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Speciation Post Synthesis: 1960-2000

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Abstract:	<p>Speciation - the origin of new species - has been one of the most active areas of research in evolutionary biology, both during, and since the Modern Synthesis. While the Modern Synthesis certainly shaped research on speciation in significant ways, providing a core framework, and set of categories and methods to work with, the history of work on speciation since the mid-20th Century is a history of divergence and diversification. This piece traces this divergence, through both theoretical advances, and empirical insights into how different lineages, with different genetics and ecological conditions, are shaped by very different modes of diversification.</p>	
Response to Reviewers:	I have now included relevant citations, expanded and developed one further section, and made a number of minor corrections and additions.	

Title:

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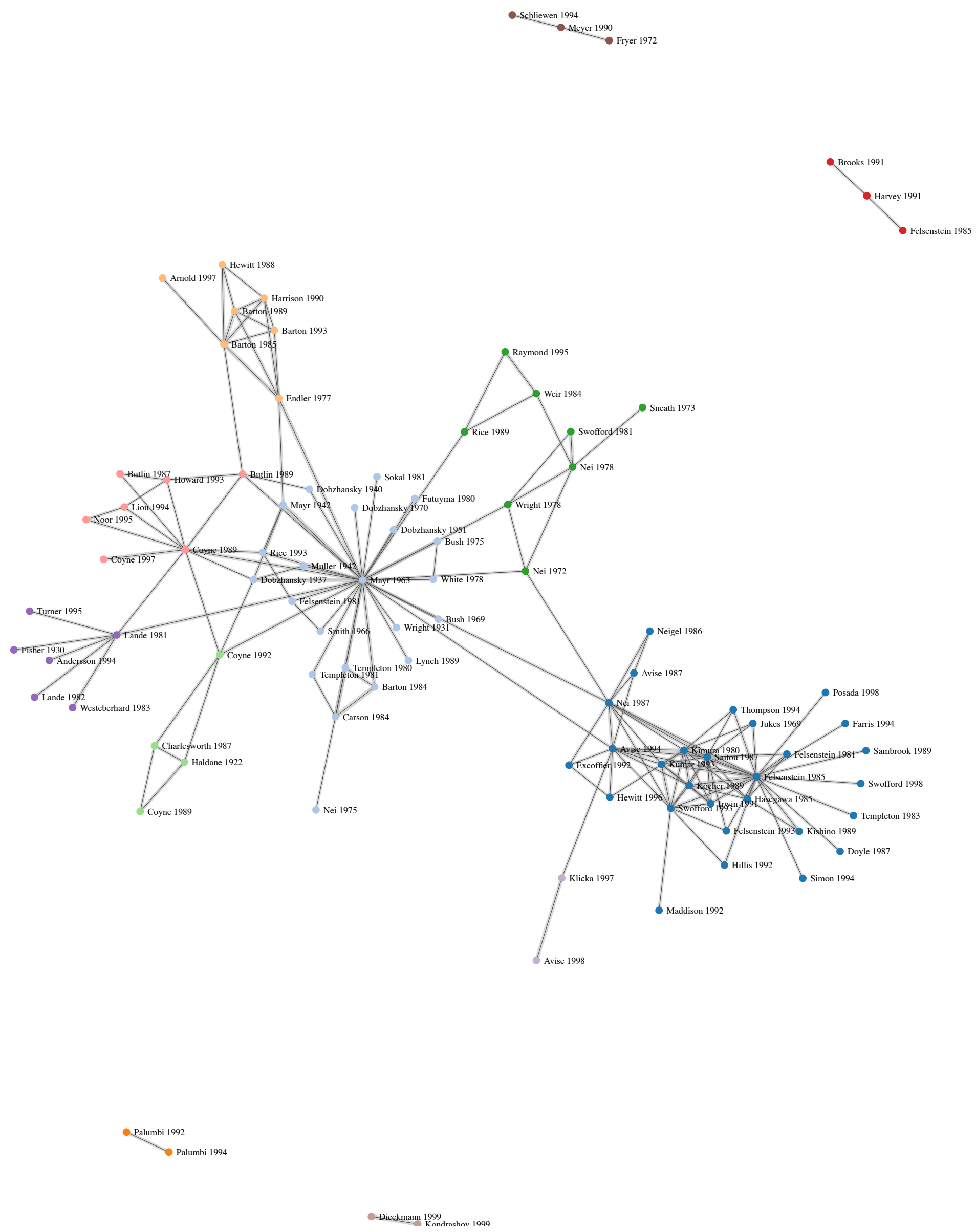
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Speciation Post Synthesis: 1960-2000

Speciation – the origin of new species – has been one of the most active areas of research in evolutionary biology, both during, and since the Modern Synthesis. There have been over 1500 publications on this topic in from 1960 through 2000 alone (Web of Science search, Feb. 2016). It would be impossible to do justice to the many contributions evolutionary biologists have made to this vast field of research (at least in under 10,000 words). So, the below will focus on several of the most influential figures in this literature, and their major contributions to thinking about speciation since the Modern Synthesis,¹ focusing on the period from 1960-2000 (see figure 1).

How has influence been measured? A brief word about methodology is in order. The figure below was constructed using Web of Science search of “speciation” as a topic, under the general heading of “evolutionary biology.” Frequency of citation was used to limit inclusion, and co-citation frequency was used to generate pathways, or “branches” leading out from ancestral “nodes”. A paper is shown if it is cited at least m (32) times in total and is cited together with some other paper at least n (16) times. An edge is shown between two papers if they are cited together at least n times. The colors are assigned in accordance with the [Louvain algorithm](#), which seeks to maximize the modularity of the graph, i.e. the fraction of the edges that fall within the given groups minus the expected such fraction if edges were distributed at random (Waltman, et. al. 2013; credit to G. Gandenberger for the design of this figure, 2015).

As the graphic illustrates, evolving ideas about speciation during this period can be viewed as a branching tree with lines of descent, adaptive divergence, and horizontal gene flow. In keeping with this image of descent with modification, the following narrative is organized around concepts that have played key roles in the speciation literature itself: founder effect, cohesion of the gene pool, speciation in sympatry, isolation by distance, tension zones, and adaptive divergence. This choice of framing is not merely a rhetorical conceit. Ernst Mayr and Theodosius Dobzhansky acted as “founders” of much of this literature in a variety of meaningful ways. Their conceptualization of the problem of speciation shaped much of the subsequent research, narrowing the field to a specific set of problems, and restricting what might count as legitimate solutions. Mayr in particular actively engineered a cohesive research program, excluding views he thought inconsistent with the consensus developed by synthesis authors on speciation (see, e.g., Provine, 1989, 2004 for a discussion of Mayr’s influence on this literature).

Despite Mayr’s influence and efforts at building and reinforcing consensus, a central challenge to Mayr’s view came in the form of critique of the idea of “homeostatic

¹ Historians disagree about how to date the Modern Synthesis, or indeed, whether we ought to grant that the “synthesis” was a discrete historical event, let alone whether there is such a thing as the “synthetic theory” of evolution (see, e.g., Burian, 1988; Smokovites, 1992, 1994a, 1994b; Cain, 1993, 2000, 2009; Depew and Weber, 2011; Delisle, 2011). There is no doubt that the “synthesis” was a period defined in part by the participants (see, e.g., Mayr and Provine, 1998). The best compromise on this issue is to grant that when and how the “synthesis” began and ended is at best vague, and that what defined it was in large part the interests and activities of scientists who at least saw themselves as concerned with a (more or less) common set of questions, whether or not they agreed on most of the answers. Some have argued that there has in fact been “two” syntheses: an “early” and “late” synthesis, one consisting largely in the “synthetic” theoretical work of Haldane, Fisher and Wright, and a “later” synthesis (see, e.g., Sarkar, 1992, 2004).

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4 gene complexes,” and the “coadaptation” of the gene pool, which served as a force
5 preventing speciation in conditions where there was gene flow. Empirical and fieldwork
6 on a variety of species suggested that the modes of speciation Mayr discounted in fact
7 play a significant role in some cases. For instance, Bush, Feder, Smith, McPherson and
8 Berlocher’s (1988) work on *Rhagoletis pomonella* (the apple maggot fly) challenged
9 Mayr’s convictions about the possibility of speciation in sympatry, as did Schliewen,
10 Tautz and Paabo (1994), and Seehausen’s (1997) work on Cichlid fish flocks in Africa.
11 Fieldwork on Hawaiian *Drosophila* by Carson and Templeton, as well as Templeton’s
12 “transilience” model prompted a rethinking of the mechanisms undergirding Mayr’s
13 model of peripatric speciation, or “founder effect.” Experimental work by Rice, Hostert,
14 Mooers, and others challenged Mayr’s claim that speciation in peripherally isolated
15 populations occurred via founder effect.
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19 Advances in genetics and molecular biology in the 1960s led to the development
20 of tools for better characterizing the extent and nature of genetic divergence between
21 species. The significance of these advances in molecular biology is illustrated by the
22 massive influence of Nei’s paper on genetic distance, which clearly forms a node with
23 multiple lines of descent, linking work on speciation and systematics. Further challenges
24 to Mayr’s views came from theoretical work by Maynard Smith, Lande, Barton, and
25 Charlesworth. Together with experimental work on *Drosophila* by Coyne, Orr, Rice and
26 Salt, these authors’ models and arguments gradually transformed biologists’
27 understanding of the evolutionary genetics of speciation. This theoretical work
28 overturned many assumptions about the genetics of populations common to the founders.
29 Key studies on a diverse array of species in the wild (see, e.g., Endler, 1977; White,
30 1978; West-Eberhard, 1983; Hewitt, 1988; Meyer, et. al., 1990) led to a diversification
31 of perspectives on the major modes of speciation. What were previously viewed as
32 marginally influential mechanisms and modes of speciation were found to be quite
33 important in some lineages, and indeed key factors in their diversification (e.g., clinal and
34 hybrid zones, a potential role for reinforcement, and sexual selection).
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39 In sum, while the Modern Synthesis shaped research on speciation in significant
40 ways, providing a core framework and set of categories and methods to work with, the
41 history of work on speciation is a history of divergence and diversification. There is,
42 today, a far more permissive, or, if you like, speciose, array of views about how
43 speciation can go forward than previously. This is in large part due to theoretical
44 advances, but also to an impressive array of experiments, fieldwork, and thus growing
45 awareness of how different species, genetics, and ecological conditions yield very
46 different modes of diversification.
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49 **The Founder Principle and Cohesion of the Gene Pool**

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51 “[Founder effect is]... the establishment of a new population by a few original
52 founders... that carry only a small fraction of the total genetic variation of the
53 parental population. The descendent population contains only the relatively few
54 genes that the founders brought with them, until they are replenished by
55 subsequent mutation or by immigration.” (Mayr, 1963, p. 124)
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4 “The phenotype is the product of the harmonious interaction of all genes. There
5 is extensive interaction not only among the alleles of a locus, but also among loci.
6 The main locale of these epistatic interactions is the developmental pathways.
7 Natural selection will tend to bring together those genes that constitute a balanced
8 system. The process by which genes that collaborate harmoniously in the gene
9 pool is called “integration” or “coadaptation.”...The result of the coadapting
10 selection is a harmoniously integrated gene complex...” (Mayr, 1963, p. 185)
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14 The two above quotations capture both two central speciation theories of Mayr,
15 and might describe Mayr’s own influence on speciation research in the latter half of the
16 20th Century. Speciation was one of the central problems of the Modern Synthesis.
17 Speciation was, in fact, the central theme around which the precursor to the Society to the
18 Study of Evolution was founded. Dobzhansky, Julian Huxley and Alfred Emerson
19 organized the *Society for the Study of Speciation* at the 1939 AAAS Columbus meeting,
20 drawing together experts from different sub-fields in biology: genetics, paleontology,
21 biogeography, systematics, and ecology. Though short-lived, this served as a community
22 infrastructure for the sharing of tools, information, and expertise on the topic of
23 speciation, and eventually became folded into the Society for the Study of Evolution
24 (Cain, 2000; Smokovites, 1994).
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27 Many of the first papers published in the Journal *Evolution* were either directly or
28 indirectly on the topic of speciation: the role of selection in generating novel adaptive
29 groups, sexual selection, chromosomal inversions in generating reproductive
30 incompatibilities, hybridization in plants, and geographical distribution brought to bear
31 on diversification. Indeed, the topic of speciation in many ways grounded the emergence
32 of the synthesis itself, serving as an exemplary case of the advantages of a new “unified”
33 biology.
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36 Thus, one of the “founding” narratives of the Synthesis was that the problem of
37 speciation required a new, synthetic approach to evolutionary biology – one that
38 integrated insights from genetics, biogeography, systematics, paleontology, zoology and
39 plant biology. According to Mayr, despite the title of his book, Darwin did not “solve”
40 the problem of speciation: “Darwin’s book was misnamed, because it is a book on
41 evolutionary changes in general and the factors that control them (selection and so forth),
42 but not a treatise on the origin of species” (Mayr, 1942, p 147; see Mallet (2005) for a
43 different view). In the introduction to his influential *Animal Species and Evolution*
44 (1963), Mayr compares the attack on the question of how we arrived at the diversity of
45 life on earth to an attack on a many-walled city by a number of separate armies.
46 Genetics, paleontology, and systematics are different strategic means of attacking the
47 same suite of problems. We are to envision the separate subdisciplines of biology as
48 having a common aim and cohesive view of the common problem and plausible
49 solutions.
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53 Mayr deploys metaphors such as these strategically. His project in this book, and
54 indeed, in his career more generally, was to identify the questions that unify the discipline
55 of evolutionary biology, and arrive at a cohesive view of how to solve these problems.
56 The problem of the origin of species – which stands at the intersection of micro- and
57 macroevolution, fruitfully illustrates Mayr’s vision for the future of biology, insofar as
58 biologists who study phenomena at different temporal and spatial scales can contribute to
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4 common solutions. A central commitment of Mayr was that “The real problem of
5 speciation is not how differences are produced but what enables populations to escape
6 from the cohesion of the gene complex and establish their independent identity.”(Mayr,
7 1963, p. 297).

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9 Mayr was committed to the idea that the challenge of overcoming “cohesion of
10 the gene pool” meant that speciation in sympatry (or, within the host range of the species)
11 should be extremely rare, and that “geographic isolation is ordinarily a prerequisite for
12 speciation”(Ibid., p. 276). Mayr developed these views in part due to his conversations
13 with Bruce Wallace and Larry King at Cold Spring Harbor, as well as his understanding
14 of Dobzhansky and Lerner’s views on the cohesion homeostasis of the gene pool (cf.
15 Provine, 2004). Mayr was convinced that “each gene acts on every other gene” in
16 development. The extent of interactive effects of genes in development meant that all
17 genes in a species needed to be “coadapted,” making the transition to new species
18 especially difficult. However, during a “founder event,” a “sudden reduction of
19 population size in the founder population” would expose resulting homozygotes to
20 selection, and more generally, “produce a sudden change of the genetic environment of
21 most loci,” leading to a “genetic revolution.” (Mayr, 1954, pp. 169-70). According to
22 Mayr, “during a genetic revolution the population will pass from one well integrated and
23 rather conservative condition through a highly unstable period to another new period of
24 balanced integration. The new balance will be reached after a great loss of genetic
25 variability” (p. 172). This line of argument, and the presuppositions he made about the
26 genetics of natural populations that supported the argument were, as we shall see, to meet
27 with significant resistance.² Mayr’s idea that speciation requires overcoming a “unity” or
28 “cohesion of the genotype” became an issue of contention, generating decades of debate.

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30 Of course, Mayr was not the only “founder” in the origins of the species problem.
31 Both Dobzhansky’s (1937) *Genetics and the Origin of Species* and Mayr’s (1942)
32 *Systematics and the Origin of Species* treat the problem of speciation as one of central
33 motivating questions of evolutionary biology, and both books are not simply summaries
34 of relevant data, but also offer programmatic statements about how best to pursue the
35 problem of speciation. If we look at the accompanying figure, it is not unreasonable to
36 see Mayr’s work as creating a bottleneck effect with respect to speciation research after
37 the Modern Synthesis. His arguments placed a good deal of weight on a family of
38 theoretical and empirical commitments that, in the end, collapsed under the weight of
39 new evidence and theoretical work by scientists, many of whom were students of
40 Dobzhansky and Mayr.

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42 How did they shape subsequent work? First and foremost, Mayr’s commitment to
43 the biological species concept (BSC) defined the problem as one of generating
44 reproductive isolation. According to Mayr, species are “groups of interbreeding natural
45 populations that are reproductively isolated from other such groups”(Mayr, 1942).
46 Similarly, Dobzhansky (1970) defines species as “systems of populations; the gene
47 exchange between these systems is limited or prevented by a reproductive isolation
48 mechanism or perhaps by a combination of such mechanisms.” Thus, the problem of
49 speciation became a problem of characterizing the mechanisms of reproductive isolation.

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² However, these arguments about sympatry vs allopatry go back to Darwin’s time and were active in the late 19th/early 20th C – e.g. in the work of David Starr Jordan. See Coyne and Orr (2003) for a discussion of this earlier history of the speciation debate.

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4 This way of narrowing the field and defining the problem had two effects. First, focus on
5 reproductive isolation made most subsequent speciation research largely irrelevant to all
6 non-sexual species, which includes a good part of the history of life on earth (before the
7 origins of sex, about 1200 mya). It also complicated the problem of how to assess
8 genuine species. For, as many plant biologists were swift to point out, hybridization was
9 extremely common in plants, and barriers to gene flow between species were much more
10 porous than Mayr insisted. Critics of the biological species concept expressed skepticism
11 about whether species in general were merely conventional categories (Ehrlich, 1961,
12 Ehrlich and Holm, 1962, 1963; Ehrlich and Raven, 1969), as well as concerns about
13 putting this concept into practice (Sokal and Crovello, 1970).

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17 Peter Raven reflects on his experience as a student entering the community of
18 plant biologists in the 1960s. He studied with Herbert Mason at Berkeley, and Harlan
19 Lewis and Margaret Lewis at UCLA, both of whom instilled in him some skepticism
20 about the ease of applicability of the biological species concept in the context of plant
21 biology:
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24 Herbert Mason – he was really a philosopher and a botanist... He taught a class
25 on phylogeny... From him I first began to develop my ideas about species.
26 [Namely:] Species are not uniform, and somewhat arbitrary constructs, without
27 particular definition... The trouble with applying the BSC species concept in
28 plants is that you can hybridize them. And mammals don't follow the BSC either.
29 There's introgression of wolves into coyotes; there was no reason to think that
30 this concept applied; it was just that Mayr was stubborn... By the time I was at
31 Stanford at the 1960s, we [plant biologists] thought Mayr was wrong... in things
32 like plants... the shorter-lived things have sharper barriers to hybridization...
33 Trees and shrubs have no barriers to hybridization – ecological barriers only.
34 They [species demarcations] are ultimately arbitrary, but that doesn't mean
35 they're not real. (Raven Interview, August 2015)
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40 According to Raven, as early as the 1960s, many plant biologists granted that in theory,
41 Mayr had provided an organizing concept of species for research. However, in practice,
42 zones of hybridization were relatively common in many plants, and it was far from clear
43 that species were as “cohesive” or genetically “unified” as Mayr supposed. In other
44 words, many plant biologists were skeptical of the narrowing of the field of speciation
45 research as Mayr had envisioned it (see Kleinman, 1999, for a discussion Anderson, a
46 plant biologist whose views on speciation also challenged Mayr's). This was the first of
47 several subsequent challenges to the theoretical cohesion of the synthesis.
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49 To be sure, by treating the problem of speciation as the problem of reproductive
50 isolation, one could thus narrow and define a research program: “a set of general
51 assumptions about the entities and processes in a domain of study, and about the
52 appropriate methods to be used for investigating the problems and constructing the
53 theories in that domain.” (Lauden, 1977, p. 81) Dobzhansky and Mayr did exactly this:
54 they not only defined “species,” but also catalogued various mechanisms of pre- and
55 postzygotic reproductive isolation, characterized the major “modes” of speciation,
56 described a family of methods of investigating speciation, and articulated a relatively
57 unified view on how common these modes of speciation were. Dobzhansky's (1937)
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4 classification of “isolating mechanisms” became a canonized and reproduced in
5 textbooks and publications. The major modes of speciation were, according to
6 Dobzhansky and Mayr, allopatry, or speciation due to geographical isolation, versus
7 sympatry, or speciation occurring within the same territory. Different mechanisms might
8 be in play in one or more of each case – ranging from the most simple (adaptive
9 evolution to novel ecological niches), to far more complex (e.g., drift, followed by radical
10 change in genetic background, making available variation for selection). Mayr and
11 Dobzhansky gave detailed summaries of the best available data of relevance to arguments
12 about the modes and mechanisms of speciation – ranging from biogeographical data to
13 ecological data on habitats, niches, extensive information on biochemical
14 polymorphisms, descriptions of karyotypes, seasonal cycles of mating, results of
15 experimental hybridization, to information regarding ethological isolating mechanisms
16 (e.g., pheromones, courtship behavior, mating calls). They argued that the major mode of
17 speciation was allopatry, or geographic isolation, followed by responses to selection to
18 novel environments. Moreover, they offered theoretical arguments that such a mode of
19 speciation was predominant. Dobzhansky devoted a chapter of his *Genetics and the*
20 *Origins of Species* to a discussion of the work of Fisher, Haldane and Wright, showing
21 the relevance of classical population genetics models to theorizing about species
22 divergence. In particular, he drew upon Wright’s idea of the adaptive landscape:
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29 If the entire ideal field of possible gene combinations is graded with respect to
30 adaptive value, we may find numerous “adaptive peaks” separated by “valleys.”
31 The “peaks” are the groups of related gene combinations that make their carriers
32 fit for survival in a given environment; the valleys are the more or less
33 unfavorable combinations. Each living species or race may be thought of as
34 occupying one of the available peaks in the field of gene combinations. The
35 evolutionary possibilities are twofold. First, a change in environment may make
36 old genotypes less fit... the species may either become extinct, or it may
37 reconstruct its genotype to arrive at the gene combinations that represent the new
38 “peaks.” The second type of evolution is for a species to find its way from one of
39 the adaptive peaks to the others in the available field...” (Dobzhansky, 1937, p.
40 187)
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44 This metaphor of the adaptive landscape, and Wright’s views about the favorable
45 conditions for evolution, shaped Dobzhansky’s views and in turn shaped subsequent
46 research into speciation. Dobzhansky cites Wright, who, in his view, “argues very
47 convincingly that the differentiation into semi-isolated colonies, is the most favorable
48 [condition] for progressive evolution.”(Ibid, p. 190). According to Dobzhansky,
49 geographical isolation of a relatively isolated ‘founder’ population could lead to fixation
50 of novel gene combinations in light of novel environmental conditions. We see here one
51 of the first articulations of the “founder” principle, drawing in part upon Wright’s views
52 about the significance of small population size in generating novel adaptive gene
53 combinations. Dobzhansky was simply transposing Wright’s shifting balance model for
54 evolution in interbreeding populations to the species level. Indeed, the “problem of
55 speciation” as articulated by both Dobzhansky and Mayr bears a striking resemblance to
56 the “problem of evolution” as Wright understood it: we require a “trial and error
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mechanism” by which populations can “shift from one adaptive peak to another.” This was all based on Wright’s assumption that non-additive effects of genes produce a multipeak landscape. Wright reasoned from the existence of epistasis to the existence of the adaptive landscape. The “peaks” on the landscape represented optimal gene combinations, or, in Mayr’s words, “harmoniously integrated gene complexes.” (Though, Mayr argued that he was far more influenced by Lerner and Wallace than Wright. He claimed no influence of Wright (Mayr, Personal correspondence, 1999). The argument that followed from this view was that with too much gene flow, any novel adaptive gene combinations would be “swamped”; so, a population should not “shift” to a new adaptive peak. These views on speciation were to have a lasting influence, well into the 1960s.

In sum, the synthesis authors can be viewed as a founder population, attempting to advance a relatively small sample of possible views on species and speciation, but nonetheless a “cohesive”, or unified theoretical and empirical stance. This was a research program, defining the study of speciation in the 20th Century in at least six ways:

1. In the questions asked
2. In the answers given
3. In terms of the relevant evidential considerations and norms of confirmation
1. In terms of the relevant theoretical considerations
2. In shaping subsequent central controversies
3. Classification of modes and mechanisms of speciation
4. Key organisms studied

Table here:

Questions	Entities:	Methods	Answers: speciation processes & mechanisms	“Standardized” key systems studied
What are the major modes of speciation? The genetics of speciation?	Species, races, subspecies, clines BSC	natural history, experimental and cytological genetic studies,	Modes of speciation: allopatry, parapatry, sympatry, peripatry (founder effects)	Heliconius, Corvus, stickleback, and Drosophila
How does biogeography affect speciation patterns?	Isolating mechanisms: allopatry, sexual selection, drift, founder effects	inbreeding studies, experimental work, theoretical models	Mechanisms: mutation, chromosomal duplication/deletion, selection, Geographic isolation / ecological factors (habitat, climate, etc.) Chromosomal duplication, deletion, Drift, Sexual selection	
Are species more likely to arise on islands or isolated places? If so, why?	reinforcement Interactive gene “complexes”	Disciplinary sources of evidence: systematics, cytology,		

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Are different lineages/clades more or less likely to speciate? Why?	The adaptive landscape	genetics, population genetics, biogeography, ecology, paleontology		
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The Modern Synthesis bequeathed to the latter half of the 20th Century an ‘integrative’ picture of the problem of speciation: shared theoretical and empirical commitments, as well as a practical sharing of intellectual resources across previously disparate domains: genetics, natural history/biogeography, the “new” systematics, zoology, ecology, and paleontology. The integration was achieved in part via a standardization of the problem space – the entities and processes to be investigated, and the methods or evidential and theoretical considerations of relevance. Dobzhansky’s experimental and field work on chromosomal changes in *Drosophila*, and work by his students, shaped decades of research on speciation. Mayr’s work on birds – and more generally, on relatively isolated island species - became paradigmatic exemplars in much of the literature as well. By creating a common language and theoretical framework, and identifying key systems for study, architects of the synthesis constrained the problem space, making robust generalizations and answers to key questions possible.

Integration – the sharing of methods, evidence, and a defined set of problems – is a great tool for moving forward in science. However, standardization of a problem space also runs the risk of oversimplification, and homogenization of what is in fact a diverse array of problems. Despite appearance of the large degree of consensus, there were in fact many open questions about the genetics of populations, the constraints that needed to be overcome for the origin of novel species, and the relative significance of different modes of speciation. The apparent consensus at the time of the synthesis treated such issues as more or less resolved: most speciation was, it was thought, due to adaptive responses to novel environments, subsequent to geographical isolation. This consensus began to be challenged by the mid-1960s, especially Mayr’s assumptions about the “homeostatic gene complexes” and the difficulty of speciation in hybrid zones, or the challenges facing the possibility of speciation in sympatry.

Speciation in Sympatry

“In sympatric speciation, premating reproductive isolation arises before a population shifts to a new niche.” (Bush, 1979, p. 352)

Guy Bush did not set out to prove Mayr wrong. In fact, Bush was first inspired to take on the problem of speciation in sympatry after writing a paper in a graduate seminar at Harvard taught by Mayr. The break with the consensus view, in other words, came from within the very home of the founder: speciation in sympatry. The title of Bush’s term paper for Mayr was, “Sympatric Speciation: a Factor in Evolution?” and Bush’s answer

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4 was a resounding “no.” Bush’s interest was in insects, and he realized that the case of
5 *Rhagoletis* – which some had argued was a persuasive case of speciation in sympatry –
6 would “provide an excellent group to study the process of host race formation while at
7 the same time allowing me to fulfill my goal to become an insect systematist.” In the
8 1860s, a natural historian and correspondent of Darwin’s, Benjamin Walsh, reported that
9 a new kind of pest had arrived on local apple trees; this was *Rhagoletis pomonella*, or the
10 apple maggot fly. Apples were newly introduced into North America; their former hosts
11 were the North American hawthorns. The fly burrows into and lays eggs in the red fruit
12 that grows on hawthorne trees, but appeared to have split from the ancestral group in
13 sympatry – or, within “cruising range” of the ancestral lineage. Mayr was deeply
14 skeptical of sympatric speciation, and was initially at least very supportive of the idea for
15 Bush’s dissertation; Bush explains: “I embarked on a mission to demolish the claims that
16 species of *Rhagoletis* had evolved by colonizing new hosts in the absence of geographic
17 isolation”(Bush, 1998, p. 429).
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21 By the time he had finished his dissertation, however, Bush became convinced of
22 the opposite view he set out to prove: “Contrary to my original views, if mate and host
23 choice were tightly correlated, new host races and eventually distinct species of
24 *Rhagoletis* could evolve sympatrically after all.” Bush ultimately argued that mate
25 recognition and host preference, as well as allochronic isolation, or differential timing of
26 mating due to different times of fruiting of hawthorne and apple, had generated a novel
27 species of *Rhagoletis* in sympatry. He needed to assume that host selection was heritable,
28 and diapause and emergence times were under genetic control, but provided these
29 assumptions were met, a new species could arise. This was absolutely in opposition to
30 Mayr’s views, which were forcefully put forward in *Animal, Species and Evolution*
31 (1963). Mayr argued that the likelihood of speciation in sympatry was very low, due to
32 the continued presence of gene flow:
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38 One would think that it should no longer be necessary to devote much time to this
39 topic, but past experience permits one to predict with confidence that the issue
40 will be raised again at regular intervals. Sympatric speciation is like the Lernean
41 Hydra which grew two heads whenever one of its old heads was cut off. There is
42 only one way in which final agreement can be reached and that is to clarify the
43 whole relevant complex of questions to such an extent that disagreement is no
44 longer possible. (Mayr, 1963, p. 451)
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48 Bush persevered, despite Mayr’s stern warning. While Mayr did not serve on his
49 dissertation committee, Bush did defend successfully at Harvard, and went to do a
50 postdoc at University of Melbourne in Australia. There he met with M.J.D. White, a
51 cytologist and evolutionary biologist, who shared his interests in insects and speciation.
52 During his postdoc, Bush and his wife collected samples of *Tephritidae*, a fly that, similar
53 to *Rhagoletis*, diversify due to specialization on specific fruit or plant species as food.
54 White and Bush together began to gather evidence against the consensus view that
55 geographical isolation was necessary for speciation. Initially, at least, this view was met
56 with either ringing silence, or severe skepticism. After presenting his first paper on
57 *Rhagoletis* at the Society for the Study of Evolution in 1966, Bush reports that
58 Dobzhansky (the chair of the session) commented that “That was an interesting story...
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4 but I don't believe it. Sympatric speciation is like the measles; everyone gets it, and we
5 all get over it" (in Bush, 1998, p. 431-2).

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7 Over the next several decades, both Bush and White amassed evidence that
8 insects, in particular, appeared to have distinctive ecological and chromosomal features
9 that made speciation in sympatry and parapatry (or in continuous ranges) possible.
10 Carefully documenting the distribution, ecology and cytogenetics of the Australian
11 morabine grasshoppers, White argued that the grasshopper, and indeed other species with
12 similar characteristics (prolific, had low vagility (relatively low mobility), and an
13 environment with very delimited niches), could diverge, even with overlapping ranges.
14 This was helped along in the grasshopper and many insects, he argued, by chromosomal
15 alterations that could forbid hybridization. Speciation could occur in a contiguous
16 population. White called this "statispatric" speciation, and argued that it was distinctive
17 due to the genetic mechanisms involved. Generalizing from this case, and drawing upon
18 the work of other cytologists such as Arason (1972, 1974), White carefully make his case
19 for speciation in insects breaking many of the rules Mayr had established. Central to the
20 argument is that different lineages, with distinctive genetics, behavior, and ecological
21 circumstances, speciate in different ways. In one of the most frequently cited articles on
22 speciation (Bush, 1975), Bush sums up the argument:
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27 ... the ways in which various groups of animals differ in these properties
28 determine, to a great extent, the mode of speciation they are most likely to follow.
29 I also reexamine the conventional wisdom that new species of sexually
30 reproducing animals arise only after a period of complete geographic isolation
31 and gradual genetic change, a viewpoint long held by most evolutionary
32 biologists. Major advances in our understanding of the relationship between the
33 structure and function of genetic systems and mechanisms of speciation in
34 different animal and plant groups now make it almost impossible to accept the
35 universality of allopatric speciation (Bush, 1975, p. 340).
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39 Theoretical work during this period, as well as experimental demonstrations of speciation
40 in sympatry (Thoday and Gibson, 1962) were equally important to overcoming resistance
41 to the very possibility of sympatric speciation. For instance, population genetic models
42 of speciation in sympatry by Maynard Smith (1966), Dickinson and Antonovics (1973)
43 and Caisse and Antonovics (1978) suggested a variety of ways in which speciation could
44 go forward.
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47 What Maynard Smith and some of these other modelers suggest is that speciation
48 in sympatry is possible when there are "modifiers" or genes associated with assortative
49 mating or habitat preferences that are linked to genes associated with adaptation to
50 specific niches. In this way, assortative mating can lead to adaptive divergence, or
51 "habitat races." However, this by itself is not sufficient for speciation; for, gene flow can
52 break down any incipient barriers to reproductive isolation (Felsenstein, 1981). Unless
53 there is tight linkage between genes associated with either habitat or mating preference,
54 speciation in sympatry is made difficult because of the antagonism between selection and
55 recombination. As selection acts to split a population, interbreeding will break up gene
56 combinations that might otherwise produce reproductive isolation. That is, there are
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4 constraints on the process of speciation that have to do not only with ecology, but the
5 genetics of populations. How might linkage between such genes become established?
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8 **Disruptive Selection, Sexual Selection and Prezygotic Isolation**

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10 By “disruptive selection,” we mean a deterministic force that generates linkage
11 disequilibrium... Several kinds of disruptive selection can lead to speciation...
12 Perhaps the simplest is spatial variation in fitness, as emphasized by proponents
13 of allopatric speciation (Mayr 1963). A second way to generate persistent
14 disruptive selection is frequency dependence... Competition between similar
15 phenotypes can also produce persistent disruptive selection through frequency
16 dependence... Sexual selection is another source of disruptive selection. ...
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20 The answer to this question, as in so many other interesting questions in biology, is sex;
21 or, perhaps, food and sex. In part in response to the controversy surrounding sympatry,
22 there was a proliferation of both empirical and theoretical work on selection associated
23 with mating or food preference might become linked, and thus accelerate speciation, even
24 with gene flow. While Bush arrived on the scene relatively early, much of the research
25 on mating preferences and their roles in speciation arrived on the scene in the last 20
26 years of the 20th Century, during which, the tide concerning the relative significance of
27 speciation in sympatry, has shifted. This was largely due to the discovery of how
28 common mating preferences and correlated characters could come to coevolve in nature.
29 In addition to the case of *Rhagoletis*, cichlid fish flocks in African crater lakes appeared
30 to present a vivid case of sympatric speciation (Schliewen et al. 1994; Feder et al. 1988,
31 1994; Filchak et al. 2000). In addition, theoretic models of sympatric speciation have
32 become more sophisticated, incorporating multilocus genetics and more or less realistic
33 ecological context (e.g., Kondrashov 1983a,b, 1986; Rice 1984; Doebeli 1996;
34 Kondrashov et al. 1998; Kondrashov and Kondrashov 1999; Dieckmann and Doebeli
35 1999).
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41 As one might imagine, this theoretical work was viewed with a great deal of skepticism,
42 as “disruptive” by Ernst Mayr. As late as 1999, Mayr granted that Bush may have been
43 right, but was still rather skeptical of the frequency or importance of speciation in
44 sympatry. Nonetheless, what much of this modeling work has elaborated upon is how
45 disruptive selection alone can lead to reproductive isolation, and especially so if that
46 character is associated with mating (whether mating preference, behavior, or timing). In
47 this vein, a vivid description comes from Kirkpatrick and Ravigne (2002):
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50 Sexual selection has fundamentally different consequences for speciation
51 than does natural selection. Sexual selection is more effective in generating
52 disequilibria and hence new species. The reason is that recombination frustrates
53 natural selection by breaking apart favorable combinations of alleles. Nonrandom
54 mating, however, brings together alleles at different loci, which allows
55 recombination to unite them in a single gamete. Recombination therefore helps to
56 generate, rather than break down, the disequilibria favored by nonrandom mating.
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4 Disruptive natural selection on a polygenic character causes a population to split into two
5 reproductively isolated populations. Prezygotic reproductive isolation in these models
6 builds up in either of two ways: first, the trait under disruptive selection simultaneously
7 serves as a basis for assortative mating. Rhagoletis is a vivid example: preference for a
8 fruit and mating occur in the same place and are so associated. Thus, genotypes with
9 intermediate values of the mating trait are directly selected against. In two-trait, or
10 double-variation, models, the trait under selection does not influence mating; instead,
11 assortative mating occurs for a second trait, and the alleles controlling that trait develop
12 chance associations with alleles affecting the selected trait, genotypes with intermediate
13 values are disruptively selected against. An example might be bright coloring in cichlid
14 fish; that is, it may happen to be the case that a bright red or blue coloring on the males
15 came to be associated genes associated with traits that affect food preferences: feeding in
16 either deep or shallow water might come to be associated with red or blue coloring, and
17 so could lead to divergent species in a cichlid fish flock. Such conditions could happen
18 as a matter of chance – traits that affect choice of mate might by chance be linked to
19 genes associated with a variety of other traits – or, they could be linked via a common
20 selective condition. E.g., blue might become more visible in some areas of the lake than
21 others, and the reverse for red coloring. A variety of ingenious experimental tests were
22 set up to try out one or more of these hypotheses (see, e.g., Rice and Hostert, 1993, for a
23 review). However, laboratory experiments can only demonstrate what is possible, not
24 what actually occurs, or how frequently, in the wild. As Kirkpatrick and Ravigne (2002)
25 reported in their review of the literature on disruptive selection, and in particular, the
26 relative roles of selection and drift, what was really needed to test these hypotheses was
27 genetic data: “One hope for resolving this issue is the prospect of locating the genes
28 responsible for prezygotic isolation. Both direct and indirect selection should leave their
29 signatures there in patterns of nucleotide divergence and polymorphism. Conversely,
30 sequence data consistent with divergence by drift would call into question the role of
31 selection in speciation.”(2002, p. S30).

39 **Genetic Distance:**

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42 “In a study of the number of gene differences between related species, Nei (1971)
43 developed a statistical method for estimating the number of codon differences per
44 gene and the divergence time between closely related species. This method
45 utilizes electrophoretic data on protein identity between different species. A
46 similar method was used independently by Kimura and Ohta (1971) for
47 estimating the divergence time between two subspecies...” (Nei, 1972, p. 283)
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51 At the same time that this theoretical work on speciation in sympatry was coming on
52 board, a sea change in the view of the adaptive integration of genes in an interbreeding
53 population was underway. As a result, the 1960s and 70s were a heady time for
54 speciation research. Lewontin and Hubby’s (1966) work on electrophoretic gels
55 challenged many assumptions about genetic variation in interbreeding populations.
56 According to Felsenstein:
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4 As soon as their paper appeared, it was immediately obvious that the field was
5 transformed: where there had been little data, there was now a lot. A wave
6 excitement swept population genetics, and extravagant promises were made
7 (Felsenstein, in Singh and Krimbas, 2000, p. 612)
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10 As a graduate student, Alan Templeton recalls feeling that “Electrophoresis changed
11 things in a fundamental way... suddenly it was possible to study variation within and
12 between species directly...” (Templeton Interview, 2015). Direct examination of the
13 genetics of speciation would be – it was thought – finally possible. Prior to this period,
14 natural history, biogeography, cytology, experimental work on hybridization, and
15 theoretical modeling were the main tools for investigating speciation. Barton concurs:
16 “The really big change was Lewontin and Hubby’s electrophoretic data. It was still quite
17 hard work. The electrophoretic data stimulated studies describing variation across a very
18 wide range of species, and generated the data on genetic distance that Coyne & Orr used
19 in their classic paper. .”(Barton interview, 2015).
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23 In other words, both new tools for sampling genetic variation in populations made
24 available in the 60s and 70s, and new ways of thinking about the extent and nature of that
25 variation, opened a new frontier for investigating the genetics of speciation. Prior to this
26 time, competing views of the genetics of populations were based on indirect inferences
27 from breeding experiments, cytology, and theoretical population genetics. Such indirect
28 inferences led to two competing schools of thought on the genetics of populations: the
29 “balance” school (represented by Dobzhansky and Sturtevant, for instance) as opposed to
30 the “classical” school (represented by Muller and Morgan) differed over whether
31 populations were highly polymorphic (balance) or relatively uniform (classical) at the
32 genetic level (Dietrich, 1998).
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35 This divide over the character of the genetics of populations was radically
36 reconfigured as new work on protein electrophoresis suggested to Kimura (1968) and
37 King and Jukes (1969) that, at the molecular level, most genetic substitutions were
38 relatively neutral with respect to fitness. The “neutral theory of molecular evolution,” as
39 it came to be called, had two significant effects on the speciation literature: it forced
40 reconsideration of longstanding assumptions about the genetic structure of populations
41 (assumptions that at least in part drove Mayr’s views on the significance of
42 “homeostatic” gene complexes), and led to new tools for testing hypotheses about genetic
43 “distance” between populations.
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46 That is, as a result of the rise of the neutral theory, and associated tools and
47 technologies, molecular biologists began to have a very significant influence on the
48 speciation literature. Nei (1971, 1972) used electrophoretic data on protein identity
49 between species as a measure of estimating divergence time between species. This
50 became a tool to test competing hypotheses about speciation in both wild and laboratory
51 populations. With the availability of Nei’s genetic distance, one could test various
52 hypotheses about the genetic bases of these species differences more directly. As is
53 evident in the accompanying figure, this tool became a central “node” around which
54 much of the work on not only theoretical and empirical work on speciation, but also
55 systematics and phylogenetic reconstruction, developed.
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58 For instance, in a hugely influential paper in 1988, Coyne and Orr (1988) used
59 electrophoretic genetic distance to investigate extent of reproductive isolation in different
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4 lineages of *Drosophila*. The paper was a landmark paper because it drew upon this new
5 genetic data to give more precise, quantitative answers to questions such as “How rapidly
6 does reproductive isolation evolve?” “Do pre- and post-zygotic isolation evolve at the
7 same rate?” Or, “How does postzygotic isolation increase with time?” Previously, the
8 only data available to answer such questions were biogeographical data (patterns of
9 distribution of species) and experimental crosses.

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11 Perhaps more important than the tool, however, was a rethinking of the genetics
12 underlying species differences. The new genetic data allowed evolutionary biologists to
13 reconceive the object of explanation, or achieve some distance from the presuppositions
14 of the genetics of population shared by synthesis founders, particularly about
15 “homeostasis” and “cohesion” of the gene pool. The neutral theory prompted a
16 rethinking of the genetics of populations, and of speciation. In other words, it gave
17 researchers some distance from presuppositions that had governed speciation research
18 since the modern synthesis.
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22 **Transilience:**

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25 “I distinguish between two basic speciation mechanisms: transilience and
26 divergence. A speciation mechanism will be classified as a transilience if the
27 isolating barriers depend upon a genetic discontinuity characterized by extreme
28 instability of the intermediate stages. The source of the instability lies in the
29 nature of the genetic system itself... the transilience cannot be induced by
30 selection alone; indeed it is characterized by *overcoming* some selective barrier.”
31 (Templeton, 1980, p. 720).
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35 Alan Templeton played an important role in this period via development of what he
36 called the “transilience” model. Recall that “founder effect” is when, following a founder
37 event, (the isolation of a small “founder population,”) reduction in population size can
38 lead to the reduction of genetic variability, changing the adaptive value of various gene
39 combinations, and, eventually, reproductive isolation. Mayr called this process a
40 “genetic revolution.”
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42 Mayr observed that many unique varieties of birds were recent colonists of the
43 remoter islands in New Guinea. He argued that speciation was more likely in small,
44 isolated subpopulations, since he believed that large panmictic species possess “genetic
45 homeostasis,” or “evolutionary inertia.” In his words, species possess “a limited number
46 of highly successful epigenetic systems and homeostatic devices, which place a severe
47 restraint on genetic and phenotypic change.” The way in which this constraint might be
48 overcome, according to Mayr is either with geographical isolation, novel environments
49 and time, or genetic bottlenecks. Population bottlenecks could occasion what Mayr
50 called a “genetic revolution”— the generation of a novel “homeostatic gene complex.”
51 Isolation and reduction of population size and genetic variation in particular, in Mayr’s
52 view, was a necessary first step in “emancipating” founder populations, insofar as loss of
53 variation in founder populations would change selection pressures, and might eventuate
54 in a new adaptive gene combination.
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58 Templeton (1981) argued that the genetic effects of founder events might lead to
59 novel selection pressures for some alleles on otherwise homogeneous genetic
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4 backgrounds. This could trigger changes at other loci, with effects cascading through the
5 epistatic genetic system, eventually leading to reproductive isolation (Templeton, 1980,
6 p. 1015). He called this “transilience”:
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9 I chose transilience deliberately. “Genetic revolution” by that time had a lot of
10 baggage with it... I wanted to get away from the idea that genetic revolution
11 involved the whole genome... If you look at Mayr’s paper, he’s got the diagram
12 where the variation plummets to zero. But, I was influenced by a paper by Nei –
13 looking at founder events and bottleneck effects, where you don’t lose a lot of
14 heterozygosity... The flaw I saw in Mayr’s work was that Mayr was having
15 populations lose genetic variation at the same time that they were responding to
16 selection. It’s inevitable in founder effects that you’re going to have shifts in
17 epistasis. If you look at a single locus, the fitness can shift dramatically
18 depending on the genetic background; Mayr was thinking on the individual level,
19 I shifted it up to the population. (Templeton Interview, 2015)
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24 Templeton’s transilience model was a far more theoretically sophisticated model of the
25 evolutionary genetics of speciation than Mayr’s “genetic revolution.” Templeton argued
26 that just by changing allele frequencies, you could change how selection is acting:
27 “You’re still playing with the same players, but the impact of natural selection changes
28 dramatically.”(Templeton Interview, 2015). Templeton’s work was one of a series of
29 papers that explored the possibility and limits of a founder effect model.
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31 Templeton partnered with Carson (1984) to defend a “founder-flush” model of
32 speciation in *Drosophila* in the Hawaiian islands. On this model, populations would
33 grow quickly, thus (in principle) addressing the problem of a dramatic loss of variation
34 that comes with a genetic bottleneck. Carson had been collecting and documenting the
35 enormous diversity of the Hawaiian *Drosophila* for years before Templeton came to work
36 with him at Washington University. The work was original and important, in that it
37 combined population genetic models, biogeographical work on species distribution, and
38 genetic data. Critics of the work argued that the “flush” stage was an ad hoc assumption,
39 however.
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43 **Tension Zones**

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45 “We believe that most hybrid zones are in fact ‘tension zones’, which we define
46 as clines maintained by a balance between random dispersal and selection against
47 hybrids.” (Barton and Hewitt, 1989)
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50 Not all agreed with Carson and Templeton’s conclusions. In fact, the 1980s and 90s
51 became a period of controversy over the evolutionary genetics of speciation. As a
52 consequence, there was both a diversification of views, as well as a growth in empirical
53 case studies, in speciation, yielding a new appreciation for the “richness and exciting
54 complexity of speciation processes”(Dieckmann, et. al., 2012, p. 383).
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56 This diversification was in part due to competing views fighting for authority over
57 the mechanisms and relative significance different mechanisms and models of speciation.
58 There was, in fact, a renaissance of thinking about the theoretical basis of the genetics of
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4 speciation, and the possibility of speciation under conditions other than geographical
5 isolation. For instance, in one of the most widely cited papers in the 1980s, Barton and
6 Charlesworth argue quite forcefully that:
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9 ...although founder effects may cause speciation under sufficiently stringent
10 conditions, they are only one extreme of a continuous range of possibilities.
11 Complete geographic isolation is unnecessary; absolute coadaptation between
12 "closed" systems of alleles is unlikely; and divergence may be driven in a variety
13 of ways, without the need for drastic external changes. Reproductive isolation is
14 most likely to be built up gradually, in a series of small steps. Inference from
15 nature or from laboratory experiments is difficult, and much of the evidence that
16 has been used to support founder effect models seems ambiguous. (Barton and
17 Charlesworth, 1984, p. 134).
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21 What is striking about this argument is that it runs almost entirely contrary to the
22 "received" wisdom of Mayr. No longer could it be accepted as a matter of course that
23 "genetic systems" were coadapted. This more or less removed Mayr's rationale in favor
24 of treating reproductive isolation as necessary, or founder events as optimal, for
25 speciation. Barton and Charlesworth demonstrated when and how hybrid zones could,
26 over time, lead to reproductively isolated groups. Their argument is, by and large,
27 theoretical; they show that "the probability that strong reproductive isolation evolves in a
28 single founder event is low under most circumstances."
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31 Barton initially entered into the debate about founder effect via his interest in
32 hybrid zones (Barton Interview, 2015). He was inspired by White (1968) and Endler's
33 (1977) work on clinal populations and hybrid zones. If, as their work suggested,
34 speciation with gene flow was possible, then how was it possible? How might the
35 balance between selection and migration shape speciation in clinal populations? What
36 were the relative importance of genetic incompatibilities, local ecology, and behavioral
37 factors in generating and in maintaining the genetic integrity of taxa? These questions
38 were very much in the air in the 1980s: how common was speciation with gene flow? A
39 flourishing literature developed at this time, suggesting various modes and mechanisms
40 of speciation that had been overshadowed by the overwhelming emphasis on speciation
41 in allopatry. For instance, West-Eberhard (1983) compiled a massive review of both
42 empirical and theoretical support for the possibility of speciation via "social competition"
43 – including, but not limited to, sexual selection and competition for mates. This led to a
44 renaissance of work on behavioral isolating mechanisms.
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48 Arguably, theoretical work drove a lot of the debate over speciation with gene
49 flow, even more so than advances in genetic methods or experimental techniques, or any
50 empirical case study per se. For much of the debate was about relative significance of
51 various mechanisms (cf. Beatty, 1997). Barton argues, "What is most remarkable
52 perhaps is that the discovery of the molecular basis of genetics in the 1960s has had little
53 effect on the intellectual framework of evolutionary biology. It opens up
54 an extraordinary amount of genetic data, and also all kinds of
55 fascinating "molecular natural history". But, the main advances in speciation have
56 depended on ideas and methods that date from the 1930s - speciation genetics in
57 *Drosophila*, studies of clines, understanding Haldane's Rule, and so on." (Barton
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4 Interview, 2015) We will turn to these advances in turn: first, the debate over founder
5 effect, next speciation genetics in *Drosophila* and studies of clines, and last, Haldane's
6 rule.
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8 In 1984, Barton and Charlesworth co-authored an influential review, responding
9 to Mayr, Templeton and Carson's arguments above founder effect. Barton and
10 Charlesworth argued that:
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12 ... it's extremely unlikely that [speciation] is going to happen in a single founder
13 event... the idea is you have two alternative stable states, each of which is
14 associated with good fitness. In between you have the hybrid, which has low
15 fitness. In order for random genetic drift to get you from state one to state 2, you
16 have to go through a valley of low fitness. The deeper that valley, the more
17 difficult a random process is likely to pass you from state one to state 2.
18 (Charlesworth Interview, 2015)
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22 That is, Charlesworth and Barton (1984), and Barton (1989) argued that the conditions
23 required for founder effect to work are very restrictive. This is because the chance of such
24 a shift occurring via drift decreases with population size and depth of valley. In other
25 words, the smaller the population size, the less likely the chance that the shift will occur;
26 but, drift is more significant in smaller populations. In sum, the conditions for peak
27 shifting via drift are unlikely to be met.
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30 Central to the dispute over founder models were more fundamental disagreements
31 about the genetics of populations, the significance of epistasis, and the strength of
32 adaptive 'integration' of genetics in populations. These can be traced back to the modern
33 synthesis, and even earlier. Barton explains, "People got kind of obsessed with Wright's
34 compelling image of an "adaptive landscape"(Barton interview, 2015). Wright's image
35 of the stable, co-evolved gene combinations yielding stable species and populations
36 shaped a research tradition that emphasized the role of epistatic interaction among genes.
37 Appeal to Wright's metaphorical descriptions of the relative "plasticity" of populations in
38 their response to selection suggested to some that special conditions needed to be in place
39 for speciation to occur. One such special condition was isolation and founder effect. In
40 contrast, Fisher argued that any number of means of "traversing" the genetic landscape
41 were plausible. This is in large part because Fisher imagined that there were multiple
42 different "dimensions" of the landscape – indeed, a potentially infinite number of ways in
43 which selection alone could permit populations to shift to new "adaptive peaks." This
44 was first mentioned in correspondence with Wright, which Wright actually conceded
45 (Fisher's correspondence to Wright May 31, 1931, cited in Provine 1986, 274; Fisher
46 1941).
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51 A theoretical solution to the problem of how species could evolve hybrid sterility
52 without passing through an was already available in the work of Bateson (1909) Muller
53 (1939, 1940, 1942) and Dobzhansky (1936), sometimes called the "Bateson-Dobzhansky-
54 Muller" model. Orr (1995) gives an excellent summary of the model:
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57 This fundamental problem was finally solved by Dobzhansky (1936) and Muller
58 (1939, 1940) early in the modern synthesis. Each produced genetic models
59 showing that two populations could come to produce completely sterile or
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4 inviable hybrids even when no substitution caused any sterility or inviability
5 within either population. Their models were very simple: two allopatric
6 populations begin with identical genotypes at two loci (aa, 66). In one population,
7 an A allele appears and is fixed; the Aabb and AAAb genotypes are perfectly
8 viable and fertile. In the other population, a B mutation appears and is fixed; aaBb
9 and aaBB are also viable and fertile. The critical point is that, although the B
10 allele is compatible with a, it has not been “tested” on an A genetic background. It
11 is thus possible that B has a deleterious effect that appears only when A is present.
12 If the two populations meet and hybridize, the resulting AaBb hybrid may be
13 inviable or sterile. (Orr, 1995, p. 1805)
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19 Experimental and theoretical work in the 1980s and 90s demonstrated that not only that
20 this picture of the evolution of reproductive incompatibility possible, its likelihood could
21 be increased under a variety of different conditions (see, e.g, Orr, 1995). Contrary to
22 Mayr’s assumptions, speciating populations need not cross fitness valleys to evolve
23 reproductive isolation.
24

25 At the same time, there was mounting experimental evidence for the role of
26 disruptive selection in speciation, even without geographic isolation. For instance, Rice
27 and Salt (1988) were able to generate incipient reproductive isolation in sympatry, by
28 selecting strains of *Drosophila* that mated preferentially in different habitats. This work
29 both challenged and refined many of the assumptions that informed the founders of the
30 modern synthesis. What the work of Barton, Charlesworth, Coyne, Orr, and others in the
31 1980s and 90s suggested is that while there are a variety of ways in which speciation can
32 go forward, there are some modes of speciation that are more or less likely, given the
33 frequency with which one might expect initial conditions to hold. Moreover, there was
34 growing awareness that one can think about mechanisms that both prevent and promote
35 speciation operating at both the phenotypic and genotypic level. Barton explains: “You
36 can think of it at two levels: genotype and phenotype. Think of a single trait under
37 stabilizing selection: at the underlying genetic level, many combinations of genes can
38 produce that phenotype – and so shifts between adaptive peaks need not involve changes
39 at the phenotypic level... The shifting balance idea didn’t depend upon there being peak
40 shifts at the trait level. You can also think of peak shifts involving traits under disruptive
41 selection. In the 1984 paper, I was exploring both kinds... .. Mayr was emphasizing
42 interaction. Everyone would accept that there’s a lot of interaction at the physiological
43 level. However, that doesn’t imply that you cannot make small adjustments and
44 incremental progress [at the genetic level]” (Barton interview, 2015).
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49 Barton’s views notwithstanding, there was a growing raft of data that seemed to
50 suggest that the barriers to speciation Mayr imagined were simply not there. By way of
51 just a few vivid examples: Careful work on cichlid fish in African lakes demonstrated
52 that a single ancestral population gave rise to a diverse array of species, due only to
53 unique selective conditions (Meyer, et. al., 1990). Speciation in sympatry was suspected
54 in this case, and sexual selection may have driven this as well. The the barriers to
55 speciation due to gene flow simply did not exist as Mayr envisioned them.
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58 In sum, both theoretical and empirical work in the 1980s and 90s opened up the
59 possibility that even if there may be many genes in interaction in development, there is in
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4 fact a great deal of “give” between the genetic and phenotypic level. The possibility of
5 divergence between populations and the emergence of reproductive isolation did not
6 require such a radical transformation in the genetics of populations as Mayr and
7 Dobzhansky had argued.
8

9 Indeed, today, talk of “speciation genes” suggests that one or a few relatively
10 minor genetic changes could lead to reproductive isolation in some contexts. While the
11 Modern Synthesis brought together the micro- and the macro-, genetics and phenotypic
12 change, it also tied them together far more closely than was warranted by the evidence.
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15 **Conclusions and Open Questions**

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17 The founders of the modern synthesis defined species and the problem of
18 speciation, which in turn shaped the tools and methods appropriate, relevant evidence,
19 theoretical considerations, answers given, and key organisms studied. Because of their
20 own research interests and backgrounds, Mayr and Dobzhansky both focused primarily
21 on sexual species, devoting relatively little attention to plants, and none to the diversity of
22 microbial life. To be sure, Stebbins was very important in the synthesis, and later
23 Antonovics’ work was important for understanding that populations could speciate in
24 parapatry – both worked with plants. However, architects like Mayr were concerned to
25 present a relatively “cohesive” picture of speciation theory. In many ways, the modern
26 synthesis is as much a story of exclusion as inclusion (see, e.g., Dietrich, 1995;
27 Kleinman, 1999, 2009). Shoring up a consensus view involved adopting a relatively
28 narrow field of vision. The synthesis defined the study of speciation in the 20th Century in
29 at least six ways:
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- 33 5. In the questions asked
 - 34 6. In the answers given
 - 35 7. In terms of the relevant evidential considerations and norms of confirmation
 - 36 8. In terms of the relevant theoretical considerations
 - 37 9. In shaping subsequent central controversies
 - 38 10. Key organisms studied
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42 However, despite an appearance of consensus, as early as the 1960s, there was, in fact, a
43 diversity of views about everything from the nature of species to competing
44 presuppositions about the genetics of natural populations, to appropriate methods of
45 investigation – e.g., the relative importance of natural history, biogeography, and
46 theoretical population genetics. In other words, under the “veil” of integrative or
47 synthetic agreement on some fundamental principles were many disputed open questions.
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49 Current open questions concern the character of species, the genetics of hybrid
50 zones, the ongoing debates over the relative importance of different mechanisms and
51 modes of speciation, the extent of epistatic interactions between genes, the relative
52 importance of adaptive divergence versus drift, the relative roles of sexual and natural
53 selection, the ecological conditions that promote speciation, the possible role of
54 “reinforcement” in speciation, the importance of hybridization, particularly in plants, the
55 possibility of speciation “genes” driving change, the role of phenotypic plasticity, the
56 biases in the literature produced by focus on specific model organisms, such as
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4 *Drosophila*, and the genomic bases of reproductive isolation, the possibility of a “semi-
5 permeable genome”, and so on.

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7 The case of this research program highlights an important paradox. On the one
8 hand, conformity is effective: agreed upon definitions of common terms and problems
9 enabled scientific workers with very different presuppositions, methods, and evidence, to
10 share their work and learn from one another. On the other hand, however, disagreements
11 over open questions – sometimes quite heated – were exactly why speciation became
12 such a booming area of research in subsequent decades. The disagreements fueled
13 research well into the late 20th and early 21st century. Indeed, disputes about speciation in
14 part fueled research in neighboring fields, on questions ranging from the extent and
15 nature of genetic variation, to the pertinence of molecular biology and genetics to
16 evolutionary theory, to the problem of apparently neutral variation. Protein
17 electrophoresis, the discovery of such extensive amounts of genetic variation, and
18 accompanying debates about whether and how such genetic variation was maintained,
19 was arguably what in part spurred the almost exponential increase in literature around
20 speciation in the 1980s and 90s.
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