Points to discuss:
  Why do we need a unified account?
  How do we apply a unified account?
  What advantage is the dynamical view?
  What about species pluralism?
ABSTRACT

A Unified Approach to Species
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There are a number of different species concepts currently in use. The variety results from differing desiderata and practices of taxonomists, ecologists and evolutionary theorists. Recently, arguments have been presented for pluralism about species. I believe this is unsatisfactory, however, because of the central role of species in biological theory. Taking the line that species are individuals, I ask what might individuate them. In other work I have argued that dynamical systems are individuated by their cohesion. I present here a version of a cohesion concept of species that accounts for the advantages of other species concepts, and is open-ended enough to accommodate additions to or changes in biological theory. On my account biological forces combine like Newtonian forces, to work on a common locus. Just as we might have an electromagnetic system, we might have an ecological species, if the dominant source of cohesion is ecology, but there is no certainty that biological species will divide up into elegant single principle types anymore than there is for physical systems.
1. Introduction

The "species problem" is the question of how to form species concepts that are useful to biologists and that also reflect the natural order. The problem is generated by different desiderata for species according to the roles that they play in biological theories and practices. The main division is between the requirements of taxonomy and those of evolutionary theory. Secondary splits arise within taxonomy from requirements of simplicity and convenience of classification on the one hand and naturalness of classifications on the other, while differing emphases on genetic versus ecological factors in evolutionary theory lead to splits there. The approach I propose here can partly satisfy these different desiderata in a way that is motivated by the underlying processes that form and maintain species. It cannot fully satisfy all desiderata, because these processes do not necessarily result in the neat, well-behaved species that taxonomy, ecology and evolutionary theory tend to presume. It can, however, explain such failures in a uniform way, and can even predict them, if enough is known.

Taxonomy tries to produce classifications that let each organism be identified within a hierarchy of increasing specification (a specification hierarchy, after Salthe 1993) in order to easily catalogue and compare organisms. Species are one of the lower taxonomic units in this hierarchy, and hold the special place of representing the minimal naturally distinct divisions. Lower units are considered varieties, whereas organisms that transgress species boundaries are generally hybrids. Within taxonomy there is a tension between finding a well behaved hierarchical classification and finding one that corresponds to natural distinctions. At least part of this tension results from differences about what makes a distinction natural, but the tendency of nature not to fit our preconceptions of orderliness is also a problem. Species are also part of the theoretical apparatus of evolutionary theory, which tries to explain their origin and history, at least in general terms. Any evolutionary account of species will need to consider both the genealogical and ecological forces that shape and distinguish them (Wiley 1978). The constraints placed by these various desiderata are not easy to satisfy.

My proposal is an extension of Michael Ghiselin's radical solution to the species problem (Ghiselin 1974). It has its roots in the evolutionary species concept proposed by Simpson (1961), later taken up by Wiley (1978, 1980, 1981), who augmented it with his conception of cohesion (which plays a significant role in Wiley and Brooks 1982, and an even more central role in Brooks and Wiley 1988). Cohesion was later seen as definitive of species by Templeton (1989). My approach differs from Templeton's, in that while he sees his approach as a replacement of prior species concepts, borrowing some of their advantages, my approach treats competing species concepts as representing legitimate aspects of what composes a species. Rather than trying to choose among competing concepts, I synthesise them in a way that is extendable. The basic idea is that species are historically and spatially distributed dynamical systems, individuated by dynamical properties including both their internal and external interactions. All complex dynamical systems are individuated by their cohesion (Collier and Hooker 1998), and species are no exception.
Although my position is not pluralistic (for examples of fully pluralistic approaches, see Mishler and Donoghue 1982, and Ereshefsky 1992), since it presumes a unified species concept, it is pluralistic in the sense that it assumes the validity of the intuitions behind the current competing species concepts. In some respects my position resembles that of Philip Kitcher (1984). My main disagreement is that I do not think that species can be reduced to *sets* or any other sort of logical construction (at the least, either move would be a category error, confusing a formal abstract entity with a concrete particular). To extent that species exist naturally, they have independence from any categories we may apply to them. I accept the Hull (Ghiselin 1974, 1987, Hull 1976, 1978, 1980) thesis that species (inasmuch as they exist) are historical individuals, and not sets, though they are that too, rather trivially. My approach should support the slowly maturing program for the unification of biology started by Brooks and Wiley (1982, 1986, 1988, Van der Vijver et al 1998, and Collier and Siegel-Causey 1998) in terms of complex self-organising systems. It has the additional advantage that it can accommodate new ways of distinguishing species; though as will become clear, there are limits to potential candidates.

2. *Individuation of complex dynamical systems* In order for the concept of species to be scientifically useful, organisms must form recognisable groupings that are not completely arbitrary, or nominal. For example, it would not do to classify organisms according to their order of discovery, even by location, however useful this means of classification might be to the field worker. *Any* classification must organise biota according to properties that members of the same class have in common. A *natural* classification may use either intrinsic qualities or relations, but the properties used must be independent of the classifier. Species classifications must be natural, since species play a central role in the naturalistic theory of evolution. If we presume the cogency of classification into species, then, there will be recognisable natural properties that are shared by members of the same species. We can conclude, then, that if it is possible to classify organisms by species, organisms must fall into natural groupings, and it must be possible to classify according to patterns of natural properties. Whatever these properties are, they must be in some sense causal, or else they are of little use for explanation of the role of species in the evolutionary process.

There are three ways that have been recognised in the literature on explanation (following Salmon 1984) to explain natural unity. These are:

1) essential properties (natural kinds, archetypes)
2) stable properties (resistance to internal or external perturbations)
3) cohesion (causal relations that make physical wholes out of parts)

Essential properties (often but not necessarily associated with idea of *natural kinds*) produce good classifications if there are a relatively small number of ways in which different fundamental processes can interact to form stable configurations, it is possible to catalogue those configurations, and to classify things according to which configuration they take. It may be possible to produce higher order classifications if there are relatively few ways that the various configurations can combine to form more complex configurations. An example would be the physical elements and their chemical properties, which combine to form chemical compounds. Biological taxa are not like this. The number of possible biological configurations is immense, and only a few of these actually occur. In higher taxa, for example plants and animals, classification by natural kinds may be more useful, because the possibilities are more limited. Even here, though, for any list of typical properties of plants
and animals, there will be members of some other class that have most of those properties. In fact all leading current approaches to species guarantee this. Biological taxa, at least at the lower levels, and arguably at the highest levels, are not natural kinds in any interesting sense.

Stable properties across a group of organisms alone are not sufficient for biological classification, since the similarities can be coincidental. Some classifications might be preferable because they are more stable than others, but there is no guarantee that there is a unique most stable classification. Stable classifications are objective in the sense that they represent non-subjective similarities, but are not objective in the sense that they must be unique. They provide interesting regularities to be explained, but do not require a non-accidental explanation. Purely numerical methods can at best produce stable classifications. These classifications can provide interesting evidence for biological theory to explain, but we are just lucky if stability alone produces a unique classification.

We can take the stability approach somewhat further by testing for species unity by testing the stability of species themselves, either by experiment or observation. The basic notion of stability in a complex dynamical system is resistance to perturbation, internal or external (Christensen et al, in preparation). Intuitively, a system in some state is stable if small perturbations to its conditions eventually die out and the system returns to (sufficiently near) its original state. That is, stability concerns how constrained the dynamical behaviour of systems is under perturbation, whether these perturbations originate internally within the system or externally to it. We might find, for example, that some species have little or no stability: they mix without constraint when put together, and form and disrupt independently of ecology. Alternatively, we may find that there apparent species stability is merely an epiphenomenon of underlying organism dynamics, and that testing shows that changing organism dynamics alone (say, putting animals in zoos) changes their species membership, or makes it irrelevant. There is ample evidence against this possibility, but any adequate species concept should allow the possibility that there are really no such things as species, anymore than there are stellar constellations.

Stability is a complex multidimensional dynamical concept, specified relative to the tolerances and the time scale chosen. For example, human skin is stable against small blunt pushes, but tears once the magnitude is sufficiently increased and cuts quickly once the pushing instrument is sufficiently sharp. The central organs of the body are normally remarkably stable over timescales of a year, but certainly not over a timescale of a century. Their functional stability is also a highly sensitive function of the kind of perturbation applied, e.g. being stable against relatively high values of overeating but unstable against relatively small applications of poisons or specific kinds of abnormal cells. The multidimensional concept of stability must therefore be carefully specified so that it picks out all of the relevant dynamics of the systems involved.

Nonetheless, the concept of stability per se does not have the right logical form for individuation, nor does it tell us anything but the consequences of some process or processes; it does not tell us how a stability was achieved or why the system has the kind of stability it has. A gas in a rigid container is stable against adiabatic perturbation, but largely because of the container, rather than gas internal organisation. The stability of human skin against a small blunt push, though the molecular biochemistry may be complex, is essentially accounted for in terms of an elastic restoring force, so that during the whole process neither
the structure nor the function of the skin essentially alters. The stability of human psychological functions under neuronal damage suffered near birth, on the other hand, represents a complex regulatory structural and functional change of a marvellous kind which permits other areas of the brain to take over functions which the damaged areas can no longer perform.

A rock is relatively stable because the formation of its structures is so energetically favoured, i.e. its molecular bonds correspond to relatively deep energy wells so that it requires a substantial perturbation energy to break them. For this very reason, however, rocks show little or no plasticity, adaptiveness or resilience. Species, on the other hand, can be quite robust, even though they have relatively weak energetic stability, and can change, adapt and resist both external and internal perturbations (up to a point).

Systems are collections of dynamically related elements of some kind (organisms, in the case of species). To individuate dynamical systems we need to specify the dynamical relations between components of a system that make them components of the same system, and distinguish them from other systems and components of other systems (cf. organs vis-a-vis component cells and super-system bodies). There are two aspects to this that need to be kept in balance: An individual is something more than merely a stable pattern, but neither are all individuals closed, statically stable systems. The first aspect requires providing a sense of belonging together, an interactive ‘gluing’ that binds a system together as an integral unity, while the second aspect requires a sense of interactive organisation that allows systems to be open and adaptive, exchanging energy and materials with their environments and being altered by those interactions, yet remaining an individual system. We need a suitable dynamical unity relation (Perry, 1970) $U$ such that $a U a_j$ implies that $a_i$ and $a_j$ are both dynamical components of $S$ but, unlike simple part/whole specifications, we require a specification of $U$ that has both dynamical and organisational aspects. Like the purely logical relation of identity, the unity relation is an equivalence relation, but unlike identity, it relates different entities (the system components), and its specific nature depends on the kind of dynamical object it unites.

Although stability (resistance to perturbations) of some kind is necessary for system integrity, stability is not a unity relation, because it is a property of the whole system, not a relation among dynamical components of a system. The dynamical unity relation formed from the closure of these relations is called cohesion (Collier 1988). The cohesion of a crystal is the collection of all the inter-atomic bonds that bind crystal atoms to one another in the rigid but brittle crystal lattice formation, that of rubber all the inter-molecular bonds that hold the rubber molecules together yet allow it to stretch and twist, while the cohesion of a living cell is the collection of all the complex inter-molecular relations which together maintain cellular biochemical processes and structures, and that of a flock of birds is the complex set of sensory signals relating avian bodies that maintains a dynamical unity to the flock during its manoeuvres.

The essential idea of cohesion is that of an emergent system property (see Collier 1988, Collier and Muller in preparation) that is insensitive to relevant local variations in the system components, including in those non-linear interactions that formed it. Consider, e.g. the property of lift for a kite flying in the wind. The lift of the kite is the net effect of the impulses of molecules hitting the kite on its two sides, averaged by the cohesive forces that hold the kite together. It is the averaging process, physically embodied in the interaction of
the cohesive kite and the individual air molecules, that produces the lift, which can be felt as tension on the kite line. The specific thermal motions of the molecules making up the kite do not appear at the level of the kite structure as motion but only as heat in a stable macro object because they are dissipated, ‘averaged out’, by the cohesive molecular structure of the kite. Similarly, the specific motions of the individual air molecules are not relevant to the net effect of lift, only their average is. The kite is insensitive to both kinds of individual molecular motions, except to separate them into heat and lift, because of its cohesion. If the cohesion of the kite is disrupted, say by being ripped, the averaging is severely reduced and lift largely disappears. The cohesion of the kite is essential to the existence of its lift. In this case cohesion is clearly dynamical but also captures the relevant organisational feature of the kite. Its role here is indicative of the centrality of cohesion to virtually all important dynamical system properties (in fact to all but the simple linearly additive properties, like total rest mass). The cohesion of species should explain their stability in the face of changing organisms, ecological conditions, behavioural patterns and other traits, but should also explain why this stability fails when speciation occurs.

Because of the power of the cohesion concept for analysing dynamical system properties, it provides the right tool for understanding system identity and individuation in general. It provides a dynamically grounded unity relation which has the same kind of multi-dimensionality as has stability. But while stability of some kind is necessary to system identity, it is cohesion that is needed to identify the dynamical relations involved. The stability of the gas in a rigid container is due to the cohesion of the container, not of the gas, that of the rock and of the skin against blunt pressure is due to local molecular cohesion (hence whole-system passivity) while that of intelligent functioning is a global organisational property of all the interacting system components (hence whole-system active). Now consider a liquid filled balloon, distorting irregularly as the liquid moves about, and expanding as it rises into the atmosphere; it is the molecular cohesion of the balloon that provides this system with its continuing identity even though it will never repeat its shape or internal liquid state, so none of these properties are stable. Instead, there is a complex, very general molecular connectivity property which is stable, but it requires analysis of the balloon cohesion to identify it. Thus it is cohesion, rather than stability per se, which provides the right dynamical approach to system individuation. Similarly, species might be extremely variable and flexible, held together by a complex dynamics. System cohesiveness also thereby grounds a distinction between essential and accidental system properties; the essential properties, those that constitute the identity conditions for the system, being those that provide the full complement of cohesion relations constituting the stable unity relation required for that kind of system.

Like stability, cohesion is not only multi-dimensional but also a matter of degree. Many different dynamical variables can be involved in cohesive relations, and these relations can be stronger or weaker. Even the cohesion of two clay pots of identical properties in all respects except that one is merely dried and the other kiln fired are radically different in strength, let alone the differences between cells and computers. This complicates the cohesion criterion for individuation because relative strengths as well as kinds of cohesion must be taken into consideration. This is not a disadvantage, however much it is an inconvenience, because it forces a more realistic analysis of individuation. In the case of species, relative cohesion along only one dimension can easily lead to misclassification. We need to look at the complete closure of cohesion, which may involve a number of separate, perhaps interacting factors.
Taking into consideration the kinds and strengths of cohesion in a system, we can construct a *cohesion profile* for the system. This will assign a strength of cohesion to each dimension of system cohesion for each state of the system. We can then (partially) compare the relative cohesion of systems in the usual variety of ways. Here is the simplest (and crudest): average the cohesion strength over the dimensions of cohesion for a given system state and then over system states, weighted by their probability of occurrence, doing this first for the internal dynamical interactions of the system and then for its interactions with the system’s supersystem. If the former is significantly greater than the latter, the system is distinct from its supersystem, and from other subsystems of the supersystem. The significance condition is somewhat worrisome, since it is not an all-or-nothing affair, however much we might prefer absolute criteria for individuating distinct systems. But it is also not how things are empirically; with respect to the accidental/essential distinction, e.g. accidental properties may or may not be able to be changed in practice (a leopard can change the positions of its legs but not those of its spots, though both are accidental properties) and while having a heart is essential to the leopard, though its particular size is not, it is much closer to essential that, given the leopard’s activities, its heart is the size it is. Getting individuation right is actually a matter of entering all the cohesion relations, in their proper degrees or strengths, that constitute the unity relation for that kind of thing. With respect to individuation within an encompassing environment, if there is only a very small difference between a system’s internal and external cohesion strengths, we might well be reluctant to distinguish the system from its environing supersystem. This might occur, for example, when there is a question of whether a population is a subspecies or a separate species. Fortunately, there are good reasons, to think that the processes underlying speciation ensure significant differences in the weighted average cohesion strengths of external and internal interactions, so that species are usually well individuated.

Cohesion is always a dynamical matter, though we often identify and summarise a complex, typically largely unknown, cohesive dynamical process in other functional terms (Collier 1988, cf. Hooker 1981). Consider a flock of birds. Unlike a simple collection of objects, a flock is a dynamic system that remains cohesive long enough to have dynamical consequences. Clearly, a flock is not distinct because of deep energy wells, nonetheless, flocks are fairly robust, wheeling and turning together in such a way that potential disruptions, such as avoiding intervening bodies in the flight path, reveal the cohesiveness of the flock. If we try to explain the cohesiveness of a flock in terms of whole-flock functions, we can go only so far. Plausible functional explanations of flocks include protection from predators and reduction of the effort required for flight in individual birds. Although these explanations can account for why we observe flocks if flocks are dynamically possible, they do not explain why flocks are dynamically possible. Thus functional explanations of flocks are inevitably incomplete. The immediate explanation of flock cohesion is to be found in the connections between observations by birds of their near neighbours in the flock and their control of their own motion. (The latter may be according to relatively simple rules about how far to stay from neighbours.) This explanation of flock cohesion, however, cannot explain why birds follow these rules and hence cannot explain the appearance and persistence of flocking. This latter explanation will invoke function in a standard way through the theory of natural selection: birds that don’t have flocking ability simply don’t survive as well as birds that do, but both types of birds are likely to appear because of evolutionary dynamics, so we find flocking. As the last phrase indicates, it is the specific dynamical processes of production of natural variation in flocking tendency, selective elimination of less-flocking
types by acts of predation or starvation, and the differential reproduction of variants, not their functional characterisation in gene frequencies, that grounds the evolutionary explanation. Particular flocks, then, persist because of their internal cohesion, but flocking persists because of the cohesion on bird lineages imposed by natural selection. Unless sufficient care is taken about the cohesive closure, it is all too easy to confuse explanations of the persistence of individual flocks with explanations of the persistence of flocking behaviour. This all applies, mutatis mutandis, to species. To understand species, we must both understand the existence and survival of particular species, as well as their origin. The explanations need not be the same, but they should have some dynamical connection.

Rather than beating around the bush, looking for some common characteristics in current species concepts, I will present my hypothesis directly. Modern biologists recognise that there are natural divisions of biota into distinct groups. These groups are not always as distinct as we might like for the purposes of neat classification. Various considerations pull systematists in different directions. What I propose is that the various species concepts are analogous to the different causes in physics before the Scientific Revolution. Just as Newtonian mechanics unifies causes under the concept of force, while allowing for different forces that act on a common object, the unity of species (to the extent it occurs) is the net effect of biological forces. In order for this idea to work, there must be some common locus of action of these forces. On current neo-Darwinist theory this locus is the genetic makeup of the species, or rather in the pool of genes represented by its individuals. I will expand on this in what follows.

This doesn't tell us, however, which properties to use for classification. The simplest way to go is to assume that all observable traits are equally relevant, and to classify according to overall similarity of observable traits. To achieve some objectivity, it is helpful (but not strictly necessary) to numerically quantify the properties, and locate each organism in a trait space according to the numerical value of each of its traits. We then determine species by identifying via statistical methods which organisms fit best into clusters of similarity. This is the method proposed by numerical taxonomists, or pheneticists (Sokal and Sneath, 1963). According to Sokal, species are:

... dense regions in a hyperdimensional environmental space.

I won't go into the problems with this method in detail, because they will be familiar in general to philosophers, and they have been dealt with for the particular case of taxonomy by Mark Ridley (1986). Ridley pointed out that there is no unique best way to quantify properties, and even if there were, there are various cluster statistics that can give different results. Furthermore, the addition of more data can lead to arbitrarily radical re-classifications. Lastly, there are so many phenotypic properties that can be chosen that systematists are likely to choose for examination those that they expect, for whatever reasons, to give correct classifications, for example, the sexual organs of plants. A completely unbiased technique would choose the traits to examine at random. No systematist would do this. So much for the objectivity of numerical techniques.
The advantages of cohesion:
1. Pattern without process underdetermines classification. Cohesion permits various (in principle) ways to test proposed classifications.
2. Cohesion explains stability, since the properties underlying cohesion will be stable as long as the cohesive entity persists (because, by definition, cohesion is required for the identity, and hence, continued existence of the entity).
3. Cohesion is essential to the identity of the cohesive entity (by definition), so the properties that make up the cohesion of an entity are essential to its identity. Despite this, the particular components of the cohesion of a species are arbitrary.
4. Cohesion explains why sexual species are better defined than clonal species. It also explains some difficulties (e.g. hybridisation).
5. Because cohesion is a causal process, classifications based on cohesion are more useful for fitting into natural laws, including evolutionary theory.
6. Because cohesion is causal, classifications based on cohesion can be useful for manipulating (controlling) evolutionary processes.

The main problem with cohesion as a criterion for individuality is that causal processes are not directly observable. Sokal's criticisms of the biological species concept raises this objection specifically (Sokal and Crovello, 1970). On the other hand, strictly empirical predicates are rare in advanced theories, so Sokal's demand may be out of place. Given the problems with finding a unique best cluster pattern, along with the advantages of unifying the notions of species in evolutionary theory and taxonomy, sacrificing some observability is probably the best move. The question becomes, how much should we sacrifice?

The approach which sacrifices the least is due to Kluge (1970). He suggests that all we need to take into consideration is that organisms come in lineages, and that species are historical entities. Certainly this gives us more data to constrain similarity clusters (they must remain clustered through time), but it is unclear that the additional data will resolve the problems raised by Ridley. A further assumption from evolutionary theory is that the clusters must originate by fission (descent with modification). This is the only assumption consciously used by the pattern cladists. Ridley argued that the same problems of underdetermination will arise even in this case. It is fairly obvious that no finite set of additional assumptions is guaranteed to eliminate the problem of underdetermination. Acknowledging this, we should allow an open-ended admission of processes, as long as they can be supported by evolutionary theory or by independent test, or preferably both.

There are three promising candidates in the literature for process based species concepts. First, because of its eminence and longevity, is the biological species concept, associated most closely with Ernst Mayr (1969, 1970). This concept applies most easily to sexually reproducing species, but it can be adapted to clonal species as well. In brief it goes as follows:

Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.
Perhaps this notion would be better called the reproductive isolation species concept. It is a relational species concept, because what is important are the reproductive relations between members of different species, or more accurately, their lack of reproductive relations. Speciation, on this account, results from isolation mechanisms. The connection to evolutionary theory is straight-forward. Species are held together and differentiated from other species by gene flow, but the exact amount of gene flow possible between related but different species is not specified. This species concept entails that speciation is by reproductive isolation.

Paterson (1985) has criticised Mayr's concept because it focuses on a negative property that cannot be easily observed. He suggests what he calls the recognition concept of species, according to which the cues that allow members of a species to be mutually fertile are definitive of the species. His definition is as follows:

We can, therefore, regard as a species that most inclusive population of individual biparental organisms that share a common fertilisation system. How much this differs from Mayr's concept is a matter of interpretation, but is simplest to say that it is a version of the biological species concept that focuses on one particular mechanism for restriction of gene flow. This interpretation of the recognition species concept follows from the assumption that sharing a common fertilisation system is the only way to transmit genes. This is a reasonable assumption for sexual organisms. The recognition species concept is therefore logically a restriction on the biological species concept, and shares most of the same advantages and disadvantages. What matters in both cases is gene flow, or, rather, potential gene flow. The recognition concept, however, is explicitly restricted to sexually reproducing organisms, since the cohesion mechanism itself, not just what it relates, as in the biological species concept, requires sexual reproduction.

Sokal and Crovello (1970) criticised the biological species concept on the basis that determinations of gene flow are made largely on phenetic grounds, so the concept is not superior to the phenetic concept of species. Their argument fails, though, since the biological species concept does not imply that all traits are equally important for classification: those that are directly involved in gene flow take precedence. The fact that phenetic evidence is used to infer species boundaries doesn't imply that species can be defined purely phenetically. Use of the biological species concept constrains the evaluation of phenetic evidence, but its classifications are not implied by phenetic evidence alone.

Ehrlich and Raven (1969) point out some more serious problems with the biological species concept. First, as Sokal also argued, the concept is restricted to sexually reproducing species, but non-sexual organisms also can be classified into species. This suggests that isolating mechanisms are not the only ones that are relevant to the determination of species. The biological species concept can be modified to take this problem into consideration by considering trans-temporal, diachronic, or vertical gene flow, which can be diminished by mutations and selection processes (leading to differing Waddingtonian canalisations). Restrictions on vertical gene flow could also account for some differentiation between sexually reproducing species. This move is not open to the recognition species concept, because of its explicit invocation of fertilisation systems. Even for the broader biological species concept, however, the move is somewhat ad hoc.

Second, Ehrlich and Raven point out that many populations remain parts of the same species although the populations have been isolated for many years, even millions of years.
Many species have sub-populations between which there is only minimal gene flow. Therefore, they argue, the absence of gene flow is not a good indicator of different species. They also demonstrate that, in many cases at least, the effects of selection dominate those of horizontal gene flow. Similar amounts of gene flow can, depending on the pressures of selection, lead to speciation or not. To some extent, their arguments can be met by noting that they consider only synchronous, or horizontal gene flow, and that vertical gene flow needs to be considered as well. On the other hand, as they point out, selection is a major force guiding vertical gene flow, so it is unreasonable to attribute the cause of species cohesion to gene flow rather than selective forces.

Considerations like these have led to the ecological species concept that is associated primarily with Van Valen (1976), though it is clearly present in Ehrlich and Raven. It is especially useful for plants, but has applications to animals as well when there are gradations of forms across different environments. The essence of this concept is that gene flow is not the major factor in the distinguishing of species, but that ecological factors contain and distinguish divergent species. Van Valen's main example is the North American oaks (Quercus). In my own experience, I was genuinely surprised that Californians identified certain trees as oaks that bore no resemblance (barring acorns) to the oaks I had grown up with in Eastern Canada. My trips across the continent by car, however, convinced me that the trees did indeed intermingle, and they do hybridise. There is a more or less continuous gradation of phenotypes from one coast to the other, and similar gradations exist within one region from one environment to another.

Simpson (1961) anticipated the difficulties presented by interbreeding species in his criticisms of Mayr's biological species concept, but proposed the evolutionary species concept, which relies on vertical gene flow. Van Valen rejects gene flow as a determinant of species in favour of "adaptive zones." Species are distinct according to their adaptive zone. This idea is directly applicable to animal species as well as to plants. Imagine, if you will, two varieties of lizards that live in different parts of the desert, say high desert and low desert. They may interbreed when they come together, but the offspring may not be well adapted to conditions under which either normally lives, and the hybrid descendants typically die off over time because they do not do very well in either of the home ranges. Although they varieties can interbreed, making them one species by the biological concept of species, the varieties are ecologically separated.

On the ecological account, the genetic variation of a species is contained by the adaptive zone of the species, not by reproductive isolation. According to Van Valen (1976):

A species is a lineage (or closely related set of lineages) which occupies its own distinctive adaptive zone minimally different from that of any other lineage in its range, and evolves separately from all lineages outside its range.

This definition allows a certain amount of vagueness that reflects vagueness in the idea of an adaptive zone. Van Valen points out that adaptive zones can grade one into the other, unlike rooms in an apartment block, but more like living areas in an Iroquois longhouse.

A major problem with the ecological species definition, pointed out by Wiley (1978), is that different species can occupy the same ecological niche. This will be necessary if one species is to supplant another through competition, a widely supported mechanism for
evolution. Otherwise, the definition is a special case of the evolutionary species definition. The evolutionary species definition in turn is a variety of phylogenetic species concept.

The phylogenetic species concept has become increasingly popular because of its connections with evolutionary theory. It attributes species unity to a common evolutionary heritage. What matters is descent, or lineage, and divergences in lineage. The concept developed with large animals, but has also been applied to microbiota as the study of microorganisms has moved from considerations of pathogenicity (the previous basis of classification), towards concerns about physiological processes. The concept has been championed by Ed Wiley (1978, 1980, 1981) and Joel Cracraft (1983, 1987). Wiley proposed the following:

A species is a single lineage of ancestral descendent populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate. (Wiley, 1978)

On Cracraft's version the concept goes as follows:

A species is the smallest diagnostic unit including individual organisms in which there is a parental pattern of ancestry and descent. (Cracraft, 1983, 1987)

a) "smallest" (bush vs. tree)
b) "diagnosable" (no easy operational definition, since process is hidden, but requires a unique set of ancestral and derived characters)
c) reproductive cohesion (reproductive community defined by lineage)

Both definitions emphasise descent through a lineage. Cracraft's definition differs from Wiley's primarily in that it is closer to an operational definition, and he stresses this aspect in his discussion of the differences between the two definitions. He uses the notion of a diagnosable unit, where Wiley uses the notion of evolutionary tendencies and historical fate. Unless "diagnosable" is interpreted in terms of actual diagnoses of taxonomists, Cracraft's definition leaves open what makes a unit diagnosable. In a similar way, Wiley's definition leaves open what maintains the identity of a lineage, and what gives a lineage its own evolutionary tendencies and historical fate. When these are cashed out, there are some similarities with both the biological species concept and the ecological species concept, since both reproduction and ecological forces are involved in forming a diagnosable unit, or in keeping lineages separate and determining evolutionary tendencies and historical fate. Wiley (1978) points out that some degree of reproductive isolation is a corollary to his definition. The main difference in the evolutionary, or phylogenetic concept is the emphasis on vertical cohesion. Cracraft (1983) explicitly excludes reproductive disjunction (central to the biological species concept), unlike the definition of species given in (Eldridge and Cracraft, 1980), but he notes that some form of reproductive cohesion is required by his definition.

Each of these three species concepts, like the general concept of cohesion, admits of degrees: they are fuzzy concepts that allow a certain amount of arbitrariness at the edges. Each explains the stability of species in terms of evolutionary forces acting to contain the genome of species, and each identifies species in terms of cohesion that is generated by these forces. There is a direct relation in each case between the forces that form species and those that guide evolution. In each case the result will be more or less discrete phenotypic groupings that can be identified phenotypically as long as the right phenotypic traits are chosen for observation.
Van Valen (1976) suggested that ecological factors be added to resemblance and cladistics in taxonomy. This suggests that he did not see his ecological species concept as fundamentally opposed to the reproductive and phylogenetic concepts, but as complementary. Mishler and Donoghue (1982) argue for a plurality of cohesion inducing mechanisms in addition to genetic cohesion, which they attribute to Wiley and Brooks (1982) through either a misreading or overly narrow reading. The cohesion of Wiley and Brooks was not based merely in reproductive relations, but also in the forces that constrain and make possible reproductive relations. This idea was taken up by Templeton (1989), and articulated to cover a broad range of cohesion mechanisms (though, apparently, the source of the idea got lost in the process). These mechanisms break into two sorts, broadly genetic and ecological. The genetic mechanisms are further divided into mechanisms supporting genetic identity through gene flow, and isolating mechanisms that restrict gene flow, while the ecological mechanisms are divided into replaceability mechanisms that promote genetic identity through descent from a common ancestor (genetic drift) and displaceability mechanisms involving selection that either promote identity through fixation or that alter demographic exchangeability. These mechanisms can work together or in different directions, and differently in different types of organisms or at different times. Species are the net effect of these forces. According to Templeton:

... a species (is) an evolutionary lineage through the mechanisms that limit the populational boundaries for the action of such basic microevolutionary forces as gene flow, natural selection, and genetic drift.

On the cohesion concept of species, species are the net result of evolutionary forces acting on the genome. The various different forces act additively on a single locus, the genome, in much the same way that the various Newtonian forces work additively on a single locus, a particle or physical location. These forces may act together, or may act against each other. When one force dominates, it is the primary source of species identity, but generally there will be more than one source.

Following Wiley, it is possible to divide cohesion into two components: horizontal, which constrains the constituents through their current interactions, and vertical, which constrains the constituents through historical restrictions on variation. Sexual species are cohesive due to reproductive closure. Asexual species and higher taxa are cohesive due to historical constraints. Ecological forces and genetic drift are horizontal forces that constrain both sexual and asexual species. Generally cohesion is lost, producing divergence, but in principle it is possible for cohesion to be formed, producing convergence of phylogenetic lines. This possibility should be reflected in classification schemes, which may need to be reticulated rather than branching when convergence occurs. Cohesion is the natural basis for biological classification. Natural classification in biology is possible only to the extent that cohesion is strong enough to determine distinct classes. This sometimes happens, sometimes not. The cohesion basis for classification justifies using phylogeny as a taxonomic criterion, and supports cladistics at the level of species and below. For higher taxa, though, loss of cohesion can occur within the descendants of an original population, justifying some of the conclusions of evolutionary taxonomy, which would distinguish birds from dinosaurs, although they belong to the same clade. Cohesion is subject to degrees; this explains the varying applicability of classification to different biological entities. More cohesive taxa are more distinct, whereas less cohesive taxa are more questionable, and less useful.
My main argument is cautionary towards those who would wish to have a single operational definition of species, but it does not sanction pluralism in classification. Instead, I suggest that there are several factors that might equally contribute to species membership, and that the alert systematist should be aware of these various factors, rather than relying on some "tried and true" method of classification. Sometimes, the requirements of classification into species cannot be met by objective considerations, in which case some discretion by systematists is justified, but they should make clear the subjective criteria they are using, rather than trying to justify them on objective grounds. In other cases, one or another biological force will dominate, so we might want to distinguish between ecological species, recognition species, phylogenetic species, and so on, just as we distinguish between gravitational systems, electrical systems, and so on in physics. We may find other forces that lead to cohesion, and add them to the list, as long as their locus of action is on the species genome.

The cohesion concept of species can explain both why species are sometimes well-defined, and why in other cases they are not. It also permits a direct conciliation of the needs of taxonomy and evolutionary theory, though its emphasis is on the latter. Taxonomy through phenotypic comparison is possible as long as the relevant traits are used for identification. Preliminary identification of taxa without evolutionary theory is possible because there are traits that are peculiar to particular species as a result of evolutionary forces. More refined taxonomies, however, will need to take into consideration the specific evolutionary forces at work, and proposed taxonomies will need to be tested against the existence of the requisite forces. A fully refined taxonomy cannot be produced without input from evolutionary theory. Unless taxonomy and evolutionary theory are unified, we are probably doomed to a dizzying plethora of species concepts produced by differing operational criteria used by practising biologists. Avoiding this is as good a reason as any for unification.

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References


Gray, R. and P. Griffiths (unpublished) "Extended Phenotypes and Developmental Systems".


**Endnotes**

1. There are other differences as well. I will argue that Templeton’s concept is incomplete, since it is more a patchwork of mechanisms with no obvious common measure, which makes
evaluation of his approach difficult if not impossible.

2. For an extended version of a similar argument, applied to each of the leading views of species, see (LaPorte 1997).

3. These are an extension of the regularity notion, according to which natural regularities must be robust. Armstrong (1983) has expounded and criticised this view, pointing out that there may be equally justifiable but different classifications, which would admit an unacceptable element of conventionality into nature. It is important to recognise that this is an ontological issue, not an epistemological one. Omniscience would not help.

4. This sort of error might seem obvious, but it is rampant in much sociobiological literature in which individual or group behaviour is often explained in terms of ultimate evolutionary causes despite the significance of particular circumstances in determining particular behaviours (e.g. Alexander 1979, 1987; for criticism see Brady 1989, Collier 1991).

5. There have been other proposals of possible loci of action for evolutionary forces, for example Russell Gray and Paul Griffiths (unpublished) have argued the developmental systems are preferable to genes as units of selection. I don't find this proposal implausible, but if it turns out to be correct, my account can be modified accordingly.

6. Wiley (1978) argues that phenetic differences need not appear between evolutionarily distinct lineages. This is true if we restrict ourselves to qualities and ignore relational properties. Sokal and Crovello (1970) however, allow very broad properties to be phenetic. Whether these properties can be identified operationally is another question. Wiley is no doubt correct if phenetic properties must be operationally identifiable.

7. See Templeton (1989) for a list of more specifically biological advantages of using cohesion for classification. Some, but not all, of his advantages overlap the ones I list.

8. Joel has told me that diagnosability does not present special problems, but I think he is overly optimistic about the empirical skills of biologists. If Cracraft's definition is strictly operational, then it runs afoul of the problem that Wiley raised, following Hull (1971), for the phenetic definition of species, mentioned in a footnote 3 above.

9. This was suggested to me by criticisms made on an earlier version of this paper by Kim Sterelny and Mohan Matthen.