

Predator–prey coevolution: interactions across different timescales

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SUMMARY

Using a simple predator–prey model we studied the consequences of interlocking processes that occur on ecological and evolutionary timescales. Various evolutionary attractors are shown, one of which is a system of two prey and two predator quasi-species packed in an alternating pattern. This pattern, which proves to be very robust, is studied in more detail to investigate the interaction between evolutionary and population dynamics. The evolutionary and the population dynamics both show complex periodic behaviour, with the same two dominant periods. The two prey quasi-species as well as the two predator ‘quasi-species’ oscillate synchronously, albeit out of phase. It is this temporal pattern in the population dynamics which drives the evolutionary dynamics and evolutionary dynamics which force the population dynamics to periodic behaviour with much shorter periods than if there were no evolution. This mutual influencing of the periodic behaviour is an interesting consequence of the interaction across different timescales. It is further shown that the evolutionary dynamics are essential for the maintenance of different species in the system.

1. INTRODUCTION

In ecology we usually assume that evolution is a slow process so in ecological models parameters are kept constant. In evolutionary studies we usually assume that population dynamics is a relatively fast process, which can be represented by a quasi steady state, or at least a ‘quasi attractor’. These assumptions are even incorporated in the relatively recent models of coevolutionary dynamics which aim at combining population dynamics and (co)evolutionary dynamics (see, for example, Marrow *et al.* 1992; Marrow & Cannings 1993; Dieckmann & Law 1994; Rand *et al.* 1994) as well as in models that study the evolutionary consequences of (ecological) spatial self-structuring (Boerlijst & Hogeweg 1991*a, b*; Boerlijst *et al.* 1993; Van der Laan *et al.* 1994).

In this paper we study the consequences of interlocking timescales of population and evolutionary dynamics. To this end we use a standard Lotka–Volterra type ecological model in which distinct phenotypes are represented as different state variables.

We assume a simple linear relation between genotype and phenotype. Thus, we represent the phenotype landscape as a simple one-dimensional axis and mutation can then be modelled as diffusion along this axis. The phenotype affects only the interaction between predator and prey. Moreover, it is not the absolute value of the phenotype that is important here but the difference in the phenotype of the prey and the predator. The interaction is strongest if the difference is zero and falls off with a gaussian function if the difference increases. We deliberately exclude the effect

of the phenotype on other parameters of the predator and prey equations to concentrate on the interaction only, which is obviously the essential factor in coevolutionary dynamics.

In the studies presented here we assume a circular phenotype space, i.e. a phenotype axis with periodic boundaries. Such a phenotype space can represent for instance the 24 h of the day or the 12 months of a year. The phenotype can then be interpreted as a property such as the timing of feeding activity (on a 24 h axis) or the timing of budbreak or flowering of plants and the hatching of herbivorous insects (on a 12 month axis).

2. THE ECO-EVOLUTIONARY MODEL

A simple discrete Lotka–Volterra type model has been used with equations

$$\left. \begin{aligned} \Delta X_i / \Delta t &= aX_i - bX_i \sum_{j=1}^n X_j - cX_i \sum_{j=1}^n \alpha_{ij} Y_j \\ &\quad + \mu[0.5(X_{i-1} + X_{i+1}) - X_i]: \\ \Delta Y_i / \Delta t &= -dY_i + ecY_i \sum_{j=1}^n \alpha_{ji} X_j \\ &\quad + \mu[0.5(Y_{i-1} + Y_{i+1}) - Y_i]. \end{aligned} \right\} \quad (1)$$

X_i = population of prey with genotype i and Y_i = population of predator with genotype i , the prey populations of different phenotypes are assumed to share a common resource. The phenotype-dependent

Table 1. *Parameters of the eco-evolutionary model*

symbol	internal range	parameter denoted
a	1.0	natural rate of increase for prey
b	0.005	prey competition parameter
c	0.0055	interaction parameter (fixed part)
α	variable	interaction parameter (evolvable part)
d	0.5	mortality of predator
e	0.73	efficiency of predator
θ	0.00001	threshold density
n	60	total number of phenotypes (length of axis)
μ	0.001	mutation rate
σ	0.4 to 0.6	standard deviation of Gaussian interaction curve

interaction parameter α_{ij} is a function of the differences between the phenotypes of prey and predator and the phenotype axis for both prey and predator consists of n discrete phenotypes. Because we assume our phenotype axis to be wrapped around as a circle, there are two ways (directions) to determine the difference between the phenotypes. The shortest distance along the phenotype axis is used to determine the interaction parameter α , and this distance is scaled to the maximum distance, which is $n/2$:

$$\text{dist}(i,j)_{\min} = \min[|i-j|, (n-|i-j|)]/1/2n.$$

The gaussian function for the interaction parameter then becomes:

$$\alpha_{i,j} = (1/\sigma) e^{(-\text{Dist}(i,j)_{\min})^2/2\sigma^2};$$

and α ranges from:

$$1/\sigma \text{ to } (1/\sigma)e^{(-1/2\sigma^2)}.$$

Note that the surface under the gaussian interaction curve is not equal for different values of σ because the tails of the distribution are not used for determining the interaction strength α (see also figure 2). Thus generalist predators (high σ) have lower total interaction strength. In the model mutation occurs by the discrete 'diffusion' of a proportion (μ) of every population with phenotype i to populations with phenotype $(i-1)$ and $(i+1)$.

To prevent diffusion of extremely low concentrations over phenotype space, we define a threshold (θ) for population density. If the population density of a phenotype is below this threshold, the phenotype has a probability of becoming extinct that is inversely proportional to its density. A system with $\theta = 0$ appears to have qualitatively the same properties as the system presented in this paper. The default parameter setting of the eco-evolutionary model is shown in table 1.

3. PATTERN FORMATION IN PHENOTYPE SPACE

The standard deviation of the gaussian interaction curve (σ), which determines whether a predator is a specialist (small σ) or a generalist (large σ), is the key

parameter of our model. In figure 1 we present the results of simulations with three different degrees of specialization of the predator. For each value of σ the behaviour of the system is shown with two different initial configurations. In the top three figures the simulation starts with one prey and one predator species of the same phenotype ($\alpha_{ii} = 1/\sigma$), whereas in the bottom three figures the results are shown with a random initial configuration (i.e. four prey and four predator species of randomly chosen phenotypes). Several interesting phenomena can be observed in figure 1.

(a) *Formation of quasi-species, speciation and extinction*

All simulations show the formation of one or more 'quasi-species' in both prey and predator. A quasi-species is a small ensemble of species with related genotypes. The emergence of quasi-species introduces an extra level into the model; in addition to the local population (one lattice point) and global population (the entire lattice) an intermediate or meso-scale entity can be distinguished. This meso-scale population consists of all members of a quasi-species which may wander over the lattice. Models of molecular evolution have shown that the evolutionary dynamics of quasi-species is quite different from that of 'pure' (i.e. one lattice point) species (Huynen *et al.* 1993; Huynen & Hogeweg 1994). In our model the quasi-species appears to be important in the process of speciation (speciation here means the branching of one quasi-species into two distinct quasi-species). The actual speciation event is preceded by an increase in the size of the quasi-species (i.e. an increase in the number of different phenotypes that form the quasi-species). In the top three figures, for example, which start with one prey and one predator species, speciation events can be observed during the initial period for all three levels of specialization. If the predator is a specialist ($\sigma = 0.4$), several successive speciation and extinction events can be seen.

As the meso-scale population and quasi-species are the main objects of interest in the remainder of this paper, we will refer to them by simply using the words population and species, whereas the entities at other levels will be denoted by the use of the adjectives local and global.

(b) *Multiple versus single attractors*

Multiple attractors are present in this system for all degrees of specialization. However, the system with intermediately specialized predators ($\sigma = 0.5$) attains in most cases the same attractor. This evolutionary attractor consists of a system with two prey and two predator species, which are distributed in turn along the phenotype axis. This pattern, which we will call the 'alternating pattern', is an evolutionary attractor with interesting properties, each predator species being positioned on the phenotype axis in such a way that it interacts with both prey species. Thus neither predator specializes entirely on one prey. Oscillations can be observed in both the evolutionary and the ecological

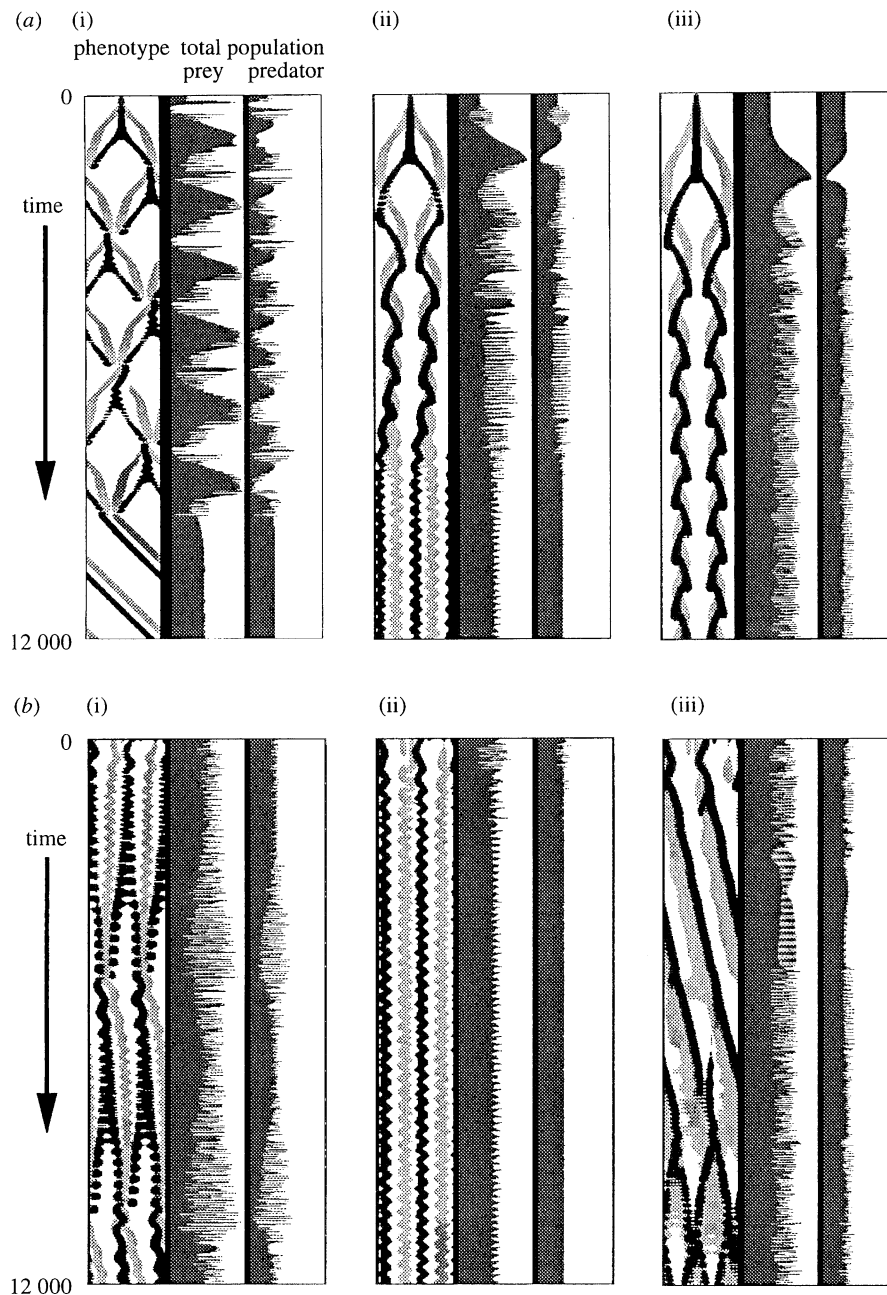


Figure 1. Time series of evolutionary and population dynamics, with (a) symmetric and (b) random initial configurations and with (i) $\sigma = 0.4$, (ii) $\sigma = 0.5$ and (iii) $\sigma = 0.6$. In the three columns of each time series, time ranges from $t = 0$ to 12000 with a display-interval of 15 time steps. The first column of each time series shows the phenotype axis of both prey (grey) and predator (black). Only the phenotypes with a local population density higher than 0.01 are indicated. The other two columns show the total population density of prey and predator on a horizontal axis which ranges from 0 to 200.

population dynamics. On this evolutionary limit cycle the alternating pattern is maintained indefinitely.

(c) *Predator chases prey, prey chases predator*

Predator-prey coevolution is often described as an 'arms race' (Dawkins & Krebs 1979) or 'Red Queen dynamics' (see for example, Van Valen 1973; Stenseth & Maynard Smith 1984): predators chasing prey in phenotype space continuously but without making any real 'progress'. This chasing behaviour can be observed in the transients and in some attractors. Figure 1 shows that after the branching of prey and predator, each prey species is being chased by one of the predator

species. Because the phenotype axis is circular, this behaviour results in surrounding of the prey. At this stage the interaction between prey and predator is high, resulting in complex oscillations and an increase in the size of the quasi-species, this enables the prey to escape in the other direction and the process of surrounding starts again. This surrounding and escaping behaviour appears to be an evolutionary attractor if the predator is a generalist ($\sigma = 0.6$). If the predator is a specialist ($\sigma = 0.4$) the evolutionary attractor is an example of the more classical case of 'Red Queen dynamics'. Because the phenotype axis is assumed to be cyclic, this Red Queen behaviour is also a cycle but on another spatial scale.

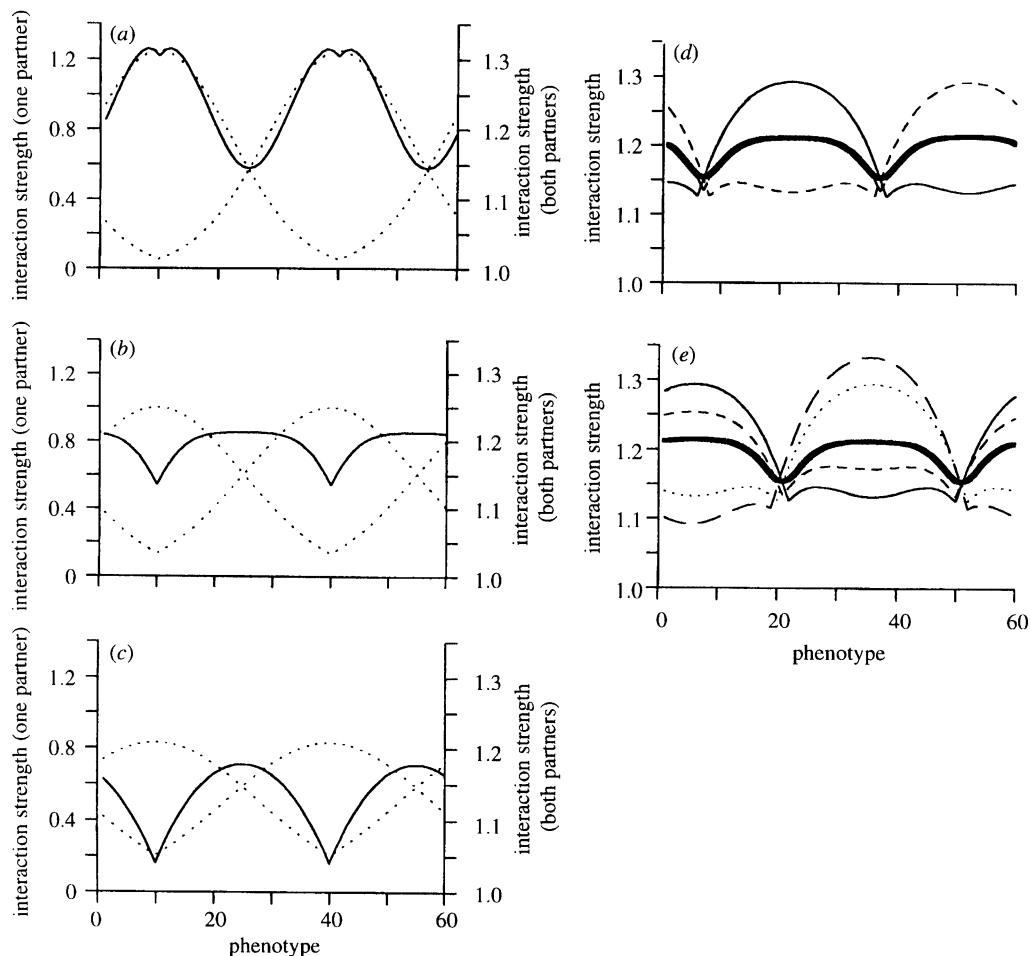


Figure 2. Interaction strength as a function of phenotype. (a) $\sigma = 0.4$, (b) $\sigma = 0.5$ and (c) $\sigma = 0.6$ show the interaction strength with one partner, either at phenotype 10 or 40 (dotted lines), and the total interaction strength with both partners, 10+40 (solid lines). Figure *d* (interaction with prey) and *e* (interaction with predator) show the total interaction strength, recorded from a simulation with alternating pattern ($\sigma = 0.5$), at five arbitrarily chosen time steps ranging from t 100 to t 500 and averaged over 5000 time steps (bold line).

More interesting is the presence of chasing behaviour in the attractors, where the predator is either specialist or generalist and the simulation starts with a random configuration. The system as a whole seems to switch between two different attractors: the alternating pattern and a pattern with the two predator species each completely specialized on one prey species (a 'matching pattern'). The chasing behaviour, which can be seen during the switching between these two patterns, is qualitatively different for the specialist and generalist. In the case of a specialized predator ($\sigma = 0.4$) the predators are chasing the prey: they extract themselves from the alternating pattern by each branching into two species. The resulting four predator species move two by two to the closest prey species. During this process the oscillations of the population dynamics become larger and one of each converging pair of predator species becomes extinct. This results in the matching pattern of completely specialized predators. However, prey successfully escape this pattern and the alternating pattern is restored again. The above mentioned behaviour repeats itself on a time-scale of approximately 6000 time steps. If the predator is a generalist, the story is completely reversed ($\sigma = 0.6$). The two prey species appear to chase the predators by branching behaviour, thus evolving

towards the matching pattern whereas the predators extract themselves from this pattern in order to restore the alternating pattern. This difference in behaviour between the system with specialists and the system with generalists is easy to understand from figure 2*a-c*. In these graphs the solid line indicates the total interaction strength, given two interaction partners at positions 10 and 40 on the phenotype axis. Predators are expected to maximize this total interaction strength, whereas prey is expected to move to the minimum of the curve. Therefore, if predators are specialists (see figure 2*a*) their preferred position will be the same position as that of the prey. Prey, however, will prefer the position between two predator species. This curve is qualitatively different for the generalist predator (see figure 2*c*): here prey has minimum interaction if positioned at predator phenotype whereas predator has maximum interaction strength in between the two prey species. One should realize that these curves change continuously during the eco-evolutionary simulation due to the (periodic) movement of all species along the phenotype axis. Figure 2*d* (interaction with prey), 2*e* (interaction with predator) shows interaction curves which have been recorded at different moments during a simulation with $\sigma = 0.5$. The average curve (bold line) is shown in each graph.

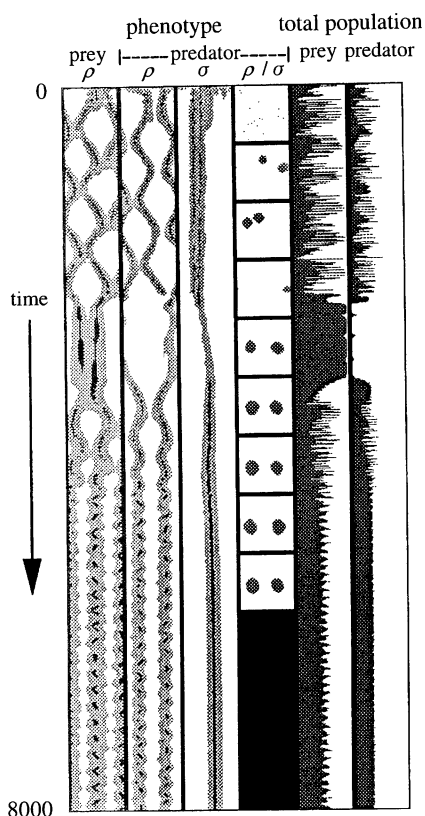


Figure 3. Time series of evolutionary and population dynamics with evolution of specialization (σ). In columns 1, 2, 3, 5 and 6 the time ranges from $t = 0$ to 8000 with a display-interval of 10 time steps. Column 4 shows the 2D-phenotype space of the predator at $t = 0, 1000, 2000, \dots, 8000$ (from top to bottom). The vertical axis of this 2D-plane defines the interaction as in the default models (phenotype ρ), whereas the horizontal axis defines the degree of specialisation (σ) of the predator and ranges from the $\sigma = 0.15$ to $\sigma = 0.75$. Column 1 shows the phenotype axis of prey. Column 2 shows the projection of the 2D-phenotype space on axis ρ (all local predator populations with same phenotype σ are added). Column 3 shows the projection of the 2D-phenotype space on axis σ (all local predator populations with same phenotype ρ are added). The local population density of each phenotype is indicated using three colour codes: white for 0, grey for < 10 , and black for ≥ 10 . Columns 5 and 6 show the total population density of prey and predator, respectively. The horizontal axis in these two columns ranges from 0 to 200.

(d) *Specialist or generalist?*

Given the above results and the dependence of behaviour on the degree of predator specialization (σ) it would be interesting to study the evolution of σ rather than use fixed values for σ . To this end we extended our model by adding a second predator-phenotype axis. The position along this second axis defines the standard deviation of the interaction curve (σ) and the phenotype space of the predator thus becomes a two-dimensional plane. The interval of σ ranges from 0.15 to 0.75 and the mutation rate used was $\mu = 10^{-2}$ (for mutation in both dimensions). It is obvious that the evolution of the degree of specialization critically depends on the way the penalty for being a generalist is implemented in the model. In our model we find that for most initial configurations,

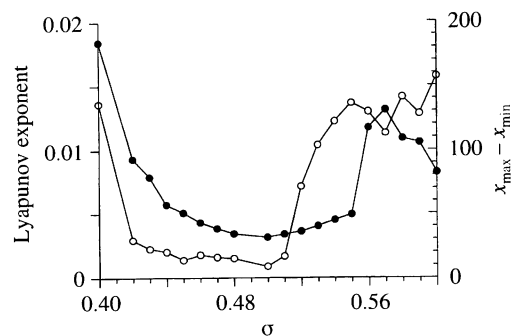


Figure 4. Lyapunov exponent (open circles) as a function of σ . First Lyapunov exponent averaged over 50 000 time steps (from $t = 100\,000$ to $150\,000$) and the difference between maximum and minimum prey population size ($x_{\max} - x_{\min}$; filled circles) during the same time-interval, in a simulation starting with a random initial configuration. Parameters as in table 1.

the system eventually moves towards the alternating pattern with $\sigma = 0.486$ (see figure 3). This attractor has a low Lyapunov exponent and relatively small fluctuations in total population density as shown in figure 4. If the total interaction strength is kept constant for all values of σ (i.e. without the penalty for generality), evolution towards maximum σ occurs in most cases. The predator in our eco-evolutionary system evolves to an intermediate degree of specialization. In this pattern both the ecological and the evolutionary attractor consists of a limit-cycle with complicated periodic behaviour, in which the time-scales of ecological and evolutionary dynamics are interlocked. The total population density, therefore, remains relatively constant when compared to the other attractors (see figures 1, 3 and 4).

4. INTERLOCKING TIMESCALES

(a) *Dynamics of the eco-evolutionary attractor*

The alternating pattern (using the evolved value $\sigma = 0.486$) has been analysed further to study the effect of interlocking timescales. To this end we analysed both the time series of the population dynamics (prey and predator density in each of the four species) and the time series of the evolutionary dynamics (interaction parameters for the resulting four predator-prey relations) for different mutation frequencies (μ) using spectrum analysis (*FFT*). The results, which are summarized in figure 5, show that both the evolutionary dynamics and the population dynamics consist of a complex periodic behaviour with two dominant periods. Furthermore, both periods depend on the mutation rate: high mutation rate gives short periods, low mutation rate gives long periods (see figure 5a). The two prey species as well as the two predator species oscillate synchronously, albeit out of phase, and this results in an almost stable population density for total prey and predator (see figure 1; $\sigma = 0.5$). The alternating pattern and concurrent evolutionary and population dynamics cause both predator species to switch between the two prey species instead of specializing on one of them. However, when interaction parameters are averaged over time it

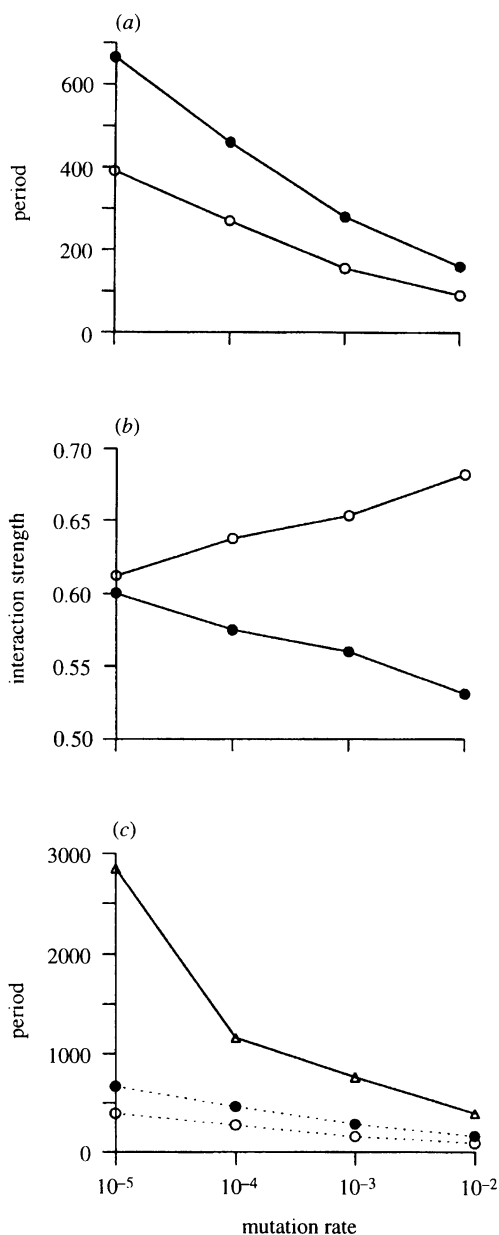


Figure 5. The effect of mutation rate on the evolutionary and population dynamics. (a) The two dominant periods in the dynamics of the four quasi-species: evo/eco (small) (open circles), evo/eco (large) (filled circles). (b) The mean interaction parameters for the four quasi-species: γ_{11} and γ_{22} (open circles), γ_{12} and γ_{21} (filled circles). (c) The period of population dynamics in the ecological model that has fixed interaction parameters (from figure 5b): evo/eco (small) (open circles), evo/eco (large) (filled circles), eco (mean interactions) (open triangles).

appears that each of the predators does partly specialize on one of the prey species (see figure 5b). This implies that two predator-prey pairs can be distinguished, with high average interaction strength within a pair (open circles) and low average interaction strength between a prey and predator of different pairs (filled circles). This difference in average interaction strength is largest if the mutation rate is high.

(b) Dynamics of non-evolving populations

The population dynamics of this system was studied in more detail by using an ecological model without

evolutionary dynamics. The model, which is a derivation of the eco-evolutionary model (1) as presented above, consists of two prey and two predator species:

$$\begin{aligned}\Delta X_1/\Delta t &= aX_1 - bX_1(X_1 + X_2) - cX_1(\gamma_{11}Y_1 + \gamma_{12}Y_2); \\ \Delta X_2/\Delta t &= aX_2 - bX_2(X_1 + X_2) - cX_2(\gamma_{21}Y_1 + \gamma_{22}Y_2); \\ \Delta Y_1/\Delta t &= -dY_1 + ecY_1(\gamma_{11}X_1 + \gamma_{21}X_2); \\ \Delta Y_2/\Delta t &= -dY_2 + ecY_2(\gamma_{12}X_1 + \gamma_{22}X_2).\end{aligned}$$

This model was studied with parameter setting as in table 1, and with the mean interaction parameters γ as observed in the eco-evolutionary model for the four different values of mutation rate μ (see figure 5b). The population dynamics of this ecological model show the same trend as observed in the eco-evolutionary model: a large difference between the mean interaction parameters γ (as observed for high mutation rate) gives a short period, small differences give long periods (figure 5c). However, the absolute value of the periods is much higher in this two-prey-two-predator ecological model than in the eco-evolutionary model. Therefore, in this case the addition of evolutionary dynamics to an ecological model does result in population dynamics with shorter periods.

(c) Stability of ecosystems

The use of the observed interaction parameters rather than their averages in this ecological model results in the extinction of one of the predator-prey pairs. At any time, therefore, the interaction parameters are such that some of the species would become extinct if the interaction parameters were invariant over time. Thus, in this stable interlocked eco-evolutionary attractor 'ecological' persistence does not occur.

5. DISCUSSION

Here, we demonstrated the existence of several different evolutionary attractors in the eco-evolutionary model. Because the alternating pattern has a large domain of attraction at intermediate degrees of specialization, it would be interesting to investigate whether there are any examples in nature that show such alternating niche-packing along a circular phenotype axis (time axis). For instance, it is well known that in coral reef ecosystems fish species that graze on coral or algae will actively feed either during the day or during the night and that predator fish species around coral reefs forage mainly during the dawn and dusk (Hobson 1973; Ehrlich 1975). It is possible that this observed alternating niche-packing could be the result of elementary self-structuring properties of a system of coevolving fish species. Once organized in this pattern, subsequent adaptations to the timing of feeding could have generated specialized phenotypic properties like those observed in these fish species.

In our model we observe complex periodic behaviour during the transient period, before the system organizes itself into the alternating pattern. Pattern formation in phenotype space has also been observed in a model which combines competition and evolutionary dy-

namics (Maxwell & Costanza 1993). In a model which studies the influence of predation on aspect diversity in prey populations, Levin & Segel (1982) estimate the intrinsic 'diversity' wavelength of their system. The wavelength in our system depends critically on the degree of specialization (σ) and stable solutions with more than two prey and predator quasi-species exist when σ is sufficiently small. However, preliminary results indicate that the basin of attraction of these alternative stable solutions is much smaller than that of the alternating pattern with two prey and two predator species. Therefore, the pattern we studied in our system consists of two coexisting predator species interacting with the same two prey species.

In a comparable model of predator-prey coevolution, Rand *et al.* (1994) show the existence of one or more fixed-point equilibria (ESAs) in phenotype space. The occurrence of simple evolutionary point-attractors in their model is probably due to the fact that in their model only the prey species can evolve whereas the predator species has fixed parameters. Our study shows the presence of complex (periodic) evolutionary attractors, if both prey and predators can evolve.

Comparing the robust attractor of our eco-evolutionary model to ecological models of two-prey-two-predator systems we note that models of two-prey-two-predator systems can show very complicated behaviour; a system with two loosely coupled predator-prey pairs exhibits a wide range of different types of behaviour: entrainment, period-doublings of cycles, chaos and intermittency (Vandermeer 1993). Similar results have been reported for predator-prey systems in two patches. Here the level of diffusion between the two patches determines the degree of coupling between the two predator-prey pairs (Nisbet *et al.* 1992; V. Jansen, unpublished results) and it is interesting to observe that the pattern formation in our model together with the evolutionary dynamics prevent the occurrence of these potentially present types of behaviour. A comparable result has been reported by Kaneko (1989*a, b*) who used coupled map lattices (CML) for the study of spatio-temporal chaos and demonstrated that chaotic behaviour can be suppressed by spatial pattern selection. The 'stabilizing' effect of evolutionary dynamics has also been reported in a host-parasite coevolution model with evolvable mutation rates (Kaneko & Ikegami 1992). If here is a strong interaction between parasites and hosts a high mutation rate is sustained and the combination of evolutionary dynamics and chaotic population dynamics results in a system with weak high-dimensional chaos ('homeochaos'). Their system shows 'dynamic stability' (low-amplitude fluctuations) due to high mutation rates. Preliminary results of our eco-evolutionary model that incorporates evolvable instead of fixed mutation rates also show evolution towards high mutation rates. In the long term, however, branching of one (ecological) species into two species with different mutation rates can be observed. Interestingly, the evolution of low mutation rates only occurs if $\sigma = 0.486$, which is the evolved degree of specialization, whereas the mutation rates remain high if $\sigma = 0.5$.

In addition to the above-mentioned spatial organization, our system also contains temporal organization. Both prey species as well as both predator species oscillate with the same period but in opposite phase, and in our model this drives the evolutionary dynamics. Pahl-Wostl (1993) shows that temporal self-organization also occurs in a model of various non-evolvable predator-prey pairs distributed along a body-mass axis and that this results in more efficient utilization of a common resource.

Summarizing our results on the interlocking of processes that occur on different timescales, we conclude that it is the evolutionary dynamics which drive the system into an attractor characterized by two coupled predator-prey pairs. In this attractor the oscillatory population dynamics force the evolutionary dynamics and vice versa. Our model demonstrates that the traditional separation of ecological and evolutionary processes obscures essential properties of the system. Evolutionary dynamics is essential in order to maintain the different species in the system.

The authors thank T. Ikegami and Ingrid Seinen for helpful discussions and Sheila McNab for linguistic advice.

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Received 19 September 1994; accepted 13 October 1994

Because this paper exceeds the maximum length normally considered for publication in *Proceedings B*, the authors have agreed to make a contribution to production costs.