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Insect Speciation Rules: Unifying Concepts in Speciation Research

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selection-recombination antagonism, species boundary continuum

Abstract

The study of speciation is concerned with understanding the connection between causes of divergent evolution and the origin and maintenance of barriers to gene exchange between incipient species. Although the field has historically focused either on examples of recent divergence and its causes or on the genetic basis of reproductive isolation between already divergent species, current efforts seek to unify these two approaches. Here we integrate these perspectives through a discussion of recent progress in several insect speciation model systems. We focus on the evolution of speciation phenotypes in each system (i.e., those phenotypes causally involved in reducing gene flow between incipient species), drawing an explicit connection between cause and effect (process and pattern). We emphasize emerging insights into the genomic architecture of speciation as well as timely areas for future research.

Speciation

phenotype: a trait whose divergence contributes, directly or indirectly, to a reduction in gene flow during speciation

INTRODUCTION

The promise of discovering general principles to explain the origin of species has inspired students of speciation since Darwin. Insects offer among the best, if not the best, systems with which to study the multitude of processes that cause speciation. This is, in part, due to the tremendous diversity of insect taxa that offer representative “models” for the study of distinct mechanisms of speciation, thus capturing the diversity of process that is the hallmark of evolution and speciation. In addition, insect models often come with practical advantages. Insects can frequently be reared in the lab; present the possibility of hybridizing races, subspecies, or species for genetic studies of natural variation; and enable the study of large samples for hypothesis testing. The most comprehensive and convincing studies of speciation garner evidence in the testing of specific hypotheses from a diversity of disciplines, including ecology, phylogenetics, evolutionary process, behavioral ecology, genetics, and genomics. As such, insects have served prominently in the development of these approaches.

The identification of general causes of speciation, in insects or any taxon, has been a difficult and elusive task, however, for several reasons. First, speciation occurs within lineages characterized by unique biological and demographic characteristics, complicating the identification of common processes in diverse taxa. Second, as with evolution in general, multiple mechanisms, rarely acting alone, are involved in speciation (34). Third, universal definitions of species entities have evaded evolutionary biologists for decades, at least in part owing to the first two impediments discussed above.

Despite the multifarious nature of the speciation process and its varied taxonomic outcomes, many argue that species have one key feature in common—reproductive (or genetic) isolation from other species. Mayr (108) argued fervently that this characteristic is basic to species-level diversity and is the defining criterion of species rank (under the biological species concept), where species are groups of organisms that are reproductively isolated from other such groups. Some have even gone so far as to assert that understanding the origin of species is equivalent to understanding the origins of reproductive isolation (23).

Many have argued that the emphasis on reproductive isolation in the study of speciation has come at a cost, however (72, 146). An alternative approach is to place intellectual emphasis on the evolutionary processes that cause lineage divergence, a tradition traceable to Darwin’s *On the Origin of Species* (28). Such an emphasis is not without precedence, as many models focus explicitly on phenotypic divergence (e.g., divergent natural and/or sexual selection) (173). Moreover, other speciation models focus on population genetic consequences of changing demographics and genetic drift (64). Although these models explicate mechanisms of character differentiation and cladogenesis, they typically do not make an explicit connection to reproductive isolation. Thus, the evolution of taxon diversity, as opposed to the effect of divergence on genetic cohesion, is modeled.

It is not hard to see that prevailing species concepts loosely align with this duality. On the one hand, the biological species concept emphasizes future reproductive isolation as paramount to species status. Research emphasis is placed on the tractable question, What is the nature and origin of reproductive incompatibility? On the other hand, concepts such as the phylogenetic species concept or the ecological species concept emphasize the origins of differentiation. In such approaches, research emphasis is placed on the tractable question, What is the history and consequence of character change? The current conceptual challenge in the study of speciation is to bring these two perspectives together to ask, What is the history and consequence of character change that has resulted in the severance of gene flow between species?

Previously, we argued that the study of “speciation phenotypes” leverages a conceptual framework for connecting pattern and process in speciation (146, 147). This approach shifts emphasis

away from efforts to characterize the genetic basis of reproductive isolation, which may reflect historical causes of speciation, to the characterization of diverging phenotypes of incipient species, the evolutionary forces causing those phenotypes to evolve, and the consequences (whether direct or indirect) of this phenotypic divergence to contemporary patterns of gene flow. Although single studies of speciation are unlikely to achieve this result, we suggest that a comprehensive understanding of the speciation process requires demonstrating (*a*) axes of differentiation, (*b*) speciation phenotypes (i.e., traits whose divergence contributes directly or indirectly to a depression of gene flow), (*c*) which evolutionary forces cause the divergence of a speciation phenotype, (*d*) the genetic architecture underlying the speciation phenotype, and (*e*) how speciation phenotypes trigger further genome evolution and the establishment of species boundaries.

Here we highlight a diversity of insect speciation models to evaluate the progress in the study of speciation phenotypes. We discuss the patterns and processes of speciation in key taxa with guidance from the conceptual framework outlined above. We also suggest where future research is needed to generate a richer, more integrative view of the speciation process.

Genetic architecture:
the underlying genetic
basis of a phenotypic
trait

HELICONIUS BUTTERFLIES

Heliconius butterflies display a stunning diversity of brightly colored wing patterns, which act as adaptive signals to warn potential predators of their unpalatability (**Figure 1a**). Color pattern divergence, resulting from predator-imposed selection to match different unpalatable mimicry models (99), isolates populations and species of *Heliconius* in at least two ways. First, color patterns act as mate recognition cues, and male mate preferences often lead to strong assortative mating among individuals that share similar wing pattern phenotypes (20, 77, 84). Second, hybrid offspring typically have recombinant, nonmimetic wing patterns that are subject to intense predation (80, 97).

Axes of Differentiation

Although color pattern divergence and mate preference evolution are the most well-understood axes of differentiation within the *Heliconius* radiation, host-plant use and microhabitat choice also differ between closely related species. For example, *Heliconius melpomene* and *Heliconius cydno* are recently derived sister species that occasionally hybridize (98) but remain distinct and broadly sympatric throughout a large portion of the Neotropics. There is substantial racial diversity among populations of *H. melpomene* and *H. cydno*, which tracks, respectively, with geographic variation in the Müllerian wing pattern phenotypes of *Heliconius erato* and *Heliconius sapho*/*Heliconius eleuchia* (10). Mimetic convergence between distantly related species pairs of *Heliconius*, one from each of two major subclades (pupal mating/ESS clade versus nonpupal mating/MCS clade) (159), is typical of the genus. In this case, each pair of “comimics” also differs in their use of microhabitat (*H. melpomene* and *H. erato*, open areas, versus *H. cydno* and *H. sapho*, forest understory) (36), larval morphology (11), and patterns of host-plant utilization (153).

Identifying Speciation Phenotypes

Predation against novel color patterns generates geographically divergent selection among intraspecific racial populations of *Heliconius* and, as a result, leads to a reduction in gene flow due to extrinsic hybrid inviability (96). Color pattern divergence is also directly tied to the evolution of premating isolation in *Heliconius*, at both the intra- and interspecific levels, owing to divergence in male preference for wing color pattern cues (77, 109, 112, 113). Male mate choice in *Heliconius*, in turn, may coevolve with color pattern as a function of (*a*) direct selection of alleles at preference

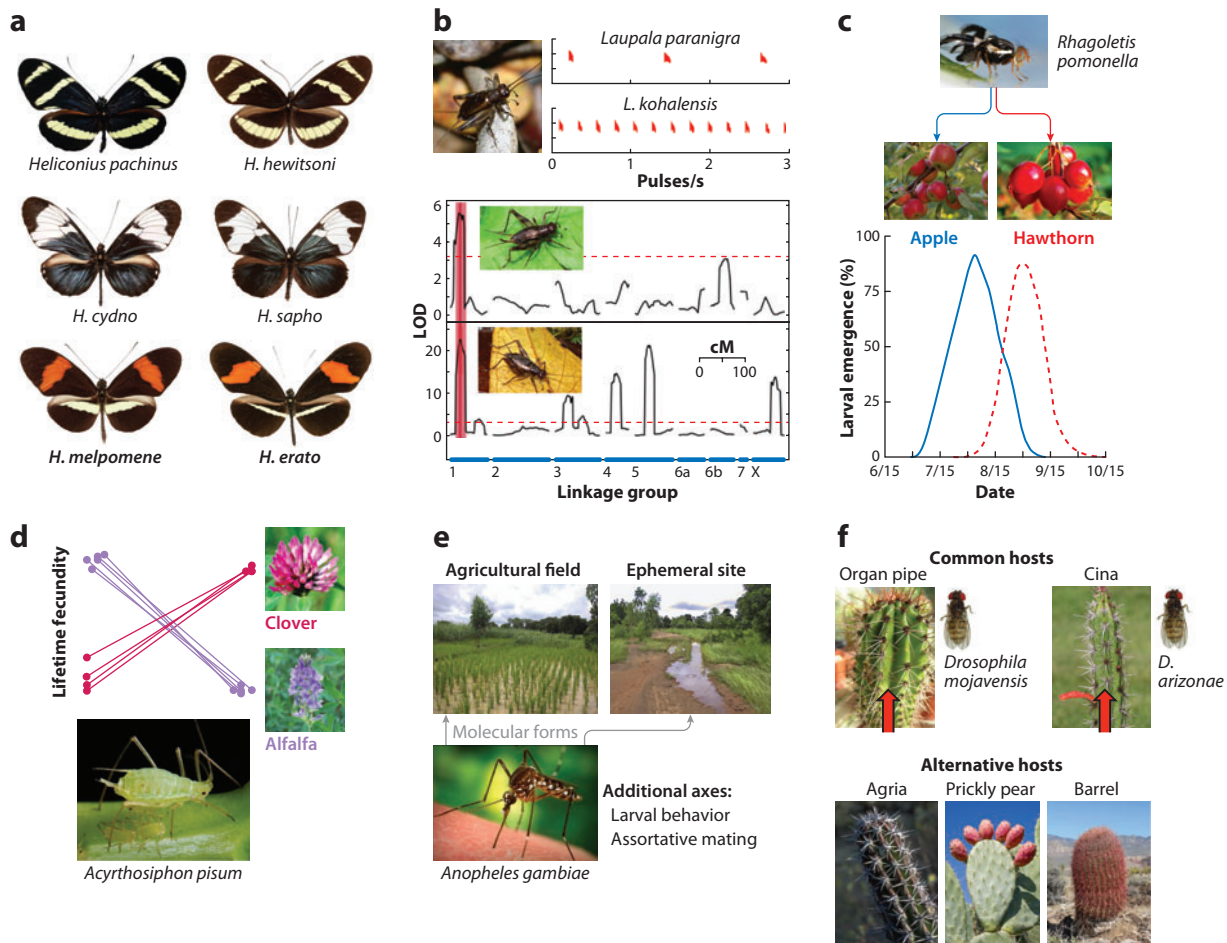


Figure 1

Axes of differentiation and candidate speciation phenotypes. (a) *Heliconius* butterflies displaying convergent (columns) and divergent (rows) Müllerian wing patterns. (b) Acoustic divergence among two species of Hawaiian *Laupala* crickets (top), and colocalization of QTL for female preference and male song (reproduced with permission from Reference 145). Red dashed lines indicate the 5% significance threshold based on permutation. (c) Host races of *Rhyacionia pomonella* depicting peak larval emergence from *Malus pumila* apple and *Crataegus* hawthorn (modified with permission from Reference 56). (d) Lifetime fecundity of *Acyrthosiphon pisum* (pea aphids) feeding on *Trifolium pratense* (red clover) and *Medicago sativa* (alfalfa) (modified with permission from Reference 17). (e) Larval habitat and behavioral divergence associated with ephemeral or permanent oviposition sites (photos courtesy of C. Constantini). (f) Divergence in host utilization among geographic races of cactophilic *Drosophila* species. Abbreviations: cM, centimorgan (distance based on the recombination frequency between markers); LOD, logarithm of the odds (to the base 10). A LOD score of 3 or more is generally taken to indicate that two markers are close to each other on a chromosome. A LOD score of 3 means the odds are a thousand to one in favor of genetic linkage.

loci, (b) correlated evolution with locally adapted mating choice signals, or (c) disruptive sexual or ecological selection against hybrids (85). Evidence suggests that *Heliconius* color patterning loci are tightly linked to alleles underlying variation in male preference (86) as well as female mating outcome and hybrid sterility (112). This is important because tight physical linkage reduces recombination between loci underlying adaptive traits and their associated preferences and may facilitate the maintenance of positive assortative mating in this system.

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

As discussed above, color pattern divergence among geographical races of *Heliconius* comimics is driven by purifying selection for local mimetic convergence, the associated evolution of male mate preferences, and strong disruptive selection against nonmimetic, recombinant hybrid phenotypes (77, 100, 109). Divergence time estimates for the Müllerian comimics, *H. erato* and *H. melpomene*, predate the Last Glacial Maximum (9), and historical inferences of population demography suggest that *H. melpomene* diversified more recently than did *H. erato* (57). These findings have been interpreted as evidence that the resemblance between geographic races of these two species reflects mimetic “advergence” by *H. melpomene* onto the pre-existing template of *H. erato* warning patterns (131), rather than phylogenetic codivergence of the two species. However, the initial evolution of warning color patterns remains controversial (95).

Adaptive introgression: the selectively favored movement of alleles from one species or population into the genetic background of another via the process of hybridization

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

Heliconius color patterns are controlled by a small number of major Mendelian loci (148) that underlie the evolution of both convergent and divergent mimicry phenotypes (79, 84). The genetic basis of these major color patterning “switch” genes has been extensively reviewed elsewhere (83), but several insights bear repeating. First, comparative mapping studies have shown that the genetic variation underlying similar color pattern elements in different *Heliconius* species localizes to a small number of homologous genomic intervals (79, 84), suggesting a conserved genetic basis for wing pattern development. Second, larval expression domains of the transcription factor, *optix*, and the signaling ligand, *WntA*, are correlated with red patterning (134) and patterns of melanin formation (105), respectively. Third, at least in some cases, chromosomal rearrangements (e.g., inversions) play an important role in the origin and maintenance of *Heliconius* mimicry polymorphisms (78).

Connection Between Divergence of Speciation Phenotypes and Species Boundaries

Color pattern divergence in *Heliconius* occurs across all levels of the species boundary continuum (94) and can be achieved by changes in a relatively small number of loci. In fact, there is accumulating evidence that adaptive introgression of patterning alleles among populations of *Heliconius* may be more common than previously recognized (29), thus supporting the hypothesis that hybridization is an important source of adaptive novelty in this system (66, 94). As discussed above, this divergence results in barriers to gene exchange among different wing pattern phenotypes of *Heliconius* owing to elevated rates of predation on recombinant patterns and through positive assortative mating driven by the evolution of male mating preferences.

In summary, the available data support the hypothesis that Müllerian warning color patterns are speciation phenotypes and that their divergence is predictably and repeatedly associated with the evolution of diversity at both the intra- and interspecific levels. Future research in this system is likely to be aimed at (*a*) the debate over whether advergence or codivergence best explains the mimetic resemblance between *H. erato* and *H. melpomene*, (*b*) the importance of Wright’s (177) shifting balance in the initial establishment of novel warning patterns, (*c*) adaptive introgression and the evolving species boundary, and (*d*) the evolution of genetic and developmental interactions among the regulatory network of color patterning genes that underlie the spectacular diversity of *Heliconius* wing patterns.

LAUPALA CRICKETS

The genus *Laupala* (Gryllidae: Trigonidiinae) is a group of flightless cricket species native to the rain-forested slopes of the Hawaiian islands (125, 143), offering rare insights into the process of speciation for several reasons. First, the genus is entirely endemic to the Hawaiian archipelago, and its phylogenetic history is understood, revealing an older to younger island radiation (111). Second, repeated speciation events have followed the colonization of each island, resulting in species-rich assemblages within islands. Third, the age of the youngest island, Hawaii, and the dramatic diversity of its endemic *pacifica* clade yield the highest speciation rate yet estimated among invertebrates (111). *Laupala* crickets occur at mid-elevations within humid environments, typified by dense foliage and leaf litter. However, there are no known host-plant dependencies, and species are both morphologically and ecologically cryptic (125). The similar lifestyle among species narrows focus to other aspects of differentiation, namely the reproductive system. Thus, *Laupala* offers an unusual opportunity to isolate the effects of evolution in the mate recognition system on speciation.

Axes of Differentiation

In *Laupala*, the most conspicuous axis of differentiation is male song. As with most crickets, males sing a long-distance calling song to which females respond when locating a mate. Songs are simple, consisting of long trains of pulses produced by wing stridulation (**Figure 1b**), but they can vary in multiple temporal features. Females show differential preferences for variation in these song characteristics (144), and across the range of the variable *Laupala cerasina*, pulse rate and pulse-rate preference have coevolved (69). A second rhythmic behavior that varies among *Laupala* species is the diurnal timing of acoustic activity. Peak male singing behavior differs significantly between sympatric species (26, 55) and correlates with the timing of mating (30, 54).

Furthermore, courtship in *Laupala* is extraordinarily elaborate: It lasts 6–8 h; involves the serial transfer of smaller, spermless microspermatophores; and is followed by transfer of a larger, sperm-filled macrospermatophore (30). Throughout courtship, males and females antennate extensively. Although tactile or chemical cues may be detected during antennation, astoundingly diverse, long-chain cuticular hydrocarbons (CHCs) (contact pheromones putatively used in mate choice) vary among species (116, 117). This is intriguing because, in addition to their role in desiccation resistance, CHCs play a role in a variety of social interactions among insects including courtship (73).

Identifying Speciation Phenotypes

Due to their role in pair formation, song and song preference may be speciation phenotypes in crickets generally and in *Laupala* particularly. To date, these traits alone have been studied for their impact on patterns of mating between differentiated forms in *Laupala*. Grace & Shaw (69, 70) found that females from acoustically distinct, neighboring populations of *L. cerasina* display assortative acoustic preference and that this preference predicted a high probability of mating. In addition, sexual isolation between *L. cerasina* and its sister species *Laupala eukolea* appears largely based on strong assortative mating generated through acoustic preference for songs of conspecific males (121). Sympatric congeners also display strongly differentiated songs and song preferences in sympatry (110), consistent with the hypothesis that these traits are rapidly evolving speciation phenotypes.

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

Several studies support the hypothesis that features of male calling song experience intense sexual selection (110, 122, 144). Furthermore, females display unimodal preference functions, suggesting stabilizing selection on pulse rate. Mean pulse rate preference is also well matched to mean pulse rate of a given species (69, 110). Interestingly, mismatches in mean pulse rate and preference have been measured and suggest a mechanism of divergent evolution by female choice (69, 122). Once divergence has occurred, evidence shows that assortative mating mediated by long-distance acoustic preference behavior should contribute to reduced gene flow between populations and species differentiated by pulse rate (110). However, explanations for why these preferences exist and diverge remain to be investigated.

Pleiotropy: the control of multiple traits by a single locus

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

Interspecific studies clearly show that acoustic trait differences are controlled by many, small-effect genetic factors (35, 147, 176). Two independent species crosses have been studied. In the *pacifica* group, *Laupala kohalensis* [~3.7 pulses per second (pps)] and *Laupala paranigra* (~0.7 pps) are closely related species that differ in pulse rate by approximately 25 standard deviations (147). Quantitative trait locus (QTL) mapping studies have corroborated the quantitative genetic nature of this species difference (147). Remarkably, preference QTL colocalize with song QTL to the same regions of the genome, suggesting either tight genetic linkage or pleiotropy of genetic effects on both song and preference variation (176). In the *cerasina* group, a genetic correlation has been documented between male and female traits (70). Furthermore, a cross between *L. cerasina* (~2.5 pps) and its sister species *L. eukolea* (4.0 pps) has revealed a comparable quantitative pattern of inheritance, with approximately five underlying genetic factors responsible for each pulse rate and pulse rate preference. As seen in the *paranigra/kohalensis* cross, the X chromosome explains a relatively small effect in the *cerasina/eukolea* cross.

Connection Between Divergence of Speciation Phenotypes and Species Boundaries

As described above, divergence in song and acoustic preferences in response to divergent sexual selection likely contributes to the establishment of species boundaries between closely related populations of *Laupala* by reducing gene flow. The available data also suggest that tight genetic correlations between these traits facilitate the maintenance of species boundaries once established. Future work aimed at identifying the specific genetic basis of male song and female preference should (a) allow a test of the hypothesis that parallel examples of acoustic divergence among pairs of *Laupala* species reflect repeated divergence in the same QTL; (b) help clarify whether the observed colocalization of QTL contributing to song and preference in mapping crosses is the result of tight linkage or pleiotropy; and (c) elucidate the proximate mechanisms underlying variation in male pulse rate at the genetic, cellular, and developmental levels.

RHAGOLETIS POMONELLA: THE APPLE MAGGOT FLY

Tephritid fruit flies in the genus *Rhagoletis* have been heavily investigated as a potential case of incipient sympatric speciation via host-race formation (12, 13, 44). In the mid-1800s, a larval host shift from their native host, hawthorn (*Crataegus* L. spp.), to varieties of domesticated apples

(*Malus pumila* spp.), contributed to the formation of two “host races” of *Rhagoletis pomonella*, which are isolated as a result of a combination of host-specific mating, oviposition preferences, and host-associated fitness trade-offs (12, 14, 44) (**Figure 1c**). The system has been important in evolutionary biology not only as a model of sympatric divergence, but also as an early example of extrinsic hybrid inviability arising as a consequence of antagonistic pleiotropy related to host fidelity (4, 45).

Axes of Differentiation

The primary axis of differentiation within the *R. pomonella* sibling species complex is host-plant utilization, and evidence suggests that olfactory cues play an important role in host location and host discrimination (25, 59, 91). However, although early studies of peripheral chemoreception in *Rhagoletis* suggested that changes in receptor or receptor neuron specificity may underlie olfactory preference (1, 2, 124), subsequent investigation found no evidence that peripheral coding was directly correlated with olfactory behavior (123). This suggests a complicated basis for olfactory behavior in this system even if the novel odor preference for apple has arisen recently (48).

A more recent study challenges that assumption and suggests that historical and ongoing gene flow from flies infesting a variety of hawthorn species in the southern United States (2, 3, 45) may have been the source of chemosensory variation in this system (128). Populations of *R. pomonella* in the southeastern United States differ along the same ecological axes differentiating host races in the northern United States, including fruiting phenology, the color and size of host fruits, and, importantly, their olfactory and behavioral responses to volatile compounds emitted from the surface of ripening fruit (2, 3, 19). Interestingly, although southern flies are not attracted to the apple volatile blend, they respond behaviorally to volatile blends from southern hawthorn species that include volatile olfactory cues used by apple maggot races; therefore, it is possible that standing behavioral variation in downy hawthorn flies may have predisposed them to evolve sensitivity to apple olfactory cues (128).

Identifying Speciation Phenotypes

Host fidelity is the key barrier to gene flow between races of *R. pomonella* (44, 46, 50). Divergence in host-plant utilization directly causes prezygotic isolation among host races of *Rhagoletis* because mating and oviposition occur on the fruit of their hosts (50). Migration between hosts is thought to be as high as ~6% per generation (50), indicating that host choice alone is an insufficient barrier to maintain the observed ecological differentiation between host races. Eclosion-time differences also isolate host races and arise as a consequence of differences in host phenology, which impose strong selection on the timing and duration of diapause (52). Recent work indicates that geography and introgression may have played an important role in providing the genetic variation to initiate the switch to apple (45, 51, 128). Population divergence in sympatry, however, was clearly triggered by the host shift, and the fact that host fidelity both directly and indirectly limits gene flow between host races suggests it is an important speciation phenotype in this system.

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

Sympatric divergence among populations within the *R. pomonella* sibling species complex arises from ecological pressures associated with the colonization of novel hosts (12, 13). Host-plant identification involves visual, olfactory, tactile, and gustatory cues (60). Apple flies use olfactory cues for long-to-intermediate range behavioral orientation, a combination of visual and chemical cues to locate fruit within the tree canopy, and a suite of sensory modalities (tactile, visual, gustatory,

etc.) when fruit is located. Host fidelity is tied both to host-plant identification and to avoidance of non-natal hosts (60). Studies of courtship in *Rhagoletis* suggest that, although visual cues based on wing and body markings are important for courtship initiation (12), males are unable to discriminate the sex or species identity of other flies prior to copulation attempts (129, 130). In the absence of evidence for additional mate recognition divergence, it is reasonable to assume that host fidelity plays a primary role in isolating host races (44, 50).

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

Genetic divergence among apple and hawthorn host races of *Rhagoletis* was initially demonstrated for a small number of allozyme loci ($n = 6$) that are correlated with postdiapause development and, hence, the timing of adult eclosion (56). All six of the major allozymes that differentiate host races of *R. pomonella* reside within one of three large chromosomal inversions (51). Coalescent genealogies based on widespread geographical sampling of flies from the southern United States and Mexican hawthorn populations suggest that at least some of the inversion polymorphisms that currently characterize differences between northern host races of *R. pomonella* are the result of historical introgression (45).

A major obstacle to speciation with gene flow is the expectation that recombination will quickly break down linkage disequilibrium between loci favored by ecologically divergent selection, thus preventing the accumulation of additional genomic barriers to gene exchange (164). Within inverted chromosomal segments, however, recombination is drastically reduced, thus alleviating selection-recombination antagonism (53). Although inversions protect suites of coadapted alleles from recombination, they also present a significant challenge to traditional genetic-mapping approaches for elucidating the genetic architecture and/or genetic basis of traits underlying adaptive differentiation, such as postdiapause development. Despite these challenges, mapping work on fruit-odor discrimination suggests that as few as three loci contribute the majority of variation in preference for natal hosts (25). In conclusion, divergence among host races of *R. pomonella* likely arises via a combination of geographic variation in exposure to natal and novel hosts, the existence of pre-existing genetic variation for the recognition of volatile compounds from non-natal hosts, clinal variation in overwintering diapause optima, and strong ecological pressures related to host-plant identification and utilization.

ACYRTHOSIPHON PISUM: PEA APHIDS

Pea aphids (*Acyrtosiphon pisum*) thrive on a wide variety of plants in the legume family (Fabaceae) as well as on several cultivated legume varieties in areas outside of the ancestral geographic range. Although they are treated taxonomically as a single species, pea aphids represent a diversified complex of populations, host races, and incipient species that span the species boundary continuum (126). In North America, sympatric populations utilizing alfalfa (*Medicago sativa*) and red clover (*Trifolium pratense*) are genetically distinct and locally adapted (161, 162) (**Figure 1d**).

Axes of Differentiation

The primary axis of differentiation among North American pea aphids is ecological specialization on alternative host plants, leading to reduced performance on non-natal hosts (161–163, 167). Behavioral traits are generally thought to play a key role in the evolution of host-plant divergence (63). Not surprisingly, in *A. pisum*, behavioral acceptance of a novel host is also the key factor driving host fidelity (17).

Linkage disequilibrium:

the nonrandom association of alleles at two or more loci, which could be physically on the same chromosome

Selection-recombination antagonism:

the breakdown of nonrandom associations and linkage disequilibrium generated by disruptive selection due to recombination during meiosis

Beyond host performance and behavioral preference divergence, aphids also display remarkable phenotypic variation in the geographic composition of their reproductive lineages. Pea aphids are cyclically parthenogenetic insects that reproduce clonally throughout the spring and summer but produce sexual forms in the fall. However, these “sexual lineages” may coexist with other reproductive lineages that are strictly parthenogenetic (i.e., asexual) (62). Interestingly, pea aphid populations also display a male dispersal polymorphism, with some populations producing only winged (alate) or wingless (apterous) males and other lineages that produce both adult male phenotypes in equal frequencies (7, 15).

Color polymorphism (red versus green) also characterizes pea aphid populations, and color variation influences susceptibility to parasitoids as well as predation rates (92). The two morphs also differ in their ability to utilize alfalfa hybrids selectively bred for aphid resistance (87), and behavioral differences exist in their response to disturbance (8). Taken together, these results suggest a complex relationship between color and fitness in this system (16). Finally, although less well investigated than other known axes of differentiation in this system, one intriguing finding is that host races differ substantially in their complement of obligate (*Buchnera*) and facultative endosymbionts (27, 115, 149). Strikingly, there is evidence of strong interrelationships between patterns of genetic differentiation, facultative symbionts, color morph, host-plant use, reproductive mode, and male sexual (alate versus apterous) phenotypes (61).

Identifying Speciation Phenotypes

Host fidelity among *Acyrtosiphon* lineages, arising as a consequence of strong host-plant preferences (17, 167), generates considerable premating isolation (163, 167). In addition, although host migration rates may be as high as 10% (163), strong selection against migrants and reduced hybrid performance in parental environments reduce gene flow among host-plant races and is an important source of postmating reproductive isolation in this system. The association between life-history traits described above and natal host performance suggests that traits related to host acceptance and feeding behavior may be important speciation phenotypes as well as key targets of divergent selection. In addition, because sexual reproduction in aphids takes place exclusively on the host plant, a secondary consequence of host preference divergence is reproductive isolation resulting from assortative mating (74, 169).

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

Host-plant acceptance and host fidelity are complex traits. Thus, it is fair to ask what evolutionary forces favored the initial evolution of behavioral preferences for alternative hosts. Within *Acyrtosiphon* populations, there is generally some genetic variation among clonal genotypes in the relative use of the two plants over and above the differences between population means (168). Dispersal by a clonal fundatrix to a non-natal host, although expected to be rare given evidence for divergent selection on winged adults for accurate habitat choice (167), would lead to strong disruptive selection on fecundity and/or additional fitness measures (163). Genetic coupling of host acceptance preferences and host performance traits (see below) is then expected to have greatly facilitated resource specialization in this system.

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

QTL mapping experiments using crosses between clover and alfalfa races indicate that host acceptance and performance are polygenic. These studies also found evidence for close physical linkage

between loci controlling the two traits and/or pleiotropy (74, 168). In addition, outlier analyses subsequently confirmed that divergent AFLP F_{ST} outliers significantly cluster around fecundity and host acceptance QTL (170), and a larger study using ~400 microsatellite loci recently revealed that 5 of 11 significant outliers map to positions close to olfactory receptor genes or several genes that encode salivary gland proteins (75). A more explicit candidate gene approach employed by Smadja et al. (152) found a handful of loci showing elevated genetic differentiation between pea aphid host races, almost all of which corresponded to either odorant-binding or gustatory receptor genes.

Connection Between Divergence of Speciation Phenotypes and Species Boundaries

Taken together, the above studies suggest that speciation among pea aphid host races is primarily driven by divergence in host-plant acceptance and performance, which may be controlled by a small handful of tightly linked, or pleiotropic, chemosensory genes. However, more work needs to be done to tie conclusively the genetic variation in these loci with the observed phenotypic differences among host races. Furthermore, the observed interrelationships among host-plant use, polymorphism in color and male dispersal phenotypes, as well as the composition of symbiont communities, deserve further investigation. Finally, an assessment of sexual isolation and/or an analysis of chemical mate recognition cues is needed to rule out the possibility that sexual selection also plays an important role in this system.

ANOPHELES GAMBIAE

The *Anopheles gambiae* species complex is comprised of seven closely related, morphologically cryptic mosquito species that are incompletely isolated (174, 175). *An. gambiae* sensu stricto (s.s.), the major vector of malaria in sub-Saharan Africa, is further subdivided into two partially isolated molecular forms, M and S, which were originally characterized by the identification of several fixed single-nucleotide polymorphisms in the rDNA of the X chromosome (43). The M and S molecular forms are further subdivided by inversion karyotypes into five distinct chromosomal types (31, 65), and the relationship between molecular and chromosomal forms varies as a function of geographic and ecological distributions (21).

Axes of Differentiation

Where the M and S forms are sympatric and synchronously breeding, there is strong assortative mating, possibly mediated by differences in female wing morphology (139) and divergent song types (127), but premating barriers are incomplete (157, 158). In addition, the S-form larvae are primarily associated with small, ephemeral, predator-free rain pools. In contrast, the M-form larvae exploit larger, more persistent bodies of water associated with anthropogenic habitats, suggesting that the two forms are further isolated by ecologically dependent postzygotic isolation arising as a consequence of fitness trade-offs in these alternative larval habitats (90) (**Figure 1e**).

Identifying Speciation Phenotypes

Coluzzi et al. (21) first hypothesized that adaptation to different larval environments was pivotal to speciation in this system, and the finding that genetic differentiation among forms is strongly correlated with ecological zones supports this view (22, 101, 178). Furthermore, reciprocal

Genomic islands of speciation: highly differentiated genomic regions between closely related species experiencing reduced recombination in hybrids, presumably because of structural variation or the action of disruptive selection

transplant experiments suggest that in the absence of predators the two forms outcompete each other in their respective larval habitats but that the M form significantly outperforms the S form in both habitats when predators are present (32, 33). Both larval forms display behavioral plasticity in response to predators (67), spending less time foraging and more time engaging in behaviors consistent with predator vigilance, but M-form larvae exhibit a much more dramatic shift toward predator vigilance (68).

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

As mentioned above, evidence suggests that divergent selection between the molecular forms of *An. gambiae* is related to differences in predation risk in larval habitats (32). However, larval habitats within the complex range from very small, ephemeral puddles (e.g., drainage dishes, old tires) to larger, more stable sites associated with higher predation risks, and until recently it was unclear how differences in larval-site use between the two forms was mediated. One possibility is that performance differences among molecular forms, which are dependent on predation risk, have favored the evolution of distinct oviposition preferences related to the presence or absence of predator chemical cues. Consistent with this hypothesis, oviposition experiments involving water conditioned with the presence or absence of two types of potential predators, *Notonecta* sp. backswimmers or *Xenopus* tadpoles, demonstrate that certain strains of *An. gambiae* display strong oviposition avoidance in the presence of these predator chemical cues (118, 172).

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

Although the two forms appear to have diverged recently (21, 24), efforts to understand the genetic variation contributing to differences in niche preference, ecological adaptation, and assortative mating have remained elusive (18). Early efforts to characterize patterns of genome-wide genomic divergence in this system identified several small, isolated regions of high differentiation between forms located near the centromeres of each chromosome (156, 160, 174), leading to speculation that these “genomic islands of speciation” housed genes involved in ecological adaptation and/or sexual isolation. However, further investigation revealed widespread, heterogeneous divergence between molecular forms of *An. gambiae* (89) and no evidence for biased cotransmission of speciation islands (71). These results appear to call into question the speciation with gene-flow model but may also simply reflect variation in the strength of extrinsic ecologically dependent postmating barriers across populations or fluctuating environmental conditions (135).

Connection Between Divergence of Speciation Phenotypes and Species Boundaries

In summary, molecular forms of *An. gambiae* are characterized by strong differences in niche utilization, larval behavior, and female mate choice that are consistent with a recent history of ecological divergence in response to strong natural selection for niche adaptation. The genetic architecture of divergence is not fully elucidated but appears to be the result of divergence in a small number of loci located in regions of low recombination; however, the lingering uncertainty about realized levels of gene flow across the genome between populations makes it difficult to predict conclusively how the architecture of adaptation will impact the future evolution of species boundaries in this system. Future work dissecting the relationship between diverging genomic

islands, habitat utilization, larval performance, and morphological correlates of song and mate choice should shed light on the shape and depth of the species boundary in this system.

DROSOPHILA

Drosophila is a diverse genus of small flies with more than 1,500 recognized species (102), representing the group of insects most intensively studied on the topic of speciation. A panoply of differentiating phenotypes has been documented. Indeed, the complexities of differentiation are often a hindrance to comprehending what first drives speciation in *Drosophila* because simultaneous axes of differentiation between closely related species characterize early *Drosophila* diversification. Although a full review of *Drosophila* speciation would require a book-length treatment, we highlight *Drosophila arizonae* and *Drosophila mojavensis* (*repleta* group, *mojavensis* species cluster), an exemplary study system for speciation. These two focal species are distributed across the arid southwestern extent of North America and Mexico, infesting the fermenting tissues of a variety of cacti, including prickly pear (*Opuntia*), as well as various columnar (*Stenocereus*) and barrel (*Ferocactus*) cacti (42) (Figure 1f).

Axes of Differentiation

Within the *mojavensis* species cluster, the most recent context of differentiation occurs among four biogeographic subspecies of *D. mojavensis* (although subspecies boundaries continue to be investigated) (42, 93, 133). Host use varies among these subspecies, with associated effects on life-history traits (39) and CHCs (e.g., 73). Additional axes of differentiation include male courtship song (38), aedeagus shape (136), body size, and mating speed (82). These differences and more, such as postmating prezygotic physiology (6, 171) and partial hybrid male sterility (132), distinguish *D. mojavensis* from its sister species *D. arizonae* (93, 103).

Identifying Speciation Phenotypes

In *D. mojavensis*, both CHC and song differences contribute to mate choice and sexual isolation (38, 73). Interestingly, data suggest that cactus substrate impacts life-history traits, which impacts CHC variation, which in turn alters the sexual selection environment for song traits (39). Thus, host environment acts as a keystone to the system, whereby changes in the fermenting host-plant environment impact multiple phenotypes involved in mate choice, with sexual isolation as a by-product, among differentiated populations of *D. mojavensis*. Such effects are variable and complex, however, as sexual isolation is not concordant with all changes in host-plant environments. Statistically significant sexual isolation is evident only between Baja California and mainland Sonora, Sinaloa, and Arizona, which diverged ~0.18–0.25 Mya on the basis of extensive nuclear sequence data (154). In contrast, sexual isolation between *D. mojavensis* and *D. arizonae*, which diverged ~0.66–1.5 Mya (107, 133), is nearly complete (106), and the species boundary may have been sealed for some time. Thus, even though hybrid male sterility, for example, is pronounced between species rather than among geographic populations/subspecies, it is likely an effect of postspeciation divergence because hybrids apparently do not form in the wild (93).

Evolutionary Forces Causing the Evolution of Speciation Phenotypes

Evidence suggests that divergence in speciation phenotypes in *D. mojavensis* is tied to host shifts, as each subspecies is associated with a distinct species of cactus (42) and is differentiated in CHCs

(37, 73, 155). Host-plant adaptation is likely, with longer development times expressed on putatively more novel hosts (i.e., organ pipe) (39). Experiments establish a connection between development time and CHC expression. They further suggest evolutionary links between evolution in developmental timing and CHC differentiation, ultimately manifest as partial (one-way) sexual isolation between the Baja California (agria cactus host plant) and mainland Mexican and Arizona (organ pipe host plant) populations (39). In addition, although female mate choice is predicted among population mating trials by variation in CHCs, “perfuming” experiments (with “attractive” CHC extracts placed on “unattractive” Baja California males) eliminate sexual isolation between female mainland and male Baja flies (37, 73, 155). Variation in male courtship song has also been linked to mate choice and sexual isolation between these same populations (38). It is unclear whether the additional axes of differentiation contribute to sexual isolation among geographical regions of *D. mojavensis*.

D. arizonae may continue to be involved in speciation within *D. mojavensis* owing to their partial sympatry in mainland Sonora. The geographic setting, coupled with a small but nonzero crossability in the laboratory, has inspired tests of character displacement within *D. mojavensis* (76, 106), interspecific gene flow (93) (also see below), and the components of reinforcement. Sexual isolation is stronger between *D. arizonae* and sympatric (versus allopatric) *D. mojavensis* (106), and the interspecific interaction may be causally involved. CHC variation can distinguish the two species (41) and is involved in the asymmetrical isolation between *D. mojavensis* subspecies (discussed above). Thus, it seems an obvious hypothesis as to the causal phenotype behind the heightened sexual isolation within *D. mojavensis*.

Genetic Architecture of Speciation Phenotypes with Influence on Patterns of Gene Flow

The genetic architectures of the putative speciation phenotypes in *D. mojavensis* (development time, CHCs, and song) are not simple, but rather involve multiple genomic regions (including both autosomal and X chromosomes), gene by environment interactions, and some degree of genetic correlation among traits and/or pleiotropy (39, 40, 73). At the level of species differences (*D. mojavensis* versus *D. arizonae*), the genetic basis of these phenotypes is presumably even more complex. Data suggest that additional mating phenotypes (e.g., sexual conflict phenotypes) may also be involved in a complex genetic fashion, as gene expression in heterospecifically mated females differs drastically from conspecifically mated females (6). Furthermore, a quantitative genetic basis to hybrid sterility between the species has also been documented (132), with contributions from multiple, interacting QTL and cytoplasmic effects.


Connection Between Divergence of Speciation Phenotypes and Species Boundaries

Extensive genetic structure has been documented in both *D. mojavensis* and *D. arizonae* and extends to the interspecific level where species boundaries are measurably well defined (93, 133). In addition, several chromosomal inversions differentiate the two species (42). Partial reproductive compatibility and geographic overlap between the two species motivated Machado et al. (93) to hypothesize greater differentiation between inverted, compared with collinear, chromosomal regions. Such a pattern could indicate greater current (cf. ancient) gene flow in regions free to recombine (in females) as the ancestral lineage split giving rise to the two species. Although evidence of recent gene flow was rejected, inverted regions showed significantly higher differentiation than did collinear regions. This discrepancy could indicate differential gene flow in the distant past;

alternatively, however, the authors point out that those chromosomes carrying inversions have repeatedly harbored inversions across the *repleta* group (137). Thus, the differentiation may predate the split between *D. mojavensis* and *D. arizonae* (93). Regardless, the lack of recent gene flow argues, despite observations of reproductive compatibility in the lab, for a sealed species boundary between *D. arizonae* and *D. mojavensis*. However, interspecific reproductive or ecological interactions in sympatric regions may have caused divergence between sympatric and allopatric populations of *D. mojavensis* (i.e., character displacement), shifting the focus of current speciation processes back to the *D. mojavensis* subspecies. The genetic architecture of phenotypic variation among differentiating *D. mojavensis* subspecies is not fully resolved, but there is currently no compelling evidence that differentiation in inverted regions is caused by divergent selection on speciation phenotypes. What we do know is that there is ample opportunity for the multigenic architecture of speciation phenotypes in this system to impact speciation islands and species boundaries and that many of the insights about speciation in this group are mirrored by other groups of *Drosophila* in which, e.g., song and CHC variation are evolving at the earliest stages of divergence (88).

EMERGING INSIGHTS INTO THE PROCESS OF SPECIATION

Here, and in the past, we have advocated for a more integrative view of the speciation process that focuses on the characterization of speciation phenotypes, the evolutionary forces driving their divergence, and the consequences of evolution of these traits with respect to the formation and maintenance of species boundaries (146, 147). Viewed through this lens, it is fair to ask what insights are beginning to emerge about speciation in general and insect speciation in particular. Although this review cannot hope to capture the full complexity of speciation in insects (see **Supplemental Table 1**; follow the **Supplemental Material** link from the Annual Reviews home page at <http://www.annualreviews.org>), several themes are evident.

 **Supplemental Material**

First, the systems considered here, and the broader speciation literature (e.g., 138, 140), demonstrate that disruptive natural selection and/or sexual selection are often involved in phenotypic divergence early in the speciation process. Second, accumulating evidence indicates that rapid evolution of sexual isolation arises as a consequence of divergence along multiple axes or modalities of sexual communication (e.g., visual, olfactory, acoustic, vibrational), and several studies have now demonstrated tight linkages between traits experiencing divergent selection and traits controlling assortative mate preferences (74, 86, 112, 113, 176). This is important because speciation may be favored when traits experiencing divergent selection also contribute to nonrandom mating via pleiotropy (so-called magic traits) or tight linkage (53).

Third, once controversial, a large literature now exists on the conditions that favor speciation with gene flow (5, 64, 81, 120, 141, 142, 151, 164). Furthermore, the genetic architecture of diverging phenotypes largely determines whether disruptive natural or sexual selection leads to widespread genomic differentiation, and presumptively speciation, or simply weak differentiation at isolated genomic regions (47, 58, 119, 165, 166). There is widespread interest in identifying such “genomic islands of differentiation” (49, 114, 150, 160), and it has been argued that the reduction in effective gene flow due to such islands may facilitate the accumulation of additional weakly selected alleles through a process termed divergence hitchhiking (47, 120, 166, 170).

Although our ability to detect such genomic regions of elevated divergence is relatively recent in most nonmodel systems, the field has a longstanding interest in this topic because it promises to elucidate the shape (genomic distribution) and depth (proportion of the genome) of the evolving species boundary (146). Recent advances in next-generation-sequencing technologies have allowed, for the first time, truly genome-wide insights into genomic patterns of differentiation, and they have led directly to the cataloging of hundreds of specific genetic changes underlying

examples of phenotypic evolution (104). Moving forward, when coupled with population genomic data, this knowledge will allow for far more rigorous and direct investigations of how phenotypic divergence impacts the evolution of species boundaries through space and time.

SUMMARY POINTS

1. Testing the hypotheses of speciation phenotypes is critical to the success of speciation studies.
2. Multiple axes of differentiation characterize even the youngest of incipient species and often include multiple sensory modalities involved in sexual communication.
3. The genetic architecture of diverging traits plays a pivotal role in whether speciation proceeds in the face of ongoing gene flow.
4. How selection shapes the evolving species boundary through the accumulation of and synergy between “islands of divergence” is an area of active research.

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