

Evolution of host plant selection in insects under perceptual constraints: A simulation study

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ABSTRACT

A major enigma in insect ecology is why many more host plant specialists than generalists exist, especially since laboratory and field experiments have indicated that specialists are usually able to use a much broader spectrum of plants than is observed in nature. It has been suggested that perceptual constraints, coupled with considerations of foraging efficiency, may play a role in the evolution of specialization. Here we investigate this notion in the context of insects selecting different types of plants, where the ratios of particular compounds in a blend of odorants provide the cues necessary to discriminate different plants from one another. The discrimination task is modelled by feedforward neural networks that are identified with particular individuals. These networks replicate with the clonal reproduction of individuals, and the strength of the synapses in these networks are able to mutate from one generation to the next. Individuals exploit the different plant types at a level determined by their perceptual response to the individual plants of each type. The fitness of individuals is determined by the relative nutritional value of each plant type and the proportion of individuals in the population exploiting that plant type. From simulations of the evolution of the perceptual networks, we are able to conclude that the probability of particular preferences evolving depends on how close the signals of the plants of different nutritive values are to one another. At reasonably high mutation rates, the more easily implemented plant preferences evolve earlier and are at a competitive advantage compared with later evolving, equally fit plant preferences. At low mutation rates, evolution stalls for long periods of time, but when change does occur it is saltational. Evolutionary equilibria typically involve guilds of complementary species that together constitute an 'ideal free distribution' in terms of the productivity of the different plants. Our results also suggest: that the mix of phenotypes in these guilds is critically dependent on the order of appearance of various combinations of specialist and generalist phenotypes; that this order depends on the difficulty of the perceptual task associated with each phenotype; that any differences in the relative utilization by a generalist of different species of plants will lead to the emergence of one or more specialists that exploit the plants most under-utilized by the generalist; and that evolutionary changes in guild structure are less frequent than mutational rates might suggest, but are saltatory when they occur. Consequently, the strategy to specialize may dominate for two reasons: specialization appears to evolve more readily in complex environments; and the ideal free distribution mentioned above is more easily matched by a group of specialists or by generalists in concert with specialists than by a generalist alone. Finally, our analysis suggests the hypothesis that oligophages or heterophages will not omit

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nutritive plants from their diet that have chemical signatures intermediate between plants upon which these herbivores feed.

Keywords: diet selection, evolutionary dynamics, feedforward networks, genetic algorithms, herbivory, niche selection.

INTRODUCTION

The concept of specialization can only be defined in a comparative sense (Futuyma and Moreno, 1988; Berenbaum, 1996). Herbivorous insects, for example, can be placed on a specialist–generalist gradient by considering the number of species, genera or families of plants that they exploit (Jermy, 1984). However, specialist strategies are more common than generalist strategies (Jermy, 1984), which constitutes a major puzzle in entomological ecology and evolution (Futuyma, 1991).

Several proposals have been made to explain selection for either specialists or generalists. The chemical defence theory states that specialization is required to overcome the chemical defences of a plant or group of plants (Swain, 1977). If a herbivore overcomes these defences, then colonization of these plants is facilitated (Feeny, 1987). Specialization has also been explained from a population ecological point of view. For example, predation might select for specialists (Bernays and Graham, 1988) or specialization might evolve to enhance foraging performance (Bernays and Weislo, 1994).

More recently, it has been suggested that specialization in insects may evolve due to limitations in the perceptual system (Fox, 1993; Bernays and Weislo, 1994; Janz and Nylin, 1997; Bernays, 1998). In a complex environment, the information-processing capabilities of an insect need to be focused on a limited number of identification tasks. Neurological complexity should allow increasingly sophisticated decision rules, and hence facilitate polyphagy. In line with this idea, Levins and MacArthur (1969) suggested that insects are constrained by their ability to discriminate among a number of suitable and unsuitable host plants. We may therefore expect the underlying features of an insect sensory neural system to be critical in determining the path taken by evolution towards particular species of insect herbivores becoming generalists or specialists.

Plant chemistry (taste and olfaction), rather than plant colour or shape (vision), is probably the most fundamental factor in the process of individual herbivores accepting or rejecting a plant (Bernays and Chapman, 1978). Some of these chemicals are volatile odours detectable at some distances, while non-volatiles (e.g. waxes) are detected by contact chemoreception or taste. Most olfactory receptors are located on the antennae (Visser, 1986). They respond to an array of odorant molecules (Smith and Getz, 1994). This response is then propagated down the antennal nerve to the olfactory lobes in the insect deutocerebrum (Masson and Mustaparta, 1990; Smith and Getz, 1994) where the information is processed and sent on to the higher levels of the brain (i.e. the mushroom bodies in the protocerebrum; see Masson and Mustaparta, 1990; Hammer and Menzel, 1995).

Some structural features of insect olfactory systems may exist that correlate with the degree of specialization across particular families of insects. Polyphagous species, for example, appear to have more chemosensory sensilla than oligo- and monophagous species (Chapman, 1988). Orthopteran insects (grasshoppers and crickets) stand out as a group dominated by polyphagous species (Bernays and Chapman, 1994). The brain of a typical

orthopteran has about 1000 olfactory glomeruli in each of its two antennal lobes (Visser, 1986). The brains of insects that have a more restricted diet (Bernays and Chapman, 1994) generally have fewer glomeruli (in some cases as few as 50; see Visser, 1986). Although other factors, such as the complexity of individual glomeruli, have some bearing on the complexity of chemosensory computations that individuals are able to perform, the chemosensory apparatus of polyphagous orthopterans suggests that they have evolved a more powerful olfactory processing system than many other herbivorous insects that are less polyphagous. This suggests that polyphagy requires enhanced capabilities in memory processing, as discussed by Dukas and Real (1991, 1993), and that neural structures associated with memory and perception are energetically costly to maintain, or only evolve at the expense of other adaptations.

Here we use artificial neural networks and population models to study the question of perceptual constraints on the evolution of feeding behaviour in insects. Each individual insect is represented by a simple network that processes plant chemosensory signals (Fox, 1993). In these networks, synapse strengths are able to mutate during clonal reproduction (Enquist and Arak, 1994). The assumption of clonal reproduction implies that we do not have to consider sexual recombination of genes coding for synapse strengths. This type of assumption is often made in evolutionary analyses (Maynard Smith, 1982; Brown and Vincent, 1987; Vincent and Brown, 1988), and the results are directly applicable to traits with additive genetic variance under weak selection in sexually reproducing species (Taylor, 1989; Kaitala and Getz, 1995; Getz, 1999; note that weak selection implies that point mutations lead to small perturbations in traits). The network is capable of selecting among plant types (i.e. resource niches), where the input to the networks is a signal that is unique for each plant type and the output is a measure of the probability to utilize that plant.

Futuyma, among others, has suggested that genetic constraints affect the evolutionary trajectory of host preferences in insects (Futuyma, 1991; Futuyma, *et al.*, 1993, 1995); but, to the best of our knowledge, this study represents the first attempt to investigate the significance of perceptual constraints on the evolution of host range in insects, using neural net models. Consequently, so as not to confound our results with other constraining processes, we have kept the genetic coding, reproduction and fitness processes as simple as possible. Thus, we focus here on how a class of neural networks (as detailed below), with their limitations and biases, will respond to selection in a number of different plant environments. We also investigate the effects of the frequency and the amplitude of mutational changes.

THE MODEL

The model we use has three components: (1) computation of the perceptual response of individuals to different plant types, (2) calculation of the fitness of individuals, and (3) generation of progeny for the fittest individuals. The first component is modelled by a simple three-layer feedforward neural network (one sensory, one hidden and one output layer; Haykin, 1994). Each network represents an individual insect, and each plant type represents a resource capable of supporting the development and maturation of a fixed number of individuals in each generation. The plants are assumed to produce a signal; that is, the input to the neural network each individual uses to discriminate among plant types. The second component, the calculation of the fitness of each individual, is based upon

(a) the response of its network to each of the plant types, (b) the productivity of those plant types, and (c) the number of individual competitors on those plants. The third component, reproduction of the fittest individuals, involves the replication and mutation of the associated perceptual neural networks using algorithms detailed below.

Our model is particularly applicable to the evolution of guilds of holometabolous insects that lay their eggs on selected host plants. Our results, however, are equally applicable to other species for which the abstraction of processes embodied in our model provide a basic dynamical framework for their evolution. Our simulations are individual based (DeAngelis and Gross, 1992) and, because of random mutations, they are also stochastic. Therefore, simulations need to be repeated many times to obtain a sense of what the most likely outcomes will be over thousands of generations.

Odour perception and network model

Plants have a number of C6 compounds that, when mixed together, constitute what is generally known as ‘green odour’ (Visser, 1986; Olías *et al.*, 1993). These universally common compounds occur in plant-specific ratios from which the plant species can be recognized (Bernays and Chapman, 1978; Visser and de Jong, 1987). A large number of species have shown sensitivity to the components of green odour (Visser, 1986).

To keep our model simple, we assume that each type of plant is characterized by a species-specific ratio that is fed into the network via two input channels (S_1 and S_2), where each channel responds to the presence of plant compounds according to its own normalized ‘tuning spectrum’ (cf. Getz and Akers, 1993). Note that limiting the inputs to two channels does not imply that only two types of chemical are involved (e.g. see Dickinson *et al.*, 1996). The input itself is preprocessed by afferent neurons to the location of this perceptual network (Fig. 1). The most likely location for this perceptual network in insects is in the mushroom bodies of the protocerebrum (for reviews, see Masson and Mustaparta, 1990; Smith and Getz, 1994). The olfactory input to the protocerebrum comes from the antennal lobes, which in turn receive their input from sensory neurons located in the antenna (Fig. 1). For simplicity, we only consider the case where the perceptual network relies upon two inputs from the antennal lobe. In actuality, this number is probably on the order of a hundred. Again, for simplicity, we ignore the complications of the effects of concentration (but see Masson and Mustaparta, 1990; Smith and Getz, 1994). In particular, we assume that H plant types exist and that the signals from these H plant types produce characteristic responses in the antennal lobes of individuals that are spaced out equidistant along the line joining the points $(S_1, S_2) = (0, 1)$ and $(S_1, S_2) = (1, 0)$. That is, plants of type h produce the response

$$(S_{1,h}, S_{2,h}) = \left(\frac{h}{H+1}, 1 - \frac{h}{H+1} \right) \quad \text{where } h = 1, \dots, H \quad (1)$$

This response, generated in the projection neurons by the sensory neuron input into the antennal lobes, is then propagated to a fully connected, feedforward neural network (Fig. 1; see Haykin, 1994, for a didactic presentation of neural network theory). We select the number of hidden units to be one less than the number of plants, since this is the minimum number generally required to separate all plants from one another; and we select the number of output units to be one.

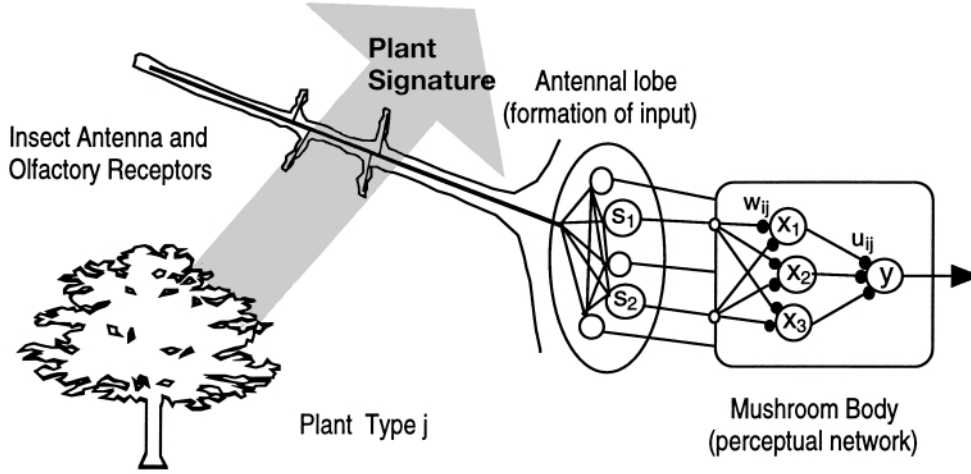


Fig. 1. Representation of the perceptual component of the model. Each plant type produces its own unique signature that stimulates the olfactory receptor cells located on the antennae of individual insects. The response of these cells is processed in the antennal lobes to produce an antennal lobe output S_i that we regard as input to a perceptual neural network located in the mushroom bodies of the protocerebrum. Our highly idealized model of this perceptual system is a three-layered feed-forward 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_{ij} , $i = 1, 2, j = 1, 2, 3$. The output x_j from each of the hidden units when stimulated, is the result of passing the input activity through an activation function (equation 2). The activity impinging on the output unit is similarly modified by the synaptic weights u_j . The response y of the output neuron is characterized by the same activation function (equation 2).

We use the common neuron (unit) activation function

$$\varphi(\xi) = \frac{1}{1 + e^{-\alpha\xi}} \quad (2)$$

where $\alpha > 0$ is a slope parameter (the higher the value of α , the sharper the threshold; we use $\alpha = 4$). We assume that an individual's preference for plants of type h is represented by the response y_h of her single output neuron, which ranges between 0 (complete rejection of plant h) and 1 (maximum preference for plant h).

Each individual in the population is represented by a unique set of weighting parameters \mathbf{W} (the matrix of elements w_{ij} , $i = 1, 2, j = 1 \dots 3$; see Fig. 1) and \mathbf{u} (the matrix of elements u_j), and hence a unique output response $\mathbf{y} = (y_1, \dots, y_H)$ to each of the H plants. In particular, the g th individual in the population is uniquely designated by the parameters $\mathbf{P}_g = (\mathbf{W}_g, \mathbf{u}_g)$ or the output response \mathbf{y}_g , where the choice of designation (parameter or output) will depend on the context. Note that, in our simulation, individual g is first created by assigning the values to the parameters \mathbf{P}_g at random from a constrained set of possible values. Also note that positive weightings are interpreted as excitatory input and negative weightings as inhibitory input. The corresponding output, \mathbf{y}_g , is then an H -dimensional vector of values lying between 0 and 1.

Finally, for clarification, we reiterate that the signal from each plant, after being processed at the level of the peripheral and antennal lobes of the insect brain, is assumed to be invariant across individuals and to be constant throughout both the lifetime of the individuals and through evolutionary time. In reality, however, this signal will show some variation across individuals and, as with the network itself, will be affected to some degree by experience and learning (Hammer and Menzel, 1995). Furthermore, in reality, we should expect: variations in the signals across individual plants of the same type; the signals themselves to evolve over time (actually co-evolve with the insect population); and, as previously mentioned, the dimension of the signal to be higher than two (hundreds of relay neurons project from the antennal lobe to the mushroom body and, at least, tens of neurons should be responding to any given stimulus at the periphery; see Laurent, 1996; Lemon and Getz, 1999). As a first pass at analysing the evolution of specialization in plant choice using a neural network approach, however, we ignore this level of detail and focus only on the evolution of choice as represented by the output response y_g from the network model defined by the parameter set \mathbf{P}_g that is fixed for the lifetime of an individual, but which mutates from one generation to the next.

Ecological dynamics and fitness

The fitness of the individuals themselves is determined by their relative abilities to use the plant signals to identify the most nutritious plants in an environment that has a finite carrying capacity (cf. the finite niche differential selection models of Levene, 1953; Dempster, 1955; Christiansen, 1975). The ecological dynamics and determination of individual fitness are based on the following idealizations:

1. Each individual has a total complement of E eggs.
2. Individuals move around and lay their eggs in a number of clutches, with individual g ($g = 1, \dots, G$) ultimately laying $c_{g,h}$ of her eggs on plants of type h . All plant types are considered as hosts by every insect individual. The value of $c_{g,h}$ should reflect both the relative and absolute responses of individuals to plant type h ; that is, $c_{g,h}$ depends both upon

$$y_{g,h} / \sum_{h=1}^H y_{g,h}$$

and upon $y_{g,h}$ itself. The latter implies that individuals who respond weakly to all plants will end up laying only a small proportion of their egg complement E . From a modelling perspective, this assumption avoids a drift in absolute response values. From a biological perspective, it is reasonable to assume that a minimum response is required to stimulate egg laying in females.

3. The collection of all plants of type h represents a resource that produces a fixed number r_h of individuals whenever more than r_h eggs are laid on that plant. This represents some host-plant-related density-dependent effect that could be due to resource limitation, predation or any other limiting factor associated with the environment in question.
4. Every egg on a particular plant has the same probability to develop to maturity; that is, the probability of successfully completing the development cycle from egg to larva to pupa to adult is independent of the individual phenotype \mathbf{P}_g and all adults are equally fecund.

Idealization (3) implies that density-dependence is infinitely abrupt (Getz, 1996), an idealization that has been used elsewhere to study competition in evolutionary contexts (Levene, 1953; Dempster, 1955; Christiansen, 1975; see also Getz and Kaitala, 1989). The simplest implementation of idealization (2) is to use the expression

$$c_{g,h} = y_{g,h} \frac{y_{g,h}}{\sum_{h=1}^H y_{g,h}} E \quad (3)$$

To demonstrate formula (3), suppose the environment has four types of plants (i.e. $H = 4$) and individual g has the same moderate response $\mathbf{y}_g = (0.5, 0.5, 0.5, 0.5)$ to all plants. In this case, individual g will lay $E/8$ of its eggs in each of the four niches represented by these four plant types; that is, it will lay only half of its egg complement E before it dies. On the other hand, if individual g has the same strong response to all plants $\mathbf{y}_g = (1, 1, 1, 1)$, then it will lay $E/4$ of its eggs in each of the four niches, thereby laying all of its egg complement E before it dies. Finally, if individual g responds only to plant type 2, but the response is maximal (i.e. $\mathbf{y}_g = (0, 1, 0, 0)$), then this individual will lay all of her eggs only on plants of type 2.

Since each plant type is limited to producing r_h individuals in the next generation, it follows from idealizations (1)–(4) that the expected number of offspring of individual g from niche h in the next generation is

$$r_h c_{g,h} / \sum_{g=1}^G c_{g,h}$$

so that its total number of offspring z_g in the next generation is

$$z_g = \sum_{h=1}^H r_h \frac{c_{g,h}}{\sum_{g=1}^G c_{g,h}} \quad (4)$$

Note that the fitness function represented by equation (4) does not explicitly or even implicitly favour a generalist selecting all suitable plants or a specialist selecting only one plant. The fitness of an individual depends on the strategies of all other individuals through the competition that arises between the progeny of these individuals to get their proportional share of the resources in that niche.

Whatever the mutational processes are that drive the variation in the progeny of the individual of phenotype \mathbf{P}_g , and whatever the details are of the selection processes that translate the real number z_g into an integer number of progeny, we should expect that at an evolutionary equilibrium the particular mix of phenotypes \mathbf{P}_g , $g = 1, \dots, G$, will represent an ideal free distribution (i.e. each phenotype is equally fit; see Fretwell and Lucas, 1970; Parker, 1970). Furthermore, at the end of the evolutionary process (i.e. reaching a mix of strategies or drifting among equivalent mixes of strategies), this mix of strategies should represent a Nash equilibrium (Nash, 1951); that is, if the g th phenotype ‘tries’ alone to change her ‘strategy’, represented by the values of the parameters \mathbf{P}_g , then she can only reduce her fitness (see Lindgren, 1990, for similar results with regard to mixed strategies).

In all the simulations discussed below, we limit our investigation to an environment with four niches (i.e. $H = 4$) with a combined productivity of the 100 individuals – that is, both $\sum_{h=1}^4 r_h = 100$ and $G = 100$.

The evolution algorithm

The algorithm used to simulate the evolution of network phenotypes \mathbf{P}_g is described by the following six steps:

1. The first generation of individuals (reproductive adults) is created by initially selecting random values between 0.1 and -0.1 for the nine synaptic weights in $\mathbf{P}_g = (\mathbf{W}_g, \mathbf{u}_g)$ for each of the $G = 100$ phenotypes considered.
2. The output vectors \mathbf{y}_g and associated fitness values z_g are then calculated using equations (1)–(4) for each of the 100 phenotypes \mathbf{P}_g .
3. These fitness values z_g , which are real numbers, are randomly rounded up or down as follows: a rectangularly distributed random number between 0 and 1 is added to z_g and the result is then rounded down to obtain the number \hat{z}_g (i.e. all numbers of the form $n.x$ will be rounded up to $n + 1$ with probability $0.x$ and down to n with probability $1 - 0.x$).
4. The 100 phenotypes are ranked in descending values of z_g . The number of progeny assigned to each phenotype is \hat{z}_g . The total number of progeny should add up to a number close to 100. If this number is more than 100, then the lowest ranking phenotype with a single progeny will have its value \hat{z}_g reset from 1 to 0. This procedure will be repeated until the number of progeny is 100. Similarly, if the number of progeny is lower than 100, then the highest ranking phenotype with 0 progeny will have its value \hat{z}_g reset from 0 to 1. This will be repeated until the number of progeny is 100.
5. All the progeny inherit the synaptic weights of their mother, but each of these weights can mutate as follows. Monte Carlo methods are used to determine which of the nine weights in \mathbf{P}_g will be adjusted with probability π . Those to be adjusted have a random value selected from a rectangular distribution centred on 0 and of width $2d$ (i.e. between $-d$ and $+d$) added to their current value. The procedure is continued until all 100 new progeny have been assigned their mutated phenotype. These 100 progeny are then taken to be the adult reproductives producing the next generation.
6. Steps 2–5 are repeated for T generations (we use $T = 100,000$).

Population index

The number of possible output phenotypes, \mathbf{y}_g , is essentially infinite, although we can round-off the values of elements $y_{g,h}$ in this vector to the nearest integer (i.e. 0 or 1) so that we obtain 2^H categories of phenotypes. For purposes of discussion, we refer to phenotypes that consist of all 0s or 1s with at least one 1 as ‘refined’, and all other phenotypes will be referred to as ‘unrefined’. Because only the refined phenotypes lay their whole egg complement (see equation 3), evolution tends to produce only refined phenotypes. Thus the rounding-off procedure allows us to classify all G individuals into 2^H categories of refined phenotypes and then plot the proportion of each category in the population. To reflect the fact that the unrefined phenotype $\mathbf{y}_g = (0.75, 0.75, 0.25, 0.25)$, for example, is less like the refined phenotype $\mathbf{y}_g = (1, 1, 0, 0)$ than is the unrefined phenotype $\mathbf{y}_g = (0.95, 0.95, 0.05, 0.05)$, we use the following index D_i , $i = 1, \dots, 2^H$, to portray more accurately the proportion (multiplied by 100 to convert to a percentage) of individuals conforming to refined phenotype category i (denoted by C_i):

$$D_i = \frac{100}{HG} \sum_{g \in C_i} \sum_{h=1}^H |2y_{g,h} - 1| \quad i = 1, \dots, 2^H \quad (5)$$

To illustrate how the index in expression (5) works, consider the unrefined phenotype $\mathbf{y}_g = (0.75, 0.75, 0.25, 0.25)$. Inserting these values in expression (5), we see that this phenotype contributes $50/G$ to the index D_i , while the refined phenotype $\mathbf{y}_g = (1, 1, 0, 0)$ contributes $100/G$. Additionally, the quantity

$$\left(100 - \sum_{i=1}^{2^H} D_i\right)$$

is a measure of how far evolution still has to go to produce refined phenotypes (the closer this quantity is to 0, the more refined the phenotypes will be).

Types of runs

Simulations were run for the following six types of environments, Ω_i , $i = 1, \dots, 6$, each being a vector of four r_h elements: $\Omega_1 = (50, 50, 0, 0)$ (i.e. niches 1 and 2 each produce 50 individuals and niches 3 and 4 produce no individuals), $\Omega_2 = (0, 50, 50, 0)$, $\Omega_3 = (50, 0, 50, 0)$, $\Omega_4 = (40, 10, 40, 10)$, $\Omega_5 = (30, 20, 30, 20)$ and $\Omega_6 = (60, 0, 40, 0)$. Environments $\Omega_1 = (50, 50, 0, 0)$, $\Omega_2 = (0, 50, 50, 0)$ and $\Omega_3 = (50, 0, 50, 0)$ represent an increasing order of difficulty for the task of separating out the nutritious from the non-nutritious plants. We note from equation (1) that the ratio of the input signals $S_{1,h}/S_{2,h} = h/(H+1-h)$ progressively increases from the first plant ($h=1$: $S_{1,h}/S_{2,h} = 1/H$) to the last plant ($h=H$: $S_{1,h}/S_{2,h} = H$) as h increases from 1 to H . In particular, for $H=4$, the four ratios in question are $1/4$, $2/3$, $3/2$ and 4 . To identify the nutritious plants in environment Ω_1 as distinct from the other plants requires that the network perform one discrimination task; for example, discriminate between ratios below and above 1. To identify the nutritious plants in environment Ω_2 as distinct from the other plants, however, requires that the network perform two discrimination tasks, for example, discriminate between ratios above and below $1/2$ as well as ratios above and below 2. Thus, being a generalist in environment Ω_1 is a more easily implemented discrimination task than being a generalist in environment Ω_2 . Three discrimination tasks (discrimination levels) are required to be a generalist in environment Ω_3 .

For the six types of environments, we conducted simulations for the four cases obtained from combinations of the probability-of-mutation parameter $\pi = 0.02$ or 0.1 (probability that each synapse weight mutates) and mutation-range parameter $d = 0.2$ or 1.0 (the rectangularly distributed half-range of the mutation). In each of the cases examined, simulations were repeated 100 times to obtain a sense of the average evolutionary trajectory and its range of variation.

RESULTS

Arrangements of plants and the possibilities of categorization

One of the most striking features of our results is how the placement of the nutritious and non-nutritious plants with respect to the response-induced input ratios, $S_{1,h}/S_{2,h}$, determines whether specialist or generalists will evolve. As will become evident, this placement can be arranged in three qualitatively different ways (environments Ω_1 – Ω_3).

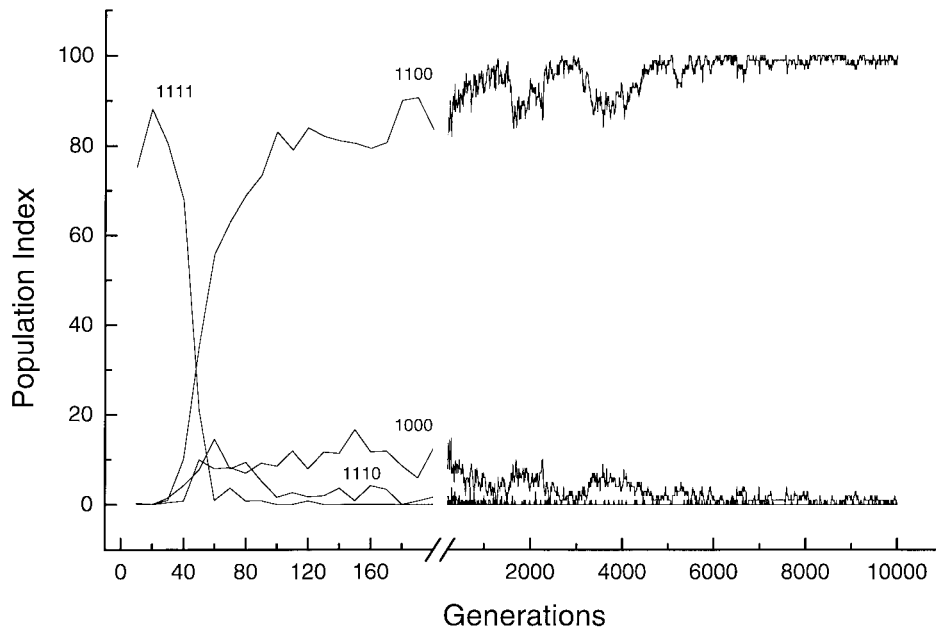


Fig. 2. The population indices D_i of the phenotypes (as labelled on the graph) plotted for one of the simulations of a population evolving in the environment $\Omega_1 = (50, 50, 0, 0)$. Only the values obtained every 10th generation are plotted and the scale of the abscissa is varied to portray both short- and long-term trajectories.

Environment 1

When the plant resource array is $\Omega_1 = (50, 50, 0, 0)$, the generalist 1100 evolves relatively quickly and soon completely dominates the population (Fig. 2). Of the 100 simulations for each of the four cases $\pi = 0.02$ or 0.1 and $d = 0.2$ or 1.0 , only one case did not result in complete dominance of the generalist (i.e. for phenotype 1100, the value of the corresponding population index was $D_i \geq 99$) after 100,000 generations (Table 1).

The sequence in which the different phenotypes reached more than 10% of the population for the case $\Omega_1 = (50, 50, 0, 0)$ and $(\pi, d) = (0.1, 1.0)$ is typically towards increasing levels of discrimination (Table 2). The non-discriminating phenotype 1111 always arises first (irrespective of the environment; see Table 3), primarily because setting the initial values of the synaptic weights at random probably produces networks that do not have the ability to discriminate among plants. Thereafter, the partially discriminating phenotype 1110 appears but quickly evolves into the fully discriminating generalist phenotype 1100, since phenotype 1110 wastes eggs in one of the two non-producing niches. This shows that phenotypes with better resource-matching displace phenotypes with less good matching.

Another equally good matching of the resources can be found by the two specialists 1000 and 0100 in equal proportion in the population. The reason why these two specialists do not dominate the population may be that the generalist 1100 has a simpler discrimination task (one level of discrimination is required) than the specialist 0100 (two levels of discrimination are required). For this reason, the generalist invariably appears before that specialist (the Order statistics are 1.8 and 7.3; Table 3), and also before specialist

Table 1. The final outcomes of the 100 simulations are listed for each of the four cases corresponding to two rates of mutation (π) and two ranges of deviation of the mutated weights (d) and for each of the six environments Ω_i considered*

Environment and evolved phenotypes	Parameter settings				
	$d =$ $\pi =$	1.0 0.1	1.0 0.02	0.2 0.1	0.2 0.02
$\Omega_1 = (50, 50, 0, 0)$					
1100 (100)		99	100	100	100
1000 (40) 0100 (40) 1100 (20)		1			
$\Omega_2 = (0, 50, 50, 0)$					
0110 (100)		14	1	96	93
0100 0010 0110		79	97		
0100 (50) 0010 (50)		6	2	4	
No Nash equilibrium		1			7
$\Omega_3 = (50, 0, 50, 0)$					
1010 (100)				58	54
1010 1000 0010		2	2	1	
1000 (50) 0010 (50)		97	89	17	1
No Nash equilibrium		1	9	24	45
$\Omega_4 = (40, 10, 40, 10)$					
1010 (60) 1111 (40)			2	49	15
1000 0010 1010 1111 (40)		1	3		
1000 (30) 0010 (30) 1111 (40)		88	55	1	
1010 (40) 1110 (30) 1011 (30)		2	3	4	
1000 (20) 0010 (20) 1110 (30) 1011 (30)		2	1		
1000 (30) 0010 (20) 1110 (30) 0011 (20)			1		
No Nash equilibrium		7	35	46	85
$\Omega_5 = (30, 20, 30, 20)$					
1010 (20) 1111 (80)		10	9	3	
1000 (10) 0010 (10) 1111 (80)		13	2		
1000 (10) 1110 (30) 0011 (20) 1111 (40)		23	3		
1110 (30) 1011 (30) 1111 (40)		45	43	3	
No Nash equilibrium		9	43	94	100
$\Omega_6 = (60, 0, 40, 0)$					
1000 (20) 1010 (80)		3	1	22	
1000 0010 1010		5	1	2	
1000 (60) 0010 (40)		90	87	55	58
No Nash equilibrium		2	11	21	42

* In each row, immediately below the environments listed in the left column, the guild or combination of insect phenotype categories (C_i) obtained at the end of each 100,000 generation simulations is listed (the population indices D_i for each of the phenotypes are given in parentheses for the cases where the Nash equilibrium is obtained).

Table 3. The order of first appearance of phenotypes (reaching a population index (D_i) of more than 0.1%) in the 100 simulations of insects adapting to each of six different environments Ω_i for the case $(\pi, d) = (0.1, 1.0)$

Ω_i		1111	0000	1110	1100	0001	1000	0011	0111	0100	1101	0110	1001	0010	1010	0101	
50, 50, 0, 0	C_i	1111	0000	1110	1100	0001	1000	0011	0111	0100	1101	0110	1001	0010	1010	0101	
	Nash			**		*				*							
	Count	100	100	100	100	22	100	28	34	100	94	2	36	8	0	0	0
Order	1.0	1.5	1.7	1.8	2.4	2.5	2.5	2.6	2.6	7.3	7.5	8.0	8.5	8.6			
0, 50, 50, 0	C_i	1111	0000	1110	0111	1100	0011	1000	0001	1001	1011	1101	0110	0100	0010	1010	0101
	Nash											**	**	**	**		
	Count	100	100	100	100	100	100	56	52	4	9	1	100	100	100	30	25
Order	1.0	1.2	2.5	2.6	4.2	4.2	4.9	6.0	6.8	7.6	8.0	8.3	9.1	9.2	10.9	11.2	
50, 0, 50, 0	C_i	1111	0000	1110	1100	0111	1000	0011	0001	0110	1101	0010	1010	1011	1001	0100	0101
	Nash					**					**	*					
	Count	100	100	100	100	84	100	99	46	99	9	100	78	46	61	22	0
Order	1.0	1.8	2.0	2.6	3.6	4.2	6.1	6.5	8.4	8.4	8.7	10.1	10.3	10.4	12.0		
40, 10, 40, 10	C_i	1111	0000	1110	1100	0111	1000	0011	0001	1101	1011	0110	1001	0010	1010	0100	0101
	Nash	**		*		**	*	*		*	*		**	*	*		
	Count	100	100	100	100	100	100	98	83	36	84	95	71	86	56	36	0
Order	1.0	1.5	2.0	3.2	3.5	4.5	5.0	7.0	9.4	9.8	10.0	10.4	10.5	10.7	11.9		
30, 20, 30, 20	C_i	1111	0000	1110	0111	1100	0011	1000	0001	1011	1101	1001	0100	0110	1010	0010	0101
	Nash	**		**		*	*	*	**	**				*	*	*	
	Count	100	100	100	100	100	100	100	91	97	82	78	7	77	28	48	2
Order	1.0	1.8	2.1	2.9	3.4	4.7	5.0	6.8	9.1	9.9	10.7	10.7	10.8	11.3	11.5	12.5	
60, 0, 40, 0	C_i	1111	1110	0000	1100	1000	0111	0001	0011	1101	0110	0010	1011	1010	0100	0101	
	Nash				**	**				**	**	*	*	*	*		
	Count	100	100	100	100	100	92	61	100	12	100	100	66	46	73	17	0
Order	1.0	1.6	1.7	2.4	3.2	4.8	6.1	6.6	7.2	9.0	9.2	9.8	10.2	10.4	10.8		

Note: The table also shows the number of simulations (counts) in which the insect phenotype categories (C_i) surpassed the 0.1% level, and the average ordinal number in these simulations. Phenotypes participating in Nash equilibrium solutions after 100,000 generations are indicated by one or two (for the most common) asterisks.

1000 (Order statistic 2.5). In addition, both specialists must appear virtually in the same generation if the combination of the specialist–generalist polymorphism is to be selectively neutral. Any specialist arising on its own will be selected against because the resident generalists will be more fit. Once the generalist – or, less likely, the pair of specialists – is established, the established phenotypes continue to dominate newly emerged phenotypes because the established phenotypes would be more refined in their category (i.e. the elements in its response vector \mathbf{y} are closer to 0s and 1s). Other factors aside, more refined phenotypes are always more successful than less refined phenotypes.

Environment 2

The environment $\Omega_2 = (0, 50, 50, 0)$ presents a more difficult discrimination task for the generalist 0110 (two levels of discrimination are required) than the environment $\Omega_1 = (50, 50, 0, 0)$ presents for the generalist 1100 (one level of discrimination is required). Furthermore, in this environment, both specialists 0100 and 0010 require the same level of discrimination as the generalist. Thus the specialists both arise on average at the same time, but later than the generalist (Tables 3 and 4). This is because fewer mutations are required for the generalist than the specialist to evolve from the preceding phenotypes 1110 and 0111 (see Table 2 for order of phenotypes appearing above the 10% population index level).

Interestingly, when the effects of the mutations are smaller ($d = 0.2$), specialization evolves much less frequently than when they are larger ($d = 1.0$; Table 1). In contrast to the previous environment, the two specialists can evolve relatively easily from the already existing generalist. Provided the effects of the mutations are sufficiently large ($d = 1.0$), for most of the simulation the specialists 0100 and 0010 co-exist with the generalist 0110 (Table 1 and Fig. 3). The proportion of specialists to generalists drifts, while the two specialists themselves track each other. The reason for this is that the levels of competition in the various niches are indifferent to replacing a pair of specialists 0100 and 0010 with two generalists 0110, but replacing any one of these three phenotypes with one of the other two upsets the competitive balance that maintains their co-existence.

The typical simulation in the case of environment Ω_2 begins with the emergence of unrefined forms of the phenotypes 0000 and 1111, where the latter dominates the population for a short period of time. Thereafter, phenotypes 0111 and 1110, which are able to reject one of the non-nutritive plants, spread in the population (Table 2). After running through the gamut of one-level discriminator phenotypes, the two-level discriminator phenotypes emerge and with them the Nash equilibrium polymorphism consisting of the generalist 0110 and specialists 0100 and 0010 evolves (Table 3).

Environment 3

The most difficult environment for the generalist phenotype to evolve in is $\Omega_3 = (50, 0, 50, 0)$, because the generalist phenotype 1010 must discriminate at three levels. Thus it is not surprising in the two cases where $d = 1.0$ that the two specialists 1000 and 0010 evolve as Nash equilibrium solutions in 186 of the 200 simulations. First, they evolve earlier than the generalist (Table 3) and, secondly, the specialists are more resistant to mutations. The simpler the recognition task that a phenotype solves, the fewer the number of involved synaptic weights, and hence the lower the probability that a mutation will be deleterious. It is surprising, however, that the outcome with two specialists is only found in 18 of the

Table 4. The order of phenotypes reaching more than 0.1% the value of the population index (D_i) in the 100 simulations of insects adapting to environment Ω_3 for the case $(\pi, d) = (0.02, 0.2)$

Ω_i																	
0, 50, 50, 0	C_i	1111	0000	1000	0001	1100	0011	0111	1110	0110	0100	0010	1101	1011	1001	1010	0101
	Nash									**							
	Count	100	98	46	40	73	73	98	97	84	82	78	0	0	0	0	0
	Order	1.0	1.0	1.1	1.3	2.6	3.0	3.6	3.7	6.9	8.4	8.5					
50, 0, 50, 0	C_i	1111	0000	0111	0001	0011	1110	1100	1000	1010	0010	1011	0110	1101	0100	1001	0101
	Nash								*	**	*						
	Count	100	100	56	40	31	100	100	69	42	38	29	6	0	0	0	0
	Order	1.0	1.0	1.1	1.3	1.8	2.9	3.4	3.7	6.6	7.9	8.9	10.0				

Note: The table also shows the number of simulations (counts) in which the insect phenotype categories (C_i) surpassed the 0.1% level, and the average ordinal number in these simulations. Phenotypes participating in Nash equilibrium solutions after 100,000 generations are indicated by one or two (for the most common) asterisks.

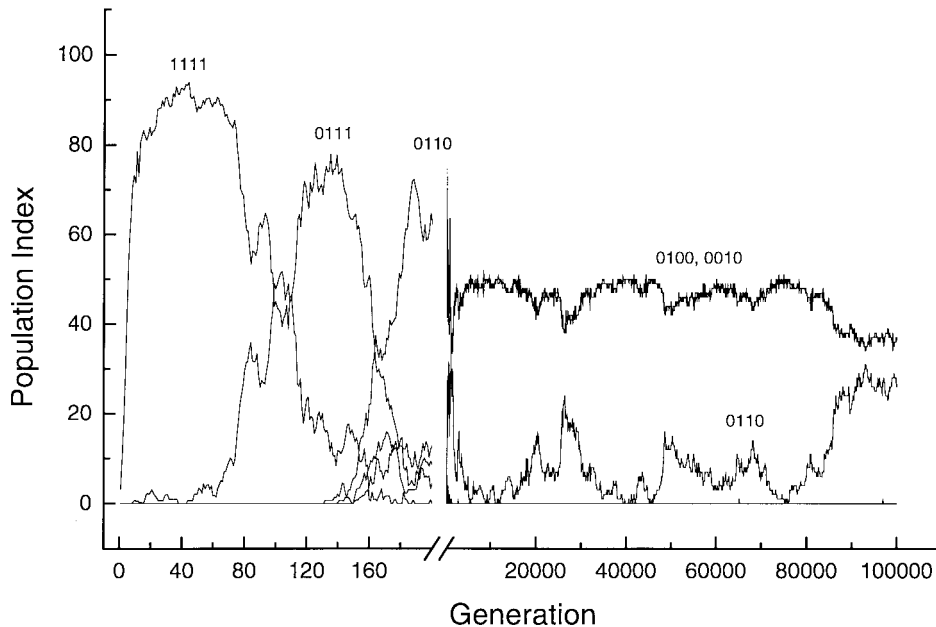


Fig. 3. The population indices D_i of the phenotypes (as labelled on the graph) plotted for one of the simulations of a population evolving in the environment $\Omega_1 = (0, 50, 50, 0)$. The values plotted are for every generation up to 1000 generations, and thereafter every 100 generations. The scale of the abscissa is varied to portray both short- and long-term trajectories.

200 simulations for the two cases where $d = 0.2$ (Table 1). The reason is that the generalist evolves before the second specialist (Table 4). As previously pointed out, if the two specialists are to spread in the population, they have to evolve from the generalist more or less simultaneously.

In a typical run for the case $(\pi, d) = (0.1, 1.0)$ (Fig. 4), phenotype 1111 dominates for the first 150 generations, after which phenotype 1110 and then specialist 1000 appear. Note, it is not before both specialists appear that the first specialist to emerge can increase, and that the two specialists together can outcompete the less fit generalist phenotype 1110. Thus, for the case $\pi = 0.02$ and $d = 0.1$, the generalist 1010 evolves shortly after the last specialist 0010, but the generalist soon disappears because it cannot compete with the two specialists. These two specialist genotypes then persist for the remaining 10,000 (Fig. 4) and 100,000 generations.

Reduced differences among niches

Although some plants may be very nutritious and others completely poisonous, many plants will be of intermediate value to the insects that consume them. To investigate how plants of intermediate resource value affect the evolution of specialists and generalists, we explored the evolution of choice in the two environments $\Omega_4 = (40, 10, 40, 10)$ and $\Omega_5 = (30, 20, 30, 20)$. In these environments, one might expect generalists which distribute their clutches across plants in direct proportion to the plants' resource values ('matchers') to

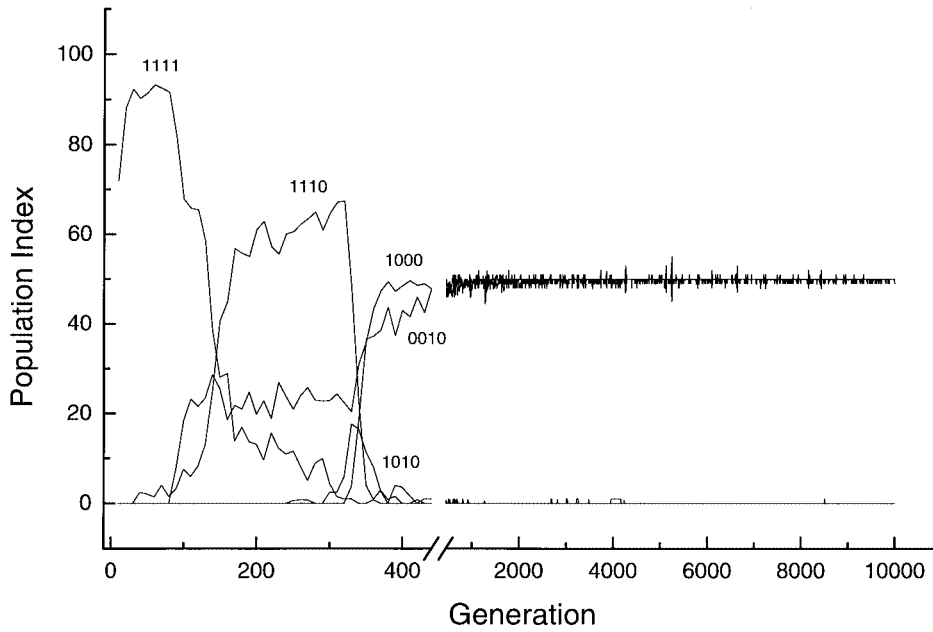


Fig. 4. The population indices D_i of the phenotypes (as labelled on the graph) plotted for one of the simulations of a population evolving in the environment $\Omega_1 = (50, 0, 50, 0)$. Only the values obtained every 10th generation are plotted and the scale of the abscissa is varied to portray both short- and long-term trajectories.

evolve, since such generalists can take advantage of low-value niches that may not be exploited by any specialists. The fitness function we use, however, does not facilitate the evolution of such phenotypes, because individuals with an intermediate response to any of the plants (i.e. unrefined phenotypes) will not lay all their eggs before they die. Such an individual strategy is always inferior to a related individual strategy that involves laying all eggs. At a population level, however, efficient exploitation of environments (i.e. exploitation without wastage of eggs or excessive competition in particular niches) can be achieved through an appropriate mix of phenotypes that constitute an ideal free distribution (Parker and Sutherland, 1986), referred to as a 'guild'.

Environment 4

As in the previous cases, the guild of insect phenotypes evolves towards a Nash equilibrium in which the proportion of phenotypes matches the productivity of the niches. When the rate of evolution is the greatest (i.e. the case $(\pi, d) = (0.1, 1.0)$), 88 of our 100 simulations in the environment $\Omega_4 = (40, 10, 40, 10)$ reached the Nash equilibrium guild of phenotypes (Table 1). This equilibrium consists of 40% of the non-discriminator 1111, and 30% of each of the specialists 1000 and 0010. This guild of phenotypes matches the productivity of the niches, because this guild implies that 40% of all the eggs are laid in niches 1 and 3, and 10% in niches 2 and 4.

On the other hand, when the effects of the mutation are reduced ($d=0.2$), the Nash equilibrium guild of phenotypes overwhelmingly is now 40% non-discriminator 1111 and

60% generalist 1010. Both this and the previous ($\pi = 1.0$) result are in accordance with the results obtained for environment $\Omega_3 = (50, 0, 50, 0)$, in the sense that the polyphagous phenotype 1111 is associated with both specialists 1000 and 0010 when the effects of the mutations are relatively large and with the generalist 1010 when the effects of the mutations are five times smaller.

A typical sequence in which the different types evolve shows a more complicated pattern than previously (Fig. 5): a greater array of phenotypes now reach the 10% level than for environments Ω_1 – Ω_3 (Table 2). Also, in this evolutionary sequence, we see that the guild of phenotypes 1110, 1000, 0010 and 0011 persists for a couple of thousand generations in roughly the ratios 30%, 30%, 20% and 20% (Fig. 5). Although this guild of four phenotypes matches the niche productivity of the environment, which could explain why the guild persists for more than a thousand generations, the guild does fluctuate and reduces to the three phenotypes 1111, 1000 and 0010, which then persists for the next 96,000 generations without itself reducing to the two-phenotype guild 1111 and 1010. The reason why the three-phenotype guild is much more stable than the four-phenotype guild (as can be seen in Fig. 5) may be because it is more simple. The phenotypes 1110 and 0011 are substituted by the non-discriminating phenotype 1111, which also is a step towards simplification with less synaptic weights being critical for the output. This process does not continue to the two-phenotype guild, however, because the fact that the two-phenotype guild involves a more complicated recognition task than the three-phenotype guild does overwhelms the processes that tend to reduce the number of species in a guild. This is the same argument discussed

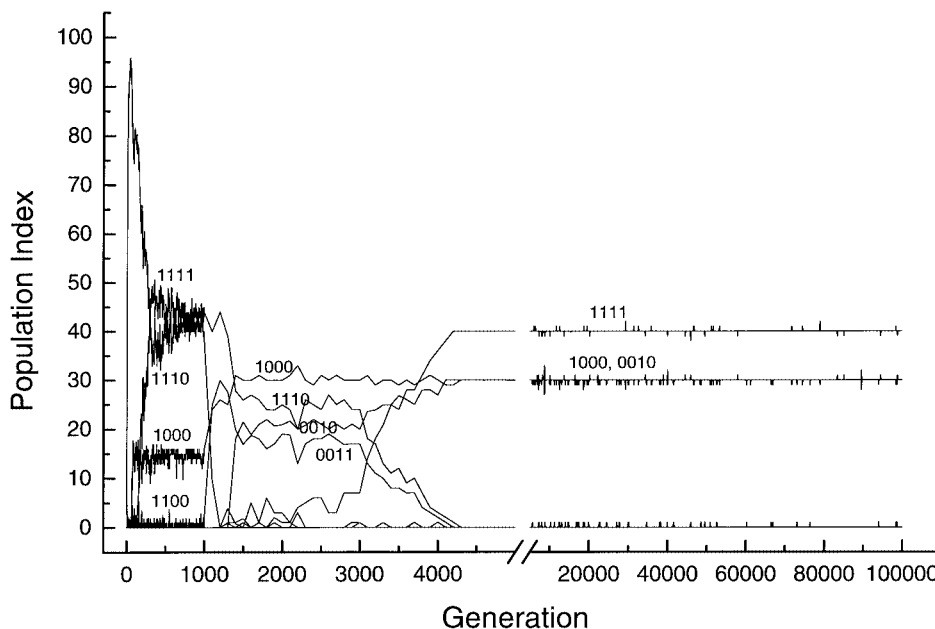


Fig. 5. The population indices D_i of the phenotypes (as labelled on the graph) plotted for one of the simulations of a population evolving in the environment $\Omega_1 = (40, 10, 40, 10)$. The values plotted are for every generation up to 1000 generations, and thereafter every 100 generations. The scale of the abscissa is varied to portray both short- and long-term trajectories.

in the previous section regarding the stability of the phenotype 1010 compared with the two specialist phenotypes 1000 and 0010.

Environment 5

When the resource values of the niches are set to be even closer to one another, as in environment $\Omega_5 = (30, 20, 30, 20)$, the stability of different guilds of phenotypes that match the environment is reduced and the outcomes less determined after 100,000 generations. For the case where the effects of single mutations are relatively small ($d = 0.2$), 97% of the simulations do not reach a Nash equilibrium solution after 100,000 generations. For the case where the effects of single mutations are relatively large ($d = 1.0$), only 26% of the runs do not reach a Nash equilibrium. When an equilibrium is reached, the guilds of phenotypes often do not include specialists: the guild 1111, 1110 and 1011 in the proportions 4:3:3 is the most common (Table 1). In one simulation, however, we see that this guild only arose around generation 97,000, having previously spent tens of thousands of generations in phenotype guild 1111, 1110, 0011 and 1000 in the proportions 4:3:2:1 (Fig. 6).

Asymmetric niches

Environment 6

We also investigated evolution in the asymmetric environment $\Omega_6 = (60, 0, 40, 0)$. In this case, it is no longer possible for the generalist phenotype 1010 to efficiently exploit the

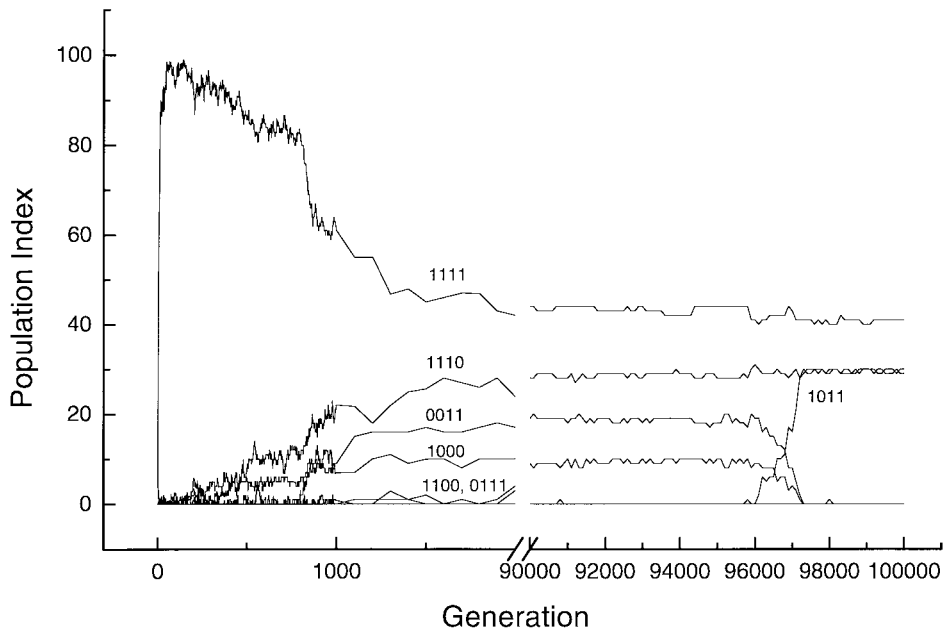


Fig. 6. The population indices D_i of the phenotypes (as labelled on the graph) plotted for one of the simulations of a population evolving in the environment $\Omega_1 = (30, 20, 30, 20)$. The values plotted are for every generation up to 1000 generations, and thereafter every 100 generations. The scale of the abscissa is varied to portray both short- and long-term trajectories.

environment on its own. Thus we see the appearance of the Nash equilibrium solution involving the generalist 1010 and specialist 1000 in an 8:2 mix. In all cases, however, a 6:4 mix of the two specialists provided the most common matching of the plant resource distribution (Table 1).

The number of simulations that do not reach a Nash equilibrium is almost identical to the case $\Omega_3 = (50, 0, 50, 0)$ (1 vs 2 when $(\pi, d) = (0.1, 1.0)$; 9 vs 11 when $(\pi, d) = (0.02, 1.0)$; 24 vs 21 when $(\pi, d) = (0.1, 0.2)$; and 45 vs 42 when $(\pi, d) = (0.2, 0.02)$). Thus the asymmetry in question does not affect the rate at which phenotype guilds evolved to Nash equilibria, only that generalists are much less likely to evolve in the asymmetric than in the symmetric case when the rate of evolution is comparatively low (for the case $(\pi, d) = (0.2, 0.02)$, 54% generalists evolved in the symmetric case while no guilds containing generalists evolved in the asymmetric case). When the generalist evolves, the specialist 1000 will need to be retained at the level of 20% of the population to provide the necessary competitive balance in the more productive plant niche (which is the first or Type 1). It is now likely that the other specialist 0010 evolves from the generalist, and the two specialists will take over due to the stability argument made earlier. In environment Ω_3 , both specialists have to evolve from the generalist more or less simultaneously, something which is less likely compared to when the specialists can evolve sequentially as is the case here in environment Ω_6 .

DISCUSSION

Although our model is a parody of perceptual, ecological and selective processes that mould the form of individual organisms, like all models in population biology it provides us with a tool for generating ideas and investigating the complexities of the evolutionary process in question. In particular, our model enables us, for the first time, to explore in depth the evolution under perceptual constraints of host-plant range in phytophagous insects.

Several selective and non-selective factors have been proposed that affect host-plant range in phytophagous insects (for a review, see Bernays and Chapman, 1994). These factors include resource availability, interspecific competition, climate, chemical defences in plants, neurological constraints, other morphological constraints, and phenological constraints. Regardless of the ultimate factors of the evolution of host-plant range, 'the evolution of behavioral patterns is the evolution of properties of the neural system' (Bernays and Chapman, 1994).

The apparent suboptimal behaviour that many insects exhibit in ignoring ubiquitous resources that would contribute greatly to their fitness is explainable in terms of the hypothesis that the evolution of feeding behaviour in insects is constrained by perceptual and memory considerations. Arguments in support of this hypothesis have been made (Fox, 1993; Bernays and Weislo, 1994), including a thorough discussion by Fox and Lalonde (1993) of the information-processing limitations inherent in olfactory perception (see also Getz and Page, 1991).

Most neurological constraint models that have been proposed in the literature assume that the herbivore does not have the neural capacity to be a competent generalist. Levins and MacArthur (1969), for example, assumed that herbivores are unable to include a new beneficial host in their diet without increasing the probability of including hosts that would incur some cost to fitness. Schneider (1987) suggested that a herbivore's image of its host plants becomes more 'blurred' as the range of hosts increases. A similar idea was presented by Bernays and Weislo (1994), who suggested that herbivores that were 'focusing' on fewer

host-plants had better recognition performance. Fox and Lalonde (1993) also made this assumption of the imperfect generalist. Although these ideas have some validity, our study was not constrained by a network being insufficiently complex to perform the perceptual task required to be a generalist.

Our results take us a step further in evaluating the effects that perceptual constraints might have on the evolutionary dynamics of plant-feeding insect guilds. The results indicate that implementation of host-plant recognition in neurological structures may bias the evolution towards specialists or generalists. Hence, our work focuses on the likelihood that evolution will take a particular path rather than on the selective forces themselves. In our system, the driving force of evolution is competition for a share of the resources provided by each plant. This force does not *a priori* favour generalists or specialists. The fitness of a given phenotype is dependent on the mix of extant phenotypes competing for the different resources. The emergence of a phenotype depends on the difficulty of the discrimination task required to express that phenotype (a more difficult task being more levels of discrimination that must be implemented by the network). The maintenance of a phenotype depends on the stability of the guild of phenotypes and how easily that guild is disrupted by the invasion of other phenotypes. Our results suggest generalizations that may well apply to an array of systems that deal with the question of evolution of niche selection.

Obviously, the simulations we present cannot be construed to mimic the actual phylogeny of feeding behaviour in any real insect clade: our model is far too simple for that. Rather, our results reveal mechanisms or rules that help us resolve the apparent suboptimality of currently observed feeding preferences in a number of species, as well as suggest hypotheses for explaining the phylogeny of diet breadth in particular clades. From our results, we propose that the following three rules have a strong influence on feeding preference, and are critical in determining whether generalists or specialists will evolve. These rules may also help explain the mix of phenotypes observed in stable guilds of herbivorous insects exploiting a heterogeneous environment of plant types:

1. The probability associated with the emergence of a particular phenotype depends both on the mix of extant phenotypes and on the difficulty of the perceptual task.
2. Guilds (of one or several phenotypes) may be displaced by more fit guilds until the resource utilization by the guild matches the relative availability of resources of varying quality (Nash equilibrium: Bulmer, 1994).
3. Guilds at the Nash equilibrium may be displaced by other more stable Nash equilibria, especially if mutation rates are high.

The essence of Rule 1 in the context of neural networks is that phenotypes solving relatively simple recognition or discrimination tasks evolve before phenotypes solving more complex recognition or discrimination tasks. This is certainly borne out by the results in Tables 2–4. The reason for this could be that the number of ways a feedforward network is able to solve a recognition task decreases with the difficulty of the task. Thus, the more possible configurations of synapse weights that lead to the emergence of a particular phenotype, the earlier we can expect that phenotype to evolve. There are exceptions to this general trend, for example the generalist 1010 in environments Ω_3 – Ω_6 , where the generalist appears relatively early. We interpret this as an increased probability for this type to evolve from intermediate types (i.e. the generalist phenotype 1010 is more likely to evolve from the

prevailing specialist 1000 than the specialist phenotype 0010 is) and, therefore, the result still obeys the extant phenotype component of Rule 1. We regard the order of appearance of phenotypes as the main explanatory factor in our results. The order of appearance determines the outcome of two competing guilds (e.g. specialists versus a generalist) having the same fitness from an optimization point of view – the first guild to evolve will often resist invasion by the other guilds (see asterisks in Tables 2–4). If a new guild is to be established, first all new guild members need to evolve from the existing phenotypes more or less simultaneously to displace the existing guild. This becomes more unlikely with an increasing number of new guild members. Second, the new guild has to be more successful than the extant one in order to spread. This is determined by Rules 2 and 3.

The importance of Rule 2 is evident from the results in Table 1, where we see that the frequencies of phenotypes in different guilds equilibrate at proportions that correspond to an ideal free distribution. Rule 2, however, not only has something to say about the final outcome of evolution, but also about the process, since the fitness of a phenotype at any point in time is affected by the distribution of other phenotypes at that point in time. This fact is dramatically illustrated in Fig. 3, where, although the proportion of specialists to generalists drifts through time on a low-resolution time scale (right-hand side of Fig. 3), the proportions of the two specialists are indistinguishable over time from one another. Furthermore, the rate of drift is remarkably slow (note the unit of time illustrated on the right-hand side of Fig. 3 is 10,000 generations). The reason for this slowness is that the proportions of the two specialists have to drift in concert subject to the constraint that the whole guild of phenotypes constitutes an ideal free distribution.

Rule 3, as with Rule 1, pertains to the degree of difficulty of recognition task performed by phenotypes and even guilds. The greater the number of levels of categorization, the more likely that each individual synapse weight is critical, and hence the more likely that mutations are deleterious. This fact is most clearly visualized in Fig. 5. Here we see a Nash equilibrium guild consisting of four phenotypes emerging after about 1300 generations. The relative frequencies of the phenotypes are quite unstable, and do not stabilize until two of the phenotypes have been substituted by a single new phenotype. Naturally, Rule 3 becomes more important with increasing effects of mutations, which is exemplified by the shift from generalist to specialists in environments Ω_3 and Ω_4 (Table 1).

We may make some conclusions regarding the comparison of our results in the different environments. Environments Ω_1 – Ω_3 represent increasing difficulty for a generalist to recognize its plants, whereas this is not true for the specialists. For reasons explained above, we see that the more complex the environment, the more likely that specialization will be the dominant strategy. If environment Ω_3 is changed so that the completely non-valuable plants are of some low value as a resource to the herbivores, we get environments Ω_4 and Ω_5 . In these environments, the evolving guilds consist of a larger number of specialists compared to environment Ω_3 . When plants become more similar in resource value, as in environment Ω_5 compared to environment Ω_4 , it seems that the guilds are more likely to consist of generalists (compare most common equilibria for these environments in Table 1). Asymmetry also seems to favour the evolution of specialization (environment Ω_6). Since most environments are likely to exhibit at least a moderate degree of asymmetry in the availability of plants of differing quality, we should rarely see generalists on their own, but most often in association with one or more specialists exploiting the plant niches that are most under-utilized by the generalist. To express this in another way, it may be difficult for generalists to evolve to match the ideal free distribution of a heterogeneous

environment, thereby providing opportunities for the evolution of specialists on the least efficiently utilized plants.

Our model suggests that three types of clades of herbivores are most likely to evolve: (a) monophages or specialists, (b) oligophages that feed on a related group of plants with a similar odour signature, and (c) non-discriminating heterophages. In other words, our model suggests that oligophages or heterophages will not omit nutritive plants from their diet that have signatures intermediate between plants upon which they feed. These predictions fit with the observation that natural clades of insect species are, primarily, mono- or oligophagous on distantly related plants. The most common situation is oligophagous clades living on a restricted group of plant species (Jermy, 1984).

In our model, we have assumed that the values of the network parameters are subject to mutation and are heritable, but are not plastic within each generation. We expect, however, that Rules 1–3 could also apply when learning takes place within networks over the lifetime of an individual, because parameter adjustments in neural networks can be used to model learning over both intra- and inter-generational time scales. We therefore expect that factors elucidated by our analysis have some validity for niche selection on ecological as well evolutionary time scales.

In conclusion, our results provide us with insights into how particular guilds of specialist and generalist plant feeding phenotypes may be influenced by perceptual constraints. First, our model clearly demonstrates that perceptual constraints influence the order in which particular phenotypes appear – the easier the perceptual task, the earlier that phenotype appears – and that this order is critical in determining the guild of phenotypes that assemble and persist for some period of time. Thus, in any real system, some understanding of why a particular guild exists will arise from insights into the difficulties of the perceptual tasks associated with particular phenotypes. With hindsight, this insight seems obvious. Less obvious is the insight that guilds with several phenotypes arise and persist for long periods of time, but are eventually replaced in a saltatorial manner by guilds that are more stable. This suggests that many extant guilds of herbivorous insects are not necessarily the most optimal long-term configurations. Whether the most stable configurations ultimately evolve depends on whether the background environment remains constant for long enough to prevent extant configurations from being disrupted. Finally, the model suggests two reasons why specialization is the dominant strategy in insect communities: the required neural settings for specialists are easier to evolve and are more resistant to mutations (in a general sense) compared with generalists. Specialists are required in guilds to make up an ‘ideal free’ matching to the resource values of the host plants.

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