

Selection, Space and Diversity: What Can Biological Speciation Tell Us About the Evolution of Modularity?

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Abstract. Modularity is a widespread form of organization in complex systems, but its origins are poorly understood. Here, I discuss the causes and consequences of modularity in evolutionary systems. Almost all living organisms engage in sexual exchange of genes, and those that do so are organized into discrete modules we call species. Gene exchange occurs within, but not between, species. This genetic segregation allows organisms to adapt to different niches and environments, and thereby evolve complex and long-lasting ecosystems. The process that generates such modularity, speciation, is therefore the key to understanding the diversity of life. Speciation theory is a highly developed topic within population genetics and evolutionary theory. I discuss some lessons from recent progress in speciation theory for our understanding of diversification and modularity in complex systems more generally, including possible applications in genetic algorithms, artificial life and social engineering.

1 Introduction

Many systems exhibit modular structure. By this I mean that their underlying units interact within discrete subsystems, rather than with the system as a whole (a number of other definitions are possible, mostly related to engineering and therefore less relevant to understanding natural systems [1-4]). Such modular structures appear to be a very general consequence of adaptive evolution at a wide range of scales[1,5-7]. By allowing differentiation of components within complex systems, modular structure is a key factor in the behavior of complex systems[1-4]. However, the principles governing the origins of modular structure in complex systems remain poorly understood [3,4]. Here, I discuss the evolutionary origins of one of the best-studied forms of modularity in nature, the biological species, and its implications for our understanding of ecological and evolutionary systems. It is shown that the evolution of genetic modularity has some important lessons for our understanding of modularity and diversification in complex systems in general.

1.1 What Is Modularity?

A system can be described as modular when its components form hierarchically organized, interacting subsystems[1-4]. For example, a road traffic system can be decomposed into interacting vehicles in a spatial environment, and each vehicle can then be decomposed into wheels, engines, brakes, each of which can itself be broken down

into lower-level components, ultimately to the level of subatomic particles. Thus, modules are units within a system that are themselves composed of lower level units. Secondly, these lower level units interact primarily within their own module, and their sole significant effect with regard to understanding the system is to induce a state change of that module[2,3]. The module as a whole interacts with other modules, depending on its state. In this sense, each module can be considered as a “black box” for the purpose of understanding the functioning of the system at a higher level. We need know nothing about interactions at the subatomic, atomic or molecular levels, or even the behavior of the braking and acceleration systems, in order to understand traffic dynamics. We can collapse all of these subsystems into an attribute of each car – its speed – without losing any generality in our understanding of traffic dynamics.

It should be noted that modularity is relative to the system we are interested in. Cars are modular relative to traffic dynamics. They are not necessarily modular relative to air flow, magnetism, pollution, or many other features.

1.2 Complex Systems, Network Theory, Emergence and Modularity

The terms complexity and emergence should be mentioned because they are commonly used to describe systems that exhibit modularity [3-6, 8]. Systems that are composed of a large number of interacting units are often called “complex systems”, especially when the behavior of the units is not always uniform and leads to different or surprising outcomes at larger scales [3-6, 8]. The latter phenomenon is sometimes termed emergence [8-9]. In practice these definitions are subjective. They describe our perception of system behavior, rather than an objective attribute of the system.

For example, a table is not usually considered a complex system, but it is composed of many units (atoms), the behavior of these atoms is not always uniform (they are usually, but not always, maintained in a stable configuration), and they have a collective outcome which might sometimes surprise us (the table mostly holds things up, but sometimes breaks or falls over).

Defining complex systems in terms of modularity does not resolve the definition problem: many systems that are not widely considered complex are modular with regard to some function. A table can be decomposed into modules (legs, nails and surface), each of which can be decomposed further, but whose underlying structure is generally irrelevant to understanding the system of table behaviour. As long as we understand that the table legs support (or fail to support) the table surface, we do not need to understand whether they are made of steel or wood. Thus, modularity is not a measure of complexity, although it is a common feature of systems usually described as complex.

It is often useful to view systems as networks of interacting elements [10-11]. From this perspective, modules are highly connected subsystems that share few connections with other such subsystems [11]. In network theory highly connected subsystems are termed clusters, and clustering can be measured as a continuous parameter [10-11]. In modular systems, connections within modules are qualitatively different from connections between modules [10]. This is not necessarily the case in clustering systems. Thus, modules are clusters, but not all clusters are modules. Clustering behaviour can be generated quite easily in networks, especially through scale-free growth patterns [10-11]. However, known growth patterns do not generate the functional differentiation that is observed in modular systems [11].

2 Species as Modules

The definition suggested above implies that modules are not objective phenomena, but exist only in relation to a system. Therefore, in deciding whether species are modules, we must first specify the system within which they might form modules. I will discuss two possible systems, ecology and evolution, and the commonalities between them.

2.1 Species as Ecological Modules

Species are not clearly modular in an ecological sense. Animals and plants interact with their environment as separate individuals, not as an aggregate of their species. Although the outcomes of these individual interactions may be viewed from an aggregate perspective, the aggregate view may be a human construction rather than a natural feature of the system.

We can draw a food web that describes which species eats which within a certain ecosystem, for example, foxes eat rabbits. Such a drawing is a usable hierarchical abstraction of the relationships between different organisms. However, it may be a mistake to assume that such an abstraction actually reflects an underlying modular structure. The fox species as a whole does not eat the rabbit species as a whole: rather, individual fox units eat individual rabbit units. Thus the interaction between rabbits and foxes is an interaction between many distinct units of two basic types, rather than an interaction between modules. The principle that units within a module interact primarily with one another, rather than with units belonging to other modules, appears to be violated.

Although rabbits and foxes are not modular in this sense, there may nonetheless be a system of interactions between the rabbit and fox species which can be understood from a modular perspective. It may not matter that individual foxes eat individual rabbits if there is an efficient way to summarize the interactions between all rabbits and all foxes with respect to the system in which we are interested. The assumption that ecological interactions can be summarized in this way is necessary for notions such as ecosystems and food webs to have any validity beyond mere description.

2.2 Consequences of Species Modularity in Ecology

There is a tension in ecological literature between these two viewpoints. The ecosystem view sees species as modules existing in tightly coupled interactions with other species [12-19]. In contrast, neutral theory sees species as aggregates of individuals, all separately interacting [20-21]. In the neutral view, food webs are descriptions of how interactions generally happen to occur, but they do not describe a system that can be analyzed in any meaningful way, because the interactions between individuals overwhelm interactions happening at the species level. In the ecosystem view, interactions can be meaningfully analyzed at the species level. The ecosystem view tends to assume that species interactions attain some form of dynamic equilibrium, in which each species plays a consistent role, while neutral theory focuses on non-equilibrium dynamics [22-23]. In their most extreme form, ecosystem models take the form of the

Gaia hypothesis, which proposes that ecosystems form self-sustaining complex adaptive systems [24-26].

The debate about whether species form ecological modules is far from resolved: current empirical evidence suggests that both neutral and ecosystem dynamics are important [27]. The ecological literature contains good examples of both highly specialized ecological feedback loops, and non-equilibrium neutral ecological dynamics, and few large-scale data sets are capable of distinguishing between the two models. Perhaps we need a theory that can unify these perspectives, allowing species to have varying degrees of modularity.

2.3 Species as Evolutionary Modules

At the evolutionary level, the view of species as modules is less dubious. Evolutionary systems are constituted by the interactions that determine the movement of genes within populations. Sexual reproduction implies that genes do not remain in fixed relationships with one another: instead, genes move into a new genetic environment every time sexual reproduction occurs. We term the net movement of genes within natural populations gene flow [28].

Gene flow occurs within, but not between, species. In 1942, Ernst Mayr proposed his biological species concept, which states, in its short form:

“Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups.” [28]

Much subsequent debate has centered on what exactly reproductive isolation might entail [29-30]. However, Mayr’s essential concept that species are units defined by the limits of gene flow is widely accepted and often regarded as one of the major advances of evolutionary theory during the 20th century.

Gene flow occurs slowly, over generations. Day to day interactions between individuals are therefore not as important to gene flow as they are to ecology. What is important for gene flow is the average outcome from those interactions. For example, to understand cheetah population dynamics, we need to understand not only that cheetahs eat gazelles, but that competition from lions and hyenas limits the spatial range cheetahs can occupy; that gazelles rely on pasture, which is also spatially and seasonally limited, and numerous other interactions. However, to understand the evolutionary impact of cheetahs on gazelles, we need to know only the average impact of the cheetah gene pool on the gazelle gene pool: cheetahs generate a net selection pressure on gazelles, and vice versa. In this sense, treating species as modules from an evolutionary perspective is much more clearly justifiable than treating species as modules from an ecological perspective.

2.4 Punctuated Equilibrium and Species Modularity

The view that species function as evolutionary modules potentially has some major consequences for our understanding of evolution. This is reflected in the great debate between neo-Darwinian and punctuated equilibrium theorists. Species modularity opens the door for the controversial process of selection at multiple scales, a necessary component of punctuated equilibrium as championed by Gould [31].

The view that selection can operate at the level of species as well as individuals is often regarded as nonsensical in neo-Darwinian theory for the following reason [32]. Selection at the species level occurs on a vastly slower timescale than selection at the individual level. It is, therefore, comparatively very weak. Moreover, most genes that are advantageous at the species level are also advantageous for the individual. Therefore, any consequences of species selection are likely to be trivial, and overwhelmed by selection at the level of the individual. This makes species-level selection in general untestable and therefore unscientific [32].

Gould, on the other hand, argued that after some form of perturbation, species rapidly evolve to an equilibrium state in nature [31]. Evolution to equilibrium is governed by natural selection at the individual level, as argued by the neo-Darwinian theorists. However, adaptive variations should percolate through a population quite rapidly even with weak selection, and mutations are rare. Therefore, most of the time, there will be no significant variation in adaptive traits, and therefore no natural selection. Species will remain in an equilibrium evolutionary state, unable to evolve new adaptations because the necessary variation is absent. However, they will compete with other species for space and resources, and species with superior design features will ultimately drive less efficiently adapted ones to extinction. Thus in Gould's model, selection occurs primarily at the species level.

Part of the confusion between these two viewpoints results from a conflation of scales [33]. Neo-Darwinians are interested in relating quantifiable population genetic processes to observable current evolutionary processes. Therefore, they tend to regard macroscopic evolution as something that cannot be studied in anything more than a historical sense. Paleontologists, on the other hand, are interested in the processes that generate the fossil record. The fossil record reflects only a tiny proportion of species, and only limited aspects of those species. This limitation means that paleontologists are intensely interested in the processes that generate macroscopic structures in evolution – about which neo-Darwinian theory has very little to say.

We can caricature this debate, with even-handed unfairness to both sides, as follows. Suppose a tree-dwelling mammal species has split into two forms. One of these forms has skin-flaps that are useful for aerodynamic control during leaps between trees. The other has bristles that perform the same function. Neo-Darwinians are interested in the gene-level selection process that leads to bristle and skin flap production, and the process of diversification that means bristly animals lack skin-flaps, and vice versa. Paleontologists are interested in the processes that determine whether, in the long term, animals with skin-flaps become abundant and diverse, and ultimately produce new adaptations, while animals with bristles disappear. From the paleontological perspective, it therefore makes sense to think about whether skin flaps are selected over bristles, that is, whether skin flaps are ultimately a better or worse path to aerodynamic control. This is species-level selection because there is no gene-level competition between skin-flaps and bristles: they occur in separate evolutionary lineages. From the neo-Darwinian perspective, such analysis appears excessively speculative: species with skin flaps may have succeeded while species with bristles went extinct for any number of reasons, which may or may not have anything to do with skin flaps.

However, this difference of scale also leads to a philosophical divergence that permeates the interaction between evolutionary biology and other disciplines. If species

are discrete, relatively stable units, occasionally passing through brief but dramatic periods of diversification and adaptation, then the ecosystem view becomes highly plausible. If, on the other hand, species are loose, fluctuating aggregations of genes, maintained by competing feedback processes but in a state of permanent disequilibrium, then ecosystems make far less sense. The more modular our perception of species, the more we move towards the punctuated equilibrium side of the debate; the less modular, the more we are inclined to the neo-Darwinian view. Table 1 summarizes this dispute.

Table 1. Consequences of modular and non-modular views of species

Aspect	Modular view	Non-modular view
Species interactions	Tightly coupled, no significant variation within species (specialists)	Loose and interchangeable (generalists)
Ecological dynamics	Equilibrium, self-maintaining, generally stable	Non-equilibrium, illusion of stability caused by limited human perspective
Food webs	Accurate representations of system dynamics that can be analyzed in their own right	Descriptive snapshots of what is happening at a certain time and place
Environment	Stable/predictable (except at boundaries)	Unstable/unpredictable
Evolution	Punctuated equilibrium	Gradualist

3 How Do Species Form?

Understanding speciation is one of the major theoretical challenges of evolutionary biology [28]. Among sexually reproducing organisms, genetic recombination continually breaks down associations between genes, so that genes that are mutually incompatible, even if harmless in themselves, are unlikely to persist within a sexual population. Consequently, through recombination, a high degree of self-compatibility is thought to be maintained within sexual populations. Speciation requires that this homogenizing force of gene flow be overcome. Gene flow can be restricted either by the spatial environment or by genetic changes; genetic changes are almost always required at some point (except possibly in the case of *Wolbachia* bacterial infection [34]). However, the importance of spatial isolation has been disputed throughout the history of speciation theory.

3.1 Isolation in Space

Geographic isolation (allopatry) can cause genetic divergence, because genes that could become incompatible together can evolve freely in separated populations [28]. Provided spatial separation continues for a sufficient number of generations, genetic drift and possibly founder effects and natural selection acting on the separated populations inevitably lead to the evolution of such incompatibilities between the two popu-

lations [35-36]. The evolution of co-adapted gene complexes through natural selection occurs separately within each population. Mate choice systems may also diverge when populations are spatially separated, such that hybridization does not occur when contact between populations is resumed. Eventually, the populations reach a point where successful interbreeding no longer occurs when they are once again in contact; mating between members of different populations may not occur, or hybrids may be ecologically or behaviorally impaired, inviable, or sterile. This process is referred to as allopatric speciation [28].

The converse possibility is sympatric speciation, in which reproductive isolation evolves within populations sharing a single habitat area [28]. Speciation without spatial separation remains controversial because no single, widespread mechanism opposes the homogenizing force of genetic recombination. However, recent theoretical work, as well as evidence from a variety of natural populations, shows that speciation without spatial isolation can and almost certainly does occur, albeit under relatively restrictive conditions [37].

In most cases that have been studied, it appears that spatial isolation is neither absolute nor insignificant [38-39]. Rather, genetic discontinuities occur within continuous populations where gene flow is restricted. In general, it is unclear whether hybridizing populations were previously completely geographically isolated, but have resumed contact before the evolution of complete reproductive isolation, or have always been in limited contact, as the geographic patterns produced by the two histories are usually indistinguishable [38]. Gene flow can be restricted geographically by a partial barrier, such as a mountain range that crosses a large proportion of the species range, a channel between a continent and an island, an area of sub-optimal habitat, or an ecotone with a strong selection gradient.

3.2 Isolation Without Space

There are, in addition to geographic barriers, potential barriers to gene flow that do not require any population-level geographic separation. These factors increase the probability of a member of a particular population mating with a member of its own population rather than another population. Positive assortative mating, the tendency for like to mate with like, is commonly observed and can be caused by a variety of factors such as:

- sexual competition: for example among calanoid copepods larger males are more successful in competing for access to preferred larger females;
- temporal differentiation, such as differentiation of flowering times in plants [40], or daily cycles of pheromone release in aphids [41];
- microhabitat differentiation, for example in pea aphids that prefer different feeding substrates, and tend to mate where they feed [42];
- learned social preferences. Zebrafish prefer shoaling partners whose pigmentation matches that of their early experience and tend to mate with their shoaling partners [43]. Similarly vocalizations used by both male and female crows are thought to contribute to assortative mating through homotypic flocking [44];
- sexual imprinting, where offspring learn mating preferences and displays from their parents [45].

Such limitations on gene flow are likely to occur in a wide range of populations. However, they seem, in themselves, unlikely to be sufficient to lead to speciation by drift alone. There are theoretical arguments [46] that gene flow must be extremely low in order for incipient species to persist. Two selective mechanisms can lead to strong genetic divergence in populations with little or no spatial isolation. These are disruptive ecological selection and sexual selection.

3.3 Ecological Speciation

Ecological speciation, which proposes that speciation results from disruptive natural selection, is generally accepted despite a lack of strong empirical data distinguishing between ecological and non-selection-based mechanisms of speciation [37, 47]. The reason for this acceptance is that models suggest that ecological speciation is highly likely and will occur very rapidly under very general conditions even in sympatry [39,48-50], provided it is combined with sexual selection (see below). In contrast, speciation by drift is expected to be slow even in optimum conditions and likely to be prevented altogether in spatially connected populations because it requires that two incompatible alleles be simultaneously present, but not ubiquitous in populations [39,51]. Because the average time between the origin and extinction or fixation of neutral incompatibility-causing alleles is likely to be orders of magnitude smaller than the mutation rate, simultaneous coexistence of such alleles is thought to be relatively unlikely [39]. However, inclusion of a spatial dimension in modeling may considerably modify this prediction because it can result in the indefinite persistence of neutral genetic variation.

3.4 Isolation by Sexual Selection

The possibility of speciation by sexual selection was first considered by Fisher in 1930 [52]. Sexual selection was first proposed by Darwin in 1871 as an explanation for conspicuous sexual advertisements by male animals, such as peacock tails [53]. If, by chance, a proportion of a population happens to prefer a certain arbitrary trait for mating, then individuals possessing that trait will be chosen as mates more often, and consequently produce more offspring, than individuals who lack the trait. Moreover, these offspring will have a high probability of inheriting not only the trait, but the preference as well. Thus both the preference and the trait automatically become adaptive and associated with one another. In this way an initially arbitrary mating preference can generate rapid positive feedback between selection on traits and selection on mating preferences. This positive feedback process is potentially a cause of rapid and powerful evolutionary change (termed “runaway sexual selection”) [52]. From a complex systems perspective, sexual selection is self-organizing within a population through the non-linearity of the selective process.

If sexual selection can lead to mating preferences and traits diverging between populations, then speciation might be self-organizing. This is an idea many researchers find appealing. In addition to sexual selection speciation models that assume populations have limited spatial interactions [54-55], several recent models have developed the concept of speciation by sexual selection without spatial isolation. However, there are strong constraints on the generality of this idea [56-58] and field evi-

dence is ambiguous [59]. The view that runaway sexual selection contributes to speciation events that also involve other forms of genetic divergence is less controversial [60]. In this model, speciation is initiated by ecological divergence or drift in geographic isolation, but selection against hybridization initiates runaway sexual selection for divergent mate choice systems when the populations are in contact.

A much-debated question, whose resolution is required as part of a general theory of speciation involving sexual selection, is how preferences can be maintained in the face of realistic costs to mate choice, a problem termed the “paradox of the lek”. As sexual selection proceeds, variation in display traits disappears, and positive selection for preferences consequently ceases. One model shows that costly preferences can be maintained when display traits are costly also and dependent on many loci [62]. In addition, it has been found that costly mating preferences and varying displays and preferences were usually maintained in a spatially explicit model provided the optimum male phenotype varied between localities [63].

Despite this theoretical problem, the evidence that sexual selection contributes greatly to speciation is unambiguous. In areas where populations hybridize, the parental populations retain a separate genetic identity only when different mate choice systems have evolved [64]. Species that share the same environment tend to discriminate more strongly against potential mates belonging to the other species than do species that live in different environments [65]. Indeed, some reviewers argue that divergence of mate choice systems is virtually essential for speciation [66].

3.5 Summary of Speciation Theory

Modes of speciation can be broadly classified in two ways.

1. By the spatial arrangement and consequent level of interaction of speciating populations. This includes:
 - Allopatric (no interaction);
 - Parapatric (interaction across a linear interface);
 - Sympatric (populations interact without geographic restriction).
2. By the mechanism driving speciation. Mechanisms include
 - Genetic drift (includes founder and chromosomal speciation, and speciation by chance accumulation of genetic incompatibilities);
 - Sexual selection (termed reinforcement when combined with another mechanism);
 - Disruptive natural selection on ecological traits (with or without a spatially varying component);
 - Disruptive natural selection acting on mate choice system traits. This scenario can simplify the evolution of prezygotic isolation.

Any of the above mechanisms can in principle be combined with any spatial arrangement. More than one mechanism may operate in the same speciation event, and spatial arrangements may change over time [38]. This makes empirical testing of models difficult. Most models agree that speciation should be most likely in populations with greater spatial separation (but see [56, 67]), and where there is natural and/or sexual selection rather than drift alone. In addition, empirical evidence strongly suggests that sexual selection is usually important, if not essential, for speciation [64-66].

4 What Can Speciation Teach Us About Module Formation?

Several of the findings discussed above have more general implications for the study of modularity in natural and artificial systems.

- Modularity has important consequences. I have tried to show how the question of whether species are modules, and of what systems, is central to a major dichotomy in current evolutionary and ecological thinking.
- Modules arise in genetic systems mainly through selection pressure, not through passive drift. This selection can be generated either internally (through sexual selection) or externally (through disruptive selection in the environment).
- Sexual selection is more powerful than natural selection in inducing modularity.
- Inclusion of spatial dimensions greatly facilitates evolution of modularity. Under most conditions, populations that are not distributed in some form of spatial environment will not form discrete modules.
- The absence of ecological competition is not always a good thing for module formation. In fact, if diverging populations are not permitted to evolve separate mate choice, ecological competition between them enhances their persistence by preventing spatial coexistence (Sadedin, in prep.).

4.1 Applications

A much-studied problem in the use of evolutionary algorithms is how to maintain variation in evolving solution populations to widely explore solution space and avoid convergence on local optima, while also allowing rapid adaptation [68-69]. Incorporating sexual selection and spatial dimensions in evolutionary algorithms may help in balancing these needs, permitting different solutions to take different evolutionary paths in problem-solving within the same domain.

Researchers in artificial life have sought to evolve ecologies that share the diversity of coexisting genetic modules seen in real biological systems. A common mistake in artificial life has been to assume that coexistence of different genetic modules will occur if separate ecological niches are created, that is, niche differentiation is a sufficient condition for speciation [70-72]. In fact, genetic recombination will tend to eliminate one evolving module unless spatial geometry and/or sexual selection are incorporated [54-58].

Conversely, it has often been assumed that separate niches, or separate adaptive peaks, are necessary for the evolution of differentiated modules [73-75]. This is not so. Diversification is entirely possible in connected spatial environments without separate ecological niches; indeed, separate niches may inhibit evolutionary diversification unless sexual selection is included [76-78].

In this paper I have considered the origin of modularity in biological genetic systems. It is possible, however, that other modular evolving systems have similar dynamics. One application may be in the self-segregation of human cultural groups.

Within cultural groups, ideas, attitudes and beliefs are exchanged and evolve over time. Incompatible views are often eliminated due to cognitive dissonance. Exchange of views between cultural groups is relatively restricted. Thus in an extreme form,

cultures may form social modules. The exchange of ideas within, but not between, cultural groups may be analogous to the exchange of genes within, but not between, species [32]. If so, then speciation research may help us to understand the dynamics of social conflict and cultural diversity.

Very high social connectivity (i.e., high levels of communication) might prevent the evolution of co-adapted sets of ideas forming discrete social modules. This could reduce the global exploration of parameter space by human thought, thereby hindering human creativity. On the other hand, a lack of connectivity may lead to incompatibilities which manifest themselves as hostilities. The effects of this idea for technological innovation have been explored by [4].

Spatial isolation is clearly a factor in cultural diversification and module formation. Human social networks often display small-world dynamics, meaning that the connection distance between individuals is much smaller than geometric measures would suggest [79]. Although small-world dynamics often facilitate clustering, they also enhance information transmission [12-13, 80-81]. Small-world dynamics may therefore mitigate against formation of social modules, especially in modern societies with electronic communication.

A form of sexual selection may also operate within cultural modules, and enhance their isolation. This could occur through the promotion of signals of cultural allegiance. For example, a symbol of religious adherence is likely to be associated with a preferential receptivity to ideas originating in the same religious group. This could lead to the evolution of isolated subcultures even within highly socially connected environments. Manipulation of the evolution of such allegiance signals, and of dimensions of spatial isolation, may be an effective way to regulate cultural modularity.

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