

The dimensions, modes and definitions of species and speciation

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Abstract. Speciation is an aspect of evolutionary biology that has received little philosophical attention apart from articles mainly by biologists such as Mayr (1988). The role of speciation as a *terminus a quo* for the individuality of species or in the context of punctuated equilibrium theory has been discussed, but not the nature of speciation events themselves. It is the task of this paper to attempt to bring speciation events into some kind of general scheme, based primarily upon the work of Sergey Gavrilets on adaptive landscapes, using migration rate, or gene flow, as the primary scale, and concluding that adaptive and drift explanations are complementary rather than competing. I propose a distinction between *intrinsic* and *extrinsic* selection, and the notion of *reproductive reach* and argue that speciation modes should be discriminated in terms of gene flow, the nature of selection maintaining reproductive reach, and whether the predominant cause is selective or stochastic. I also suggest that the notion of an adaptive “quasispecies” for asexual species is the primitive notion of species, and that members of reproductively coherent sexual species are additionally coadapted to their mating partners.

... evolution is a process of change or movement. Description of any movement may logically and conveniently be divided in two parts: statics, which treats of the forces producing a motion and the equilibrium of these forces, and dynamics, which deals with the motion itself and the forces producing it. Following this scheme, we shall discuss, first, the forces which may come under consideration as possible factors bringing about changes in the genetic composition of populations (evolutionary statics), and second, the interactions of these forces in race and species formation and disintegration (evolutionary dynamics).

(Dobzhansky 1937)

Introduction

Speciation is usually presented in terms of a number of antinomies, such as adaptation versus drift, or geographical terms of the speciating populations, or in terms of “active” versus “passive” speciation. In this paper, I will attempt to show that these contrasts are unable to differentiate the various kinds (“modes”) of proposed speciation processes, and I will offer a conceptual space map (Gärdenfors 2000) that does this, based on significant differences in the models as they relate to Sergey Gavrilets’ work (Gavrilets 2003, 2004; Gavrilets

and Gravner 1997; Gavrilets and Waxman 2002) on adaptive landscapes and speciation. Gavrilets' observation that selection and drift are not opposing forces, and that there are nearly equivalent high fitness corridors ("neutral networks") through the adaptive landscape, puts a different aspect on speciation and the nature of species.

In the course of disambiguating the modes of speciation, I will argue that the relevant conceptual axes are: the amount of gene exchange between members of population and between populations themselves, whether the selection that acts to maintain the overall constitution of a species is extrinsic, due to environmental pressures, or also intrinsic, due to the maintenance of a *reproductive reach* between members by elimination of hybrids, and finally whether the process that forms species is stochastic or not. Species maintained by extrinsic selection only include asexual species, and Eigen's concept of a "quasispecies" maintained at or near the optimal genome is brought into play.

The fitness landscape metaphor

Since Dobzhansky published *Genetics and the Origin of Species* in 1937, evolutionary biologists have been separated into two major camps, those who think that, asexuals and hybrids aside, speciation is merely the application of diverging natural selection and those who think that speciation is due to geographical isolation followed by local adaptation and drift (Turelli et al. 2001). These two modes have been termed *sympatric speciation* and *allopatric speciation* respectively, using terminology devised by Mayr and Poulton (Mayr 1942; Poulton 1903). Broadly, this division answers to the split between Fisherians and Wrightians (Skipper 2002). However, it is not required to equate the two terms with selective and nonselective speciation; the point is that selection *for* reproductive isolation cannot occur in allopatry, even though selection of features that result, inadvertently as it were, in reproductive isolation is ongoing in isolated populations.

In the text that set the Modern Synthesis of genetics and evolution going, R.A. Fisher offered a view of speciation, that in addition to geographical isolation allowing "the two separated moieties thereafter [to evolve] as separate species, almost in complete independence, in somewhat different habitats" (Fisher 1930), variants in the same region could also adapt to slightly different conditions, and thus hybrids would have lower fitness, although he didn't use that term, preferring instead "reproductive investment". Sewall Wright, in a paper presented shortly after the publication of Fisher's seminal book at the Sixth International Congress of Genetics (Wright 1932), argued instead that population size indicated that the role of selection could be offset by the randomness of stochastic factors, allowing populations to "cross" from one adaptive peak to another in the fitness landscape (a term he did not use in that paper, referring instead to "the field of possible gene combinations"), a metaphor that has been often used since. Recently, Sergey Gavrilets released a

book entitled *Fitness Landscapes and the Origin of Species* (2004). In it, he discusses at length the metaphor of the fitness (or adaptive) landscape, and of modes of speciation. As these two are related in his thinking, and this is itself highly germane to the current debates over both speciation and the role selection plays in that process, this paper will consider how Gavrilets' ideas impact on the conceptual analysis of speciation and species.

A fitness landscape, a metaphor introduced by Sewall Wright (1932), is best conceptualized, says Gavrilets, as a hypercube of n dimensions, one for each locus on a genome. Each point in the "space" (technically known as a "state space" or "phase space") represents a combination of some alleles in a population, and it has a fitness value assigned to it by the environment. A biologically realistic fitness landscape will typically have thousands, if not millions, of dimensions, for each possible gene and alleles. Gavrilets identifies what he calls a "supercritical regime" or a "percolation threshold" at in which there are large networks of loci of roughly identical fitness. In earlier work he refers to this as a "giant component" that extends throughout the entire system (Gavrilets 2003). It follows, according to Gavrilets, that in a suitably complex genome space, there are going to be "ridges", or as I prefer to think of it, corridors in that space which are pretty much the same fitness value, and which are very close to being the most fit in that region. Of course, no realistic organism will be optimized in all aspects of its genome, as there will likely be tradeoffs between competing fitness functions. In Gavrilets' models, fitness functions are held constant for simplicity.

As a result, selection will tend to maintain a population at the fittest local "peak" or "ridge", but there is a way in which ordinary genetic drift – random collations of effects like mating chances, stochastic sampling of gene pools, and environmental noise – will enable a population (and hence the species made up of these populations) to wander about in the fitness landscape, through these neutral corridors. In short, both selection and drift cause biodiversity in a way not hitherto appreciated widely.

This means that selection keeps organisms more or less adapted (there are lag effects, "you can't get there from here" situations, and competing fitnesses of different genes that almost guarantee that no organism will be entirely fit or well adapted), but the form of the *adaptation suite*, that is, the complete adaptive trait ensemble of the organisms, will vary in a random manner. While all, or nearly all, traits are maintained at high fitness, the particular "choice" of which traits, or rather, which adaptations, a population possesses is not forced by selection: some variety is due to stochastic processes acting within a range of local high fitness alternatives.

These nearly equivalent corridors also enable species to escape local adaptation "peaks". If they are connected as networks, as Gavrilets shows they are in realistic cases, then once you get to another place in the "corridor", you may find a different branch that will enable you to ramp upwardly in fitness. Of course if fitness functions vary with changes in the coevolution of linked species and the consequent environmental regime, then so too do the distributions of

nearly-equivalent components, and populations can then wander off in new directions. A population might evolve while remaining at a level of high fitness from the fluidity of the fitness values themselves, a point noted by Dobzhansky in 1937. For the purposes of this discussion, however, we will assume a relatively static background of extrinsic fitness values for a given species; or in other words, assume that the same environmental niches remain constantly available.

Selection and speciation

The idea that there are neutral networks – that is, ridges of nearly identical fitness value in the space of all possible genotypes for a species – suggests a way of reconciling two concepts that have been held to be opposed in the Darwin Wars: adaptation and drift. The opposition of these two processes goes back to a debate between Fisher, who first successfully argued that Mendel and Darwin could be reconciled, and who proposed the “fundamental theorem” of selection (which is not a theorem), and Sewall Wright, who suggested that Fisher’s theorem only applied to unrealistic populations (that were infinite and equally likely to mate between any two individuals), and that evolution in fact relied upon changes due solely to statistical or stochastic effects of sampling error in small populations. Wright, of course, is the inventor of the adaptive landscape. Fisher influenced the British evolutionists, while Wright influenced Dobzhansky and Mayr in America. Mayr’s account of speciation relied on the small population stochasticity of peripheral isolate populations of a species being subjected to fluctuations unrelated to selection for reproductive isolation. In effect, reproductive isolation was a side-effect of evolution in small populations. The British tradition of Haldane and Maynard Smith, by contrast, tended to ignore speciation and focus mostly on selection and adaptation.

In Gavrilets’ view, an adaptive landscape is almost always going to have roughly equivalent regions that are interconnected – that is, they form networks. But they are not low-selectivity networks – each point on the network pathway must be roughly the same relatively high fitness. In short, the networks are fitness ridges or contours along which species or populations will inscribe a Brownian trajectory, which we will call a “random walk”.

It is noteworthy that both selection and drift are in play here. The fitness is maintained, but the populations will take random directions due to stochastic effects, for any realistically sized population. So speciation may be due to stochastic effects while selection maintains the current genotype profile of a population at the local near-optimum. That is, in other words, the fitness isn’t at a *peak*, it’s a *ridge*, which is part of a series of interconnected ridges. Selection can only maximize local fitness, not where on the fitness ridge the population is. Maynard Smith (1970) called it a *continuous network of functional intermediates* in the context of protein evolution.

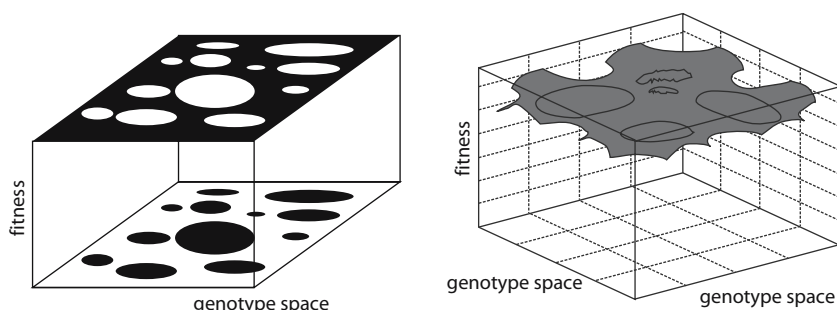


Figure 1. Gavrilets' "holey landscape". The left figure is devised for a "toyworld" case in which fitnesses are either 1 or 0 (redrawn from Gavrilets and Gravner 1997), but the right figure is for continuously varying fitnesses, with the high fitness region near the adaptive peaks, skirting low fitness basins, in a reasonably smooth landscape (redrawn from Gavrilets 2003).

Gavrilets uses a several versions of the adaptive landscape metaphor. One is that of percolation through the hypercube of the genome space (Gavrilets and Gravner 1997), but the more recent metaphor, and I must point out that it is indeed a metaphor not a model, is of a *holey landscape*, in which there is a region of high fitness in the landscape, interspersed with regions of low fitness (see Figure 1). In the high fitness region, a random walk can take you all over the place. Of course, one thing Gavrilets insists upon is the high dimensionality of the space of fitness combinations – the 3-dimensional space shown here is a necessary limitation of paper diagrams. In a space of a genome of n alleles, the dimensionality is of course n and it is, he says, mathematically highly likely in a realistic scenario that there are networks of these high-fitness ridges in an adaptive landscape.¹

It is enormously significant that selection and drift are, in effect, decoupled. They are not antonyms, they are just different processes. That makes a lot of the argument between speciation adaptationists and anti-adaptationists otiose.

Modes of speciation

Let us consider how the various kinds of speciation relate to each other. The traditional approach is to conceive of speciation as something that happens in *sympatry* or in *allopatry*; that is, in the same locale or isolated locales respectively.

¹ The editor asks why the dimensionality is not $n + 1$, given that fitness is a dimension. This is true, but the adaptive landscape model has traditionally treated the coordinates of the genome space as genomes, each of which has an associated (and variable) fitness value. The landscape itself is the range of fitness values for each genome, but the genome space is defined by the number of loci and alleles for the population under consideration. If we were to take the dimensionality to include the fitness value, then each time the fitness values changed, we would need to have a new landscape, which would undercut the operability of the approach.

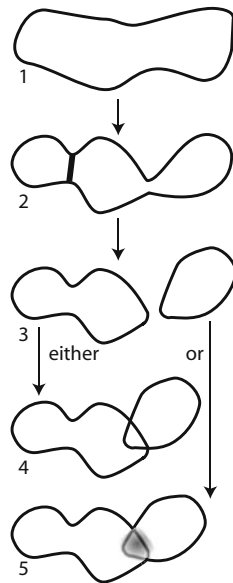


Figure 2. Mayr's model of stages of allopatric speciation. Redrawn from (Mayr 1942).

A third form of speciation is named by Mayr *peripatry*, in which peripheral populations, almost but not quite detached from the main distribution of the species, evolve independently of the rest like an isolated population would.

Mayr showed allopatric speciation with a diagram that has become iconic in evolutionary textbooks (Figure 2). The sequence is to be read from top to bottom over time. The interconnected populations or demes of the species, the *metapopulation*, fragment as conditions change, perhaps due to geological processes like mountain building or river formation. One part becomes detached, or *geographically isolated*, and it evolves in its own way, incidentally causing reproductive isolation (RI) to evolve. Note that RI is not itself the subject of selection, but happens as a side effect of other evolutionary change. This means that being a species formed through RI is not something “functional”, but this can change when species that have formed allopatrically come back into contact (steps 4 or 5).

Sympatric populations that are RI will tend to reinforce this isolation through lowered hybrid fitness, since several mechanisms will mean that hybrids actually are less fit: sexual selection, adaptive traits, chromosomal structure. In the first case, preferential mating may mean that the newcomers find it harder to find willing mates. In the second, the newcomers may be adapted to some resource or condition, while the old-timers are adapted to a different resource or condition. The hybrids will be neither fish nor fowl, and so it will mean they are less viable. In the third case, inversions, translocations, fusions and fissions make it harder for the chromosomes of the sex cells to pair up and continue development.

This led Mayr to define species, effectively, as gene pools protected against introgression (the influx of genes from other population):

... species are reproductive communities. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. A multitude of devices insure intraspecific reproduction in all organisms The species is also an ecological unit that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is a genetic unit consisting of a large, intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short time (Mayr 1963).

RI itself became the focus of a lot of research, most recently summarized in Coyne and Orr's book *Speciation*. RI was divided into subcategories, versions of which found their way into the textbooks. The primary division was between *prezygotic* and *postzygotic* isolation, or between those mechanisms that prevented the fusion of the sex cells, and those that prevented the fused sex cell, the zygote, from developing through to further reproduction. The most complete general list is this one by Murray Littlejohn (Table 1):

Note that the barriers here are not absolute – the RIMs only produce a reduced *frequency* of successful breeding, thereby causing lowered fitness of hybrids. Complete isolation is not required under (revised) RI conceptions for species to be real (as Coyne and Orr 2004 observe).

So, what is the debate? For years now, biologists working in the domain of speciation have argued whether speciation occurs in allopatry, or sympatry or some intermediate parapatry. Much of the debate has been about terms. For

Table 1. A classification of reproductive isolating mechanisms (RIMs) (From Littlejohn 1969).

Reduction of contact

(a) temporal

(b) ecological

2. *Reduction of mating frequency*

(c) ethological

(d) morphological

PREMATING

POSTMATING

3. *Reduction of zygote formation*

(e) gametic and reproductive tract incompatibility

PREZYGOTIC

POSTZYGOTIC

4. *Reduction of hybrid survival*

(f) hybrid inviability

5. *Reduction of gene flow through hybrids*

(g) hybrid ethological isolation

(h) hybrid sterility

(i) hybrid breakdown

example, if the *Rhagoletis* fruitfly that has speciated (Berlocher 1999, 2000) by moving from one host species (Hawthorns) to another (Apples) is not in sympatry, then nothing is, but it is claimed that the host species is a *kind* of allopatry. And so on. It's a messy debate, needing some conceptual clarity. Gavrilets, in his Introduction, defines these different modes of speciation in ways that, finally, make sense, relating them to each other. In the next section, I will list these and then try to organize them into a “conceptual space”.

Framing speciation

Gavrilets (2004, chapter 1) notes that one can use any of the isolating processes to classify speciation, but that the traditional way is to frame it in terms of migration between diverging populations (which is to say, it's what Mayr said in 1942). He lists the varieties mentioned above: allopatric, sympatric and parapatric, and aligns them along a single axis of migration rate (Figure 3).

Of interest here is that some of the standard modes of speciation don't appear. For example, speciation by chromosomal rearrangement (“stasipatry”, defined by Michael White 1978) is missing. It is clearly in sympatry, but there is no “migration” between the new population and the old, except in species “complex” cases like the *Sphalax ehrenberghi* mole rat in Israel (Catzeflis et al. 1989; Nevo et al. 1994a, b), which has major chromosomal races, some of which are mutually infertile, although there is introgression between them. Polyploidy – or the duplication of entire chromosomal complements, common in plants and arguably in animals (Ramsey et al. 1998; Dowling and Secor 1997) – is also missing.

Gavrilets deals with them by calling them “scenarios” and “patterns” of speciation (I will refer to these as “modes” of speciation following Wilkins 2003). He lists the following cases:

Vicariant – divergent selection and stochastic factors like drift after division of a population by extrinsic factors such as geographical changes;

Peripatric – a small subpopulation, mostly isolated, at the extreme of the parent range. The idea is that it will have both a non-standard sampling of alleles, and also be subjected to divergent selection pressures in extreme environments (for that species);

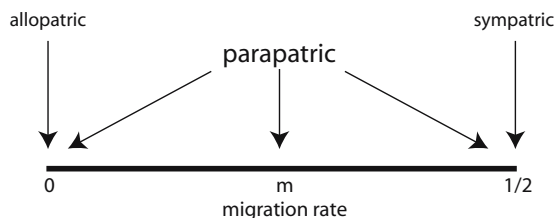


Figure 3. Gavrilets' primary axis of speciation. Redrawn from (Gavrilets 2004).

Centrifugal – central populations that carry a sample of many alleles that become isolated through, say, “island” formation (such as the mountain “islands” in the Amazon);

Punctuated equilibrium – the appearance of relatively rapid speciation and subsequent stasis as the population reaches equilibria of alleles. In my opinion, this is inappropriately included here, for it is a “pattern” rather than a “process” (or “event”) of speciation, and as such can be caused by any of the other scenarios/modes;

Chromosomal speciation – the rearrangement of chromosomes, either by duplication or insertion, fission, fusion or inversion;

Hybridization – the fusion of two genetic lineages, usually from distinct species, including allopolyploidy. In allopolyploidy the genetic complement of two species is paired up by a loss of secondary division, giving a symmetrical set of chromosomes;

Reinforcement – once hybrids are of lowered fitness for whatever reason, selection will tend to reinforce separation of the gene pools (for example, a hybrid rock and grass dwelling lizard might be less able to survive in either environment as well as the “pure” lines);

Competitive – this is Darwin’s scenario. Members of a species that are in strong selection for a limited resource may result in specialized forms that are thus in less competition with the ancestral forms that make use of some other resource;

Clinal/ecotonal – Gavrillets calls it “speciation along environmental gradients”, where limited migration and selection leads to aggregation of forms at the terminal ends of the cline;

Host shift – this is the case of the *Rhagoletis* fruit flies mentioned above, that Stuart Berlocher (1999, 2000, 2002) and colleagues have studied. Host fidelity replaces geographic isolation;

Runaway sexual selection – this is secondary selection by mate choice of polygenic traits (Lande 1981).

Now, this is a somewhat heterogeneous list, so one might wonder how to assign them to the scale above. For example, many of these occur in full sympatry – chromosomal rearrangements and polyploidy, host shift, competitive, and so on. Is there a way to separate these modes conceptually? To show that the gene-flow/geography scheme is inadequate to differentiate these distinct modes of speciation, consider the rough analysis of it in Figure 4.

Replacing percentage of gene flow for migration rate and geography as the other axis, we now get a clearer picture – sympatry–allopatry is not the only important difference between these “scenarios” or modes of speciation. So also is the relation of the populations to each other. I have placed the sexual selection example between peripheral and isolated because I doubt it would occur species-wide, and is therefore less likely to be a central population case, but it could occur in relict populations. We are left with two groups of modes – reinforcement and host race shift (in the case of almost-sympatric parapatry: again it need not be so specific), and competitive, hybrid and

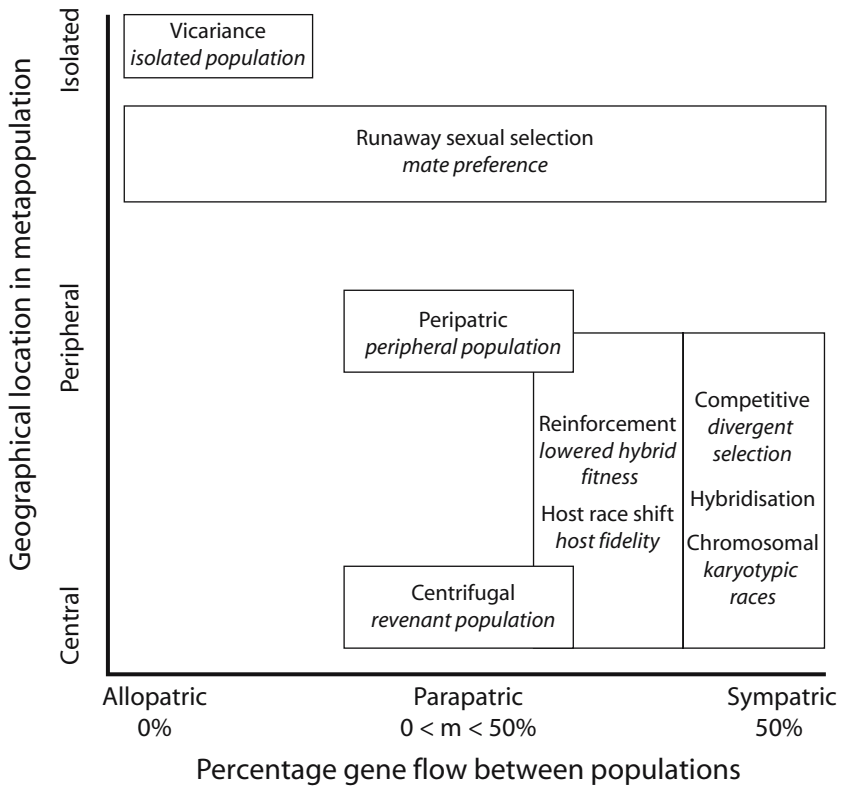


Figure 4. The relationship between percentage gene flow in sexual populations and geographical isolation, of proposed modes of speciation.

karyotypic. Each of these is distinguished by a particular mode or mechanism of speciation. We shall now explore some of the implications of this for the speciation debate, and also for the definitions of “species” used by biologists.

Reproductive reach

Two issues that face an evolutionary biologist rather sharply are these: the nature of species and how they come to be. When in the period of the fusion of Mendelian genetic and Darwinian evolutionary theory these matters were raised, initially by Dobzhansky, the obvious way to tackle the problem was by making use of the new science of genetics. Scientists will not tackle a problem for which there are no tools, although they may speculate on problems. However, give them a new tool, like Mendelian genetics, and they are off and running. This has an unwanted aspect: it can lead scientists to frame the problem solely in terms of the tools, and so it was with the matter of speciation

and species. Species were, Dobzhansky informed us, largely terminal stages in the separation of gene pools. Mayr further extended this by defining species solely as populations that were permanently isolated from exchanging genes (that is, from introgression). And this is true, for sexual species, although it is not always the case that genes are the mechanism for RI. Behavioral and developmental processes can isolate populations while massive differences in genetic structure and alleles can be included within one species. And the nature of the term “population” is suspect itself (Gannett 2003). A population is a partition of the gene pool of a species (you do not define a species in terms of populations that have no chance of reproducing together, like asparagus and elephants), but what counts as a population, or the reproductive equivalent of a population, the deme, depends on whether they are in the same or similar enough species. In the Mayr–Dobzhansky version, species define populations, and populations define species. Perhaps there’s enough shared operational understanding in the various disciplines to make non-tautological sense of the two terms, but on the face of it “population” is merely one unanalyzed term defining another, “species”.

In our diagram, several speciation modes are undistinguished, in part because what makes them different has nothing much to do with geography. Geography is only important for those speciation modes that rely upon it, like sympatric reinforcement or allopatric drift (i.e., evolution of the genetic structure of the population in isolation). But in chromosomal rearrangements, such as inversions, fusions, fissions, and duplications, geography has no real role to play as a mechanism of speciation, and is only useful as a test afterwards of whether or not speciation is complete enough to count two species where there was one, when they come into contact.

Then there are asexual, or mostly asexual, species. Dobzhansky proposed not to call them species because they failed to rely even upon reproductive isolation, and they are called “agamospecies”. A reviewer argues that asexual species lack an organizational level that sexual species have at that taxonomic level. My argument is that sexual species have only the added organization that members must be reproductively compatible with other members, and that asexuals do form species. Certainly bacteriologists consider that their organisms form species (see Moreno 1997; Cohan 2001, 2002). A better term is Manfred Eigen’s (1993) notion of a “quasispecies” (from “*qua si*”, as if), in which there is a genetic coordinate in the space defined by the genomes of these organisms (or, in the case of viruses, pseudoorganisms) that is the default, or “wild-type” (*wt*), even if no strain of them actually instantiates it, around which all the others cluster (Figure 5). This naturally raises the question why they cluster there, and in the case of viruses, for which he developed the notion, the reason is clear. They cluster about the genome of the most efficient utilizer of the host cell resources. In effect, the *wt* is a fitness “peak”, and variants that stray too far will be of lowered fitness (unless they cross a fitness valley and start moving up the new slope).

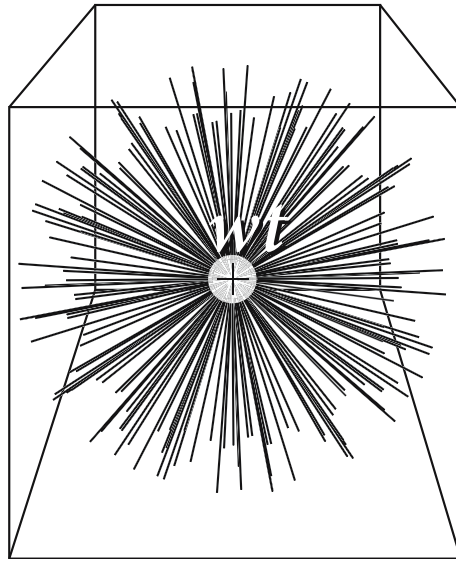


Figure 5. The Euclidean distances of the genotypes of each actual strain of an asexual lineage will not be too distant from the locus of the most locally fit genotype (wt), according to Eigen's Quasispecies concept of asexual species.

In the case of selectively reinforced speciation in sexual organisms, of lowered hybrid fitness, this is also the case. These populations or variants will be maintained by selection for some environmental niche or mode of living. So we can perhaps see that reinforcement of species here is effectively equivalent to quasispecies, only now, being sexual, it is not the elimination of strains that are not near the fitness "peak", but of hybrids that are between them. The same thing is true of host race speciation – here the selection is for the host resource availability. So the common element here is selection, and we can perhaps collapse them into one mode, differentiating them on the basis of what the resources are, ecologically speaking.

Competitive speciation – Darwin's favorite – is likewise a case of selection, but what about karyotypic races and hybridization? Or sexual selection? In each case, what counts here for fitness is whether there are mating opportunities. If you have a karyotypic difference that happens to match sufficiently with the ancestral karyotype, then speciation does not occur. But if the changes make it harder to mate, then eventually mating with those of similar karyotype is fitter than mating with the parental form. In hybridization the same thing is true – the hybrid form often cannot easily mate with either parent successfully, so it forms its own species. Sexual selection is clearly about being able to mate. The major difference here is what does the selecting. Rather than it being the *extrinsic* environment, it is the *intrinsic* one. If you cannot find a mate among one morph of the population, but you

can with the other, then eventually the lowered fitness of those that try to mate both ways will tell.

And that leaves vicariant speciation, misleadingly called “allopatric speciation” or speciation by geographical isolation and independent evolution. Originally proposed by Moritz Wagner (1868), it is the form of speciation most defended by Mayr and those in his research tradition. There is selection going on, of course, but not against lowered fitness of some morph or allele or karyotype, but solely selection *for* local conditions, which forces genetic changes that eventually make it difficult if not near impossible (nothing physically possible is actually impossible in biology) for the now sympatric populations to interbreed. In short, so far as reproductive compatibility is concerned, the two populations just... drift. Selection maintains them at local fitness peaks, but they acquire inadvertent changes that make them reproductively isolated when they get back together, if they do. I want to propose a notion here I shall call “*reproductive reach*” (RR), the inverse of reproductive isolation. Any two populations have a RR distance that is locally determined and context-dependent. It determines how much gene flow can occur between them if they are sexual reproducers. And it specifies for any two organisms whether their progeny will be fit enough to continue a reproductive lineage. The acquisition of RI depends on whether the conditions leave the two organisms outside the RR of each other. It need not be absolute, but if the fitness of a progeny of any organism is severely lowered (and having none at all is about as severe as it gets) then that form or variant is outside the RR of its parent or parents.

Now this has an interesting consequence. A sexual species becomes just a special variety of asexual species. Where the fitness peak of asexual quasispecies is entirely extrinsic, being dependent on host/environmental defenses and resources, the fitness peak of sexual species can be either extrinsic or intrinsic. It’s about, in the end, how many progeny you can have. We might even say that quasispecies is the primitive or basal notion of *speciesshood*. Sexuality just adds extra dimensions to ways of being species. Vicariant speciation relies on local fitness peaks, but put them back in sympatry and it’s also about the fitness determined by the reproductive reach of the two organisms involved. Since we can now say, with Gavrilets, that drift and selection are not mutually exclusive (because, remember, there are fitness ridges in any complex genome space along which an adapted population can take a Brownian trajectory) we can say that all speciation is, indeed, about selection, no matter whether ecological, sexual, or developmental. So we can dispense with geography in our taxonomy of speciation altogether, except as an index to differentiate the kind of process that modifies RR.

To illustrate this, consider two species, a sexual member of the whiptail lizard clade, and a sexual one (Cullum 1997, 2000). One is selected for physiological fitness alone, while the other is selected for both physiological fitness and mating fitness. In the case of the whiptails, this is a secondary loss of sexuality rather than the primary addition of sexuality, but it applies in anal-

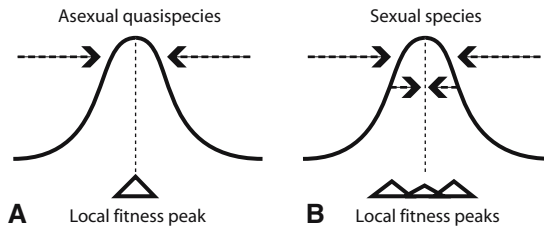


Figure 6. A quasispecies is maintained as a cohesive genotypic cluster purely by extrinsic selection (left). A sexual species is maintained in allopatry as a cohesive cluster by both extrinsic environmental selection and also intrinsic reproductive selection (right).

ogous cases. We can represent what *makes them species* (that is, what confers specieshood) as being selective clustering about the “optimal” genotype (Figure 6). This is a distinct issue from what maintains them as separate species when in sympatry again with a related species. In that case it is both reproductive selection, and environmental selection, against hybrids (assuming that members of the asexual species can facultatively be fertilized; or that both species are sexuals).

Does this make Darwin right and Mayr wrong? Of course not; Darwin *was* very vague about the modalities and reasons for speciation, and he thought that direct reinforcement of diverging selection mostly drove it. As a matter of fact, it is entirely probable, as Coyne and Orr (2004) document, that vicariance drives most sexual speciation in animals (but not necessarily plants – or gamete broadcasters in the animal world either. If you sow your seed, so to speak, broadly, then what maintains your isolation will be extrinsically selective). But geography is a secondary aspect of speciation. And it need not be the most important for all groups of organisms.

So the allopatry–sympatry axis of percentage gene flow is the spindle, as it were, around which myriads of particular processes acquire fitness in RI by exceeding the reproductive reach of the original genomes, for sexual species. Geography’s in there, as are chromosomal rearrangements, and host race speciation, etc. We need to revise our terminology to avoid the useless disputes of the past about what “the” mode of speciation is. What counts in the end is the rather obvious fact that the number of progeny, relative to alternatives, makes a new species.

The nature of species and speciation

If we accept the distinction between mode of speciation (geographical relation between populations) and rate of gene exchange, the mechanisms of speciation that fail to be distinguished that way – mostly chromosomal rearrangements and selection-based – add extra axes or dimensions to the notion of RI. Depending on how many actual mechanisms there are we can have a number

of different ways of attaining species-hood. Add to this the ways of being asexual species, and we get a rich field, one that is more complex than the usual ways of framing the issue.

The traditional RI conception of species known as the “biological” species concept was invented by Theodosius Dobzhansky in his 1935 paper, and revised in the text that effectively kicked off the modern synthesis, *Genetics and the Origin of Species*. Mayr contrasted this with the “typological” conception he claimed, wrongly,² was the default view before he “corrected” Dobzhansky’s view. Dobzhansky’s was a description of the process but not a definition of the concept of species, he said. I think he was wrong about that. Dobzhansky’s definition sure looks to me like a definition. Mayr added little – an undefined term “population” and some passing acknowledgement of ecological and geographical aspects. In terms of our chart, Dobzhansky treated the gene exchange as primary. It was Mayr who added geography, and this is important not as a mechanism for reproductive isolation, but as a condition that leads to it.

Why does it matter that two populations are in a geographical relation in speciation? Surely this is because Mayr’s own version of speciation relied upon geography as the proximal mechanism for independent evolution that gave speciation as a by-product. It is special pleading. Geography matters to Mayr because in his preferred model geography is the primary mechanism of sexual isolation. But if isolation is achieved in many ways, and it surely is, even on Mayr’s own account (he did accept allopolyploidy from the beginning, for instance), then we have an interesting situation. Speciation is something that occurs in multiple modes, using many mechanisms ranging from gamete surface molecules, to behavioral differences, to ecological adaptations, to genomic structure and so on (see the papers in Hey et al. 2005). So there is a high dimensionality to speciation itself. For every aspect of RI, for karyotypic change, for ecological isolation and reinforcement, as well as geography, speciation exhibits a plurality of causes. And in the case of non-RI speciation, such as quasispecies/asexuals, the causes can be purely ecological.

So let us work out the conceptual variables of speciation processes that we need in order to distinguish the various general speciation modes:

First, we have the distinction between speciation that involves gene flow and speciation that doesn’t. Quasispecies do not, usually, exchange genes between populations (viruses can superinfect a cell and crossover their genes; and some gene flow can also occur in asexual species due to endogenous insertion). Speciation that involves the rate of gene flow between populations ranges from pure allopatry or infertility (0% gene flow) to pure sympatry or fertility (50%

² In a forthcoming book on species, I cover the history of the species concept and conclude that the only sense in which people were “typological”, or “essentialist” which Mayr added later, before Darwin was exactly the sense in which all later systematists including Darwin were typological or essentialist – in terms of diagnosis or identification. People didn’t suddenly become smart after Darwin, nor were they mindlessly Aristotelian and bad observers before him.

gene flow), with most being a mixture (parapatry). Cases of near-sympatry must require isolating mechanisms such as selection against hybrids.

Second, we have the distinction between *intrinsic* and *extrinsic* selection. Intrinsic selection involves selection against the background of the rest of the population. It includes mate selection, lowered hybrid fitness, and developmental incompatibilities. Extrinsic selection involves selection against only the extra-specific environment.

Third, we have the distinction between determinate speciation and random or Brownian speciation. In the latter case, the “location” of the population in genome space is a matter of stochastic sampling, with no constraints imposed on viability or fitness. Neutral drift is a case where no selective coefficient, extrinsic or intrinsic, is a cause of speciation, and so it will be regarded as having a high stochasticity (although *some* selection is going to occur on the organisms, so it will not be entirely stochastic).

We can illustrate this with a diagram (Figure 7) to illustrate how to disambiguate modes of speciation.

Each of these three axes is independent of the others. A nascent species/population may be maintained at its genomic location by extrinsic selection and yet be able to randomly traverse the equal fitness ridges in the fitness landscape. Each axis is a notional, or abstract, variable. The concrete aspect for a given case will be something physical, like a pairing problem for chromosomes or a haplotype block, or cell surface identifiers on gametes, or a developmental abnormality that precludes viable zygotes, and so forth. Nothing is required and many things may be sufficient to achieve specieshood.

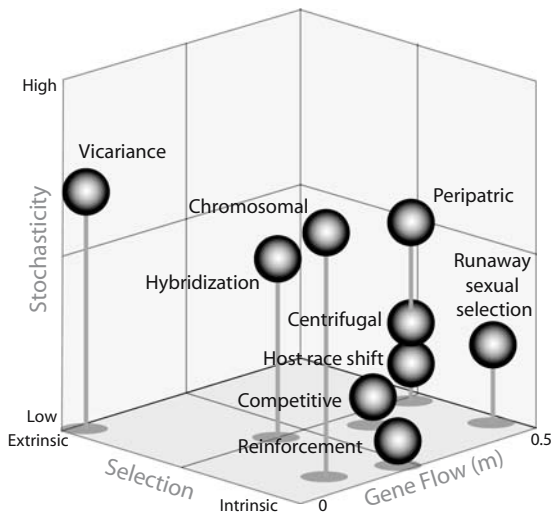


Figure 7. Modes of speciation. The modes from Figure 4 have been assigned subjective estimates and mapped in the three-variable conceptual space (see text). No account is taken of deviation on any axis, which will depend on both the theoretical models and empirical data.

The multiple causal origins of species does not in itself force the conclusion that species are not real. There is a physical fact of the matter whether organisms with particular genomic and developmental configurations (the physical properties) will have an average number of progeny, but having that number of progeny is something that occurs in many different physical ways.

What counts is the persistence of the genomic and developmental configurations C by reproduction (in a particular class of environments E). The fitness of asexuals is determined solely by their ability to produce viable offspring in E . The fitness of sexuals is determined by some mixture of viability in E and their reproductive reach. This multiple realizability explains why we observe species when we do. The phenomenality of species is a physical outcome of the relation between the observer's assays or discriminative capacities and the progenitive properties of the organisms' C in E . If we know what to look for, then we will see the clustering of properties. From a heuristic perspective, species are phenomenal objects (*iff* we have the right assay). They are clusters in genome space (and possibly also in phenotypic or morphological space as well). Speciation is the process of attaining this phenomenal quality. For instance, in cryptic species pairs we may not be able to discriminate the differences, though the organisms can, or they will not be sexual species. Or we may over-discriminate when the assayed properties do not match the reproductive reach of the organisms. But overall, species are real when there is discontinuity in the number of progeny that maintain the relevant causal processes of reproduction; that is, when differential fitness and stochastic processes cause clustering.

Conclusion

In summary, a species is some object of the relevant kind (a lineage of a population) that is maintained by causal physical processes through selection and gene flow. All species are lineages, as de Queiroz has argued (de Queiroz 1998), and as Richard Boyd has argued, they are homeostatically maintained kinds (Boyd 1999a, b), but neither homeostasis nor lineage is sufficient to identify species. We must in the end make recourse to reproduction rate and gene-exchange in the case of sexual species, and selection in all cases, to distinguish species from subspecific and supraspecific cases. When in sympatry the rate of reproduction between putative species-populations is close to the maximum (50%), we do not have species. When it is closer to the minimum (0%), we do. When asexuals maintain their ecological niche in sympatry, we have species. When they facultatively exchange niches, we don't. And so forth.

If we adopt a nominalistic perspective, and say that all there is in the biological domain here are organisms and their progenitive relations (parent-progeny causal lineages), then there is no answer to give. "Speciation" is just a convenient name we give to a process that resembles in our eyes some other process we might have observed or inferred. The only thing in common

between speciation of *Rhagoletis* flies and cats or carrots is that we choose to represent them as species whose lineages have, on the aggregate, formed some phenomenally salient branches. Others such as De Queiroz, argue for a “metapopulation lineages” account – what makes carrots, cats and fruit flies species is that their metapopulations have divided. The problem with this account is that “metapopulation” is itself a vague and difficult concept, possibly circularly defined in terms of “species”.

Therefore, let us treat species, as many have been inclined to do,³ as lineages of selectively favorable genetic and developmental complexes, and allow that nevertheless, a range of actual or possible processes can divide them. The adaptive landscape metaphor is indeed a bridge between microevolution (evolution within species) and macroevolution (evolution between species) as Arnold et al. (2001) said.

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³ Hugh Paterson’s Recognition Concept of (sexual) species (Paterson 1993) and Alan Templeton’s Genetic Cluster Concept (Templeton 1989, 1998) fall under this heading. Both focus primarily upon the positive processes that cause homeostasis, which is to say, cause species to be.

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