

Corals: pointing to a different evolution

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Abstract: For most marine organisms, ocean currents are the vehicles of larval dispersal and are therefore the pathways of genetic connectivity. These paths repeatedly and continuously change over time, creating changes to the distribution ranges and genetic compositions of species. Geographic space and evolutionary time interact: species units diverge, then re-form into different units. For corals, this creates 'reticulate' patterns in both space and time. In geographic space, species are typically distinct in any single region but lose their identity as taxonomic units over very great distances. When these patterns are envisaged in evolutionary time, species have no time or place of origin and there are no distinctions between sympatric and non-sympatric concepts of origination. Differences between species and subspecies taxonomic levels and between species and 'hybrids' are arbitrary and/or unrecognizable. Reticulate evolution is driven by the physical environment, not biological competition. Rates of evolution and extinction (which occur through fusions as well as terminations of lineages) are similar over long geological intervals. Reticulate evolution gives the overall impression of punctuated equilibria, as is frequently observed in fossil records. Taxonomic, systematic and biogeographic concepts of neo-Darwinian and reticulate evolution are mutually exclusive, except where single species form genetically cohesive, reproductively isolated, units. In the latter case, natural selection as the driving force of evolutionary change becomes dominant over environment-driven reticulate change.

Key words: corals, evolution, biogeography, taxonomy, systematics, reticulate evolution

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1. INTRODUCTION

Species have long been regarded as the fundamental units, or 'building blocks', of Nature – units which can be named, described and studied (MAYR, 1942, reviewed; GOULD, 2002). They have thus been contrasted with other taxonomic levels that are supposedly human-created and therefore matters of taxonomic opinion. When this concept of species is applied to corals over very large geographic ranges, it breaks down. In reality, most species are only clearly defined units in limited geographic space (VERON, 1995). When that space is progressively increased (as, for example, viewing a particular species in one country, then in many countries), it becomes progressively *not* that species. The fundamental reason for this is that coral species exist in both geographic space as reticulate or interlinked patterns that change continuously, not as geographically uniform units. This creates a dilemma, for humans cannot easily communicate in terms of continua: they need discrete units of some form or other.

When this issue is considered in evolutionary time, not just in geographic space, the issues that arise make it necessary to consider evolutionary change in a way that is different from that which has become generally accepted in both the popular and scientific literature. Reticulate evolution represents a paradigm that cannot be mapped directly onto traditional views of species, yet is highly explanatory of a wide array of palaeontological, taxonomic, systematic and biogeographic issues that have been debated throughout much of the twentieth century.

2. THE CONCEPT

If a hypothetical evolutionary tree is placed in an imaginary cube of space and time (with the top of the cube representing geographic space at present time) and the tree is viewed from above, we see the branches that exist today, each branch being a single species. A single branch can then be envisaged as a distribution map. If the cube is divided into layers like the pages of a book, each page will be a distribution map of that species at a different time. If the pages are turned, the pattern will change. These changes are not just distribution changes, they are also genetic changes occurring in response to changes in ocean currents. As a result, a species (or map) at one point in time is not the same as it is in another point in time: it will have been genetically as well as geographically changed. The changes do not occur uniformly, rather they occur irregularly and to varying degrees at different times. Geographic space and evolutionary time interact so that species and components of species diverge and converge. This creates a three-dimensional 'reticulate' pattern in space and time (VERON, 2000).

2.1. Reticulation and surface circulation

Reticulate evolution is driven by changes in surface circulation patterns that cause changes to the dispersal patterns of larvae. If currents remained constant throughout evolutionary time, the oceans would be divisible into source areas (where the larvae come from) and destination areas (where the larvae go to) and there would be general

uniformity in species and their distribution. However, with the exception of the most major equatorial and continental boundary currents, surface currents are not constant. Sea levels fluctuate over 100 metres, oceanic passages are opened and closed by tectonic movements, and the earth undergoes cyclical climate changes due to variations in the tilt of its axis and the shape of its orbit around the sun (Milankovitch cycles; BRADLEY, 1985). These, and probably several other types of geo-climatic events, cause variations in ocean currents (WILLIAMS et al., 1993). These changes open and close genetic contacts, generating reticulate patterns.

To understand how changing ocean currents effect genetic connectivity, it is helpful to envisage what would happen to dispersion if all the ocean currents stopped. Every reef, island and headland would be genetically isolated. In time, through natural selection augmented by genetic drift and mutations, the corals of each location would gradually become distinct from those of every other location. In time, every location would develop a unique fauna and every species would have a distribution range of just one location, and there would be millions of species worldwide. If the very opposite is now envisaged – where ocean currents are so strong and so variable that the corals of every location came into frequent genetic contact with those of every other location – every species would eventually become dispersed to every location. All species would be found everywhere they could grow and there would only be a small number of species worldwide. It is certain that these imaginary extremes never happened, but what *has* happened is that the Earth's circulation patterns and climate has oscillated within these extremes (FRAKES et al., 1992), causing constant changes in dispersion, constant changes in genetic connectivity – causing reticulate patterns to arise. Reticulate evolution is a mechanism of slow arbitrary change rather than a mechanism for progressive improvement.

2.2. Reticulate re-packaging

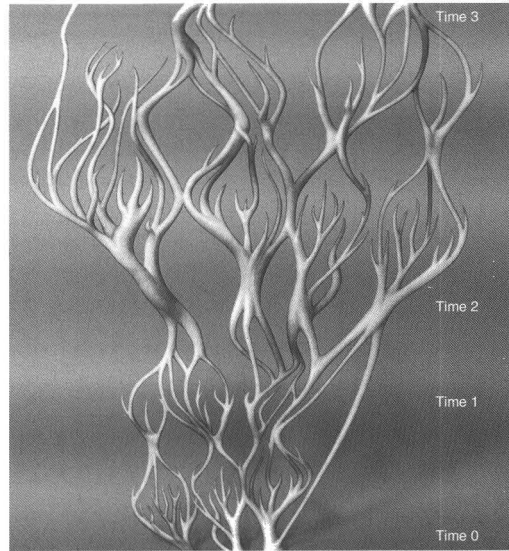
When components of a species diverge (break apart) as a result of weak ocean currents, each may form a separate *geographically* isolated species. When these components converge (re-combine) as a result of strong ocean currents, they may again become a single species or they may have diverged enough form more than one *genetically* isolated or semi-isolated species. They may also have genetic components of other species. This is reticulate 're-packaging' (VERON, 1995) and it occurs constantly at all scales of space and time. The re-packaging is not confined to a single phylogeny or evolutionary clade, but involves many clades simultaneously (Fig. 1) and the re-packaged units may arbitrarily be called species, subspecies or hybrids.

There is a balance between species diversity and dispersal capability, a balance maintained or changed by ocean circulation patterns. If currents weaken, diversity will appear to increase because genetic isolation increases, creating pockets of semi-isolated taxa that are indistinct from their relatives. If currents strengthen, diversity will appear to decrease because genetic isolation decreases, causing taxa to become widespread through genetic intermixing. These taxa will be relatively well defined.

In effect, changing currents cause genetic diversity to be endlessly repackaged in cycles that have variable impacts and frequencies. Substantial biogeographic change

Fig. 1:

A hypothetical view of reticulate evolutionary change in genetic paths of a group of species. At the bottom (Time 0), the group forms three distinct species, each of which is widely dispersed by strong currents. At Time 1, the group forms many indistinct small species units that are geographically isolated because currents are weak. At Time 2, the group forms three or four species that are again widely dispersed by strong currents. Over the long geological interval to Time 3, the group has been repackaged several times. Note: (a) no species has a time of origin, (b) the amount of evolution and extinction is similar over the geological interval represented by the diagram, (c) there are no differences between mainstream species (represented by the thicker branches) and subspecies taxonomic levels (represented by thinner branches), (d) there are no differences between 'species' and 'hybrids', (e) the total amount of genetic information represented by this diagram has not greatly changed, but has been re-packaged into different 'species' units, (f) extinction occurs through repackaging as well as terminations of lineages, (g) a single species at Time 0 and a single species at Time 3 may have few, if any, morphological distinctions. This will give an impression of evolutionary stability. Conversely, a single species at Time 0 and single species at Time 1 will give an impression of rapid evolutionary change. When combined, the overall impression may be one of 'punctuated equilibria', as is frequently observed in fossil records.



may occur at intervals of thousands of years or less and these may be associated with sufficient repackaging to form geographic races or varieties. Major cycles, or the additive effects of many cycles, may create species-level changes.

2.3. Reticulation, syngameons and systematics

The concept of the syngameon, first recognised by botanists (GRANT, 1981) and introduced to the marine world through corals (VERON, 1995), is important for the understanding of reticulate evolution and resulting geographic patterns. A syngameon, by definition, is a reproductively isolated unit. In concept, so is a neo-Darwinian species (reviewed many times, e.g. FUTUYMA & MAYER, 1980). In reality, syngameons are nothing like any of the mainstream concepts of species as they incorporate geographic variation and the spectrum of genetic links that geographic variation creates among different species.

A syngameon may be a single species, or it may be a cluster of different species (e.g. BURGER, 1975) which have variable genetic links (genetic flow through cross-fertilisation)

with other members of the syngameon. Where a syngameon contains several species, a single component species may be distinct at a single geographic location but, because it intergrades with other species at other locations, it will become submerged in a mosaic of variation at other locations. The geographic range and morphological variation of the single 'species' will depend on taxonomic decisions. These decisions will be arbitrary if they impose divisions in natural continua rather than reflect natural units. The syngameon as a whole is not morphologically observable unless its component species are determined genetically or experimentally (through cross-fertilisation trials) in every part of the syngameon's distribution range.

The reasons why syngameons are not used in operational taxonomy are (a) they can only be determined with any degree of certainty through exhaustive cross fertilisation studies in all geographic regions where their component species occur, (b) they are not likely to have distinguishing morphological characteristics and (c) they would likely include so many morphological species that they would need to be re-divided into sub-units of some kind in order to be useful. This issue will always force taxonomists to make arbitrary decisions as to what particular species are. In the context of systematics, cladistics, a widely used method of determining phylogenies, is not applicable to reticulate systems (e.g. SOBER, 1988). This restraint is seldom heeded in genetic analyses: the impact of reticulate evolution on cladistic methodology is likely to be substantial once its existence becomes more widely recognised than it currently is.

2.4. Reticulation and taxonomy

With corals as with most plants, most species *do* exist as more-or-less definable units in single geographic regions, such as the Red Sea or the Great Barrier Reef. However, widespread species commonly show sufficient geographic variation that they could reasonably be divided into several separate 'sibling species' were it not for the fact that these smaller units form continua with each other. For example, the majority of corals of the Red Sea also occur in the Great Barrier Reef, but many are sufficiently distinct at these distant locations that they would be classified as separate species if they were found growing together (VERON, 1995).

In traditional taxonomy, geographic variation within a species is accommodated by creating divisions within the species, such as varieties, races or geographic subspecies (e.g. AVISE, 2000). In reality, geographic variation repeatedly overrides the morphological boundaries of individual species. In other words, natural continua go beyond the taxonomic or morphological boundaries of individual species. This cannot be accommodated by creating divisions within species. The problem remains if the species unit is 'split' into smaller units or 'lumped' into larger units and it is not solvable by further or more detailed study. Ultimately, the only unit in Nature that is real is the syngameon.

2.5. Reticulation and dispersion

Dispersal of most terrestrial animals is an active undertaking. It requires a capacity for mobility, it allows choice of direction, and there is a high probability of surviving the

journey. Dispersal of most marine animals is passive: ocean currents control it. It requires little effort, there is no choice of direction, and there is a low probability of survival. For these reasons, adult animals undertake most dispersal on land, whilst in the ocean larvae usually undertake dispersal. Reproduction and dispersal, for most marine animals, are therefore closely linked subjects. Only some larger vertebrates – oceanic fish, reptiles and mammals – are able to defy the currents and undertake active dispersion. For the rest of marine life, the pathways of dispersion cannot be controlled, or (except for timing) even selected for. This has major significance for all aspects of coral biology, including taxonomy and evolution.

Because most marine organisms (including corals) are dispersed by larvae, the paths of the currents are the paths of gene flow – the paths of genetic connections. Currents are largely responsible for creating, and breaking, the distribution ranges of species. For most species, these ranges are very large, so large that the genetic composition of a species in one part of the range may be very different from that in another. For corals, as with many other major groups of plants and animals, this variation in genetic composition reaches a point where variation *within* species merges with variation *between* species. When this happens, geographic patterns are created where the morphological boundaries of species (the limits to what a taxonomist might call a species) become arbitrary. Importantly, distribution patterns are the outcomes of dispersal by currents: not just the currents of today, but all the currents that existed during the evolutionary history of the species (VERMEIJ, 1978).

2.6. Reticulate and neo-Darwinian evolution

Figure 1 summarizes the core reasons why reticulate evolution is sharply contrasted with the traditional neo-Darwinian concept: in reticulate systems, species can have no time of origin, nor place of origin. They are semi-arbitrary components of continua rather than units, and are continually re-packaged in space and time.

The subject of neo-Darwinian evolution is dominated by varying emphases on three broad notions: (a) that species exist in Nature as more-or-less reproductively isolated units of some kind, (b) that these units compete in different ways or are modified by the environment and (c) that the 'fittest' units survive (e.g. HUXLEY, 1942). Implicit in these notions is an assumption that species have a time and place of origin (where evolutionary trees branch) and that they are units where time and geographic space do not interact as described above. The concepts of reticulate evolution and the traditional view of evolution are not compatible – they are two paradigms that become increasingly mutually exclusive with increasing geographic space and evolutionary time. (This is comparable to 'flat earth' and 'spherical earth' paradigms: discrepancies become progressively more important with increasing geographic area.)

There is a point, however, where reticulate evolution interlinks with the traditional Darwinian view of natural selection through competition and survival. Competition affects relative abundance, but only in specific environments, times and places. In other environments, times and places, the dynamics are likely to be different. The outcomes of competition will initially be of local significance, but if repeated in many places, they can presumably cause total extinctions. They will not, however, create evolutionary change unless the competing species is a cohesive units of some kind.

The same issues apply to adaptations to environments: species *can* adapt to environmental pressures if they are cohesive units. If any given species is mobile enough to maintain genetic cohesion in the geographic space it occupies in few-enough generations to be able to maintain cohesion, then they can adapt as a single unit. Clearly this can happen with highly mobile organisms like birds and large mammals. For other organisms, the larger the space they occupy and/or the less mobile they are, the less cohesive they will be. Marine organisms that rely on larval dispersal clearly have a minimal chance of cohesion.

It can generally be said that species that are alive today are only those small fragments that have not gone extinct (e.g. STANLEY, 1979). Ever-changing reticulated systems are not prone to extinction and are resistant to major evolutionary movements. For this reason, evolutionary change large enough to be revealed in the fossil record is extremely slow. At the present point in the earth's history, sea levels have been approximately constant for many thousands of years and there has also been an extended interval of climatic stability. The earth is likely to be in a period of weak ocean currents that are providing the mechanism for re-packaging species into small units. The stage reached by each individual species will be different as it will depend on genetic dissimilarity with other species, dispersal ability, abundance and distribution range. These factors all vary geographically. The decision as to what an individual species is will, in concept, change with evolutionary time, but it will always be arbitrary.

2.7. Reticulate evolution in the fossil record

Species in the coral palaeontological literature usually have little in common with those of extant coral taxonomy. The reason is simple; corals have a wide range of morphological variation depending on the environment in which they occur. For example, colonies of *Pocillopora damicornis* (Fig. 2), one of the most studied of all corals, may have

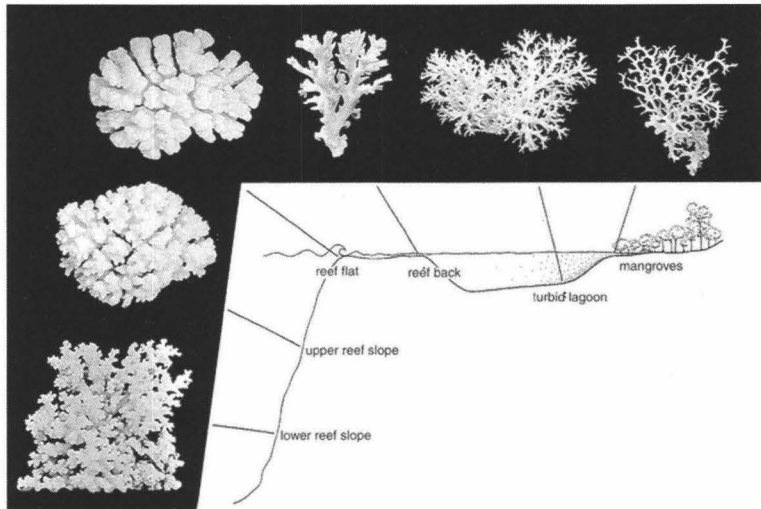


Fig. 2:
The growth forms of colonies of *Pocillopora damicornis* from a wide range of environments at the same geographic location (from VERON & PICHON, 1976).

almost nothing in common if collected from very different habitats. Most of this variation is phenotypic although it is likely that there will be genetic selection for survival in particular habitat types. These variations are readily observed underwater, but not in a fossil sequence. If of *P. damicornis* illustrated were to be observed as fossils, the observer may conclude that there are many species involved or else that evolutionary change had occurred whereas in reality what did occur was an environmental change.

Being a relatively new concept, reticulate evolution has not yet been recognised except in the fossil record and except in the '*Montastrea annularis* complex'. Its primary areas of impact are in evolutionary and taxonomic concepts and theoretical biogeography. However, it is highly explanatory of the concept of punctuated equilibria in evolution where reticulate evolution creates long intervals of change without improvement and neo-Darwinian evolution creates short intervals of directional change.

3. SUMMARY AND CONCLUSIONS

The main conceptual differences between neo-Darwinian and reticulate systems are summarised in Table 1. It is stressed that this is a check-list only and that there are alternative interpretations, as well as exceptions, applicable to different taxa.

Much of our present understanding of systematics reflects a human need to divide natural continua into units. In Nature, genetically isolated taxonomic units are uncommon, as evidenced by domesticated plants and animals (where almost no species are now considered to be genetically isolated), by developments in taxonomy (where species units are increasingly being 'lumped' or considered 'fuzzy'), by discoveries of lateral gene flow among species (e.g. KING, 1993) and by the recognition of geographic subspecies and 'hybrids' and in wild and semi-wild populations. Reticulate evolution predicts, and explains, these observations. It is also a substantial theoretical advance on vicariance theory as a source of explanation of species originations and biogeographic links between geographic patterns and evolutionary processes.

As a paradigm, reticulate evolution (embracing the concept of continua over units) advocates caution in the interpretation of experimental results and in decision-making about conservation. As with some forms of cladistic analysis, there is usually a presumption of the existence of units (i.e. of genetic isolation) in experiments and observations involving wild populations. Similarly with conservation: laws are based on species. There is an assumption that species can be conserved in refuges, or (in the case of corals) marine parks. If however these species vary geographically, then only parts of this variation can thus be conserved. Far more importantly, if species are linked in genetic networks (analogous to links in ecological networks) it is the networks as well as the species that will need to be conserved if flow-on effects of cutting links ('islandisation') are to be avoided. At the present rate of degradation of coral reefs, this requisite is clearly becoming unattainable: even genetic highways such as the Maldives-Chagos Archipelagos (SHEPPARD & SEAWARD, 1999) are now less effective as stepping-stones than they once were.

Reticulation calls for the conservation of connectivity as well as for the conservation of species. This means the conservation of stepping-stones along dispersal pathways, not only for re-seeding after denudation, but to actually maintain systematic order.

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