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Artificial neural networks in models of specialisation, guild evolution and sympatric speciation

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11.1 Introduction

The existence of sympatric speciation has been a contentious issue because empirical support was scarce and the underlying theoretical mechanisms were not as fully understood as we might like (e.g. Futuyma & Mayer, 1980; Rundle & Nosil, 2005). The view on sympatric speciation is currently changing, however. Recent theories demonstrate how ecological adaptations can drive speciation (Dieckmann *et al.*, 2004; Doebeli *et al.*, 2005). In concert with theoretical development, empirical evidence corroborating this view is accumulating (Barluenga *et al.*, 2006; Panova *et al.*, 2006; Savolainen *et al.*, 2006). An obstacle for sympatric speciation is the exchange of alleles between lineages and the homogenising effect of recombination in sexual reproduction (Felsenstein, 1981; Rice & Salt, 1988). The current view on sympatric speciation is therefore that disruptive selection for evolutionary divergence has to be correlated with assortative mating and reproductive isolation (Felsenstein, 1981; Rundle & Nosil, 2005). This can be through linkage between ecological genes and mating genes, or a pleiotropic effect of ecological genes on mating behaviour. Orr & Smith (1998) make the distinction between extrinsic and intrinsic barriers to gene flow. Extrinsic factors are physical barriers in the environment that prevent encounters between individuals. Intrinsic factors are genetic traits that increase pre- or post-zygotic reproductive isolation. They define sympatric speciation as ‘the evolution of intrinsic barriers to gene flow in the absence of extrinsic barriers’.

Host races have been defined as populations of a species that are partly reproductively isolated from one another as a direct consequence of adaptation to different hosts (Abrahamson *et al.*, 2001). Host races in phytophagous insects are believed to be precursors to full species, an idea that goes back to 1864 (Walsh, 1864), these being the first candidate examples for sympatric speciation. Specialisation on hosts is a prerequisite for host races to be reproductively isolated, and if the isolation evolves as a correlated character to specialisation, it may lead to sympatric speciation (Rice & Salt, 1990).

Resource competition between phenotypes with fixed and limited diet breadth is the driving force of current theories of sympatric speciation (Dieckmann & Doebeli, 1999;

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Geritz & Kisdi, 2000). Among insects, diet breadth does not seem to be limited. Laboratory studies show that larvae feed and grow equally well on plants other than those chosen by the female to oviposit on (Dethier, 1947; Ballabeni & Rahier, 2000). It is still unknown why females are so restricted in diet breadth, and why specialists are more common than generalists in insects (Jermy, 1984; Jaenike, 1990). It has been proposed as a major enigma in the evolution of insects (Futuyma, 1991). Other theoretical explanations for host specificity in insects include avoidance of interspecific competition or predation, reduction of parasitism, and increased probability of mate finding, but the empirical support is often circumstantial at best (Futuyma & Moreno, 1988). Recently, host specificity in insects has been suggested to be the result of limitations in brain function, more specifically in the recognition systems that process information (here host signals) for effective recognition of suitable host plants (Holmgren & Getz, 2000; Bernays, 2001).

Here we review some of our work on evolution of host-plant selection in insects using artificial neural networks as models for the plant recognition mechanism in insects (Holmgren & Getz, 2000; Norrström *et al.*, 2006). We present some new insights from the synthesis of our results. We explain why insects can become specialised, and how disruptive selection creates guilds of specialists as a result of evolution on recognition mechanisms. In addition we examine the evolutionary dynamics during coevolution of the exploiter species and their hosts. Finally we show that reproductive isolation can evolve in diploid and sexual populations, without being correlated to host-recognition genes. The results reveal a new and unexpected process that drives sympatric speciation. Although the model is inspired by insect-plant systems, it may be regarded as an example of a more general exploiter–victim system in which the evolution of the exploiters' recognition systems is critically influenced by the ability to assess resource quality of hosts/victims. We set out to present a framework for exploring the importance of specialisation for speciation, with the aim to stimulate further theoretical and empirical work.

11.2 Recognition system and ANN design

A niche-breadth model of exploiter evolution under neural constraints needs to be sufficiently detailed with regard to signals produced by victims and the ability of the exploiters to perceive and respond to these signals to adequately address the questions at hand. The plant victims, for example, produce signals of varying complexity dependent on a few key chemical compounds that occur in plant-specific ratios, but are collectively known as 'green odour' (Visser, 1986). To keep things simple, we let the plant signals in our model be represented by two odorants, the minimum needed for odour quality to depend on component ratios (Getz & Chapman, 1987). Insects, as exploiters for example, perceive these plant signals and compute an output signal coding for a behavioural action – in our models we take this action to be laying versus not laying eggs on a potential host plant.

For simplicity, we modelled the perceptual system as a perceptron (Haykin, 1994), rather than a dynamic neural network (Getz & Lutz, 1999), which captures the perceptual constraint feature seen in insect exploiters when selecting among victims with different

phenotypes (c.f. Getz & Smith, 1990; Getz & Akers, 1997). The perceptron is a three-layered feedforward network with an ability to differentiate and categorise input signals once the perceptron has an appropriate set of weighting values for passing on information from one layer of nodes to the next. Our perceptrons had two inputs, implying that victim signals were points in a two dimensional odour space. The output layer has only one node which state corresponds to a preference/rejection response. In our simulations, these weightings evolve between generations by mutations and the relative fitness achieved from host-plant (i.e. victim) selection, where fitness is measured as the expected number of eggs that will successfully mature into new adults. In short, we have a mutation-selection algorithm on the synaptic weights of replicating perceptrons (see Appendix for more details).

In an initial study we assumed that the exploiters were represented by a unique perceptron reproduced as haploid clones (Holmgren & Getz, 2000): that is, from one generation to the next depending on the fitness of the represented individual, zero to two new perceptrons were created and then mutated with predetermined probabilities and size of weighting perturbations. Models with clonal reproduction exclude genetic exchange between exploiter lineages, and are thus insufficient to model how reproductive isolation and species arise in sexual populations. In a follow-up study, we developed a diploid genetic structure coding for the synaptic weights (Norrström *et al.*, unpublished).

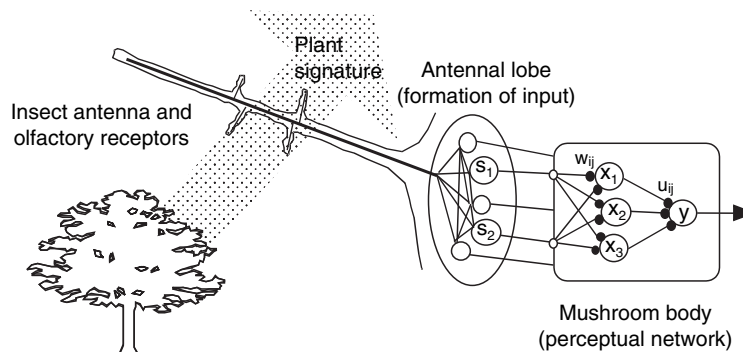


Figure 11.1. A diagram of the perceptual component of the model. Each plant type produces its own unique signature that stimulates the olfactory receptor cells located on the antenna of individual insects. The response of these cells is processed in the antennal lobes to produce an antennal lobe output S_i that we regard as input to a perceptual neural network located in the mushroom bodies of the protocerebrum. Our highly idealised model of this perceptual system is a three-layered feedforward neural network. For simplicity, we assume all compound specific signals are represented by the two inputs (S_1 and S_2), which are then propagated to a layer of hidden units (large labelled spheres). The strength of these input signals is modified by synaptic weights (small solid spheres) $w_{i,j}$, $i = 1,2$, $j = 1,2,3$. The output x_j from each of the hidden units when stimulated, is the result of passing the input activity through a sigmoidal activation function. The activity impinging on the output unit is similarly modified by the synaptic weights u_j . The response y of the output neuron is characterised by the same activation function as in the hidden units. From Holmgren & Getz (2000).

11.3 Stimulus-response functions and specialisation

How well the recognition system of an exploiter is performing, in terms of identifying suitable victims, is ultimately determined by the number of eggs in each generation maturing into new adults. We constructed exploiter-fitness functions using an insect herbivore as our leitmotif (see Appendix for fitness function of exploiters). The fitness of each exploiter is a function of the response to the input signals from its victims. One may think of an insect herbivore as having the option of choosing among a number of different types of plants, where each type produces a characteristic odour. In the model, each insect samples the odours of all plants in the environment. The response or preference of insect g , $g = 1, \dots, G$, for plant type h , $h = 1, \dots, H$, is identified with the output $y_{g,h}$ of perceptron g to input signal h . One approach to constructing a fitness function is to assume that the decision to lay a clutch of eggs on a specific host plant depends on the strength of this response relative to alternative hosts. This may seem to be a reasonable approach at first. However, if the absolute signal strength is an excluded factor, genetic drift decreases the insects' sensitivity to plant odours because there is no selection on sensitivity (confirmed in unpublished simulations). Insects searching for host-plants respond behaviourally by flying upwind in plumes of host-volatiles only if these volatiles are presented over a threshold concentration (Olsson *et al.*, 2006). Thus, there is biological reason and a computational necessity to add a dependency on the signal strength to the relative response to each plant odour type. Thus we used the expression

$$e_{g,h} = \frac{y_{g,h}^2}{\sum_{h=1}^H y_{g,h}} \quad (1)$$

to calculate the relative clutch size, i.e. the number of eggs, e , laid by exploiter g on plant type h . The egg load affects the fitness function used to calculate the number of insect offspring (Eq. A1)

If response function (Eq. 1) is at all realistic, it has some significant consequences for insect diet breadth. The function selects for an all-or-none response of insects to their available hosts. For example, in an environment of two plants, an insect with the intermediate response [$y_{g,1} = 0.5$, $y_{g,2} = 0.5$] will according to Eq. 1 lay [$e_{g,1} = 0.25$, $e_{g,2} = 0.25$], i.e. in total only half of its egg complement. In contrast, an insect with a maximum response to one plant and a zero response to the other [$y_{g,1} = 1$, $y_{g,2} = 0$] will lay [$e_{g,1} = 1$, $e_{g,2} = 0$], i.e. its total egg complement on plant one. Thus, intermediate responses have the logical consequence that insects do not lay their full egg complement, and is as a strategy less fit than all-or-none response strategies.

Now consider an environment of various host plants that are neither perfect hosts nor completely noxious, but provide some intermediate resource in terms of the number of eggs that can successfully hatch and produce viable offspring. With the bimodal preference/non-preference response of insects, one generalist type can not exploit this environment. A

complete generalist will distribute their eggs evenly among available plants. Intra-phenotypic competition on the plant of the lowest resource value will limit population growth, thereby leaving the more valuable plants underutilised. Under these circumstances, selection favours guilds of insects with relative numbers selected to match the values and optimally exploit the plant resources in the environment. The same conclusion holds if competition on host plants affects the quality of offspring, e.g. the size or fecundity of mature offspring.

In all its simplicity, the hypothesis that insects behave in accordance with both their absolute and relative responses to plants of different types may explain the observation that many insects are more restrictive in their diet than needs be from a nutritional point of view (e.g. Wiklund, 1975; Ballabeni & Rahier, 2000). As discussed below, our work suggests that the herbivorous insects exploiting a particular ecosystem have evolved into a guild where the different ecological niches arising from host plant variation are occupied by a number of more or less specialised species.

11.4 Specialisation when resources are fixed

In order to study the evolutionary process of specialisation versus generalisation, a range of resources must be included in the model. In the initial study focusing on the evolution of niche breadth we used four fixed (i.e. non-evolving) resource types (Holmgren & Getz, 2000). In particular, we investigated the evolutionary process of insects in several different ecological backgrounds from both a resource-signalling and resource-value point of view. Some of these environments represented a more difficult resource-discrimination than others. The victims reproduced clonally and an insect–plant leitmotif was used to discuss and interpret the results.

11.4.1 *The ideal free distribution*

The spectrum of plant types used in our first analysis constituted an ecological resource space or, equivalently, a set of ecological niches (Holmgren & Getz, 2000). We identified the niches with the plants themselves, and assigned a niche value v_h to the h -th population of plants of type h , $h = 1, \dots, 4$. Thus we identified the resource space using the set $[v_1, v_2, v_3, v_4]$ and normalised the analysis by setting $\sum_{h=1}^4 v_h = 100$, which we interpreted as the carrying capacity of the environment (in our simulations this normalisation to 100 represented the actual number of exploiters that could survive to reproduce from one exploiter generation to the next, but could also be interpreted in terms of relative units).

Natural selection will favour exploiters occupying empty niches – i.e. the number of individuals produced by these exploiters will increase until the ecological niches are all fully occupied. In analogy to the ideal free distribution (Fretwell & Lucas, 1970; Holmgren, 1995), we expect the number of exploiters to match the resources. In several different environments with four non-evolving plant types, we showed that insect phenotypes evolved to equilibrium levels (numbers) that matched the plants' resource values (Holmgren & Getz, 2000). For example, in the case of the resource values of the

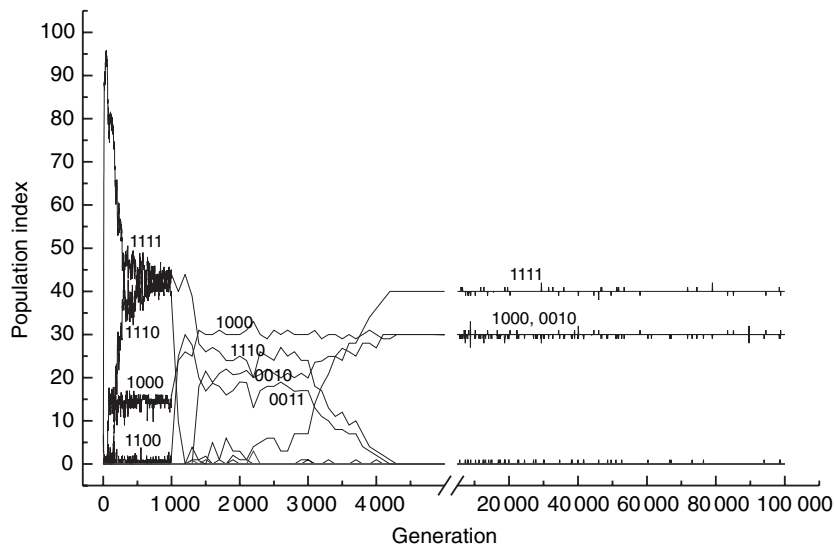


Figure 11.2. The values of the population indices of the phenotypes (as labelled on the graph) in the population are plotted for one of the simulations of the population evolving in the environment four plant types of the values as resources: 40, 10, 40, 10. The population index reflects the number phenotypes and their purity. Phenotype labels denote an array of preference to the four plants, in which 1 is preference and 0 is rejection. Because of the response function chosen for the insect phenotypes, they will tend to be all-or-none responses to each plant (see text for details). Values obtained every generation until 1000 generations, and thereafter every 100 generation are plotted. The scale of the abscissa is varied to portray both short- and long-term trajectories. From Holmgren & Getz (2000).

four plants being [40, 10, 40, 10], insect phenotypes evolved to match so that the numbers produced by each plant type was also [40, 10, 40, 10] (Figure 11.2).

Recalling that insect phenotypes evolve an all-or-none response (or close to it), we can conveniently represent each insect phenotype by an array of preference digits, one for each plant. For example, a phenotype denoted (Post *et al.*, 1999) will lay eggs on plant types one and three, but reject plant types two and four. Simulations were initiated with naïve perceptrons, in which the synaptic weights were randomly set to small values. The simulations were then run for 100 000 generations (for more details see Holmgren & Getz, 2000). In the period of 1000–3000 generations (Figure 11.2) the first niche had 40 insects: 30 of the specialist phenotype [1000] and 10 of the generalist [1110], the second niche had 10 [1110] phenotypes, the third niche 40 comprising of 10 [1110] phenotypes, 20 [0010] specialist phenotypes and 10 [0011] phenotypes, and the last niche had 10 [0011] phenotypes. Simple arithmetic indicates that the phenotypes of this guild are numerically matching the value of the plant resources.

Interestingly, the above guild begins an evolutionary transformation after 3000 generations so that at 4000 generations the matching of plant phenotypes is accomplished by 40 [1111] generalist phenotypes in concert with the two specialists phenotypes, [1000]

and [0010] of 30 individuals each (i.e. occupying niches 1 and 3, respectively). For reasons discussed below, this latter guild is more stable than the one above that arose first. Note that, resource matching is a predicted equilibrium of any exploiter-resource system unless the spectrum of exploiter types (i.e. guild) gets trapped in a non-optimal solution, from which there is no evolutionary escape if mutational perturbations are absent (as in simulated annealing optimisation processes: Haykin, 1994).

11.4.2 The evolution of guilds

Resource matching is a game-theoretic outcome in which no single exploiter phenotype can evolve independently of the frequencies of other phenotypes. From the simulations we conducted, we concluded that exploiters evolve in guilds of several exploiters utilising available resources in concert and in numbers matching the resource abundance and resource value. In Figure 11.2, the transitorily stable resource-matching guild of 30 [1000], 30 [1110], 20 [0010] and 20 [0011] phenotypes is ultimately replaced by a guild of 40 [1111], 30 [1000] and 30 [0010] phenotypes. The transition period is short in comparison with the phases during which the guilds prevail.

The geological record indicates that sudden turnovers of whole guilds of species seem to occur (Gould, 2002). Some rapid turnovers of extinct guilds may be the result of catastrophes, such as meteorite impacts on earth (Alvarez *et al.*, 1980). Species compositions in terrestrial and aquatic systems are also known to exhibit rapid turnovers when alien species are introduced (Crooks, 2002). In addition to catastrophes and major perturbations, guilds of specialists and generalists, unable to match their resources, are vulnerable to invasions of new species forming new guilds. In Figure 11.2, the guild prevailing from generation 1000 to 3000 is matching its plant environment less robustly or resiliently (Amemiya *et al.*, 2005) than the succeeding guild (after 4000 generations), because the former guild is more sensitive to mutations than the latter and more affected by inter-phenotypic competition. In reality, environments may change catastrophically or gradually, and a guild of species whose interactions are characterised by inter-specific competition may be unable to track those changes. As a consequence, a rapid turnover of species will follow, thereby establishing a new guild. Species in guilds have frequencies that are mutually dependent because of resource matching. As such, they are resistant to invasion of phenotypes that temporarily disrupts this matching. The more mutations and new exploiter phenotypes required to obtain a new matching guild, the greater the resilience of the existing guild to persist.

Appearance of a new species may not be sufficient to over-throw an existing guild. Sometimes two or more are required to invade in concert (Holmgren & Getz, 2000). When an invasion has started, existing phenotypes quickly lose fitness as their interdependence with other phenotypes weakens. Because a simultaneous increase in fitness of new phenotypes and fitness loss in old ones is required, turnover rates of guilds when they occur are relatively fast. This is not a group-selection argument: selection still acts at the individual level although the fitness of individuals is dependent on the composition and frequency of the different species in the guild of competitors.

11.4.3 Evolution of specialists versus generalists

Returning to the fact that the response of each clonally evolving insect phenotype in our system is close to all or none, in many situations resource matching can only be accomplished by a guild where some insect phenotypes are specialised on one or a few plants. In our simulations we found that the most stable guilds evolving to match their host-plant environment are those that minimise the degree to which niches overlap among the members of the guild. The reason is that guilds exhibiting considerable niche overlap are more vulnerable to changes in phenotype numbers due to inter-phenotypic competition within shared niches. If mutations of phenotypes lead to erroneous host choices and small deviations from the ideal free distribution, generalists are more likely than specialists to experience reduced fitness from over-crowded plants. Reduced fitness leads to decreased population size of the phenotype, which will lead to other plants in its diet being underutilised.

In reality, deviations from the ideal free distribution can be due to mutations on other phenotypes or changes in resource abundances. Guilds composed of specialists are less affected by inter-phenotypic competition and can more readily track a changing environment. In addition, specialists have a more simple discrimination task than generalists, given that simpler tasks involve fewer critical synapse settings in perception networks than more complex tasks. As such, the perceptual networks associated with simpler tasks are potentially less likely to be hampered by harmful mutations. An exploiter phenotype that utilises two types of plants with sufficiently similar chemical signatures to be able to lump the two plant types into one perceptual category, has no more complicated a task than a specialist exploiter that needs to identify a single plant type. The most extreme case of this would be the generalist that treats all existing plants as one category. For this reason we should expect guilds to be made up by specialists on single plant species (monophages), intermediate specialists utilising a few similar host plants (oligophages) and indiscriminant generalists (heterophages).

In summary, our simulations suggest that disruptive selection for specialisation in a heterogeneous resource environment could arise because of the following two mechanisms. First, selection for sensitivity to signals produces individuals that have an all-or-none response to the different host phenotypes so that only guilds of insects that specialise to some degree will be able to fill up available resource niches. Second, selection favours resource-matching guilds of exploiter phenotypes that perform relatively simple host-choice perceptual tasks robust to mutations.

11.5 Specialisation when resources evolve

In a follow-on study, we allowed the victims to evolve in terms of the signals used by the exploiters to detect these victims (Norrström *et al.*, 2006). As in the previous study, each exploiter was identified with a 3-layer perceptron with weights subject to mutations. Again, with focus on specialisation and disruptive selection, reproduction was assumed to be clonal for simplicity and to eliminate gene flows between genetic lineages. Specialisation and disruptive selection among sexual organisms is within the scope of future

work. Also, victims were still represented by a point in a 2D signal (odour) space. Initially three groups of victims were introduced, differing in their relative palatability: high, intermediate and low. The fitness of each victim depended on the number of victims within the same group and on the attack rate represented by a weighted sum of all exploiters – the weighting being determined by the exploiter response functions to that particular victim.

11.5.1 Red queen evolution

The conflicting interests of exploiters and victims induce a continuously changing system that cycles over time. Exploiters are continuously selected to discriminate among victims of different palatability. Victims of high palatability are selected to become similar to victims of low palatability thereby reducing the intensity of attacks. Victims of low palatability are in turn selected in the signal space to escape from approaching highly palatable victims – that is, to move away from their high palatable mimics. This results in a directional movement of victims in the signal space, driven by the exploiters' continuous adaptation to discriminate among victim types. By measuring all exploiters' responses to many locations in the signal space and calculating a response average in these locations we create a response landscape. Lowlands in the response landscape mean low average response, hence little exploitation, and highlands mean high average response and high exploitation. In the exploiter response landscape (Figure 11.3), the victims move downhill to avoid attacks (e.g. Figure 11.3c), with the least palatable victims in the lead. Because there is variation in each victim cluster, as indicated by the width of the tubes in Figure 11.3, there can be differential selection on the victims within each palatability cluster. While the signals of victims evolve, the ability of exploiters to discriminate among these victims also evolves. For most of the time, the relative distances among the mobile victim clusters in the signal space are more or less constant, reflecting the presence of a red-queen evolutionary process (Van Valen, 1973). For a short time, though, this process is arrested when threshold and saturation constraints come into play (Figure 11.3d)

11.5.2 Mimicry evolution

Geometrically, the red-queen process arrests in 'corners' of the signal space (Figure 11.3d). In these corners signal cues are either saturated or absent. Selection now enables the most palatable victims to become perfect mimics of least palatable victims. Holmgren & Enquist (1999) suggested that an equivalent process can explain the evolution of Batesian mimicry, including the saturated colouration visual mimics and models often exhibit. In this phase of the process, the exploiters are unable to distinguish between these two victim types, and hence their individual response surfaces will relax and become flat over the whole signal space. This releases the palatable and unpalatable victims from differential selection due to lack of discrimination by the exploiters, thereby allowing the victims to drift apart in the signal space. In this way the mimetic resemblance is degraded.

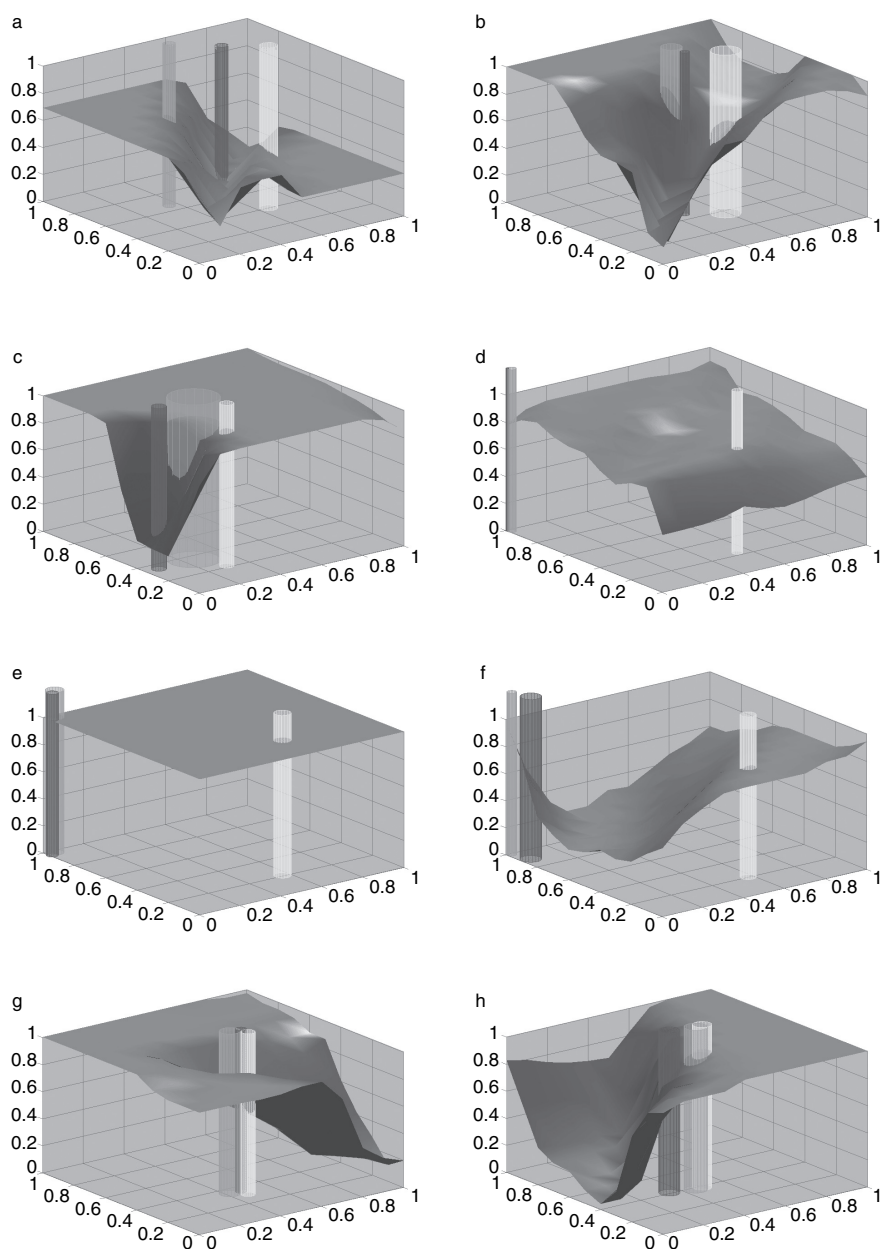


Figure 11.3. Victim-cue (e.g. host plants) phenotypes and exploiter-response phenotypes (e.g. phytophagous insects) are plotted above the 2D signal space. The two bottom axes represent signal strengths of cue phenotype. The surface shows the average response of all exploiters to a hypothetical signal at any point in the signal space. The vertical columns represent victim clusters: medium grey – undefended, light grey – intermediate, and dark grey – defended. The centre of each column is at the average of the victim cue-phenotypes in the cluster in question and the radius is the

11.5.3 Cyclicity of specialists and generalists

When host clusters are discriminable, the exploiters evolve to specialise on the palatable and intermediate host clusters. Once the unpalatable model and its mimics are driven to perfect mimicry in one of the corners of signal space, the exploiters become complete generalists. This process is cyclic (Figure 11.3) with the period length determined by the evolutionary response, i.e. changes from one generation to the next, according to Fisher's (1930) fundamental theorem of natural selection. The evolutionary response is a function of additive genetic variance, in our model determined by mutation rates, and the selection differential (Maynard Smith, 1998) given by the elevation differences in the response landscape of the perceptrons (Figure 11.3). The cyclicity is a consequence of the continuous changes in the host signal phenotype and the constraints on the strength on each of the two components of the signal. At signal saturation, first variation in signal traits degrades; second, differential selection on plants becomes vanishingly small. In the next phase, changes are determined by mutation rates alone. In this evolving plant environment, host races readily evolve. If exploiters reproduce sexually by mating among individuals sharing host plants, the reproductive isolation between host races will disappear when they come together on the same host. In this case, sympatric speciation would not be possible unless reproductive isolation is upheld by other mechanisms than assortative mating linked to host-plant preference.

11.6 Exploiter asexual versus sexual reproduction

The models described above are based on clonal reproduction in the exploiter population. No attention was paid to the homogenising effect of genetic recombination among lineages produced by sexual reproduction and recombination (Rice, 1984). In a recent study (Norrström *et al.*, unpublished), we extended our model by adding sexual reproduction and diploid genetic coding of the synaptic weightings in our perceptron representations of individual exploiters. An unlinked mating gene that could hold an allele for random or for assortative mating was added. In this case assortative matings were confined to individuals on the same

Caption for Figure 11.3 (cont.)

standard deviation. The images are captured after a simulation of exploiter–victim coevolution. (a) The simulation is initialised with the plants lined up on the diagonal. The insects have learnt to respond to the plants: two specialists, one on each edible plant has evolved (not seen in figure). (b) The most edible plant cluster has approached the noxious plant cluster. The runaway movement with the most edible plant following the least edible one, has started. (c) The chase moves to the border of the signal space. The intermediate plant is following behind. (d) The chase has been arrested in a corner, and the intermediate plant has been left behind. (e) The insects have stopped discriminating between plants. (f) The two plants in the corner have drifted apart because of the lack of selection on signals. Becoming separated, the insects are now starting to discriminate the plants again. The chase has been re-initiated. (g) The chase has been moving towards the centre and attracted all plants in the middle. (h) The chase is now continued toward a border of the signal space, and the procedure repeats from (c) and onwards. The figure is from Norrström *et al.* (2006).

host plant. We allowed for the equivalent of genetic cross-over to occur during meiosis by rearranging genes for perceptron weights among chromosomal-like structures (see Appendix for more details). We kept our four resources: two of equal value and two noxious. We can repeatedly confirm that also sexual populations evolve two specialists. In this case they are reproductively isolated homozygotes, i.e. sympatric speciation by definition.

We inhibited mutations of the mating gene during the first 20 000 generations. During this period, a polymorphism of two chromosomal haplotypes, here named A and B, arise. The two haplotypes are combined in three genotypes, two (AA and AB) expressed the same specialist phenotype on one resource and the third genotype (BB) express the specialist on the other resource. When mutations are allowed on the mating gene, the assortative mating allele invades and becomes fixed in the population. The protected polymorphism turns into two reproductively isolated, homozygote specialists (AA and BB). This suggests that stable polymorphisms can evolve as a result of disruptive selection, being a prior state to reproductive isolation and sympatric speciation. It also shows that genes for assortative mating can invade uncorrelated with ecological genes.

The initial evolution of a protected polymorphism evolves to match the available resources through mapping three genotypes on two phenotypes. This is possible with a multi-locus model and synergistically interacting genes. With genotypes expressing functional phenotypes, including heterozygotes, it is not obvious why assortative mating invades and eliminates the heterozygotes. The number of erroneous phenotypes in the population diminishes from 19.6% to 8.5% after invasion of assortative mating, thereby the mutation-selection balance for deleterious alleles settles at a lower level. Thus, there is selection for assortative mating either to get phenotypes more robust to mutations, or enhance the reductional selection of deleterious mutations. Experimental mutations on all prevailing phenotypes exhibit similar proportions of increased erroneous phenotypes and actually more during assortative mating (15.4%) than before (14.6%). This leaves us with the hypothesis that selection against deleterious mutations is more effective during assortative mating, which could be the case if deleterious mutations are silent in heterozygotes. When analysing the genotypes from our simulations, we see that the heterozygote actually has a number of silent alleles that are expressed in homozygote form. To understand how these alleles work, we have to recall the structure of the neural net and how the alleles affect its performance. Our nets have three sensory neurons, each capable of having a threshold response at a given ratio of the two input compounds. This threshold response is a linear discrimination controlled by four alleles, which in our case is an allele complex constituting a functional unit. The output of the three sensory neurons are thus governed by three allele complexes, and combined in the output neuron which can perform nonlinear responses. Simple discriminations require only one critical allele complex, whereas a complicated discrimination requires critical settings of many allele complexes. In our simulations, critical allele complexes exhibit much less variation than noncritical ones. We can thus understand the underlying genetics as three super-loci occupied with super-alleles (but let us call them loci and alleles from now on for simplicity). The output neuron later

combines the output from the alleles but the combination is elemental and left out of the description for clarity. The loci can have three discrimination alleles: d1 discriminates between resource 1 and 2 in homozygote form, d2 does the same but between resource 2 and 3 and d3 discriminates between resource 3 and 4. We also find a modifier allele, m, which modifies the expression of d2 to become like d1. The allele m does not perform any discrimination in homozygous form. There is also an inhibitor allele, i, that inhibits the expression of d-alleles so that the sensory neuron does not perform any discrimination. In homozygous form the i-allele also does not perform any discrimination. The allele arrangements of the genotypes in the polymorphism are:

Locus	Genotypes		
	AA	BB	AB
1	m m	d2 d2	m d2
2	d1 d1	i i	d1 i
3	i i	d3 d3	i d3

We can see that AA expresses d1 to become specialist on resource 1, whereas the other loci are silent. Genotype BB expresses d2 and d3, which is required to become specialist on resource 2. The heterozygote AB expresses d1, because the expression of d2 is modified by m in locus 1. Loci 2 and 3 are silent because of the inhibitor alleles. Hence, deleterious mutations on d1 and d3 are silent in the heterozygote, and thus not subject to selection. Since homozygote lineages, mating assortatively, need no modifier or inhibitor alleles the selection against deleterious mutations is stronger in homozygote specialists than in the polymorphism. Thus, the model demonstrates that species can arise sympatrically because deleterious mutations can more effectively be removed from the population. As the pre-zygotic barrier (of assortative mating) has evolved, heterozygotes are rare and the selection on m as a modifier is relaxed. As m loses its modifying property, the homozygotes in addition become post-zygotically isolated (Norrström *et al.*, unpublished). This is the evolutionary end result we can expect to observe in nature.

F₁ hybrids between host races of phytophagous flies have a markedly reduced behavioural response to parent host odours and mixtures of them (Linn *et al.*, 2004). This is convincing evidence for a significant genetic component of the host preference trait. The lack of intermediate and parental-like responses indicates a synergistic interaction between ‘preference alleles’ in heterozygote form. Electrophysiological measurements on olfactory receptor neurons suggests that it is genes for olfactory receptor proteins in dendritic membranes that interact synergistically and elicit hybrid-specific responses to host volatiles (Olsson *et al.*, 2006). The host races of these insects exhibit already pre-zygotic (by mating only on host plants) and post-zygotic isolation (by the disability of hybrid offspring to find host plants), which is analogous to the end state of our simulations. The fact that host-related, reproductively isolated lineages in some insects are morphologically

indistinguishable and lack other allozyme or genetic differences (see Olsson *et al.*, 2006 and references therein), suggest that the speciation process is driven by disruptive selection on the host-recognition trait. These may be incipient species in early stages of speciation, or recently arisen species according to the species definition of Orr & Smith (1998).

11.7 Conclusions

It has been shown that disruptive selection on morphological traits with innate limitation effects on niche-breadth can give rise to sympatric speciation if reproductive isolation evolves as a correlated character (Dieckmann & Doebeli, 1999). Such traits are typically related to the feeding apparatus, and its size sets the boundaries of suitable resources. Trait examples from cases of sympatric diversification are shell size in marine snails (Panova *et al.*, 2006) or jaw length in fish (Rundle & Schluter, 2004; Barluenga *et al.*, 2006). In many phytophagous insects, the recognition mechanism itself seems to be under disruptive selection (Linn *et al.*, 2004). There are no innate niche-limitations to this trait, so we need to understand why specialisations evolve before we can understand speciation based on the resource recognition trait. We have shown that generalists are more susceptible to mutations and their larger niches overlap link perturbations (due to mutations) between genetic lineages (Holmgren & Getz, 2000; Norrström *et al.*, 2006). In either case, disruptive selection depends on resource competition between individuals.

The underlying genetics of the trait under disruptive selection is of importance for the evolutionary response. Traits governed by additive genetics typically produce hybrids between incipient branches that are intermediates, which prevents the population from branching into two lineages (Geritz & Kisdi, 2000). Even if there is selection against intermediates because they experience the highest resource competition, it is not strong enough to counteract the homogenising effect on an incipient branching population. For traits expressed by synergistic interaction between genes, however, hybrids may express any phenotype. In this case disruptive selection results in a polymorphism (Norrström *et al.*, unpublished). The population has branched into two phenotypes, expressed by two haplotypes in Hardy–Weinberg equilibrium.

To meet the criteria of species, branched lineages in a population have to become reproductively isolated (e.g. Orr & Smith, 1998). The two scenarios with different genetics also have different causes for the selection of assortative mating. When ecological traits have additive genetics, assortative mating arises to avoid the less fit intermediate hybrids. Hence, the population branches in concert with the establishment of assortative mating. Therefore, ecological and mating genes need to be correlated (e.g. Felsenstein, 1981; Dieckmann & Doebeli, 1999). When ecological traits are expressed by synergistically interacting genes, the population is likely to be branched when an assortative mating mutant arises in the population. Hybrids or heterozygotes are as fit as other genotypes, but they are likely to have genes that are silent in heterozygote form. We see that regulatory genes evolve in order to make a haplotype compatible both to itself and its match in the stable polymorphism (as described above). Silent genes are not subject to selection and accumulate harmful mutations that are expressed in, and deleterious to

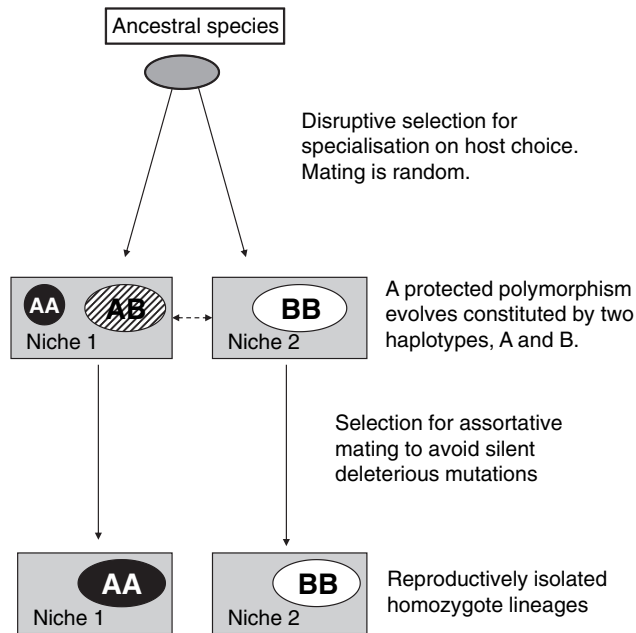


Figure 11.4. Selection on the ecological niche recognition mechanism can result in sympatric speciation. First, there is disruptive selection for specialisation on two niches represented by squares. Specialists evolve in a protected polymorphism with two haplotypes A and B. The genotypes mate randomly and consequently are in Hardy–Weinberg equilibrium. Heterozygotes have silent alleles that carry harmful mutations. These are expressed in homozygote offspring. Assortative mating homozygotes invade the population and thereby avoid harmful mutations in their offspring. Two species reproductively isolated by pre- and post-zygotic have evolved sympatrically.

homozygote offspring. So in this case, mutant assortative mating homozygotes invade the population because they avoid silent deleterious mutations carried by heterozygotes that will be expressed in their offspring (Figure 11.4).

If sympatric speciation results from specialisation on biological resources, the resource may coevolve with its exploiters. When exploiters are entrained in a cyclic coevolutionary processes with their victims, selection for generalists and specialists may shift back and forth (Norrström *et al.*, 2006). Recent investigations reveal new dynamic properties of the specialisation process (Janz *et al.*, 2001; Nosil, 2002). They question the view of the specialisation process as always going from generalisation towards specialisation; hence suggesting that specialisation is not an evolutionary end-point. Janz *et al.* (2001) investigated the phylogeny of the nymphali butterfly tribe Nymphalini. They concluded that there is no directed evolution towards specialisation and that the changes in host range show a very dynamic pattern. Nosil (2002) used phylogenies from 15 groups of phytophagous insects to investigate the rates of evolution towards specialisation and generalisation. They found that the rate of the evolution towards specialisation is significantly higher than the

rate toward generalisation. In some cases, however, the rate of generalisation was higher, or equal to the rate of specialisation. These observations that niche breadth is a variable trait in some taxa, and it can both be widened and narrowed by evolution.

11.8 Appendix: Model description

The model has a structure with a population of exploiters (e.g. insects) and an environment of victims (e.g. plants). Both exploiters and victims are equipped with traits essential to the model and will be explained below. Traits are constants or subject to mutations. Each individual exploiter and victim is evaluated by a fitness function. New generations are created by letting the most fit individuals reproduce. The offspring inherit the parents' traits but mutational changes and crossover (in the sexual model only) may occur. Generation times in evolving plants are longer than in insects. The model is a general exploiter-victim model, but was originally inspired by phytophagous insects and their host plants. Below, the models are described, but for all details we refer the reader to our original publications.

11.8.1 The exploiters

The exploiter population is modelled individually, each being equipped with an artificial neural net. We use a three-layer, feedforward perceptron as a model for the perceptual system of the exploiters. The perceptron has two input nodes and one output node. The number of hidden nodes in the intermediate layer varies between 3–6. The net is fully connected with synapses in a feedforward fashion. So called 'bias signals' were applied to the nodes. Synapse values were limited to ± 10 . Each node (except the input nodes) is activated by a standard sigmoid threshold function (see Holmgren & Getz, 2000). The output of the ANN is bounded between 0–1, and represents the exploiter's preference to the victim whose two signal cues are applied to the input nodes.

The fitness W_g^E of exploiter i depends on the resource value of the victims (h) it attacks (v_h), the intensity of the attack (e.g. the number of eggs the exploiter lays) on the victims ($e_{g,h}$; eqn 1), and the probability of attack success (e.g. the eggs hatching), and is given by the function

$$W_g^E = \sum_h e_{g,h} \frac{1}{1 + \left(\frac{e_h}{v_h \varepsilon_{1/2}}\right)^a} \quad (\text{A1})$$

Here a is a parameter that determines the abruptness of the effects of density dependence. Parameter $\varepsilon_{1/2}$ sets at which value of the total attack of plant (e_h) the sigmoid fitness function returns half its maximum value. Hence, the number of offspring in the next generation is density dependent on each host. When individuals of the generation are created the nodes are subject to point mutations with a given probability. A mutation incurs a change to the weight drawn from a rectangular distribution with given limits. The probability of mutations and the limits of the rectangular distribution varied as a part of a sensitivity analysis. The fitness determines the number of offspring in the next generation.

In the sexual model with diploid, sexually reproducing insects, each insect has two vectors representing the parts of the insect's genome that codes for the structures associated with host plant selection in the insect's nervous system. Stored in the vectors are values representing the genetic expression of each gene in the above-mentioned parts of the genome. Each position in the vectors corresponds to a specific synaptic weight in the insect's ANN. The value of a specific synaptic weight is the intermediate value of the two corresponding values in the vectors. During reproduction each parent produces a gamete that will become one of the offspring's vectors. The gamete is created by copying values from one of the vectors into the gamete and proceeding down the vector. With a given probability, crossover occurs, and the values of the gamete are instead read from the other parent continuing at the position where the crossover occurred. There are no restrictions on the number of crossovers that can occur during the creation of a gamete. The direction of the copying is always the same; hence the positions of the new values in the vectors correspond to the same synaptic weights as in the parents. A value in the gamete may mutate with a given probability. During mutation the value is modified with a random value within a fixed range.

11.8.2 The victims

In simulations where victims, e.g. plants, do not evolve, they are represented as homogeneous populations with different traits. When plants evolve, plant populations are modelled as a group of individuals that share their value as a resource to the exploiters, but exhibit variation in their signals. The signals consist of two cues that are subject to mutational changes with a fixed probability and drawn from a rectangular distribution of a given range. Range and probability have been varied as a part of a sensitivity analysis.

The fitness W_h^E of victim h is a sigmoid function of the size of the population of which it is a member (P_h), its egg-load (e_h) and its resource value to exploiters (v_h):

$$W_h^V = \frac{\beta}{1 + e^{\delta(dP_h + c_1 e_h + c_2(v_{MAX} - v_h) - \gamma)}} \quad (\text{A2})$$

Parameter β determines maximum fitness, δ is a slope parameter, and d is the intensity of density dependence. Parameter γ is a population growth rate parameter. Parameter v_{MAX} sets the maximum resource value a victim can have. The cost parameter for an egg-load is c_1 , and for the defence against exploiters c_2 . We require $c_1 > c_2$ since the victims trade off predation costs by expending fitness currency on defence (Norrström *et al.*, 2006). The number of offspring of each plant in the next generation is given by rounding off the fitness upwards or downwards to the nearest integer. Which one is determined by distance-weighted probability.

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