive selection diminishes future opportunities for change.

The issue of whether the negatively directed elimination can result in positive reinforcement can be examined by way of changes to populations. If a segment A1 of a population A develops a competitive advantage over the general population the issue is whether the promotion of A1 is necessarily associated with a decline in the remainder of A. Such a negative feedback arises where they compete for the same limited resource but does not arise where A1 occupies new territory. Moreover, as the A and A1 populations then do not compete the question of relative fitness or suitability does not arise. The benefit and hence promotion arise from the avoidance of competition.

The general situation is that competition is central to survival but development depends on the avoidance of competition. Evolutionary change therefore does not solely depend on the outcome of competition arising through direct interaction between individuals.

This identifies a basic deficiency in the term promotion of the fittest; fittest for what? The lack of a reference prevents the application of a rational analysis. Another issue with using survival of the fittest in addressing natural selection, apart from the tautology, relates to the need to differentiate between the process and outcomes. Natural selection is a process, as is the avoidance of competition. Survival of the fittest is an outcome, as is increasing the benefit to individuals.

The objective with evolution given here is increasing benefit to the individual and this establishes the direction in evolution. The means by which it is achieved is selection directed at eliminating competition. In practice complete elimination of competition is likely rare, hence the realised outcome is usually a reduction in competition. With survival of the fittest selection is based on individuals fighting for the same resource or territory.

Reducing competition can be achieved by several means including:

- Eliminating or suppressing competitors (competition).
- Avoidance of competition (use of different resources, as is most simply achieved by occupying different spaces)
- Collaboration or working together.

With this analysis selection in evolution is directed towards the elimination of competition where this can involve the avoidance of competition as well as elimination of the unsuited.

Eat without being eaten

The above considerations address how an individual can obtain increased benefit. As with Darwin it addresses how change can arise through natural selection. However, for change to be able to occur there must be prior existence and persistence. Evolutionary development is built upon survival.

Survival can be address by way of risk, and for biota the main risk relates to eating without being eaten. For plants the eating involves obtaining energy from the sun, as well as matter from the atmosphere and soil. For some bacteria the resources derive solely from inorganic minerals. These are the primary producers. However, for most biota the resource they acquire (eat) comes from other organisms. Biological systems (ecosystems) revolve around the cycling of resources developed by primary producers through other organisms.

Breeding is essential for survival but breeding cannot occur without growth, and growth involves the acquisition of resources by way of energy and matter. As the matter in organisms occurs in the most appropriate form for organisms there is a strong tendency for organisms to acquire their resources from other organisms. Humans identify it as involving predation, pathogens and symbiosis but for nature it is recycling with both live and dead organic material being recycled. Life tends to make most use of material that has been developed into an organic form.

Survival of a population, and hence species, depends on the chances of the component individuals surviving to breed. Overall the numbers produced must be greater than the numbers breeding to allow for losses. Extreme numbers of progeny are often produced to compensate for the potential losses, as with seed production by plants and the larvae of many marine invertebrates. Where the numbers of progeny are small mechanisms have evolved to improve the chances of them surviving to breed.

Selection to reduce the risk of insufficient individuals surviving to breed arises with collaboration and the avoidance of competition. The pollen of one individual is often freely available to all other individuals. The same applies with gene transfer with corals on the Great Barrier Reef and fish that reproduce by combining the eggs and sperm of many individuals in swarms. Such a collective response has typically arisen where losses of progeny are very high because of high predation and/or a low probability of a new individual finding a suitable environment.

It is axiomatic that selection must promote the survival of sufficient breeding individuals to replace the losses. Given the uncertainty as to risks the number of replacement breeding individuals tends to be greater than the parent population hence life has a large potential for growth in numbers. The growth of populations is usually restricted by the environment rather than a capacity to breed. From this analysis selection is fundamentally directed towards reducing the risk of parents not being replaced by their progeny where replacement involves the progeny surviving to breed.

The question this raises is how this management of risk relates to selection being directed towards reducing competition. The simple answer is that maintaining an existing competitive ability tends to maintain the status quo while development depends on improving relative to others. Any improvement in a competitive situation equates with a reduction in competition. Reducing competition reduces the risks associated with progeny surviving to breed. Natural selection can be regarded as reducing the risk of parents not being replaced by their progeny with natural selection being directed towards reducing that risk.

The different means of reducing competition have different levels of risk for individuals. Avoiding competition and collaboration reduce risk for individuals both in acquiring resource and breeding. Eliminating or suppressing competitors through competition has high individual risk. Such competition is fundamental to survival as that is how organisms acquire the resources needed for growth. However, with breeding such competition is usually constrained. Breeding fundamentally depends on collaboration between males and females and, while conflict can occur, it is usually ritualised. There are numerous examples where individuals in populations compete strongly for food but collaborate to breed. Conflict between males in breeding is common but is seldom fatal.

This identifies the possibility of evolution operating at different levels of organisation. Competition for food (resource) can result in selection operating on individual organisms while collaboration in breeding can result in selection also relating to populations.

This analysis differs from those commonly applied in not being restricted to the examination of a particular species by way of interactions between individuals within populations. The elimination of competition that determines evolutionary direction by way of realised outcomes need not arise from competition between individuals, populations or species as it can occur through physical factors such as climate change. Selection is effected through interactions between individuals and the entire environment.

Nature of the Environment

The environment can be subdivided into physical and biological components noting that organisms change the physical environment as well as being a biological component. The environment for organisms is not just the physical environment. An organism can directly affect others, as with predation and symbiosis, or indirectly affect them by changing physical factors such as humidity, temperature and water availability.

Some scientists express the view that ecology is simply the combination of physiology and physics. The interactions between organisms and between organisms and their physical environment negate this notion. The whole is much more than the sum of the component parts.

The basic elements of the environment needed by organisms for growth and survival are energy and matter. For most animals the source of the energy and matter are the same in being other organisms. For primary producers such as plants the sources of energy and matter differ. Their energy derives from the sun while the matter derives from the water, atmosphere and/or soil. Some microbes have the ability to directly derive their energy and matter from minerals.

While energy and matter are physically interchangeable biological organisms are not known to convert energy to matter. For example, photosynthesis acquires energy by transforming rather than creating chemical elements. Plants therefore depend on the provision of matter by way of elements. Moreover, these elements must often be provided in a particular form. The availability of necessary elements (matter) is as important as the availability of energy.

Physical Environment

The chemical reactions that form the basis of life take place in aqueous solution. While carbon is the backbone of life, water is the medium through which life operates. Water is the foundation of life and primary design criteria for life involve the maintenance of water in an appropriate form. This is most obviously achieved by membranes but the innate structure of water allows for the spatial separation of elements without the need for membranes. Liquid water occurs in high and low density structural forms and this differentiation is promoted by proximity to surfaces. The different structural forms of water have different affinities for different ions and this separation of ions allows for the occurrence of different chemical reactions in different parts of aqueous solutions.

For terrestrial biota both the availability and form of water are important as gaseous exchanges with the environment essential for survival invariably result in the loss of water. Terrestrial plants best illustrate the design constraints this imposes. Plants harvest atmospheric CO_2 to produce carbohydrates using solar energy wherein the exposure to the atmosphere needed to obtain the CO_2 inescapably results in a loss of water. The water needed to replace that lost to the atmosphere is usually extracted from the soil. The energy used to extract the soil water derives from the atmosphere at no cost to the plants, apart from the cost of building the necessary infrastructure, but the availability of soil water usually becomes limiting at some time. Plant survival depends on the ability to maximise the CO_2 gained per unit of water loss and to survive periods of restricted water availability.

These water considerations apply equally to terrestrial animals wherein water losses arise through the disposal of wastes as well as the need for gas exchange with the atmosphere. Respiratory systems essential for gaining oxygen and expelling CO_2 are designed to minimise water losses, and the water content of solid and liquid wastes is reduced prior to disposal.

Most life operates at temperatures encompassing the liquid range of water. In practice the upper limit is generally around 60 degrees centigrade (C) due to protein denaturation. The lower limit to physiological activity is around 6 C but some 'simple' organisms have mechanisms to allow them to function at temperatures below 0 C.

The rate of chemical reactions depends on temperature and this determines the activity of organisms. In general, physical reactions double for each 10 C increase in temperature whereas biological reactions increase two to three fold. However, this increase in the rate of biological reactions only applies within favourable temperature ranges. Respiration reflects the overall metabolic activity and for plants this saturates at around 50 C, rapidly declining to zero at slightly higher temperatures.

Some organisms have evolved to circumvent this limitation by maintaining a constant temperature (homothermy). The penalty is the high energetic cost of maintaining a constant temperature.

Most organisms depend on oxygen to release the energy from other material needed for life. For primary producers the physical environment additionally provides all of the other elements needed for life. The simpler organisms such as bacteria and fungi can extract these from the soil and rocks but this ability is greatly diminished in higher plants. The form of the element determines its availability. This limited ability of higher plants to extract elements from the soil results in the development of higher plants depending on micro-organisms.

Biological Environment

The biological environment is all important for non-primary producers as it represents their source of energy and matter. The survival of most animals depends on their predation of plants and/or other animals. The existence of animals depends on the prior existence of life and their survival depends on the continued existence of other forms of life.

The existence and survival of higher plants similarly depends on the prior and continued existence of other life forms. Most of the nutrients needed by higher plants are initially extracted from the physical environment by micro-organisms which put them into a form accessible to higher plants.

Nitrogen provides an example as higher plants cannot use the abundant atmospheric nitrogen despite nitrogen being needed for protein formation. Little atmospheric nitrogen is converted to a form accessible to higher plants through natural physical processes such as lightening. Virtually all nitrogen used by plants derives from microbes by way of the fixation of atmospheric nitrogen and the recycling of nitrogen in dead organic mater. Some plants form symbiotic relationships with bacteria or blue green algae to promote access to nitrogen.

The above has life evolving through different forms of organisms 'collaborating'. Evolution has involved the development of synergistic relationships between different forms of organisms similarly to the collaboration with genes. This accords with the ecological representation of the web of life but contrasts with the current representation of the biological environment for evolution which has individuals competing with each other to eat and reproduce most.

While organisms collaborate there is also competition, and like organisms usually compete more than unlike. In addressing evolution the issue is which is more important in determining change, competition or collaboration. While this question may be impossible to definitively answer the genetic change involved in competition leading to 'survival of the fittest' is small whereas the potential for change through combining the capabilities of different organisms is large.

Collaboration has been important in evolution, and may be more important than competition. The ability to compete is essential for survival but progress may be determined more by collaboration than by competition. This conclusion accords with the suggestion that evolution is determined by the elimination of competition where this can involve avoidance as well as elimination of the unsuited.

Impacts of Organisms on the Environment

The above identifies that organisms ultimately degrade the resources essential for their survival where this is a physical inevitability. However, organisms can improve their local environment despite the decline in the overall environment, just as organisms improve their condition while the overall system declines. While the improvement in the local environment can only be sustained while resources are available this development is a common characteristic of organisms. Life promotes the development of conditions favourable to life.

The most general example of life promoting the development of conditions beneficial to life is given by the development of vegetation on bare rock or sand. The system gradually accumulates resources needed for development resulting in an increase in the amount of life. The increase in the amount of organic matter continues until the losses of resources from the system exceed the gains.

The above example addresses ecosystem development but individuals can similarly develop conditions to their benefit. Improving access to water provides a number of examples with sphagnum moss using vesicles to maintain hydration and plants such as mulga (*Acacia aneura*) channeling water down stems to increase the effectiveness of soil water storage. There is empirical evidence of vegetation promoting increased rainfall but, while some associated mechanisms may be known, the main mechanism is not. Humans represent the ultimate example of organisms modifying the environment to their benefit.

Mutualism

Mutualism addresses the dependence of one organism on another. Dependent or positive mutualisms are common, as with bacteria in the gut of many animals providing nutrition from food that would not otherwise be available, and by breaking down toxic substances. Similar relationships arise between soil microbes and plant roots whereby the microbes provide elements in a form that can be used by plants while plants provide the organisms with food (energy and matter) they need for survival. While many of these relations are general some are highly specific, as arises with mychorrhizal bacteria.

Negative mutualisms (antagonisms) are most common as organisms represent an ideal resource for other organisms. Humans are non-specialists, or omnivores, and consume a very wide range of organisms from microscopic yeasts to the largest of animals such as whales. Virtually all in the animal kingdom survive by consuming other organisms, plants or animals where corals are a potential exception. Some in the plant kingdom directly consume other organisms but most obtain their energy from the sun and their matter (nutrients) from the atmosphere, mineral soil and the recycling of dead organic matter.

Antagonisms are often general, as with humans exploiting a wide range of foods, but they can also be highly specific. These associations are usually described as being parasitic, as with a leach that only lives in the anal canal of hippopotami. Microbes involved in antagonisms are described as pathogens.

The issue for evolution is whether the mutualism involves direct exchange of genetic information between the different organisms. If not then the mutualism does not change the evolutionary process compared to if mutualism did not occur. The different organisms simply represent part of the environment. The only significance of the mutualism then is that advantage can be gained through collaborative arrangements and does not solely depend on competition.

The collaboration identified above relates to dissimilar organisms and so could be said to have no significance for the flow of genes. However, collaboration also occurs between similar organisms, as with communal breeding by fish. The release of sperm and eggs is coordinated between all individuals in a population to prevent all of the eggs from being consumed by predators. Cooperation has played a role in genetic evolution.

The issue of exchange of genetic information between dissimilar organisms in mutual relationships is best addressed by others. There does not appear to be clear evidence for support in the development of organisms but there is evidence that interactions between organisms can result in heritable genetic changes.

Evolution v Revolution

The evolutionary record is characterised by the sudden emergence of new groups (Orders) that are distinctly different from the prior life forms. The fossil record appears to indicate the occasional rapid occurrence of major change as well as incremental change.

Evolutionary changes are generally said to arise through a progression of small incremental changes. Indeed, that is the definition of evolution. From a genetic viewpoint there is no clear explanation for this apparent revolutionary situation. Possibilities include:

a. Transitional forms not being observed because of the incomplete evolutionary record.
b. The magnitude / rate of change possible through selection being greater than thought.
c. There being a disconnect between the occurrence of genetic change and its expression.
d. The change arising through the capabilities of different forms of organism being combined.

Support for point (c) arises from the consideration of selection being negatively rather than positively directed. The negatively directed selection does not eliminate genes that have no influence under the prevailing conditions: there can be genetic change that is not immediately expressed. The potential therefore exists to accumulate genes that in the future can result in major change due to their interaction with other accumulated genes and/or changes in the environment. Interaction between accumulated genes provides a means of producing apparent rapid change. While individual genetic changes are still incremental, and hence evolutionary, the expression of change is rapid and hence appears revolutionary.

With point (d), developments in genetic knowledge have demonstrated the feasibility of transferring genetic information between very different life forms. It is technically possible. The difficulty lies in demonstrating that it has naturally occurred.

CHANGES IN ORGANISMS AND COMMUNITIES OVER TIME

Organisms are considered along with communities as they are interlinked. Organisms evolve within communities and communities are a product of the component organisms. Evolution is a consequence of the environment as well as the genetic complement.

The information in the tables below identifies the nature of changes from early in evolution to now, and what might occur in future. The identification of changes does not indicate that organisms similar to those at the beginning of life do not now exist, as they do. The changes identify that while evolution started with particular life forms many other forms have evolved over time. Evolution has increased the diversity of life forms and there have been patterns to the changes.

The tables compare what could be regarded as the maximal development of particular characteristics with those for the earliest condition. They also predict what could be expected in future based on the loss or decay of existing capabilities. They examine evolutionary decline as well as development. The maximal states are based on known occurrences and therefore do not (cannot) take account of future developments. The projection for decline is based on the characteristics of change in the species complement of declining plant communities where the eventual outcome comprises a mixture of organisms that currently exist but occurring within a highly degraded community.

The condition usually identified for the decay situation is a mixed community where this relates to the losses occurring across all life forms. While evolutionary development involves building upon what exists the decay logically mainly arises through a random loss of existing species. The applicability of the assumption of random loss depends on the absence of catastrophic change that preferentially affects particular life forms, as is suggested to have occurred with dinosaurs. Given the uncertainties as future changes the suggested conditions are only indicative, i.e. broader than ball park.

The main conclusions are:

- There are developmental patterns
- There have been losses
- The temporal patterns of development and loss are different

General patterns

Organisms were originally small and simple and capable of rapid continuous reproduction. Organisms that now exist and are considered to be highly evolved are large and complex, have few progeny and reproduce intermittently. They have also decreased their dependence of their level of physiological functioning on the physical environment. With animals this mainly arises with homothermy but humans have taken it much further. With plants it mainly involved protecting spores (pollen) so that reproduction does not depend on the occurrence of a film of water.

The general changes with individual plants are an increase in size, longevity, complexity and a reduction in reproduction. Plant populations have increased in complexity and decreased in density. Plant communities have increased in biodiversity, complexity, production and biomass.

As with plants the general changes with individual animals include an increase in size, longevity, and the complexity of individuals, and a reduction in reproduction and the dependence on environmental conditions. However, they also include the development of parental care. The developments for populations and communities of animals are the same as for plants.

Plants			
	Beginning	Maximum	Decay
Individuals			
Life span	short	long	mixed
Complexity	low	high	mixed
Size	small	large	mixed
Reproduction rate	rapid	slow	mixed
Reproduction (dependence on a free water film)	dependent	independent	mixed
Populations			
Complexity	low	high	mixed
Density	high	low	low
Breeding	continuous	episodic	mixed
Competition	high	high	high
Communities			
Biodiversity	low	high	moderate
Functional complexity	simple	moderate & complex	moderate
Biomass	low	high	mixed
Production	low	high	moderate to low
Interdependence	low	high	low and high
Competition	high	low to high	moderate to low

Animals			
	Beginning	Maximum	Decay
Individuals			
Life span	short?	long	mixed
Complexity	low	very high	mixed
Reproduction	rapid	slow	mixed
Size	small	large	mixed
Parental care	none	extended	mixed
Physiology	isotherms	homotherms	mixed
Populations			
Complexity	low	high	mixed
Density	high	low	low
Breeding	continuous	discontinuous	mixed
Sibling care	none	occurs	mixed

Communities			
Biodiversity	low	high	moderate
Functional complexity	simple	moderate & high	moderate & high
Biomass	low	high	mixed
Production	low	high	moderate to low
Interdependence	low	high	low and high
Competition	high	high	moderate to low
? The answer depends on whether the division of one unit into two eliminates the parent unit.			

Basic Growth and Decay Functions

The basic developmental functions involve growth and decay with the simplest form of developmental relationships being a constant rate of gain or loss. A constant rate of growth produces an exponential increase in the amount or number of organisms present as the realised gain depends on what is present. Curve A is indicative of a population breeding without any constraints or limits to growth. A pair of rabbits produces four which all breed to produce 12 which breed to produce 26 etc. However, there are always limits or constraints to growth and the typical growth cure for organisms is sigmoidal or S shaped (B). The sigmoidal curve represents exponential growth within limits. This form of relationship typically arises with the increase in biomass of individual plants as well as numbers in populations such as bacteria and animals.

Curve C characterises radioactive decay where the rate of loss is constant: the amount lost is proportional to the amount present. This form of loss is characteristic of the changes in the numbers of new recruitments (cohort) after an initial density dependent phase following episodic recruitment with plants. A cohort comprises members of a population having the same age. With episodic recruitment a population comprises a number of cohorts.

The curves in D represent a combination of B and C and so combine resource limited growth with losses that depend on the numbers present where the latter can be unrelated to resource availability. The rate of loss is one hundredth of the amount present for the upper curve and one fiftieth for the lower curve. This form of curve is seen with temporal changes in the numbers of species within animal orders and the biomass of plant communities.

The applicability of the form of curve depends on the attributes being studied. The sigmoidal curve is typical for biomass accumulation of annual plants but not for production or resource utilisation. The curve indicates that biomass accumulation is close to zero for an extended period towards the end of growth but the respiration needed for maintenance means that production stays at a reasonably high level. Production does decline towards the end of growth but not as much as indicated by the sigmoidal curve.

The basic considerations illustrated by these curves are:

- Life exponentially expands to occupy the available space.
- The level of development is constrained.
- The development of life results in losses.
- The amount of loss depends on the numbers/amount present.

Numerous examples exist for the first three points. Evidence exists for the fourth, and it is the simplest form of decay relationship. However, situations exist where losses exceed those expected with exponential decay, as with density dependent thinning of plants. This represents resource limited loss which can be additional to normal exponential resource independent losses.

Curve D is characteristic of temporal changes indicated for the number of species within animal orders but the data have limitations. If applicable this form of curve indicates that the genetic capacity of a new order is effectively set when it first arises, and the growth phase represents the development of different expressions of that capability within the given constraints. The decline represents the random loss of expressions of capability.

Few data are available to test the applicability of the response function with the main constraint being the provision of detailed information over a sufficiently long observation period. Another issue is that the idealised curves in D effectively assume that the organism is unaffected by other life forms, hence the analysis does not necessarily take account of interactions between components within systems. However, this lack of considerations of interactions is not significant if the reasons for the decay are inherent in the organism as they then arise independently of external factors.

The build up and decay of plant communities on coastal sand dunes over a period of 500,000 years illustrates constraints associated with the applicability of curve D (Walker et al. 1981) with the theoretical basis being given by Tunstall (1978). The nature of the sand is effectively independent of the time of deposition, and in leaching situations most nutrients must be acquired from the sand. The development of the vegetation therefore reflects the ability of biota to acquire, store and use matter derived from the sand.

The general temporal pattern of development as indicated by vegetation on dunes of different age is grassland, shrubland, open forest, tall dense forest, open forest, shrubland with sparse trees, low shrubland and very low sparse shrubland with sedges. The pattern of biomass accumulation mirrors curve D. Biomass rapidly builds up to a maximum followed by a long period of gradual decline.

Development of the vegetation arises through the release of nutrients from sand grains by microorganisms. Higher plants cannot access many nutrients directly from the sand so the development of the vegetation depends on microbial activity. Leaching of the nutrients is constrained by uptake and storage by higher plants with the nutrients being recycled by microbes. There is a synergistic relationship between microbes and higher plants. The growth phase of the curve represents the situation where the level of acquisition of new nutrients from the sand exceeds the losses through leaching.

The supply of new nutrients declines with time as there is a limit to the nutrients contained in the sand. The loss of nutrients without replacement means the system eventually begins to decline. Storage and recycling can delay the onset and slow the rate of decline but cannot prevent it from occurring. In a resource limited system where there is loss this decline is inevitable.

The data on species changes in the system are not definitive but the number of higher plant species increases during the growth phase of the system. The number of these species may decline during the extinction phase but the system maintains a high level of diversity of higher plants.

The conceptual basis for this analysis derived from consideration of simple component replacement plant population models, and is illustrated by observations of spatial variability in a poplar box (*Eucalyptus populnea*) woodland (Tunstall & Torssell 2004). The component replacement models were based on development being resource limited but with the resource limits varying with species / life form. The woodland observations related to spatial patterns of tree development and variations in the relative amounts of trees, shrubs and grasses in communities. Given the definition of a community the different components must be sufficiently close to interact hence the vegetation represents mixtures of individuals of different species.

There appeared to be a spatial mosaic of patches of trees wherein each patch contained individuals in two or, rarely, three size classes. The tree sizes within patches were distinct indicating the occurrence of cohorts associated with episodic recruitment. It was subsequently shown that tree recruitment depended on the level of tree development with significant recruitment only occurring where the level of adult trees is low (Tunstall & Reece 2005). Spatial patterns of tree development reflect temporal patterns of recruitment giving a time-space equivalence. Temporal changes are reflected in the spatial patterns.

The pattern of development, schematically illustrated in Fig.2, has fluctuating levels of tree development arising from the control of recruitment by existing individuals. The life cycles of the trees represent a strong control on recruitment.

The generally accepted view of vegetation development was that vegetation develops to a maximum sustainable by the environment represented by the climax (Clements, 1916). This effectively states that vegetation utilises all of the available resource. For this to arise the variations in trees illustrated in Fig. 2 would have to be compensated by changes to other parts of the system. Fig 3 illustrates that this does not occur. There is an upper limit to the sum of grass and woody components but there is a wide scatter of points within that limit. In particular, low abundance of grass can occur at low abundance of trees. The vegetation present at any time or in any location does not necessarily represent the maximum that the environment can support. There is unutilised resource where this arises because of the control of vegetation development by the life cycles of the plants.

The occurrence of unutilised resource is further illustrated by the abundance of mosses and lichens in pine forests in Central Sweden (Fig. 4). Limits exist to the combined development of mosses and lichens relative to the development of pines but those limits are rarely reached. The same situation arises with mosses and lichens on their own but they differ in their responses to the occurrence of pines. Mosses have a synergistic relationship as some cover is necessary for mosses to occur and maximum moss occurs at a reasonably high cover of pines. Lichens have an antagonistic relationship with pines with maximum lichen occurring at zero pine cover. The same forms of relationships also arise between pines and shrubs such as *Vacinnium spp* (synergistic) and *Rubus ideaus* and *Caluna vulgaris* (antagonistic).

The poplar box woodland example represents a self-regenerating system wherein recruitment occurs through the interaction between fluctuations in climate and the life cycles of the trees. It appears that the existing trees exercise control on what recruits as well as when. However, communities exist where the replacement of lost trees has not occurred. In 200+ and 400+ year old pine stands in USA and Sweden respectively only a few degraded live trees remain and the biomass and growth potential of the systems are well below the maximum levels. These stands illustrate natural patterns of system decay but may exist because the exclusion of fire has removed the natural trigger for tree recruitment. The northern vegetation has effectively developed subsequent to the last glacial period and so is not as highly evolved as Australian vegetation.

Evolutionary significance of the patterns

The sand dune example represents the evolution of a biological system and so illustrates evolutionary patterns in a system having a constant energy supply but limited by the supply of matter. Initial development of the system depends on microbes, but maximising the development depends on a synergistic relationship between microbes and higher plants. The microbes prosper along with the higher plants.

The same life forms can be present at different stages in the succession with microbes common to all. However, development of higher life forms is nutrient (matter) restricted at early and late successional stages and energy restricted when nutrients are plentiful. There is always competition for matter but competition for energy increases as matter becomes increasingly available.

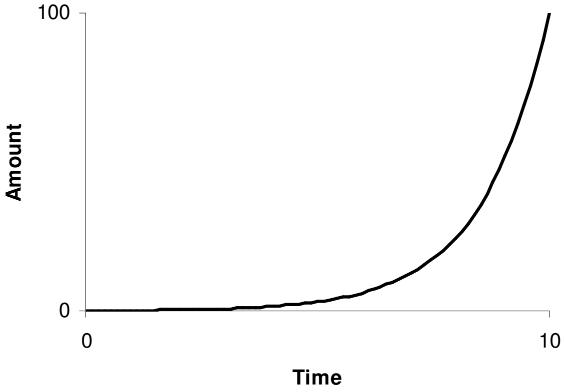
The matter restriction does not necessarily preclude the existence of higher life forms but it does suppress their development. A large tree species typically present in forests, *Lophostemon costata*, can occur in the most degraded system but only as a small prostrate plant that would not even be regarded as a dwarf shrub.

This example illustrates:

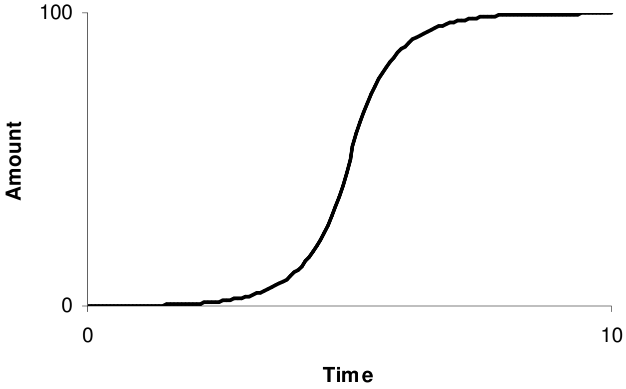
- The build up of a system through the accumulation of resource.
- The decay of a system where the rate of loss of matter exceeds the gains.
- The most developed system axiomatically has the highest biomass but it likely also has the highest production. It contains the largest individuals.
- The system develops through synergistic relationships between different life forms rather than competition.
- The different developmental stages tend to contain a diversity of life forms with the highest life forms still existing at the greatest levels of decline observed.

The examples on the composition of woodlands and forests identify that:

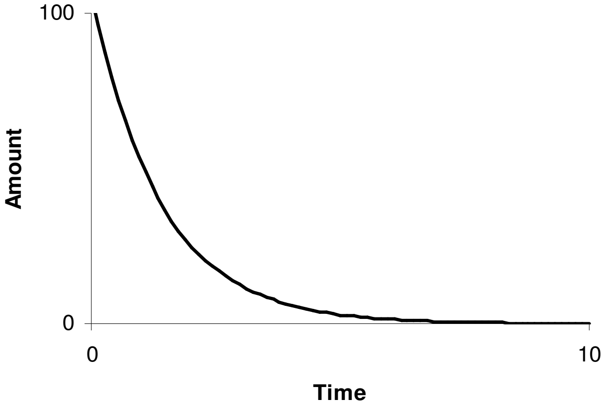
- Recruitment (reproduction) is needed for a species to continue to exist.
- The existing biota affects recruitment.
- The interactions between different organisms can be synergistic or antagonistic.
- Biological systems do not necessarily utilise all of the available resource.
- Maximum levels of resource utilisation cannot be sustained due to the life cycles of the organisms.



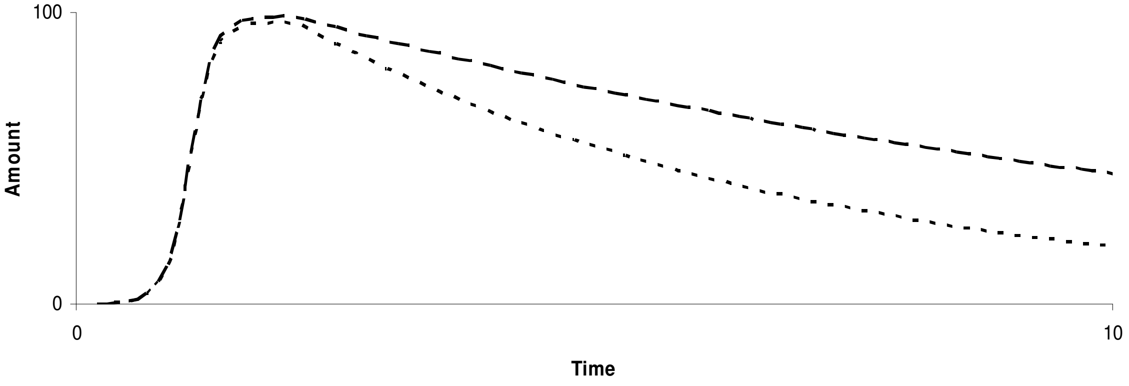
A Positive exponential
(unrestricted growth)



B Sigmoidal curve
Limited growth



C Negative exponential
(constant rate of decay)



D Combined restricted growth and decay
Decay rate 0.01 — — — — , 0.02 ....

Fig. 1 Basic growth and decay relationships.

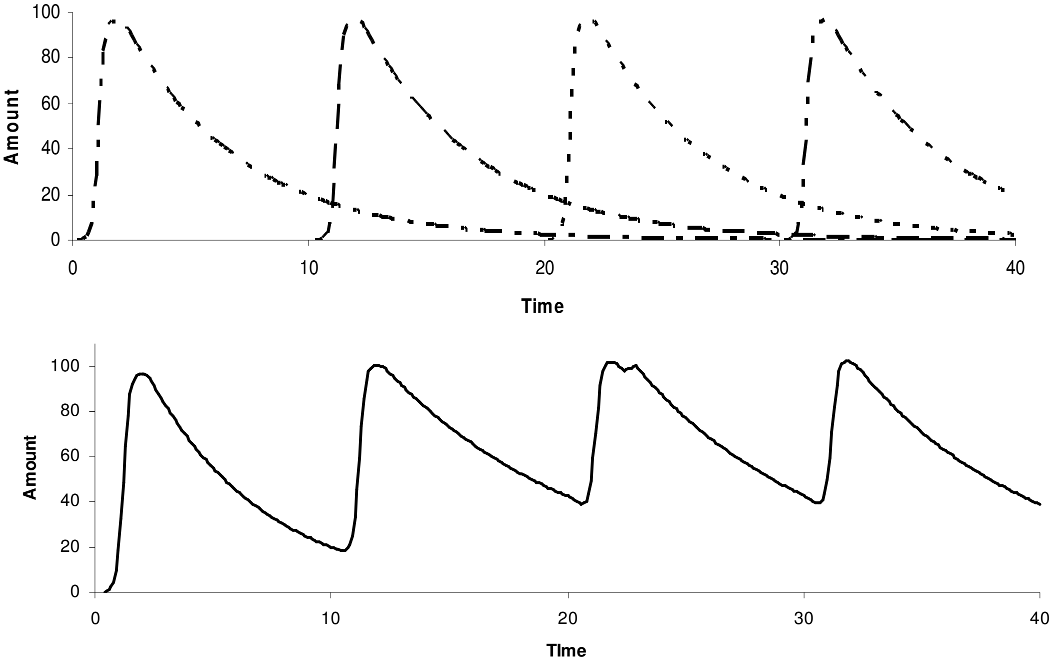


Fig. 2 The relative yield of grass versus the combined projected foliage cover of shrubs and trees in *Eucalyptus populnea* woodland systems.

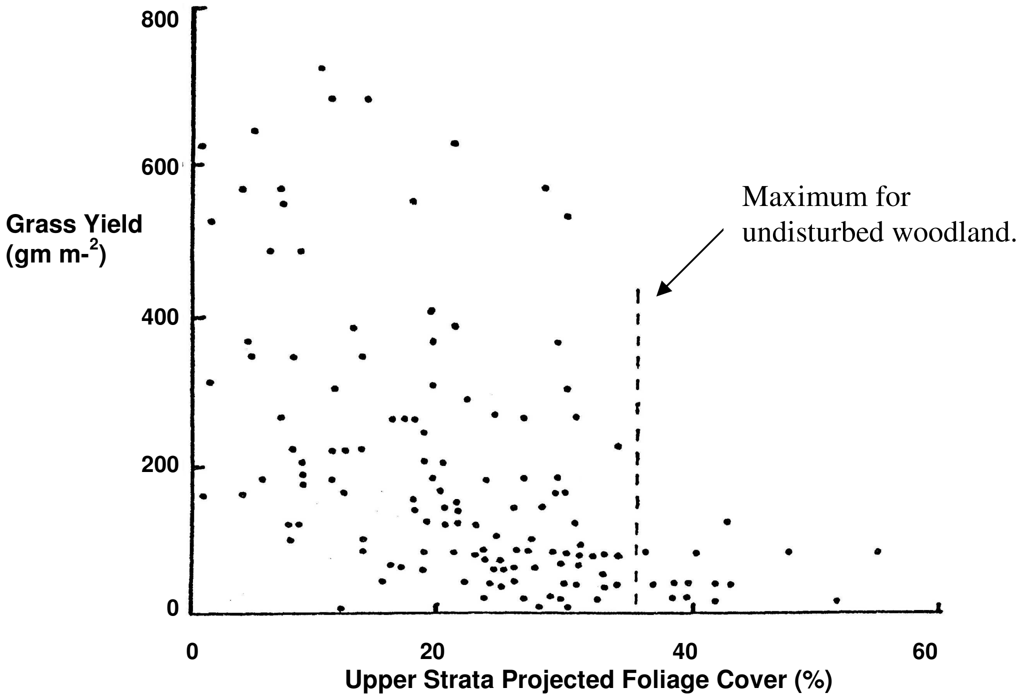


Fig. 3 The relative yield of grass versus the combined projected foliage cover of shrubs and trees in *Eucalyptus populnea* woodland systems.

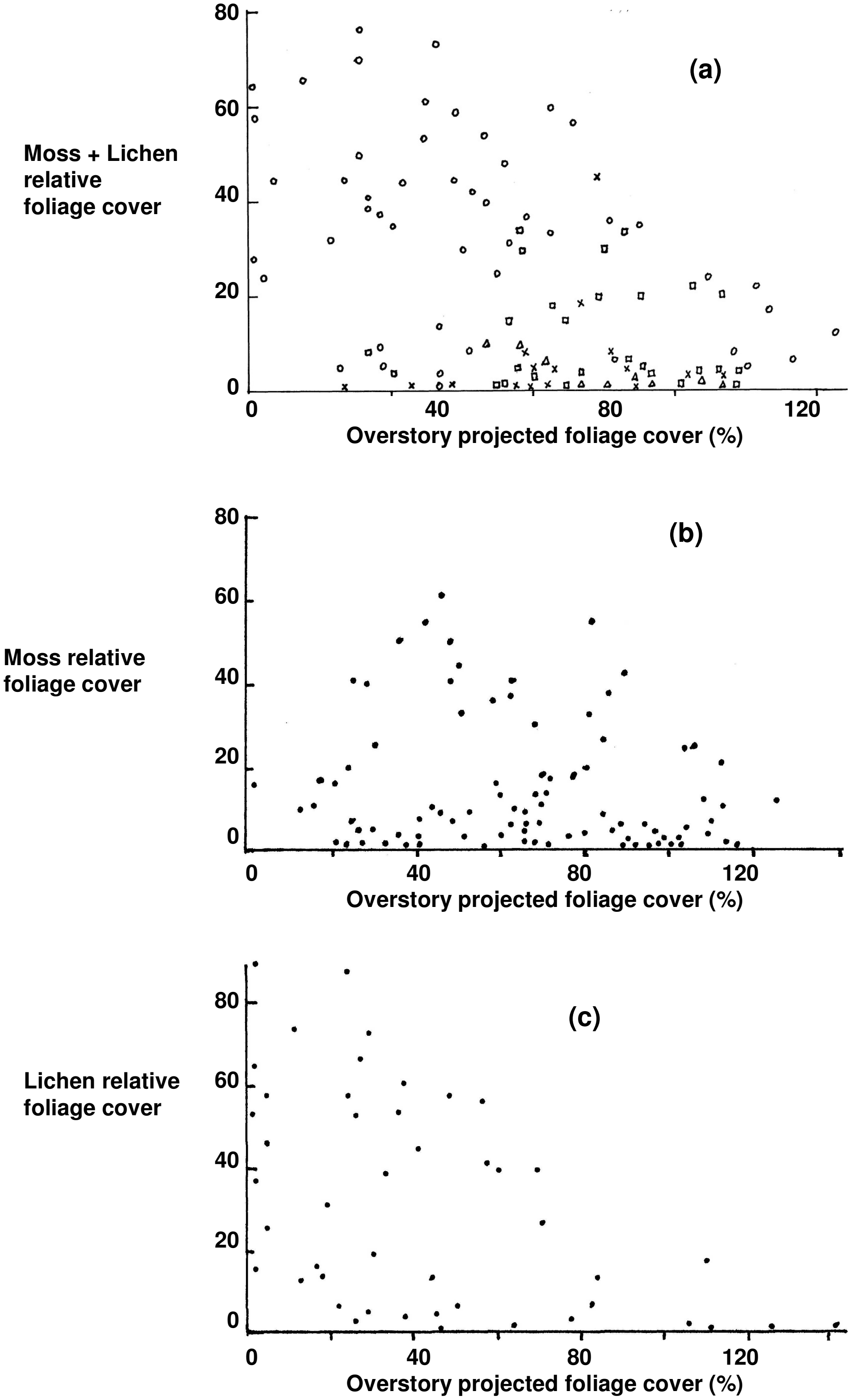


Fig. 4 The relationship between the relative foliage cover of mosses and lichens and the cumulative projected foliage cover of all other components.

(a) Mosses + lichens (all systems)
(b) Mosses (all systems)
(c) Lichens (pine systems)

HOW MANY SPECIES?

The basic Darwinian scheme has species evolving in relation to their conditions. In this situation evolution occurs as a consequence of a change in the physical and/or biological environment. In a stable environment there would be no evolution. However, the biological environment is always changing due to the finite life span of individuals so there is no stability. Evolution will occur as long as life persists.

With the Darwinian scheme the number of potential species depends on the diversity of conditions. As organisms change the environment the number of potential environments could increase with increase in the number of species. If unrestricted this would produce an exponential growth in species as in the unrestricted growth curve. Such unrestricted growth in species numbers has not occurred and the sigmoidal function appears most appropriate. This raises the issue as to what constrains the growth in the numbers of different species, as well as the fundamental question as to why distinct species arise?

A significant issue is whether the array of viable gene combinations can represent a continuum or whether they can only represent disjunct states as identified by species. The occurrence of a continuum of gene combinations in relation to a continuum of environmental conditions would effectively see an infinite number of viable gene combinations. Distinct species would not be expected to occur, rather there would be a continuous gradation in the forms of organisms. Clinal variations in species do arise where one environmental factor exhibits a marked gradient but the general situation is that distinct species greatly outnumber the number of clines. The surviving gene combinations tend to represent discrete or disjunct states represented by species.

Clinal variations represent a gradual continuous change in a species typically associated with a strong environmental gradient. The organisms at each end of the environmental gradient appear distinctly different but there is a gradual change in form along the environmental gradient. Transplant experiments have been used to demonstrate that the changes are genetic and not a direct response to the immediate environment. The organism is usually identified as a single species because of the occurrence of all intermediate forms along the gradient.

Environmental Continuum

This issue is equivalent to that addressed in the debate last century of whether plant communities represent a continuum or a series of disjunct states. The main concepts developed in plant ecology to characterise succession or evolution in plant communities are the climax, the individualistic `hypothesis' and the continuum. The first views vegetation as an organism developing through a number of seral states into a climax which represents maximal community development under the prevailing conditions (Clements 1916). The individualistic concept (Gleason 1927) regards vegetation as reflecting interactions between individuals and their environment while the continuum concept (McIntosh 1967; Whittaker 1975) suggests that there should be an intergrade of vegetation along an environmental gradient; a continuum of vegetation in response to a continuum of environmental conditions.

Gleason’s view of process would not be questioned as it has the outcome representing the interactions between the organisms and their environment, but it does not resolve the issue as to outcomes. It has no predictability or practicality. Clement’s view is demonstrably incorrect as the climax is not sustained. Such deficiencies were ‘accommodated’ by identifying special categories such as post climax, but such exceptions negate the rule, particularly given their number. The appeal of the climax approach is that it gives a simple description and categorisation of systems that has practical application. The difficulty with the continuum concept lies in identifying a continuum in the environment to allow testing.

The general situation with vegetation is that locally distinct communities can be recognised by the occurrence of particular mixtures of plant species. The different communities occur in different edaphic conditions and hence constitute different physical environments. The distinctive arrangement of the different community – environmental associations in the landscape, the catenary sequences, forms the basis for the Land Systems approach to natural resource mapping (Christian and Stewart, 1953).

The Land Systems approach is based on the precept that landscapes contain entities that are similar with regard to vegetation and soils (Land Units) and that these are arranged in the landscape in a definable manner. A Land System is thus defined in terms of the occurrence and arrangement of Land Units within a landscape. Arrangement is usually expressed in terms of position in a catena. This agglomerative approach is based on the concept that similar climates and geologies produce similar geomorphologies with the similarities being expressed in the patterns of vegetation and soils.

The occurrence of catenary sequences of vegetation and soils can readily be demonstrated but the repeatability of such sequences across regions has not been effectively tested. While Land Systems mapping has been applied to many areas over six decades the conceptual basis has unknown applicability.

Satellite imagery allows detailed mapping of vegetation across a region and hence allows determination of spatial associations between different forms of vegetation. The results in Fig. 5 were derived from an analysis of Landsat MSS imagery with an 80m pixel. The 80m pixel is appropriate as the optimum pixel size for characterising woody vegetation has been evaluated as being around 60m. The large size is needed to provide a reliable average of mixtures. The area encompassed around 3,000 km^2 of largely intact native vegetation. (Given in more detail in Tunstall 2007)

The discrimination between vegetation classes and the spatial resolution of mapping were enhanced by using spatial as well as spectral statistics to discriminate between classes. The spatial statistic (co-occurrence, Tunstall et al. 1984) provides a normalised probability of a pixel of one vegetation type occurring alongside pixels of other vegetation types. The within class statistic identifies the level of cohesiveness of the vegetation type or class. The within class co-occurrence for large uniform patches of vegetation is positive while it can be negative where the vegetation class occurs in small dispersed patches.

Assuming that communities represent spatially cohesive entities that have similar spectral characteristics (a community represents a spatially cohesive collection of individuals that has a distinctive appearance) the co-occurrence statistic can be used to help identify and map plant communities. Classes with low within class co-occurrence can often be combined to form a new class having a high co-occurrence. Vegetation maps produced in this way are spatially coherent and hence are not speckled. With a good classification a vegetation class is typically only spatially linked with two or three other classes, as in Fig. 5, and this indicates that there are distinct spatial patterns.

The spatial association between classes identifies their relative spatial arrangement. The results in Fig. 5 indicate that, while typical vegetation types can be recognised (the different classes), the transition between vegetation types is gradational. The results for the western area represent a transition from grassland through paperbarks (*Melaleuca spp*.) to eucalypt woodland. As the density of paperbark increases the eucalypts occur as emergents. As the density of eucalypts increases the paperbarks form an understory and are eventually excluded.

The linked sequence of grouped classes (bold numbers in Fig. 5) of 15, 22, 11, 8, 7 represents the sequence of grassland, paperbark woodland, eucalypt – paperbark woodland, open eucalypt forest with paperbarks, and open eucalypt forest. There is a continuum in the form of vegetation when evaluated across a region. This sequence occurs in the western part of the study area which mainly comprises one geological formation. The vegetation patterns mainly reflect responses to topographic and climatic variations.

The significance of the results in Fig. 5 for evolution is that they identify a continuum in the environment and, despite this continuum, there are very distinct plant species. This includes three species of paperbarks and more than 8 species of eucalypts. This indicates a continuum in environment does not necessarily result in a continuum in the gene complement of organisms.

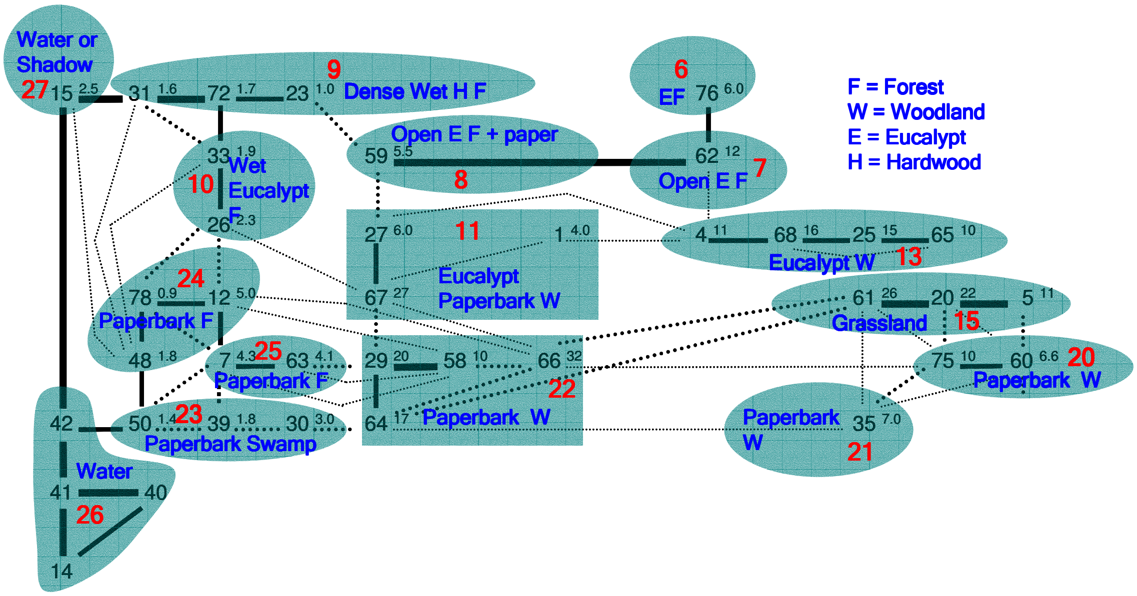


Fig. 5 Positive spatial associations between different vegetation classes. The strength of the connecting line indicates the relative strength of the association Large black numbers are the base or reference classes. Red numbers are classes formed by aggregating the encapsulated classes. The small black numbers identify the number of pixels in the class and therefore its relative extent of occurrence.

Occurrence of Species

The occurrence of species as disjunct states was originally discussed in relation to:

- The categorical nature of genes limiting the occurrence of continua.
- Spatial and/or temporal separation
- Disjunct differences in the environment.
- Changes in the environment including change induced by organisms.
- Fluctuations in environmental factors.

None of these gave a definitive conclusion apart from identifying that the occurrence of species cannot be explained by disjuncts in the environment. If the environment is the determinant of speciation then there should be numerous examples of continuous variation in the form of biota. Intergrades should be common rather than the exception.

Tunstall (2008) provides a simple mechanism that accounts for the prominence of disjuncts in the distribution of biota that are identified as species and communities.   Organisms alter the environment to their benefit. When one individual changes the environment to its benefit then other similar individuals can also benefit from that change. A mutualism develops through all of the like individuals similarly changing the environment, primarily to benefit themselves but inevitably to benefit all similar individuals. An optimum design, or species, arises through the modification of the environment by groups of interbreeding individuals.

Fuzzy boundaries are to be expected with this mechanism. So too is species drift as the environment changes as species develop. New species can occur through drift, or through splitting arising where an individual develops a new means of changing (exploiting) the environment.

The nature and level of differences between groups is not set hence the differences between species are not the same. Moreover, they change with time.

A key aspect is that only one individual initially need have the new capability. That individual will be accompanied by 'hangers on', and eventually the population will develop unique characteristics that derive from the one lead individual.

While the direction is set by an individual its implementation depends on its adoption by a population. Only through adoption by a population can a new development be maintained over time.

Adoption of a new development by a population does not identify that it is correct, the best, or has any status other than providing benefit to some in the population. Rejection of a new development by a population does not identify that it is wrong, or that it could not benefit the population. New developments are commonly suppressed by a part of the population that they could adversely impact even where they have a large potential to provide benefits to the bulk of the population.

Resource constraints

Assuming there is a limit to the total level of development of biological material in a system the issue is how this material is distributed amongst different organisms. This can depend on the non-mutually exclusive situations that different forms of organisms:

- Compete with all others to maximise their resource use.
- Cooperate to maximise their combined resource use.
- Occupy niches where they do not compete for part of the resource (avoid competition).
- Occupy niches where they compete best.

While these all represent potentially successful strategies they do not identify limits to successful combinations. They only identify that success can be achieved in different ways.

Niche

A niche is a localised environment where an organism is observed to occur and/or perform well. As with habitat a niche is defined in terms of the occurrence of the organism hence the environment is not defined independently of the organism. Niche is a descriptive term that has no analytical value. There is no value in identifying that the number of species depends on the availability of niches as niches are identified by the occurrence of species.

Biodiversity

Biodiversity is a measure of the density of species and, while not a reliable indicator of the level of co-existence of species, is a general indicator. It indicates how many species can coexist in a particular environment. The simple answer is lots.

The issue for evolution is how the biodiversity differs between different environments. Rainforests are generally held to be the optimum but the biodiversity of higher plants is similar in nutrient limited heaths. Biodiversity is similarly high in the nutrient limited coral reefs. High biodiversity is not necessarily associated with high levels of resource availability or apparently favourable conditions.

The answer may relate to the ability of particular organisms to control resource rather than the level of resource. Change in rainforests is highly probabilistic as recruitment of trees depends on the development of a gap by a falling mature tree. No single tree species can exercise control. The system is energy limited and the individuals that are best positioned to gain the energy prosper. However, given the finite life span of individuals, there is no means for one species to continue to strongly suppress others.

Heath is nutrient rather than energy limited and that limits the size of individuals and their ability to suppress others. Like rainforests, recruitment of individuals is highly probabilistic.

The contrast is given by woodlands and forests such as poplar box (*Eucalyptus populnea*) and brigalow (*Acacia harpophylla*). Their biodiversity is very low compared to rainforests and heaths with the communities are often being monospecific in the tree layer. The mechanism used by poplar box to control the resource is identified above. The mechanisms with brigalow involve the ability to rapidly use available water and to regenerate through suckers as well as seed. The rapid use of water precludes the occurrence of many other plants that can exist in the environment. Regeneration through suckering ensures the community is self perpetuating.

Conclusions

It may be that there is no intrinsic limit to the development of species but there are limits to the number of species that can co-exist in a system. The number that co-exist is determined by the ability of particular life forms to dominate and control resource where this is environment dependent.

ECOSYSTEMS

The direction with evolution given here is increasing benefit to the individual where this is achieved by avoiding or reducing competition as well as through competition. Benefit to the individual organism arises through increased use and control of resources. The increased resource use can arise through out competing others or through accessing new resources.

While developments arise from individuals they can only persist through being adopted by populations. Moreover, populations cannot exist in isolation. Developments are therefore manifest as changes to communities / ecosystems.

While the changes are manifest in ecosystems there is no means of determining the basis for the change by observations on the ecosystem. The logical situation is that the outcome C (community) depends on interactions at B (populations) which depend on interactions at A (individuals). Observations made of C and its components A can only be observed in situations where the observed outcomes are affected by interactions at B as well as A. There is no means for determining whether outcomes at C arise from interactions at levels A or B, particularly since what happens at A can depend on what happens at B. There can be unknown feedbacks.

Some suggest that within ecosystems a net increase in one organism must result in a net decrease to all others considered together. This suggests that the biological component of a system is fixed and only varies by way of the relative contribution of the different components. As the amount of live organic material in systems fluctuates greatly this suggestion does not accord with observation. Indeed, results for plant communities in Australia and Sweden demonstrate otherwise.

Ecosystems arise through the interaction between component units, like and unlike. Some interrelationships between the component biota are antagonistic and others to mutual benefit. The mutual dependencies can include collaboration to the extent of coexistence, but the benefits to the system derive from benefits to the individuals. As the different species do not interbred the selection is effected through individuals of the different species rather than combined species. This situation applies to the entire ecosystem whereby improvements to the system arise through benefits to the component units. Selection is not directed at improving the entire system even though this may be a realised outcome.

Selection being directed towards improving component units rather than the total system means that the entire system may not ‘improve’ despite improvements to the some component units. Natural selection can produce losses and net development only occurs where the gains exceed the losses. While some populations can improve through selection others can decline, and even be eliminated, hence natural selection can cause systems to decline.

Ecosystems function through the component units tending to improve their lot by competing, avoiding competition and/or collaborating. The main biological characteristic that determines patterns relates to the finite life span of the component units as this necessitates change. While the existence of an individual suppresses others this suppression is released when the individual dies. The resources acquired by a deceased individual become available to others thereby providing opportunities for the development of other forms of organisms as well as replacement by like organisms.

The accumulation of live organic material reflects the relative rates of accumulation and loss of energy where the losses occur through non-producers as well as producers. The rate of energy accumulation need not be maximal as losses by non-producers can reduce the potential production, as with damage to plants by predators and pathogens. However, some non-producers can enhance the accumulation of energy by producers by enhancing the availability of a limiting resource. The fixation and recycling of nitrogen by microbes is an example where energy fixation by vegetation depends strongly on the provision of resource by non-primary producers.

A breakdown of the composition of ecosystems is primary producers, supporters and exploiters. This breakdown is broad and some organisms can be supporters or exploiters depending on circumstances, but it does identify that many organisms do not directly contribute to production. However, even exploiters can promote energy accumulation by increasing the turnover of resources, as with grazing by herbivores. Also, exploiters that consume organisms that damage producers provide indirect benefit, as with predators on herbivores.

Exploiters can accelerate the rate of loss of energy through inefficiencies in their utilisation of organic material. Energy losses in their use of organic material are usually greater than with the source. For example, the maintenance rate of energy use by herbivores is much higher than for the vegetation they consume.

Despite these inefficiencies the general situation appears to be that the total system is greater than would arise with the sum of the individual components operating on their own. That is, the increased potential for acquiring energy arising through synergistic relationships appears to more than compensate for loss in production through antagonistic relationships and the loss of energy by non-producers.

These relationships result in ecosystems having characteristic forms as well as function. With terrestrial vegetation where most new matter is derived in-situ the primary producers (plants) collaborate with supporters to increase the acquisition of energy, while exploiters consume these to their benefit. The same situation arises with coral reefs, and with marine benthic systems dependent on bacteria that obtain energy from inorganic minerals such as sulphides.

Communities in oceans waters differ from the above as the main primary producers, the phytoplankton, are free flowing in the currents. This appears to have limited the development of synergistic relationships that promote production. Reasons could include the difficulties of constructing and maintaining protecting structures needed for synergistic relationships, and the lack of substantive benefit where nutrients are readily available. Corals notably occur in low nutrient environments.

The structure of communities is usually described by way of a food chain. Primary produces are eaten by herbivores that are eaten by carnivores that are eaten by bigger carnivores. However, dead material is eaten by scavengers and decomposers. The inefficiencies in conversion between levels results in a double pyramid whereby the amount of biota at each level decreases from the primary producers. The occurrence of decomposers as well as predators means that the structure is not a simple chain.

This triangular structure is a gross simplification to the point of being simplistic unless restricted to addressing abundance. It cannot reliably be applied to the size or form of organisms. For example, whales feed on small herbivores where this improves their returns by cutting out the middle predatory levels. Whales are at the top of the food chain in largely lacking predators other than humans but have eliminated all bar one level from the primary producers in the food chain. While this provides benefits to them it does not necessarily benefit (increase) the total system.

With terrestrial systems the primary production is based on collaboration between microbes and plants. The smallest life forms help the largest life forms acquire new matter as well as enhancing its availability through recycling. The microbes provide as well as recycle essential resources. The level of primary production does not depend solely on the primary producers. Benefits to primary producers do benefit the total system.

Rainforests and heaths have equivalent compositions of plant life forms and, for higher plants at least, can have an equivalent number of species. They also have an equivalent energy supply via solar radiation, and both have an abundant water supply albeit limiting at some times. The main difference lies in the availability of nutrients (matter) and this produces distinct differences in their form. Compared to rainforests heaths have:

a. Small plants.
b. A low rate of production.
c. A low ecosystem biomass.
d. High efficiency of nutrient retention by individuals.

The efficiency of nutrient retention is evidenced by the longevity of plant leaves. Many rainforest species have a high turnover of leaves with substantial nutrients being recycled through litter. The predominant woody heath species retain leaves for a long period. The situation is the same as forests in central Sweden where species on high nutrient soils are deciduous and those on low nutrient soils are evergreen.

The deciduous characteristic makes inefficient use of nutrients compared to being evergreen but it is not inefficient for the plant as efficiency is only important when a resource is limiting. The balance between deciduous and evergreen reflects the balance between the energetic costs of retaining leaf under unfavourable conditions and building new leaf structures. Costs of leaf retention include the need to develop leaf structures that can survive for a long time while the costs of leaf drop include the need to develop new roots.

The common outcome is that where nutrients are not particularly limiting most benefit is obtained through developing maximal leaf to acquire energy. The leaves tend to be large, flimsy and short lived, thereby giving maximum area for minimum materials. Where nutrients are particularly limiting leaves tend to be small, robust and long lived thereby minimising the need to acquire new nutrients.

The nutrient relations of the producers directly impact on the synergistic relationships as low nutrient availability reduces production and also reduces the turnover of organic matter. This in turn reduces the exploiters and these appear to be reduced in diversity as well as abundance. The highest diversity as well as abundance of animals generally occurs in nutrient rich areas. Coral reefs are an apparent exception. The waters have low nutrients but the corals concentrate them making it a nutrient rich environment for exploiters.

Comparing these situations with the suggestions that evolution tends to increase the efficiency of energy utilisation and the total energy stored in biological organisms it can be seen that the efficiency of energy utilisation is only important when energy is limiting. Evolution tends to improve the efficiency of utilisation of a limiting resource, be it matter or energy.

The total energy stored in organisms within ecosystems arises as a consequence of changes to individuals and populations. Where organisms evolve to utilise resources not previously available to life this has the potential to increase the level of organic matter within systems, and this has occurred over time. However, the accumulation of organic matter by one organism increases opportunities for the development of other organisms to exploit that resource. This development of organisms tends to reduce the accumulation of organic matter in the system because of inefficiencies in conversion. Evolution has likely increased the flow of resources in ecosystems more than accumulation, but they are obviously interlinked.

The potential for the development of organisms through the turnover of other organisms is identified in the section '*How Many Species?*'. There does not appear to be a limit on the potential number of species but the realised number occurring within ecosystems appears to relate to the environmental constraints. Species numbers are reduced where one organism can exercise control but the diversity of forms present appears to always include all existing forms from the earliest to the most advanced. Ecosystems tend to contain a diverse mixture of all life forms that have evolved in that environment.

The spread of mankind illustrates the occupation of territories by a newly evolved form. Numbers of people are low in poorly productive systems and some inhospitable environments, but mankind has occupied most terrestrial ecosystems and exploited many others, including marine environments. The exploitation by mankind usually reduces the number of species within systems but not the broad diversity of life forms.

The potential reduction in ecosystems with evolutionary development is illustrated by agriculture. The dominance of humans has greatly suppressed all other life forms and thereby produced highly degraded systems.

The unresolved issues in the above relate to risk and sustainability. If all of the potentially available matter is incorporated into organic material then the system is completely dependent on recycling. As recycling inevitably incurs losses the system then declines. The failure would be catastrophic if the matter is stored in a single organism as its inevitable death would terminate life. The sustainability of systems is enhanced by limiting the extent to which resources can be monopolised.

Catastrophic failure is the prime risk for organisms and this arises where the available resources cannot support the population. The worst situation is where all individuals of a population die and this naturally occurs when essential resources are fully depleted, as with severe droughts. Organisms that exist have developed means of addressing such restrictions, and for many the mechanism involves limiting the utilisation of available resource. Populations do not necessarily develop to the maxim level possible thereby leaving a reserve to allow for the occurrence of adverse conditions.

Conventional theory suggests that resource not utilised by one organism is utilised by another hence the strategy of incomplete resource utilisation should not work. The results for the poplar box woodland indicate that it does work because organisms can limit the utilisation of the resource by others. Resource can be controlled without being used as the life cycle characteristics of organisms allow the recruitment of new individuals to be suppressed by existing individuals. While the system has a capacity to support a greater amount of life this capacity is not realised.

In viable systems organisms tend to maximise their control of resource but their level of resource use is commensurate with their survival. This means that ecosystems represent conservative developments of organic matter rather than maximal developments even though evolution has tended to increase the amount of organic material within systems.

From the above modern agriculture inherently has high risk. Humans now control large areas wherein all other forms of organism have been greatly suppressed. The agricultural systems are unstable. This has been compounded by attempts to maximise the return to humans through use of chemicals such as herbicides, insecticides and fertilisers.

NON-GENETIC BIOLOGICAL EVOLUTION

The term non-genetic biological evolution may need revising when further considered. Its use here relates to the transfer of non-genetic information between generations but the process also inevitably promotes the transfer of information within generations. For humans it is therefore part of culture, but it is likely only a minor part as much of culture is associated with breeding and is therefore associated with genetic evolution. Moreover, it is not solely culture as non-genetic biological evolution is not restricted to humans and occurs in a large number of species including birds. Taken over the history of biological evolution it is a reasonably recent but highly significant development.

The overall path of human non-genetic evolution has been documented by anthropologists and historians, and the biological factors involved have been addressed by physiologists and psychologists. There is an enormous amount of detail information relating to non-genetic biological evolution that is not addressed here. The issue addressed is the interpretation of such information in relation to constraints on non-genetic evolution generally rather than the development of a particular civilisation. The organisation of businesses is used as an example because it is not constrained to any particular population or community and the different organisational structures are readily apparent.

While humans are used as the example they are not the only species that uses non-genetic means to transfer information between generations. A characteristic of evolutionary direction that has long been noted is the progression to a reduced number of progeny but an increased gestation period, often associated with a period of parental care. Directing reproductive effort into few individuals necessitates actions to promote the survival of the limited numbers of progeny, and survival is promoted by learnt as well as instinctive knowledge.

Parental care initially involved protecting offspring without any non-genetic transfer of information, as with live birth by sharks and the protection of eggs and young by crocodiles. It evolved to include parents training their offspring where this involves the non-genetic transfer of information between generations. This non-genetic transfer of information was initially from a parent(s) to progeny but for some species it evolved to include family groups. Humans are highly communal and this promotes the non-genetic transfer of information by increasing the educational sources and minimising the risk of a lack of continuity. Such communal organisation occurs in several vertebrate groups such as birds as well as mammals. While breeding can be restricted to selected members of the group all members usually contribute to the training.

Humans have further developed training by institutionalising it within formal education systems. Much of the parental / family responsibility for education is now often assumed by the community, and in many communities this formal education is compulsory. The functioning of such communities now depends on the non-genetic transfer of information between generations.

Developments in the human capacity to transfer non-genetic information can be charted from signaling using sounds, to simple drawings, through to the development of language and its graphic recording using abstractions such as numbers and letters. The recent developments have been large and rapid, particularly in the ability to acquire and distribute information. However, as with genetic evolution the developments build on earlier developments.

Electronic systems facilitate information transfer but the communication is based on prior developments of language and mathematics.

The application of information depends on its presentation in an appropriate form. A large number of observations may yield very little useful information. For dissemination and application the data must be transformed into information and the information used to develop knowledge. Observations are abstracted with unifying concepts being used to help understand and communicate information.

Science has played a pivotal role in the development of knowledge through the extraction of information from observations and data. Science has provided a concise and general context that promotes communication and application of information. While this alone is beneficial the other requirement addressed is reliability. The scientific method revolves around continuously testing the reliability of knowledge so that it provides a reliable basis for further developments as well as applications.

Science is currently the main factor affecting human evolution. Mankind now has a direct role in genetic manipulation and that role will likely increase. However, for humans it is debatable whether the consequences of genetic control will be greater than arise through non-genetic influences. The non-genetic influences are currently by far the most pronounced in determining changes to human evolution as evidenced by the electronic technologies used to promote the communication and application of information.

Selection

Selection is the process underpinning evolution as it determines what survives to contribute to future developments. The basic constraints are identified under natural selection and these apply to non-genetic biological evolution. However, examination of non-genetic biological evolution, particularly human, provides opportunities to address greater detail than for genetic evolution as information is more readily available and interpretable. With natural selection the somewhat abstract environment does the selecting but with non-genetic human evolution the selection is largely by mankind. It is this selection by mankind, a biological organism, that produces the commonalities between genetic and non-genetic evolution.

The basic elements of non-random selection are:

a. A diversity of elements or units to select from
b. A means of producing new elements or units
c. A logical basis for selection

Points (a) and (c) are self evident. Point (b) is necessary for development particularly where selection eliminates any units.

The logical basis for selection can involve either the achievement of a set objective or the following of a set process. Objective based selection is directed towards achieving a defined goal or end point. Process based selection has no defined end point and is illustrated by the scientific method. A hypothesis is tested and is rejected if negated. The test addresses local applicability and not applicability in relation to a global objective or goal.

The goal for evolution given in the appended *Evolutionary Direction* is maximising the resource utilisation by an individual where utilisation includes control as well as use. It involves maximising the benefit for the individual. With human organisations the issue arises as to what constitutes the individual. The smallest unit is the individual person, and this is the most applicable unit with genetic evolution. However, with non-genetic evolution there are additionally constructed units that include organisations such as communities, businesses and governments.

This hierarchy of vested interests in addressing the evolutionary goal establishes an inherent conflict in the management and operation of organisations. The underlying driver is the personal benefit hence participation by an individual in an organisation only arises where it increases personal benefit. Individuals support an organisation to the extent that it provides perceived personal benefits.

The occurrence and limitations of this situation are illustrated by remuneration packages for the CEOs of large corporations. These include large ‘performance based’ bonuses to entice the CEO to operate in the interests of the business, however, there are no penalties for failure other than non-renewal of a contract. The CEO benefits regardless of performance where this is contrary to selection in natural evolution. Obtaining improvement in performance involves the elimination of unproductive and defective elements. CEOs apply such selection to others in the business while effectively being quarantined from such negative impacts.

The units or elements being selected are the same for genetic and non-genetic evolution, namely information. With genetic evolution this information is contained in strands of DNA and hence is well defined even if little understood. For non-genetic evolution the issue is what comprises information.

The simplest breakdown of what generically could be called information is data, observations, information and knowledge. Data represent raw signals, as with the temperature of the air or the intensity of solar radiation. Observations are derived from data through interpretation. What we see represents an interpretation of the signals generated by our eyes and thus represents observations rather than data.

Information is produced by interpreting data and observations within a particular context. For example, an aerial photograph can be interpreted to map attributes such as vegetation, buildings and roads. The information is usually presented in a particular form, in this example as maps.

Knowledge represents a higher level of interpretation based around unifying concepts, but knowledge takes several forms. Views and beliefs are usually presented as knowledge even though their reliability cannot be evaluated. Scientific knowledge is meant to be reliable through being subject to ongoing testing.

Scientific knowledge evolves through the development of new ideas and their evaluation through testing. Ideas that do not pass the tests are eliminated. Moreover, science seeks generalisations that account for a large number of observations. The benefits of providing a concise context include improved comprehension, communication and application of information.

Businesses employ a process of continuous improvement in performance similar to the scientific method to determine the need for change. The performance of the business is monitored and assessed against defined objectives with changes being made to address identified deficiencies. The changes include elimination of unproductive elements as well as the development of profitable elements.

Governments similarly use planning processes to identify needs and priorities and assess performance. Many performance assessments are fundamentally deficient in assessing the implementation of process rather than the achievement of outcomes but all result in the elimination or contraction of some programs in association with the development of others. While large changes can occur within short periods the majority of programs are usually little changed. Evolutionary development is more common than revolutionary change.

A trade-off between development and reduction automatically occurs where new developments are introduced in a resource limited environment. The occurrence of a trade-off between development and redundancy is not an indicator of good planning as it is usually an inevitable outcome. It represents the normal evolutionary process.

The conclusions are that:

a. Human implemented selection routinely occurs in the operation of communities.
b. The selection is made at all levels ranging from individuals to governments and multi-national companies.
c. The selection promotes some aspects and reduces or eliminates others.
d. The changes at any time are generally small compared to the potential for change (small sections tend to be affected).

Points (c) and (d) are the same as for genetic evolution. However, as with genetic evolution there can be unplanned catastrophic change as arises with natural disasters. ‘Planned’ catastrophic change by way of revolution has generally been associated with wars and dictators.

The selection identified above involves a process of continuous improvement in performance against objectives set according to perceived benefit. It involves the assessment of information to identify what is developed and what is eliminated. The critical requirement is to ensure that all potentially useful information is available in the future. Any elimination involves the risk that something that would be beneficial in the future could be lost.

The constraint of eliminating potentially useful information is partially addressed by minimising the amount eliminated. The bulk of the information is carried forward unchanged. However, it can never be fully addressed because future requirements cannot be known. There will inevitably be mistakes whereby information that would be valuable in the future is discarded through being assessed as having no current value. Again, this is no different to genetic evolution.

The rate of information development by human societies is rapidly increasing and this raises theoretical and practical issues associated with storing and accessing information. This is addressed under Electronic Computers as they currently represent the main means of addressing the basic issue that the overheads associated with maintenance increase at a greater rate than the increase in information.

There is no apparent basis for assessing whether this potentially limiting constraint could apply to the storage and application of genetic information. A form of application would be that the number of mistakes depends on the number of genes hence the viability of the application of the genetic information decreases as the amount of information increases.

EVOLUTIONARY POSTULATES

The postulates are given as:

A. Evolution occurs as a consequence of change in the state of resource.
   (i) The rate of evolution increases with increase in the change in state of resource
B. Evolution occurs through selection operating on variability between individuals
C. Evolutionary development increases the resource utilisation by an individual.
   (i) Selection promotes increasing efficiency of resource utilisation.
   (ii) Maximising the efficiency of resource utilisation alone leads to extinction.
   (iii) Selection promotes the utilisation of new resource.
   (iv) Net direction in evolution is towards utilisation of new resource.

Points A and B relate to process and point C to outcomes.

Point A is a logical consideration that can be considered axiomatic. The growth and development of biota change the state of the resource hence in biological systems there is no stability and organisms continuously evolve. Negating the postulate requires maintaining a constant state which is impossible where biota exist. Demonstrating that organisms can remain unchanged is not a test as the postulate is that evolution arises because of change and not that change necessarily results in evolution. The postulate states that evolution cannot arise without a change in the state of resource and not that a change in the state of the resource necessarily produces evolution. The latter may usually apply but is not inevitable.

Postulate Ai is a logical extension of A as, if change provides opportunities for evolution then the greater the change the greater the opportunities for evolution. This situation arises because existing populations suppress the establishment of similar new populations, a situation that has long been recognised in agriculture. Changes that reduce the viability of existing populations provide opportunities for new populations. This postulate is obviously subject to the covenant that the change is not of sufficient magnitude to eliminate all biota.

Postulate B is the basic mechanism presented by Darwin but with a specific reference to individuals. The application to individuals is implied in the discussions by Darwin but is contrary to some suggestions.

While the basic mechanism relates to individuals the outcomes can only arise through implementation by populations. The characteristics identified in C are therefore manifest through populations and expressed in communities, ecosystems and the like. Postulate C addresses factors associated with realised directional change.

The only reference to maximising arises with efficiency where it is associated with extinction. In sustainable systems the resource utilisation is not maximised. Resource is often controlled without being used wherein this decreases competition and increases the chances of survival if conditions change.

Sub-postulates of (c)

Sub-postulate (i) is straight forward and is readily apparent with non-genetic human evolution. Many businesses operate through improving their efficiency in producing a particular product. Most businesses seek to minimise their production costs where that equates with increasing efficiency.

The applicability of sub-postulate (i) to genetic evolution is less obvious but is still clear. A large number of physiological studies have shown that plants and animals are highly efficient in utilising resources. Photosynthesis is an example whereby plants tend to maximise their CO_2 gained in relation to the water loss. This does not means that biota are always efficient as improving the efficiency of use of an unlimited resource confers no advantage. Some primitive plants exhibit profligate / uncontrolled patterns of water use.

The evolutionary development of efficiency in resource use is illustrated by the use of oil. As the resource becomes limiting effort is expended at increasing the efficiency of its use.

Sub-postulate (ii) is an inevitable outcome where resource is limited. Increasing the efficiency of use of a limited resource can delay but not prevent extinction. As at least one essential resource is invariably limited this sub-postulate is always applicable.

Sub-postulate (iii) is similar to (i). With non-genetic human evolution it is reflected in the development of new energy sources such as uranium and the efforts spent in discovering new reserves of energy and minerals. The silicon chip represents the development of a capability to gain large benefits from a resource that previously had little value.

For genetic evolution this sub-postulate is equivalent to the generalisation that biota tend to expand to occupy the available space. The transition of vertebrates from water to the land is perhaps the clearest example.

Sub-postulate (iv) is a logical consequence of the other sub-postulates. If selection for efficiency leads to extinction then progress in evolution is towards the utilisation of new resource. Again this is clear with non-genetic human evolution where most developmental effort has been expended in discovering new occurrences of resources and means of utilising materials that previously provided little of no benefit. It is less apparent for genetic evolution except for major developments such as the transition of vertebrates from water to the land.

Considerations in *Evolutionary Direction* and *Ecosystems* address the consequences of these postulates for patterns of evolutionary development and the structure of systems (the postulates actually derive from the considerations). The theoretical maximal evolutionary development is where a single individual controls all resource but, even if attained, this condition cannot be sustained if only because of the finite life span of individuals. Another factor that affects realised outcomes is the inability to achieve 100% efficiency in utilising resources wherein the inevitable leakage provides opportunities for others.

The inevitable turnover and leakage of resources prevents any individual organism, population or species from completely dominating and therefore provides opportunities for others. The existence of one form of organism therefore presents opportunities for the existence of other forms, and an ecosystem develops that incorporates interdependencies between the different forms. Evolutionary development involves building on earlier developments, hence the existence of directional changes such as from small to big, however, the existence of the big often depends on the continued existence of the prior forms. Ecosystems usually incorporate a full spectrum of life forms, and always include the earliest forms.

This evolutionary development of ecosystems containing a great diversity of life forms has resulted in suggestions that evolutionary direction is determined by the performance of the ecosystem. Organisms develop to take advantage of opportunities that arise, and this tends to ‘improve’ the ecosystem. However, the developments are determined by the opportunities for individual organisms rather than opportunities for the ecosystem. Development of an ecosystem is an outcome rather than a determinant of evolutionary development.

Selection

Selection is the process that produces evolutionary change and is therefore central to evolution. The above postulates suggest that selection is directed towards increasing the resource use by individuals where this equates with increasing the benefits to individuals. Evolution is effectively driven by personal benefit which can be described as greed or self interest.

The developments here generally accord with the postulates given in *Evolutionary Direction* but the wordings and presentations differ somewhat. This primarily applies with postulate (c) which addresses outcomes whereas natural selection is mainly discussed in terms of process. The process given is the elimination / reduction of competition wherein increasing efficiencies and accessing new resources represent means of reducing competition. The sub postulates identify the consequences of adopting the different approaches to reducing competition.

Knowledge of process usually allows prediction but this does not arise with evolution. Evolutionary changes cannot be predicted despite our knowing that individuals are attempting to increase their control within their operational framework. Reasons for this situation include the complexity of the interactions that determine outcomes, but the main reason relates to uncertainty about the constraints. The environment by way of constraints and options changes, and these changes cannot be predicted. Characteristics that provide benefit in the current environment need not be beneficial when conditions change. Characteristics that appear of little of no benefit now may be highly beneficial in circumstances that arise in the future.

Predictions usually project the current situation into the future based on observed patterns of past events. The validity of the predictions therefore depends on the circumstances for the past events continuing into the future. With evolution this constraint does not arise hence predictions based on past observations are unreliable.

The reason that previous circumstances cannot be projected into the future is that the biota change the circumstances or environment. This is most readily illustrated for human non-genetic evolution where electronic devices such as computers and satellites provide opportunities that were not previously available. It has, however, occurred throughout genetic evolution, as with the development of animals depending on the development of plants, and the development of terrestrial plants depending on the prior existence of microbes. As the plants changed so too did the animals, with changes to the plants occurring in response to predation by animals as well as changes in the physical environment.

Selection is usually described as involving competition with the fittest surviving. The mating games of vertebrates are typically used as an example. However, for most individuals competition is more likely to be detrimental than beneficial and there are numerous examples of animals avoiding or minimising competition in breeding. The mating of birds for life is an example.

Postulate (c) identifies that benefit to individuals can derive from the utilisation of new resource. If that resource has not previously been used by biota then such a development does not involve competition. Indeed, it represents the avoidance of competition. Competition is a potential but not an essential component of selection as an individual can obtain benefit by:

- Successfully competing
- Avoiding competition.
- Collaborating with others.

Successfully competing

Of the three options competition has highest risk. There can be situations where competition cannot be avoided, hence an ability to compete may be essential for survival, but the high risk places a premium on minimising or avoiding competition.

Most plants employ mechanisms to suppress others in their proximity. The main above ground mechanism is shading. Below ground mechanisms include allopathy and competition for water and nutrients. However, these mechanisms relate to growth but not reproduction.

Plants generally do not have competitive mechanisms that affect breeding other than a potential for selection based on the growth of pollen tubes in the stigma and entry into the ovum. Plant reproduction is typically highly probabilistic with copious pollen and seeds being produced but with exceedingly few offspring surviving to a reproductive age. The life span of trees results in very low recruitment as on average a tree that breeds for say 150 years would only produce a few offspring that survive to reproduce. Potential selection of the genetic complement of a few pollen tubes in the stigma is of no consequence compared to the random selection that arises through the chances of the millions of seeds occurring in a location where they can germinate and develop into mature plants.

Some animals engage in combat for the chance to breed but the combat is usually ritualised. The death of appreciable numbers of mature breeding individuals seldom benefits populations even if only the males die.

Avoiding competition

Avoiding competition has lowest risk but there are limited opportunities for such developments. Biota tend to occupy the available space hence where new opportunities arise there are usually competitors. The avoidance of competition is therefore mainly restricted to avoiding adverse interaction with individuals of the same species. This avoidance can be significant because like individuals compete more than unlike. The potential for competition is usually greater for individuals of the same species than between different species.

Humans, as with all biota, have used their mobility to invade new territories as this opens new opportunities and reduces competition with other humans. While individual plants are generally immobile the mobility is achieved through dispersal of seed and hence is effected through progeny. However, as space is finite there is a limit to opportunities to occupy new territories. Most movement has been directed at reducing rather than eliminating competition with the conditions at the new location being more favourable than those that were left.

Many perennial plants reduce potential competition from progeny by taking a number of years to become reproductive. Parent plants are well established before having to compete with their progeny.

Life cycle characteristics are similarly used to suppress competition through established plants limiting the establishment of others. Such suppression results in the incomplete use of resources hence competition is effected through control as well as the utilisation of resource.

The avoidance of competition is best evidenced in human non-genetic evolution. Monopolies are the optimum business arrangement while dictatorships have been common with governments. Many businesses depend on the conduct of research to develop new products with the investment usually being protected by patents. Evolutionary direction is determined by new developments rather than improved efficiencies in delivering existing capabilities.

Collaboration

Collaboration can be seen as a special case of competition avoidance but differs as the benefits are greater than can arise by simply avoiding competition. The combined benefit is greater than the sum of benefits obtained by individuals operating separately. Collaboration has effectively been ignored when addressing selection despite it being integral to many populations and occurring in all large ecosystems. Most of the collaborations promote growth and development where these are prerequisites to breeding. Such collaborations are typically between very different species. Collaborations that directly promote breeding generally arise within populations rather than between different species.

All symbiotic relationships represent collaboration between different species and these are common. The forms of relationship are diverse and include microbes with plants (e.g. mychorrhiza), microbes with insects (e.g. microbes in the gut of termites), bacteria with polycheat worms (marine utilisers of sulphides), insects with plants (e.g, moths in fig fruits and ants in special plant galls), insects with insects (e.g. ants cultivating and protecting aphids), and microbes with mammals (e.g. microbes in the gut of ruminants).

Collaboration is common within populations and occurs with plants as well as animals. The release of chemicals by trees in response to insect attack triggers the development of protective chemicals in surrounding trees. Coral reefs and some fish species synchronize their spawning.

Communal vertebrates almost invariably have collaborative arrangements to promote the perpetuation of the community. Some of these promote breeding by few individuals but many simply employ division of labour to promote survival of the community. The rotation of look outs with cockatoos and mere cats are examples of the latter.

Humans have taken such cooperation to a much higher level, as evidenced by the organisation of defence and education. Collaboration reduces individual risks as well as potentially providing greatly improved benefits.

So which is most important?

Competition appears important for survival. Organisms invariably compete with other organisms throughout their life and this competition appears to be greatest when they are young. Competition arises between as well as within species.

Predators and pathogens identify particular forms of relationship but for the organisms they affect they can be viewed as competitors. Competition involves the expenditure of resources to redress negative effects arising from other organisms. Competition addresses survival as an inability to avoid predation or defeat pathogens results in elimination. The prime effect of competition is to eliminate the unfit rather than promote the fittest.

Most considerations of genetic evolution focus on the reproductive aspects of competition and therefore only address competition between individuals within species for a particular part of the life cycle. While such studies can track the gene flow they seldom identify all of the reasons for the gene flow.

While competition is unavoidable the avoidance of competition is common. Opportunities for avoiding competition are limited but they are always taken advantage of. As the avoidance of competition can arise through the development of new capabilities it is a prime determinant of evolutionary direction.

There is no doubt that collaboration has been important in evolution as evidenced by the number of significant symbiotic relationships. The nitrogen cycle involving microbes and plants alone is of particular consequence as the existence of most animals depends on the growth of plants and there would be little terrestrial plant growth without the fixation and recycling of nitrogen by microbes. As collaboration between humans provides the foundation for non-genetic evolution it has been particularly influential in determining the rate as well as direction of evolution.

Competition, avoidance of competition and collaboration have all influenced selection and hence the rate and direction of evolution. The efficiencies arising from competition are evidenced in all biota hence this has received most attention. However, the negativity of competition means that it generally produces little change, as reflected in selection tending to reinforce the norm. The avoidance of competition can be achieved through the development of new capabilities and therefore contributes to evolutionary direction. Collaboration appears to have been influential in determining the rate and direction of evolution.

While competition, avoidance of competition and collaboration can be identified as influencing evolution in different ways there is no apparent basis for ascribing greater importance to one than another. They are all important and, as they need not be mutually exclusive, all can be involved in the evolution of an organism. The occurrence of collaboration does not preclude the occurrence of competition hence realised outcomes are determined by the combined selective influences. All influences have been important and this situation would be expected to continue.

EVOLUTIONARY DIRECTION

Brian Tunstall
1978

INTRODUCTION

The general directions of evolution, the phyllogenetic sequences, are well documented. The reasons for the existence of phyllogenetic sequences, the reasons for a net directional course of evolution, are not. We can say there is evolution but we cannot say why it has proceeded in a particular direction.

That organisms evolve is well accepted. How they evolve has become the study of genetics. Why they evolve, while starting as the study of evolution, has become engulfed in and is scarcely separate from genetics. This is reflected in replies to the question `what is evolution directed towards?' The usual reply is that the question is anthropomorphic, that evolution can only be considered in retrospect. This has the corollary that evolution is best studied in terms of mechanism in that even though the endpoint may not be capable of prediction the means by which it is reached may well be.

Because of the emphasis on genetics much of the current evolutionary theory has been developed around specific examples where parts of a system have been studied in isolation. This can lead to conclusions which are relevant to the system studied but are difficult to relate to the overall process of evolution. The total is not necessarily the sum of the component parts. Many mutations and recombinations of genes can occur without new species evolving. Many species can evolve without there being a net course to evolution. In such a system, where change occurs through interaction, it is more sound to investigate components by analysis of the system as a whole than to attempt to synthesize the net response from studies of the individual components. The discrete, part system studies cannot be ignored for they provide the bulk of the available factual information, but to allow for a synthesis of this information the interpretations placed on the results must often be revised in the light of our knowledge of the system as a whole.

BASIS OF ANALYSIS

It is generally accepted that there is variability, there is selection, and that selection acting on variability can result in evolution. As variability provides the raw material this is a major factor; only that which is there can be selected. But this raises the question, `why is one factor selected for in preference to another?' The explanation given is that selection, in general, favours that which is beneficial. What then is beneficial? The consensus answer appears to follow Darwin's (1859) comment that `the creature becomes more and more improved in relation to their conditions'. Selection favours factors (hence organisms) that function better in a particular environment. Terms used to describe this environment are habitat or niche and while these terms have been variously defined all definitions relate to the interaction between an organism and its environment.

The term used to describe the selection of beneficial characteristics is adaptation. Stern (1970) illustrates that this term can relate to different states but then defines one state in terms of another - `The process of adaptation will be that which leads to higher levels of a state of being'. That is, adaptation is that which leads to a higher adaptive state or, as stated by Dobzhansky (1968) `adaptiveness is the state of being adapted'. Although indisputably correct the value of such definitions is questionable.

An alternative attitude is that adaptation is a tautology because what lives must be adapted to live. Dobzhansky (1968) in defense of the term suggests that `no organism is adapted in the abstract, it can only be adapted to certain environments'. He illustrates this point by describing particular adaptations to particular environmental attributes.

The problem with such an argument is that, as with the terms habitat and niche, the environment is not defined independently of the organism. The selection of environmental attributes is based on observation and evaluation of the interaction between the organism and its surrounds. In effect, the question being asked is how does A change in relation to B when B has been defined in relation to A. The answer must depend on the relationship defined between A and B. An argument based on this form of structure, where the factors are not independent, can in retrospect provide an answer to any question. It does not however, allow for prediction or for rigorous examination of the system.

Such arguments have been extended by van Valen (1973, 1976). In the `Red Queens Hypothesis' he states *A change in the realized absolute fitness of one species is balanced by an equal and opposite net change of the realized fitness of all interacting species considered together*. This theory is developed around energy which is defined in terms of the carbon fixed by biological organisms. The term energy, as with environment, is therefore determined relative to our current perception of biological organisms and so is not independent of the organisms.

Van Valen (1976) further states that net increase in one organism must result in a net decrease to all others considered together; that the environment is fixed and finite. He then attempts to demonstrate that the resource, defined in terms of carbon fixed by organisms, is (has been) constant. Taken over full evolutionary time this precept must be incorrect. Starting from the initial organisms and progressing to the present there has been an increase in the total amount of organic matter.

Lotka (1922, 1945) circumvented the problem of non-independence of terms by approaching the problem of evolutionary direction from a physical viewpoint (using physical and chemical analogues). He concluded that `natural selection tends to make the energy flux through the system a maximum compatible with the constraints'. This was deduced by combining two prior considerations:

> *The first effect of natural selection thus operating on natural selection will be to give relative preponderance to those most efficient in guiding available energy in the manner indicated. Primarily the path of the energy flux through the system will be affected.*
>
> *Again, so long as sources exist, capable of supplying matter of a character suitable for the composition of living organisms, in excess of that actually embodied in the system of organic nature, so long is the opportunity furnished for suitably constituted organisms to enlarge the total mass of the system of organic nature. The result will be to increase the total mass of the system, and, with this total mass, also the total energy flux through the system, since, other things being equal, this energy flux is proportional to the mass of the system.*

That is, evolution tends not only to increase the efficiency of energy utilization but also the total energy stored in biological organisms within the system.

Lotka (1922, 1945) accepts that all the available energy is not necessarily used by organisms but, as with van Valen, suggests that it is the system as a whole that is tending to maximise and that the flux and not the amount of energy in the system is maximised.

Lotka justified maximisation in respect of energy flux by stating that this increases the energy available per unit time to the organisms. This is based on the whole system concept for the example given is that of growing two crops a year instead of one in a given area. Such a system increases the return to man but if this system was of advantage to wheat, why then does wheat remain an annual? Why the evolutionary tendency for organisms to become long lived?

The significance of the flux of energy through individuals is that the acquisition of new resource requires the expenditure of energy. The basis for the continuance of life is that the energy obtained must be greater than the energy expended. Where this ceases to apply life will, with time, cease to exist. As evolution is the balance between the generation and loss of capabilities so life is a balance between the acquiring of new resource and the maintenance of acquired resource.

Lotka (1922) recognized that *in evolution two kinds of influences are at work: selecting influences, and generating influences. The former select, the latter furnish the material for selection*. He does not however appear to have appreciated these two processes are opposed; one is a process of generation, the other one of elimination.

Selection is usually regarded as a process of promotion, a means by which particular organisms are favoured. However, selection cannot promote that which is not there, it can only operate on that which exists. Also, any selection, once effected, reduces the options for further selection. Selection is therefore a negatively directed process in that the number of selective options decreases with increase in selection. In effect, selection is a process of elimination and operates through the elimination of individuals. Advantage to any individual or population is conferred indirectly through the elimination of others.

Definition of terms

The postulates presented here are based on the premise that selection (in particular and evolution in general) relates to the individual and not the population or community. Dobzhansky (1968) states that such definitions should refer to both individual survival and to perpetuation of a strain or population. The point is illustrated with reference to populations where the individuals are not equal, i.e. a bee colony. This problem is also seen in the structure of organisms. Most organisms can be regarded as hierarchical organizations of individuals. A plant is composed of organs composed of cells composed of organelles composed of molecules. At the cell and organelle level the individuals may be capable of reproducing given the right conditions. At any one level there can be a number of different forms of individuals, that is, a number of populations. Given this situation the only form of definition possible is one that relates to function rather than structure. An individual organism is a collection of discrete elements where the elements are organized to operate to the benefit of the organism as a whole.

The term resource as used below is analogous to energy as used by Lotka (1922). Resource is the total energy and matter within and entering a system where the boundaries of the system must be defined in time and space. The resource utilized is the total resource controlled or used by the individual. For many organisms this could be represented by the sum of the total flux of energy and matter through the individual. Over the life of the individual this becomes the total flux through the individual which reaches a maximum at death. This definition is, however, too restrictive. An organism can benefit through controlling resource it does not use by preventing other organisms from accessing it. Such control, in effect, reduces the level of competition.

POSTULATES

The following is based on the considerations that selection operates through individuals and that selection is a process of elimination. Accepting this the Darwinian concepts can be stated as "selection, operating on variability between individuals, leads to evolution."(i)

Taking the considerations of Lotka (1922, 1945) but accepting that maximisation is in respect of the total resource utilized by the individual over its life and does not directly relate to the total flux of the community, it follows that evolution tends to maximise the resource utilized by the individual.(ii) That is, the total energy and matter used and accumulated by an individual over its life span tends to a maximum. Such resource would be the sum of the fluxes of the resource both used and controlled by the individual over its life span.

The maximising of resource utilization can be achieved through both increase in size and age but alone neither provides an optimum solution. Although in evolution there have been tendencies towards increase in both size and age the `most successful' organisms have not been the biggest nor the longest lived. Rather, it would appear that size and age must be combined with complexity (capability).

The two subcomponents of hypothesis (ii) relate to the selection (elimination) and to the generation of new capabilities (advancement). Through selection, given a finite organic capability, evolution is directed towards increasing the efficiency of resource utilization.(iii) Given an infinite organic capability evolution is directed towards utilization of new resource by the individual where new resource is resource not previously available to that organism. That is, maximum resource utilization can be achieved through increased efficiency or through increasing the resource base. Although these are independent factors they operate concurrently. To access new resource an organism must first be capable of successfully competing with other organisms; advancement requires survival. That they are independent is seen in the mechanism. Increased efficiency requires that the organism become more competitive whereas utilization of new resource can include resource not previously available to any other organism. There is also a limit to the degree of development possible through increased efficiency whereas the limit to new resource is only given by the defined temporal and spatial boundaries and taken over all time and space is infinite.

In the postulates presented there is no direct mention of reproduction although it is indirectly incorporated in postulate (i) as variability can be generated through reproduction. This indicates that reproduction is not the primary driving force in evolution, that it is associated with but not responsible for evolution. This does not necessarily mean that evolution could proceed without reproduction, only that selection is not directed by reproduction per se.

Postulate (ii) states that individuals tend to maximise their utilization of resource. As like individuals compete more than unlike individuals, and as the progeny of an individual are more like their parents than are other individuals, the conclusion is that evolution tends to minimise the reproduction of an individual. This has the corollary that to ensure survival, the survival rate of the progeny must be maximised. Thus there is an aspect of evolution that relates to reproduction in general and survival in particular.

Reproduction can be divided into sexual and asexual. Asexual reproduction can, to a first approximation, be regarded as increasing the size of an individual (this would appear reasonable for rhizomatous and stoloniferous plants but becomes tenuous when apomixis is considered) and so does not provide a source of variation other than through mutation. Sexual reproduction differs in that it provides both mutational and recombinational variability. It also usually requires a minimum of two individuals (a population). Considering both sexual and asexual reproduction, factors affecting survival can operate at both the individual and population levels.

Van Valen (1973) presents survivorship curves for a large number of plant and animal groups and concludes that the populations tend to decrease at a constant rate. This is indicative of random elimination with the numbers lost being proportional to the numbers existing. As these results represent a net balance between gain and loss they indicate that all groups eventually become extinct. However, the survivorship curves only provide information about members classified as belonging to that group and do not account for organisms derived from that group. The curves therefore demonstrate that given a population with a fixed potential extinction is inevitable. The corollary is that survival requires an increase in the potential of the organisms.

Van Valen (1973) interprets the loss of members of a group as reflecting a deterioration in the effective environment of the organisms. As the environmental deterioration is said to occur primarily through competition with members from other groups this theory requires the extinction of the members of one group be concurrent with the appearance of the members of another. However, as competition is greatest between like organisms, deterioration in environment for future generations is likely to have been caused by the parents. The reasons for the loss of members can be inherent in the population.

Evolution is a forward looking process, it is not possible to go backwards. A gene once lost if rarely regained. It is therefore possible to have `errors' in the form of losses of attributes ultimately required for survival. Natural selection, by eliminating individuals, reduces the gene complement of the population. Given constant conditions such losses would be independent of the age of any particular group but directly related to the total number of groups within the population. That is, the errors would occur at a constant rate which would depend on the gene complement of the population at zero time. This leads to the conclusion that in any population where the capabilities of the individuals cannot be (are not) increased, the population is destined for extinction. As in any system where the organisms have a finite capability evolution is directed towards increasing the efficiency of resource utilization, this can be presented as the postulate that maximising the efficiency of resource utilization alone leads to extinction.(iv)

The above suggests that in evolution there is no stability, that evolution follows either of the two directions of advancement or extinction. The mechanism of extinction is postulated to arise from organisms with fixed potential competing for a finite resource. This can readily be related to segregation and recombination of genes in a population. The mechanism of advancement is postulated to arise from organisms acquiring the ability to utilize new resource. Mutation is a means by which this can be achieved but, because of low mutation rates, problems arise in explaining the evolutionary record. It is particularly difficult to account for the major changes that appear to have occurred over relatively short periods. A possible explanation lies in the mode of action of natural selection.

An attribute can be detrimental, neutral, or beneficial. With natural selection only the detrimental attributes will be eliminated. There will be no discrimination between neutral and beneficial attributes. With selection by man only the beneficial (favoured) attributes will be promoted while the neutral and detrimental attributes will be equally disadvantaged. Man inadvertently selects against neutral attributes whereas with natural selection they are sustained. This suggests that with natural selection operating on a population the number of attributes arising from mutations will increase with time. Moreover, as the neutral attributes are not selected against but the detrimental attributes are, the relative frequency of a neutral mutational attribute in the population will tend to increase with time. A given mutation would only have to occur once to become established in the population and the absolute number and relative frequencies of attributes arising from mutation should tend to increase with time in any population.

Models of the role of mutation in evolution usually incorporate the assumption that attributes are selected for. To account for observed changes this requires that a large number of mutations should occur over a short period and that they should occur in a number of individuals. The chances against such an occurrence appear prohibitive, however if the model is changed to one where natural selection selects against the restriction of time is largely removed.

The classification of an attribute as detrimental, neutral, or beneficial is time dependent. With environmental change a neutral attribute can become beneficial or, conversely, detrimental. Furthermore, attributes taken singly could be neutral but combined they may become beneficial; there can be interaction between attributes. The requirement for evolutionary change is that a number of individuals in the population have a number of new attributes at the same time. It is suggested that with natural selection operating on mutational variability these requirements could be met.

Rate of Evolution

The first postulate presented above deals with the mechanism of evolution while the remainder relate to evolutionary direction. An aspect not included therefore is the rate of evolution.

It is generally accepted that speciation occurs most frequently following climatic change: that change in organisms is greatest where there is environmental change. That is, the rate of evolution is greatest where there is change in the state of the resource. If disturbance is regarded as that which generates a change in the state of a resource then disturbance can be said to increase the rate of evolution. This assumes, however, that the state of any resource can be said to be constant.

The environment can be regarded as the sum of random fluctuations superimposed upon a number of cyclic changes where the frequencies of the cycles can vary and need not be in phase. While at any time the state of a resource can be defined this state changes with time. As the life span of the individual is the unit of time relevant in evolution and, as this is finite, then in evolution the state of any resource cannot be regarded as being (is not) constant. It is therefore not correct to say that disturbance increases the rate of evolution, rather, with increasing disturbance the rate of evolution increases.(v) If this is extrapolated then at zero disturbance there is no evolution. That is, evolution occurs as a consequence of a change of state of resource.(vi)

Postulate (vi) suggests that under stable conditions there would be no evolution. Further, from postulate (iv), if organisms did exist and conditions became stable life would eventually cease to exist. That is, the basis for the existence of life is change in the state of the resource.

The above postulates can be presented in the sequence:

a. Evolution occurs as a consequence of change in the state of resource.
b. Evolution occurs through preferential selection operating on variability between individuals.

c. Evolutionary development maximises the resource utilization by the individual.

    (a-i) Selection promotes increasing efficiency of resource utilization.
    (a-ii) Maximising the efficiency of resource utilization alone leads to extinction.
    (b-i) Selection promotes the utilization of new resource.
    (b-ii) Net direction in evolution is towards utilization of new resource.

d. The rate of evolution increases with increase in the change in state of resource.

The above concepts are based on the considerations that selection is a process of elimination and that the fundamental unit in evolution is the individual. The first aspect can be justified on purely logical grounds and can readily be demonstrated. Even where certain characteristics are selected `for' the net effect is the elimination of the individuals without those characteristics. Those selected `for' continue to exist while those selected against cease to exist. As selection can only operate on that which exists the material for further selection is restricted to those remaining, so with continued selection the options for further selection decrease. Selection is therefore a process of the elimination of options.

The second aspect is more difficult to justify. In general, where benefit is conferred to the individual the whole population benefits. Moreover, the development of more productive populations generally results in more productive systems. Given these correlations it becomes difficult to separate cause and effect.

The contrast between the individualistic view of evolution presented here with the system view proposed by Lodka (1945) and others is analogous to the situation that exists with plant successional theory. The individualistic theory of succession proposed by Gleason (1926) views succession in terms of the interaction between individuals and their environment. The Clementsion theory (Clements 1916) has plant communities evolving through a series of seral stages (disjunct states) in a progression towards a climax. The proponents of these theories contrast their differences when there need be little conflict. The individualistic theory deals with mechanism whereas the climax concept describes observed states. There are reasons why vegetation is not static and why certain forms of vegetation persist for sufficient time over a sufficiently large area to be recognized as separate states, but the existence of these states does not preclude their having arisen from the interaction between individuals. Indeed, the observed patterns must have arisen from the interactions between plants and their environment and neighbouring plants can be a major determinant of an individuals environment.

The limitations of the individualistic theory are that we currently do not know sufficient about the characteristics of species, the factors in the environment that affect their performance, nor the interactions, to predict the outcome observed in nature. Knowledge of the mechanism does not guarantee prediction especially where that knowledge is incomplete. The limitation of the climax theory is that it describes an observed outcome without regard to mechanism. Observations that do not fit the theory are (have to be) accommodated within special categories such as post climax.

THERMODYNAMIC EVALUATION

The term resource as used above can be sub-divided into the components energy and matter. In the functioning of organisms the acquisition of matter can be regarded as a means to the end of acquiring, storing and utilizing energy. Thus, as evolution can be perceived in terms of energy transfer, thermodynamic concepts provide a means of evaluating evolutionary constraints.

Organisms represent energy rich states in a low energy environment; they are highly improbable states. The maintenance of this state requires the continuous expenditure of energy as a single organism maintained under constant conditions will, with time, cease to exist as such. This continuous expenditure of energy necessitates an increase in entropy of the system, thus life only exists and evolution can only occur where there is change in state of the system. The two effects of biological organisms would appear to be an increase in the rate of entropy increase of the total system and an increase in the range of potentials of the components within the system.

Lotka (1945) supports the suggestion of maximisation of energy flow using a simile of a reservoir on a catchment, indicating that an increase in size of the catchment and an enlargement of the outlet will each tend to increase the flow through the reservoir. This argument is erroneous as enlarging the outlet increases the possible range of flow rates but need not alter the total flow through the reservoir. Provided there is only one outlet to the catchment, no leakage and no limit to the capacity of the reservoir (all output must pass through the outlet) flow through the reservoir is independent of the magnitude of the outlet. The reservoir and outlet serve only to alter (decrease) the rate of flow while, for a given flux density of input into the catchment, the catchment size determines the quantity.

This simile may however be useful for if the sun (catchment) is regarded as a source of energy at high potential, and organisms as the collectors of that energy (reservoir) with this energy being at a lower potential than the energy from the sun but higher than the system containing them, then the organisms can be seen to decrease the rate of flow of energy through the system. In particular, the rate of degradation of energy will be decreased. Given a continuous input of energy from the sun this can only be achieved through an increase in the capacity of the reservoir, but this capacity can be increased by increasing both the size of the reservoir and the potential of its contents. That is, for any catchment the reservoir capacity can be increased by increasing the size of an existing reservoir or by building new reservoirs at higher levels in the catchment. However, within the constraint that there must be flow through the reservoirs (organisms must degrade energy to survive) the generation of a single large reservoir at either high or low potential will not maximise the capacity of the biological system: maximisation can only be achieved by generating reservoirs of sufficient capacity at a range of potentials. Within this constraint therefore, it can be postulated that capacity of the biological component of the system tends to a maximum(vii) where this can be achieved through an increase in both the magnitude(viia) and the potentials(viib) of the biological component where these factors do not operate independently.

Making the assumption that the starting point in evolution was an organism with the lowest possible potential (the initial reservoir was at the lowest point possible in the catchment) then postulate (viib) becomes: evolution tends to increase the potential of the biological component of the system.

Within the constraint that there must be flow of energy through the organic component the tendency to increase this component can be achieved through either increasing the rate of acquisition or minimizing the rate of loss. That is, the efficiency of energy use by the organisms should be maximised (organisms should gain maximum energy for a given entropy change). Also, within the constraint that there must be flow of energy through the biological component, the tendency to maximise the capacity of the biological component is a tendency to minimise the flux of that component. Descriptively these considerations suggest that the biological system tends to be organized as a series where energy is passed down this series with:

- the energy use at any point in the series being as efficient as possible,
- the spacing between points in the series being as small as possible,
- the length of the series being as long as possible, and
- the magnitude at any point being as large as possible.

The suggestion that energy flow through the biological component tends to a minimum contrasts with Lotka's postulate (1945) that evolution tends to maximise the flux of energy through the biological component of the system compatible with the constraints. The constraints appear to be the requirement for a residue of available but untapped energy and matter and a continuous input of energy into the system. Lotka's postulate suggests there will tend to be sufficient biological material to utilize the available energy and matter but the turnover of this material will tend to a maximum. Organisms should therefore tend to become short lived, but such a tendency is not in accord with observation.

Discrepancies between the conclusions derived on biological and thermodynamic considerations arise because the former are based on an evaluation of individuals while the latter are based on analysis of systems. In consequence, the biological analysis is concerned with net direction while the thermodynamic analysis provides information about the structure of the system. Also, the biological considerations are concerned with the availability of both energy and matter while in the thermodynamic analysis it has been assumed that matter is non-limiting.

Limiting the amount of matter limits the magnitude of the biological component. Under this constraint an increase in the capacity of the biological component (vii) can only be achieved through an increase in potential (viib). Thus where matter is limiting the tendency would be for all organisms to be both efficient and at as high a potential as possible. This conclusion is in accord with the postulate that evolution is directed towards increasing the resource utilization of the individual.

PHYSICAL AND CHEMICAL ANALOGUES

A number of physical and chemical concepts have been extended to evolution, namely, the end point, reversibility, and stability. The first regards that given defined conditions there is a definable end point. The second questions if A changes to B can B change back to A. The third considers the rate of change, whether the absolute or net change is zero. Given that these terms are employed it is useful to consider their application.

If the direction of evolution is towards the individual maximising the amount of resource utilized, then at the end point a single individual utilizes all resource. However, as an individual must continue to acquire resource to maintain existence such a state can only be transient. The end point, if attained, cannot be maintained, so even if an individual occupies all space it cannot do so for all time. Evolution therefore is directed towards an unattainable goal so that while it is useful to consider direction it is not useful to search for an end point.

Lotka (1945) discusses reversibility in evolution in terms of whether a change having occurred in one direction can occur in the opposite direction. In this sense evolution may be reversible, however, in that time is always positive and that evolution is tending to maximise, evolution advances (moves forward) with time. There has never been the suggestion that biological material tends to a minimum with time. Thus while evolution may be considered to be reversible it is also unidirectional.

In the thermodynamic sense reversibility means that if A(1) changes to B then B can change back to A(2). At any time, given identical conditions, the As are identical. In evolution if

A(1) changes to B and B is said to change back to A(2) then the As may be similar but they will rarely be identical. Moreover, the individuals within any of the populations may be similar but they will not be identical. A(1) changes to B only because there is variability in A. As selection eliminates, A(1) possesses attributes not present in B. Likewise, B possesses attributes not present in A(2). For evolution to be reversible the attributes lost in the change from A(1) to B would have to be generated in the change from B to A(2). Moreover, any other attributes generated during these transitions would have to be eliminated. The probability of generating identical individuals at different points in time is low; the probability of generating identical populations is less. The answer to any question on reversibility in evolution therefore depends on the accepted level of probability and/or the accepted level of similarity. Given these constraints it would appear that the concept of reversibility is not particularly useful in the evolutionary context.

Absolute stability is attained where the rate of change is zero: where there is no change. Dynamic stability is achieved where the rate of a forward process equals the rate of a reverse process. That is, while change occurs the net change is zero. In population genetics an equivalent term is fitness, the number of individuals in a given population relative to the number is the parent population. Fitness increases when the number of individuals in subsequent generations increases. It has been proposed that fitness tends to a maximum hence rate of change and instability tend to a maximum. This is a characteristic of the capacity for exponential growth. However, the fitness, and hence the stability of a population depends on the period over which it is calculated and over the life span of the population must be zero. Within the life of a population instability tends to a maximum but over the life of a population it is zero.

Individuals are never stable, populations tend not to be stable, but in the Red Queens Hypothesis van Valen (1973, 1976) suggests that for communities an equilibrium does exist. While it may be possible to demonstrate a tendency towards a dynamic equilibrium in communities there are many situations where this does not occur. Desertification is a situation where losses to a community are not compensated for by gains while the colonization of bare rock involves an increase in the amount of organic material with time. It would appear that a change in one population is not necessarily compensated for by a change in all other organisms combined.

A more concise evaluation of stability is obtained by investigating the implications of the above postulates. Postulate 1 states that evolution occurs as a consequence of change in state of resource while Postulate 2 states that the rate of evolution increases with increases in the change in state of resource. That is, evolution occurs as a consequence of instability and increases with increase in instability. There can therefore be no stability in evolution.

APPLICATION

The above concepts should be applicable to all biological systems. The only constraint should be that the systems are sufficiently large to so as to provide valid generalizations. Business systems are a product of biological components and are well distributed in time and space and so provide a valid application.

The nature of a business can be seen to be similar to an organism, given an appropriate substitution of terms. A business is based on the resources of assets (matter) and money (energy). The assets are used to acquire money, building up assets in the process, but this only occurs given a flow of money through the business. Benefit can be gained from controlling assets that are not utilized as this can limit competition from others.

The size of businesses ranges from those based on individual people to multi-national companies. The evolutionary direction has been from the small and simple to the large and complex. Large and simple businesses do occur, as with cooperatives, but the large and complex multi-nationals are the more recent and most successful.

The maximisation of resource by multi-national companies is virtually self evident. The ultimate business is a monopoly or, if that fails, a cartel. The point of interest is how that state is achieved. The Ford Motor Company promoted efficiency as the solution. Efficiency gained, but could not maintain, market dominance. The efficient production of a product that is not required leads to losses and, eventually, extinction. The way forward lay in the development of new capabilities via the utilization of new resource. This is best seen in the development and utilization of the silicon chip.

The above considerations in this section address postulate 3 and its components. Postulate 2, the Darwinian theory, can now be regarded as self evident. Postulate 1 is difficult to address in this context. Postulate 3 is also difficult to address because of the difficulty in separating cause and effect, however, development, and hence evolution, was high during the major world wars when disturbance was at a maximum.

CONCLUSION

The above considerations are designed to extend current evolutionary thinking. Some ideas are at odds to current attitudes but are regarded as being sustainable in logic. Interestingly, none are opposed to the views of Darwin (1859). When it came to the question of evolutionary direction Darwin was not prepared to commit himself and escaped the question by stating that `*physiologists say* ---'[3].

The main differences between the views presented here and elsewhere derive from viewing evolution as an individualistic rather than a system concept. The reason is that while much information can be gained from studies of black boxes the true nature of the system will only be ascertained given knowledge of the operations within the box. Thermodynamic principles indicate the constraints or boundary conditions but an analysis of the biology is required to obtain a solution that accords with function.

---

[3] The physiologist was evidently Huxley

REFERENCES

Clements, F.E. (1916). Plant succession. An analysis of the development of vegetation. Carnigie Inst. Washington Publ. 242 Washington, D.C., 1-512.

Christian. C.S. and Stewart, G.A (1953). General report on survey of Katherine-Darwin Region. 1946. Land Research Series N. 1. Commonwealth Scientific and Industrial Research Organisation, Australia. Melbourne

Darwin, C. (1859). On the origin of species by means of natural selection. pp. 490. John Murray, London IX.

Dobzhanzky, T. (1968). On some fundamental concepts of Darwinian biology. Evolutionary Biology 2, 1-34.

Gleason, H.A. (1926). The individualistic concept of plant association. Torrey Bot. Club Bull.44, 463-481.

Lotka, A.J. (1922). Contribution to the energenitics of evolution. Natural Acad. Sci. Washington. Proc. 8, 147-151.

Lotka, A.J. (1945). The law of evolution as a maximal principle. Human Biology 17, 167-194.

McIntosh, R.P., 1967. The continuum concept of vegetation. Bot. Rev. 33: 130-87.

Stern, J.T. (1970). The meaning of "adaptation" and its relation to the phenomenon of natural selection. Evolutionary Biology 4, 39-66.

Tunstall, B. R. (1978). General constraints on succession. In - Report on a workshop on succession and disturbance in Australia held at Shoalwater Bay, Queensland, 26 November to 2 December 1977. CSIRO Aust. Division of Land Use Research Tech. Memo. 78/26

Tunstall, BR (2007) Vegetation: Continuum or Discrete States? On www.eric.com.au 12pp

Tunstall, BR (2008) The Basis for the Existence of Species On www.eric.com.au 4pp

Tunstall, B. R., Jupp, D. L. B. and Mayo, K. K. (1984). The use of co-occurrence in land cover classification for the investigation of ecological landscape patterns. In `Landsat 84', Proc. 3rd Australasian Remote Sensing Conf., Gold Coast, Queensland, 147-54. (Organising Committee, Brisbane).

Tunstall, B. R. & Reece, P. H. (2005). Tree Recruitment in a Poplar Box Woodland. On www.eric.com.au

Tunstall, B. R. and Torssell, B. (2004). An interpretation of spatial variability in vegetation in a Eucalyptus populnea woodland. On www.eric.com.au

Tunstall, B. R. & Torssell, B. (2004). Analysis of competition in spruce-pine-birch communities in Central Sweden. On www.eric.com.au

Van Valen, L. (1973). A new evolutionary law. Evolutionary Theory 1, 1-30.

Van Valen, L. (1976) Energy and Evolution. Evolutionary Theory 1,179-229.

Walker, J., Thompson, C. H., Fergus, I. F. and Tunstall, B. R. (1981). Plant succession and soil development in coastal dunes of subtropical eastern Australia. In *Forest Succession Concepts and Applications*, pp 107, 131. Eds. D. E. West, H. H. Shugart and D. B. Botkin. Springer-Verlag, New York.

Whittaker, R.H. (1978). Direct gradient analysis. 2 nd. ed. In `Ordination of Plant Communities'. (Ed. R.H. Whittaker). Junk, The Hague, pp 7-51.