

## Systematics and speciation in relation to insect-plant interactions

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**Abstract.** Problems of systematics and speciation in the context of recent advances in the field of insect-plant interaction are highlighted with reference to the comparative study of speciation in relation to the population structure and genetic architecture of living organisms. The role of insect-plant interaction in the biosystematic study of some aquatic weevils, aphids and archid pollinators are also discussed besides sympatric speciation in some phytophagous insects.

**Keywords.** Insect-plant interactions; biosystematics; population structure; genetic architecture; sympatric speciation; phytophagous insects.

### 1. Introduction

Systematics is the scientific study of the kinds and diversity of organisms and of any and all relationships among them. The word 'relationship' is not used in a narrow phylogenetic sense, but is broadly conceived to include all biological relationships among organisms. One of the major preoccupations of systematics is to determine, by comparison, what the unique properties of every species and higher taxon are. Another is to determine what properties certain taxa have in common with each other, and what the biological causes for the differences or shared characters are. Finally, it concerns itself with variation within taxa. Biosystematics, in particular is given the rightful importance among biological disciplines, more because of increasing need for a correct determination of generic and specific complexes, in view of the occurrence of large-scale diversities within species which make bioecological, behavioural as well as related interdisciplinary approaches obligatory for a better understanding of these complexes (Ananthkrishnan 1987). Furthermore, modern accounts of organic evolution recognize the existence of two processes: anagenesis, phyletic change in the course of geological time; and cladogenesis or speciation, the origin of new species of organisms through splitting of pre-existing ones. Both are population phenomena. Cladogenesis compensates for the loss of species by extinction, so that no sudden or major changes in the total amount of biotic diversity occur. It is becoming more and more apparent that speciation can occur in different ways (Dobzhansky *et al* 1977). Thus, the comparative study of speciation, in relation to the population structure and genetic architecture of living organisms, is assuming an increasing importance in evolutionary studies. The aim of this review is to highlight the trends in our present understanding of the problems of systematics and speciation in the context of recent advances in the field of insect-plant interactions.

### 2. Biosystematics of aquatic weevils infesting water weeds

A typical instance of the role of insect-plant interaction in the biosystematic study of two species of aquatic weevils will highlight the significance of such studies in

future. Biological control of the aquatic weed, *Salvinia molesta* was first attempted in southern Africa with the introduction of the weevil, *Cyrtobagous singularis* from Trinidad which established (Procter 1984) but failed to control the weed in the upper Zambezi or Chobe rivers (Edwards and Thomas 1977). A closely related weevil, *C. salviniae* from Brazil, has proven to be a most effective agent for *S. molesta* in northern Australia (Room *et al* 1981), in Papua New Guinea (Thomas 1985) and in Bangalore (Jayanth 1987). *C. salviniae* was first thought to be a biotype of *C. singularis* specially adapted to *S. molesta* (Forno *et al* 1983) but was later shown to be a separate species (Calder and Sands 1985). This was substantiated by the studies of Sands and Schotz (1985), May and Sands (1986) and Sands *et al* (1986) contributing to the different impact on the weed by the two species.

### 2.1 Differences in feeding strategies

Damage by *C. salviniae* to *S. molesta* results from larvae tunnelling within the rhizome (Sands *et al* 1983), a feeding behaviour different from *C. singularis* whose larvae feed externally on submerged parts of the plant. It is possible that the longer setae of the larvae of *C. singularis* are an adaptation to external feeding, where they aid movement from one submerged part of the host to another, in contrast to the shorter setae of *C. salviniae* whose larvae tunnel internally within the rhizome (May and Sands 1986). Adult behaviour also differs, *C. salviniae* feeding mainly on buds of *S. molesta* whereas *C. singularis* feed extensively on other parts of the plant leaving more buds intact. Hence, *C. singularis* has less impact than *C. salviniae* on plant growth (Sands and Schotz 1985).

### 2.2 Differences in preoviposition period, oviposition period, the pattern of oviposition and in effects of plant nitrogen on fecundity

The pre-oviposition and oviposition periods are very variable for both species. The pattern of oviposition was markedly different for the two species, *C. salviniae* laying eggs almost continuously (92% of weeks with some eggs) while *C. singularis* laid eggs intermittently (50% of weeks with eggs). Concentration of N in the food plant had greater effect on oviposition by *C. singularis* when compared to that of *C. salviniae*. The values for the intrinsic rate of increase ( $r_m$ ) suggest that *C. salviniae* is physiologically better adapted to *S. molesta* than *C. singularis*, particularly in the higher developmental temperature range. The differences are likely to be accentuated by the greater dependence of *C. singularis* on N in the host plant, which may be due in part, to its adaptation to a different host, *S. auriculata*, a plant found to concentrate 0.4% more N than *S. molesta* when grown in a nutrient containing 3 mg/l of N (Sands *et al* 1986). Thus, differences in reproductive physiology and feeding behaviour on the same host are the major factors helping in the differential diagnosis of *C. singularis* and *C. salviniae*.

## 3. Host-selection and speciation in aphids

Many aphids intimately associate themselves with specific host plants and evolve specific feeding, gall-making and reproductive strategies. Such a selection of host

plants with intrinsic modifications to feeding and egg-laying mechanisms has been used by taxonomists as the basis for distinguishing species in the super-family with close affinities to the plant groups they are associated with (David 1977). For instance, there are some species which, due to geographical isolation, have secured new hosts in south India. *Acyrtosiphon gossipii* Mordwilko, usually feeds on some plants of Malvaceae and Leguminosae mainly in dry areas in north-east Africa and West Asia (Eastop 1971). In south India, it is exclusively found on a totally different plant, *Sesbania grandiflora*, in wetlands. It has not been possible to transfer it to other plants like *S. speciosa*, *Medicago sativa* or *Vigna catjang*. Though *Sesbaniae* David was described as a distinct species, Eastop (1971) feels it could be treated as a subspecies on account of its shorter cauda compared to those on Malvaceae.

#### 4. Pollination biology and speciation in plants

The richness and diversity of orchid speciation depends upon both the variety of pollinators to which they have become adapted and the various ways in which pollination is effected. Among the more interesting vectors that orchids have added to their repertory are males belonging to various species of Hymenoptera. An example now familiar is the phenomenon of pseudocopulation, according to which the flowers attract sexually active males by mimicking females of a particular insect species with respect to the overall form and colour pattern of the lip, and more particularly by subtle odors, produced by specific sesquiterpene lactones and hydrocarbons, as well as coatings of hairs on the lip, which produce a tactile stimulus for their copulation reaction. As was clearly demonstrated by Williams and Dodson (1972), male bees act as specific pollinators by gathering fragrant compounds, transporting them to courtship area and using them as sex attractants, the orchid flower serving as a sort of 'beauty parlor' for the sexually ambitious male.

The effectiveness of these pollination mechanisms in producing the morphological diversity by which botanists recognize and separate species was shown by Grant (1949) in a survey of the diagnostic characters used by botanists for separating species in a great number of different genera. In genera of plants adapted to pollination by specialized animal vectors, a high proportion of the morphological characters upon which species distinctions are based are concerned with the perianth, stamens and stigmas, which constitute the pollination mechanism. On the other hand, diagnostic characters in groups pollinated by less specialized vectors, or by wind or water, are based upon characters associated with vegetative adaptations or with seed development and dispersal.

#### 5. Species problem and speciation

According to Mayr (1940, 1963), 'species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'. Dobzhansky (1970) states that 'species are systems of populations; the gene exchange between these systems is limited or prevented by a reproductive isolating mechanism or perhaps by a combination of several such mechanisms'. Both these authors stress that *absolute* reproductive isolation cannot be used as the criterion of

specific distinctness. Furthermore, every species is at the same time a reproductive community, a gene pool, and a genetic system (White 1978). Speciation is, simply the evolution of a new species. It is the evolution of a new discrete morphological array of forms that interbreed only among themselves. Sibling species are reproductively isolated but are almost identical in outward appearance. Populations that are neither good races nor good species but are connected by a reduced amount of interbreeding and gene flow are recognised as 'semispecies' (Grant 1971).

Speciation is one of the main ways by which living organisms adapt in order to exploit the diversity of environments available to them. Three essential models of speciation are traditionally distinguished. In allopatric model, a single ancestral species population becomes separated into two by a geographical barrier that individuals cannot cross. However, Mayr (1978) feels that it would seem advisable to define allopatric in terms of dispersal barriers rather than purely geographically. The next stage is for the two populations to undergo different evolutionary changes in their different environments. If they diverge enough, the two populations may be classified as different geographical races, and then if they are unable to interbreed, they become different species. According to the sympatric model, much the same process of divergence can take place without the geographical separation of the populations but through instantaneous appearance of reproductive isolation. A third model of speciation, intermediate between the two extremes, is called parapatric (or semi-geographic) speciation. In this form, the divergence takes place between contiguous, rather than separated or overlapping populations. Many speciation events have been split into allopatric and sympatric categories when in fact they may have represented a homogeneous category from a population-genetic perspective. For these reasons, Templeton (1981) has given a population-genetic classification of the modes of speciation (table 1). There are two basic categories: divergence and transilience. Under divergence, the isolating barriers evolve in a continuous (but not necessarily slow) fashion, with some form of natural selection, either directly or indirectly, being the driving force leading to reproductive isolation. Transilient modes involve a discontinuity in which some sort of selective barrier is

Table 1. Modes of speciation (after Templeton 1981).

Type of speciation	Basic mechanism
<b>Divergence</b>	
Adaptive	Erection of extrinsic isolating barrier followed by independent microevolution
Clinal	Selection on a cline with isolation by distance
Habitat	Selection over multiple habitats with no isolation by distance
<b>Transilience</b>	
Genetic	Founder event causing rapid shift in previously stable genetic system
Chromosomal	Inbreeding and drift causing fixation of strongly underdominant chromosomal mutation
Hybrid maintenance	Hybridization of incompatible parental species followed by selection for maintenance of hybrid state
Hybrid recombination	Hybridization of incompatible parental species followed by inbreeding and selection for stabilized recombinant

overcome by other evolutionary forces. In a nutshell, divergence occurs because of selection, transience in spite of selection (Templeton 1981).

## 6. Sympatric speciation in phytophagous insects

Extensive work on phytophagous insects suggest that reproductive isolation between two populations may evolve while both are inhabiting the same geographic area. It is quite common to find two or more 'biological races' of a given species in the same locality, differing little or not at all in appearance, but nevertheless quite distinct in their food preferences. It has been stressed by Janzen (1968) that species of host plants of phytophagous insects may be viewed as islands in their relationship to the insects that feed upon them and that colonization of a new host plant is analogous to immigration to an unoccupied island.

### 6.1 *Subspecific differentiation in *Hyponomeuta padella**

The caterpillars of the moth *H. padella* feed on apple and on hawthorn trees. There is in this species considerable variation in the colour of the fore wings of the adults, from dark grey to white, but although the dark forms are commoner among moths developing from caterpillars from hawthorn, and white forms commoner in those from apples, the differences is only one of the relative frequencies of the different colour varieties, and the adults are otherwise indistinguishable in appearance. However, the adult moths can usually be distinguished by their egg-laying preferences, since about 80% of individuals reared on apple lay their eggs on apple trees, and about 90% of those from hawthorn lay their eggs on hawthorn. There is also a tendency for moths to mate with partners raised on the same food plant; in experimental conditions such assortive matings were about twice as common as were matings between individuals raised on different plants. Finally, the caterpillars show a strong preference for the food plant on which their mothers were raised, although they can be induced by starvation to feed on the wrong food plant; in such cases the resulting adults are often infertile. In this case, then, the two races are not completely isolated, since some interbreeding probably takes place in the wild; they are best regarded as subspecies of a single species.

### 6.2 *Sympatric speciation in *Rhagoletis**

The most detailed, and hence the most significant studies on host races of insects have been carried out on the fruitflies of the family Tephritidae (Bush 1966, 1969a, b, 1974, 1975a, b). Bush has studied especially the genus *Rhagoletis* in north America. He has considered 3 species groups in detail. The *Suavis* group includes 5 species (eastern United States to Arizona and Mexico) that feed on a total of 8 species of walnuts (*Juglans* spp.) without showing any particular specificity. They may well have speciated allopatrically. The *pomonella* group includes 4 sibling species, each of which infests fruits of a different plant family. Although difficult to separate on morphological grounds, these siblings seem to be completely isolated reproductively and are quite different biologically. *R. pomonella* originally infested only hawthorn (*Crataegus*) throughout the eastern United States, but a host race on introduced

apples appeared in the Hudson river valley about 1864 and rapidly spread until by 1916 it extended across the Great lakes region to the vicinity of Winnipeg. In the southern United States the species is still only represented by the hawthorn race.

At the present time there are minor differences in size, number of postorbital bristles, and ovipositor length between some sympatric populations of the two races. There is also striking differences in their seasonal cycles. Both have a single annual generation, but the emergence period of the apple race is from June 15 to the end of August (with a peak on July 25), i.e. about a month before the maturation of the apples, whereas the hawthorn race emerges between August 5 to October 15 (with a peak about September 12), i.e. approximately a month before the maturation of the hawthorn fruits. This allochronic isolation may prevent gene exchange between the two races.

Another allochronically isolated race of *pomonella* infests native and cultivated plums in the eastern United States. It emerges considerably earlier than the apple race, in accordance with the earlier maturation of the plums. And in the 1960s a cherry race made its appearance for the first time in Wisconsin. The cherry race must have arisen from the apple race, since the gap between the time of maturation of cherries and haws is too great for a direct shift to have taken place.

Thus, host races that are effectively isolated genetically can arise in this species from time to time when new host plants become available. A most important fact is that the insects are attracted to their host plants by visual and olfactory cues and that mating takes place on the fruits being then followed by oviposition. Bush (1974) points out that the biology of oligophagous and monophagous tephritids makes an allopatric origin of new host races highly unlikely. Migration of a few individuals to an area where a new species of fruit was present would have no effect unless these had the right genetic constitution for recognising, ovipositing and surviving on it. Most dispersal in *Rhagoletis* takes place before mating, so that both males and females would have to be attracted to the same fruits.

In place of such improbably allopatric models, Bush (1974) puts forward the following postulates in a sympatric model of *Rhagoletis* speciation (after White 1978):

- (i) The old and new host plants must occur in the same area.
- (ii) The maturation times of the two host species must overlap.
- (iii) Diapause and emergence times must be under genetic control.
- (iv) Orientation to and selection of a host plant due to a chemical cue.
- (v) Host selection is due to one main genetic locus.
- (vi)  $h_1h_1$  individuals are attracted to the original host;  $h_1h_2$  individuals are attracted to both hosts, but because of modifiers (polygenes) will move preferentially to the original host; while  $h_2h_2$  individuals are only attracted to the new host.
- (vii) Survival on the original and new host is controlled by another locus.  $s_1s_1$  individuals survive on the original host;  $s_2s_2$  individuals survive on the new one;  $s_1s_2$  individuals survive on either.
- (viii) Since mating occurs on the host plant, a high degree of homogamy is expected.

Under these circumstances one would expect that disruptive selection would lead to the rapid evolution of two races, one homozygous for  $h_1h_1s_1s_1$ , the other for  $h_2h_2s_2s_2$ . If the time of maturation of the two kinds of fruits is different, disruptive selection would also be expected to occur for the genes controlling the time of

emergence. Thus Bush and other workers on host races in Tephritidae have built up a strong case for the view that a few changes at key loci but not a major genetic revolution i.e. the replacement of a large proportion of the alleles in the original genotype can indeed lead to a switch in host plant. However, it is clear that once two sympatric host races are in existence there will begin a long process of disruptive selection, involving a change in the seasonal cycle of the new race and changes in those body and wing patterns (and perhaps behaviour patterns as well) that serve as cues in the mating ritual.

The process of differentiation into sympatric host races is explained well by Smith (1975). If for any reason a female of, for example, a plant-eating species lays her eggs on an unusual plant, two things will follow. First, the larvae will be exposed to new conditions, and intense selection of genotypes adapted to those conditions is likely; high mortality of forms reared on a new host species confirms this. Second, the females which develop on the new plant will tend to lay eggs on that plant, not because they tend to differ genetically from the rest of the species, but because they have been conditioned during larval life. Further, in species which mate soon after emergence, there is a fair probability of a female which has developed on the new host plant mating with a male from the same plant or group of plants, simply because she is more likely to meet such a male. In this way a population of insects can arise which, although not completely isolated reproductively from the rest of the species, may yet be sufficiently isolated by its habits to diverge genetically from the rest of the population. At first the main genetic change to occur in such a population will be that resulting from the intense natural selection for the capacity of the larvae to survive on the new host plant. However, any genetic changes which reinforce either the tendency to lay eggs on the new plant, or to mate with members of the newly adapted population, will be favoured by selection.

There are relatively few groups of animals in which host races equivalent to those of Tephritidae are well-known and fully documented. Monophagy, however, is equally shown in such groups as the gall-making cecidomyids and Cynipids, the agromyzids (Nowakowski 1962), most groups of parasitic hymenopterans, some aphids and coccids and certain groups of lepidopterans and sawflies. In Coleoptera there are a number of phytophagous and wood-boring families in which the species are closely adapted to a single host plant or a small range of related species. All of these are groups in which the occurrence of sympatric speciation seems probable, on the same kind of basis as in the tephritids. Leafhoppers (Cicadellidae) are another group in which it is very likely that sympatric speciation is occurring (White 1978).

### 6.3 *The role of host plants in the speciation of treehoppers*

*Enchenopa binotata* is a polyphagous membracid that occurs from Panama throughout eastern north America. In north America, it has a single generation per year and is found on 7 species of host plant. These hosts (*Ptelea trifoliata*, *Cercis canadensis*, *Juglans nigra*, *J. cinerea*, *Viburnum prunifolium*, *Celastrus scandens* and *Robinia pseudoacacia*) are evolutionarily diverse and sympatric throughout the eastern United States. Wood and Guttman (1981) have shown that *E. binotata* in north America is a complex of reproductively isolated taxa which have diverged along host lines. *Enchenopa* on each host differs (Wood and Guttman 1983) in

(i) the colouration of nymphs, (ii) oviposition sites, (iii) nymphal feeding sites, (iv) seasonal and diurnal patterns of oviposition and (v) the number of eggs per egg mass.

When females are given a choice of host plants on which to oviposit, they select the host on which they were raised. When males and females from all hosts are confined to a single cage, there are few matings by insects of mixed host origin and the length of mixed matings are considerably shorter. Even under conditions imposed by a cage, mating tends to occur on the host on which females were raised. Assortive mating within host plant species is almost assured considering disparate life histories, the mating system and the insular nature of treehopper populations. Host plants or individual trees may function as evolutionary islands with their isolated populations of coevolving herbivores as pointed out by Janzen (1968), Opler (1974) and Edmunds and Alstad (1978).

Allochronic life histories are important in maintaining reproductive isolation among members of this complex. Eggs hatch on each host (with the exception of *C. canadensis*) about the time the host is in flower. Allochronic egg hatch combined with differences in maturation produces temporal difference in mating; differences in the time of day that mating occurs further reduce the possibility of hybridization. Allochronic and diurnal differences in mating reproductively isolate adults from 4 of the 6 hosts. Members of the last pair are effectively isolated from each other by allochronic flight activity which occurs about a week apart. On one host, almost all flight activity occurs before mating begins on that host; hence, there is very little flight by either sex once mating begins and virtually none after oviposition starts. Ovipositional attractants in egg froth tend to keep females on their hosts. In fact, movements by males and females throughout the summer, even among nearby conspecific hosts, is almost non-existent.

Electrophoretically, *Enchenopa* from each host differ in the frequency and fixation of electromorphs even when collected from 2 adjacent tree species. There were even electrophoretic differences in the *Enchenopa* among individual conspecific trees located very close to each other. Genetic distances calculated from electrophoretic data indicate that *Enchenopa* on *J. nigra* diverged first, then divergence on *P. trifoliata*, *R. pseudoacacia*, *C. canadensis*, *V. prunifolium* and *C. scandens* followed in the order given. Estimates of the time of divergence by means of the molecular time clock suggest that speciation has been recent i.e. within the last 250,000 years.

Wood (1980) postulated that north American *Enchenopa* may have diverged from a tropical polyphagous ancestor. This ancestral stock encountered selection pressures to coordinate its life history with the phenology of newly exploited hosts resulting in a shift from a multivoltine life history. Colonization of north American hosts with differing phenologies and of differing nutritional quality resulted in difference in maturation that prompted allochronic life histories. Further genetic differentiation was promoted by the relative temporal permanence and spatial heterogeneity of host resources which encouraged low vagility. In this proposed model, Wood and Guttman (1981) ultimately feel that slight life history shifts of *Enchenopa* in response to host plants combined with behavioural and ecological factors are all that are needed to produce reproductively isolated species.

## 7. Conclusion

Since complete geographic isolation, if continued long enough, will inevitably lead

to speciation, we must expect that even among groups whose ecology, vagility and population structure is most favourable to sympatric speciation, there will be some cases of strictly allopatric speciation. The converse, however, does not hold; there are almost certainly groups whose general mode of life makes it impossible for reproductive isolation to develop without prior geographic isolation (White 1978).

Finally, it cannot be gainsaid that a thorough understanding of the dynamics of insect-plant interactions will pave the way for unravelling the mysteries of systematics and speciation in phytophagous insects.

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