

Chapter 12

Eco–Evolutionary Dynamics on Deformable Fitness Landscapes

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Abstract. Conventional approaches to modelling ecological dynamics often do not include evolutionary changes in the genetic makeup of component species and, conversely, conventional approaches to modelling evolutionary changes in the genetic makeup of a population often do not include ecological dynamics. But recently there has been considerable interest in understanding the interaction of evolutionary and ecological dynamics as coupled processes. However, in the context of complex multi-species ecosystems, especially where ecological and evolutionary timescales are similar, it is difficult to identify general organising principles that help us understand the structure and behaviour of complex ecosystems. Here we introduce a simple abstraction of coevolutionary interactions in a multi-species ecosystem. We model non-trophic ecological interactions based on a continuous but low-dimensional trait/niche space, where the location of each species in trait space affects the overlap of its resource utilisation with that of other species. The local depletion of available resources creates, in effect, a deformable fitness landscape that governs how the evolution of one species affects the selective pressures on other species. This enables us to study the coevolution of ecological interactions in an intuitive and easily visualisable manner. We observe that this model can exhibit either of the two behavioural modes discussed in the literature; namely, evolutionary stasis or Red Queen dynamics, i.e., continued evolutionary change. We find that which of these modes is observed depends on the lag or latency between the movement of a

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species in trait space and its effect on available resources. Specifically, if ecological change is nearly instantaneous compared to evolutionary change, stasis results; but conversely, if evolutionary timescales are closer to ecological timescales, such that resource depletion is not instantaneous on evolutionary timescales, then Red Queen dynamics result. We also observe that in the stasis mode, the overall utilisation of resources by the ecosystem is relatively efficient, with diverse species utilising different niches, whereas in the Red Queen mode the organisation of the ecosystem is such that species tend to clump together competing for overlapping resources. These models thereby suggest some basic conditions that influence the organisation of inter-species interactions and the balance of individual and collective adaptation in ecosystems, and likewise they also suggest factors that might be useful in engineering artificial coevolution.

12.1 Introduction

Conventional population genetic models of evolution generally address selection acting on genetic changes within a single population without regard for changes to the ecological context of that selection, and conversely, conventional ecological models (e.g., Lotka-Volterra models) generally address changes in the abundance of each species without regard for genetic change within each species [28, 37, 39, 42]. However, it is clear that changes in the genetic composition of a species can affect its fitness dependencies with other species (either directly, as in trophic interactions, or by changing the overlap of resources utilised, as in non-trophic interactions) and hence alter the ecological dynamics of an ecosystem. Reflexively, the selective pressures acting on a population can be greatly influenced by its biotic environment and thus ecological dynamics also shape evolutionary changes. Recently, there has been considerable interest in the interaction of ecological and evolutionary dynamics in an attempt to understand them as coupled ‘eco-evo’ processes [25, 28, 29]. Adaptive dynamics models, for example, take account of the fact that the selective pressures on a genetic variant are sensitive to ecological conditions and, conversely, that genetic changes can alter ecological equilibria [25]. These models provide a simple way to link ecological and evolutionary dynamics when the relevant timescales are almost separated (i.e., genetic changes are assumed to occur at ecological equilibrium). But when ecological and evolutionary timescales are strongly overlapping, it can still be difficult to identify general principles that help us understand their interaction [28, 29]. For example, when multiple species compete for a set of shared resources, under what conditions will competitive feedback cause them to diversify onto separate resources? And conversely, under what conditions will multiple species evolve to compete for the same resources causing continued conflict and inefficient use of resources?

Meanwhile, conventional evolutionary computation methods utilise a single population and address optimisation problems corresponding to static fitness landscapes. Cooperative coevolution [30] approaches to function optimisation utilise multiple populations each contributing a part of a combined solution. The aim of this

approach is a form of problem decomposition where each species addresses a relatively small semi-independent sub-problem and remaining dependencies between sub-problems can be optimised by virtue of evaluation in a ‘shared domain model’ [30]. Competitive coevolution approaches to optimisation problems generally use one population to represent solutions and another to represent problem instances that need to be solved. For example, Hillis [17] evolved sorting networks in one population and data sets to be sorted in the other; Juille and Pollack [19] evolved cellular automata rule sets against parameters of the initial conditions; Reynolds [33], Miller and Cliff [3, 4, 26], Floreano and Nolfi [12] and Floreano et al. [13] evolved pursuers against evaders either in simulation or using real robots. In some cases, competitive coevolution can lead to an arms race where each population continually challenges the other to improve, with the potential to keep the problem population in the zone of proximal development for the solution population [43] and also perhaps provide an open-ended adaptive pressure [44]. However, both uses of coevolution can sometimes fail to deliver these ideals. In cooperative coevolution the main problem is finding a way to automatically decompose the problem into suitable sub-problems such that different populations find diverse semi-independent sub-problems [45]. In competitive coevolution, species may ‘disengage’, breaking the mutual selective pressure, or evolve to exploit each others specific weaknesses rather than evolve general solutions, or chase each other around in endless cycles of relative improvement that fail to yield any improvement in absolute terms [44]. As is the case with natural eco-evolutionary dynamics, it can be difficult to identify general principles that help us understand when co-evolutionary dynamics will produce one type of dynamics rather than another, and, in particular, the conditions that lead to effective co-adaptation.

In natural systems there are, of course, many specific contingencies that may affect the nature of eco-evolutionary dynamics. Likewise, in any given optimisation problem, there are many domain specific, and implementation specific, contingencies that may affect the success of a coevolutionary approach. With the aim of keeping a model as simple as possible but not more so, here we introduce a very simple model of eco-evolutionary interactions that avoids case-specific details, but includes a rich space of possible inter-species fitness interactions and coevolutionary dynamics in a multi-species ecosystem. Specifically, we model the mean phenotype of each species as a point in a continuous low-dimensional (quantitative) trait space. Each point in trait space confers the ability to utilise a particular combination of resources in a continuous multi-dimensional resource or niche space [18, 22]. For example, a particular size and shape of bill confers an ability to utilise a particular size of seed, and/or a tolerance to a particular temperature or humidity enables occupation of corresponding habitats. When a species occupies a particular point in this trait space, depletion of the resources in that corresponding niche creates competition with species of similar genotypes. This provides a simple abstract representation of non-trophic ecological interactions based on niche overlap or species packing [23, 24] where the evolution and coevolution of species alters their relative location in trait space and hence their competitive interaction coefficients. This creates a simulation that captures the notion of multiple populations coevolving on a

'rubber sheet' fitness landscape – each species deforming the fitness landscape of the other – in a quite literal manner. The deforming implies that the fitness landscape is dynamic. Although other abstract approaches to modelling coupled fitness landscapes have been proposed, (e.g. [20]), by examining the mean phenotype of populations in a low-dimensional niche space (one or two dimensions), rather than in a high dimensional genotype space, this approach has the distinct advantage that it is straightforward to visualise the state of the entire ecosystem at a point in time. It also allows us to investigate some specific research questions in a simple and straightforward manner.

In particular, in the following experiments we investigate two related issues: the type of dynamical behaviour exhibited by evolutionary change and the efficiency with which an ecosystem collectively utilises available resources. For example, in this model, what are the conditions under which ecological interactions produce an ever-changing selective pressure that maintains species in a state of perpetual evolutionary change, or conversely, conditions where species equilibrate and stabilise, extinguishing evolutionary change? Also when multiple populations experience the same set of available resources, multiple species might compete for the same high quality resources, or conversely, resource competition might produce a diversifying effect causing species to spread-out and utilise different complementary resources; what factors influence the balance of these behaviours?

The first of these issues is a classic question in ecology and evolution relating to the 'Red Queen' hypothesis [39, 41] as discussed in the following section. The second issue is relevant to the balance of individualistic and collective adaptation typified by artificial competitive and cooperative coevolution, respectively. That is, although in both competitive and cooperative coevolution selection is applied at the individual level not at the collective level, in cooperative coevolution our interest as engineers is nonetheless on the collective welfare of the species in the system (the reason we do not explicitly select on collectives, biological unrealism aside, is that to do so would forfeit the potential for problem decomposition). The desirable dynamics of these two scenarios are therefore quite different. In competitive coevolution only one species represents solutions, and improvements in the other species are only desirable in so much as they motivate improvement in these solutions. In this case, we aim for each population to keep the other population under continued selective pressure, and this implies that improvement in one species confers decline in the other (a 'zero-sum' evolutionary game). Conversely, in cooperative coevolution a solution is represented by a whole set of species and we are interested in essentially the opposite dynamic, where diverse species find ways to be simultaneously good at different aspects of the problem. If they are successful in diversifying appropriately, this implies an increase in collective welfare (informally, 'everyone is better off' and the game is therefore not zero-sum), but it also implies that in successfully minimising competition, species find a way to decrease the mutual conflict and likewise the pressure for continued evolutionary change that they exert on one another. These opposites of individualistic and collective adaptation thus suggest contrasting behaviors with respect to convergence and diversification of species, and also a correspondence with continued evolutionary change and evolutionary stasis,

respectively. Thus the type of dynamical behaviour and the efficiency with which an ecosystem collectively utilises resources seem to have interesting interactions that we will investigate. Our goal is to isolate important factors which influence the balance of these different outcomes. We find that both possibilities are possible without changing the nature of the underlying game, or the level at which selection is applied, but merely by altering the coupling between ecological and evolutionary timescales.

Here we utilise our previous work with one- [9] and two-dimensional fitness landscapes [10]. The basic mechanism of the coevolutionary interactions operates as follows. In Figure 12.1 species *A* has already reached a local optimum while Species *B* climbs towards the same local optimum due to Darwinian selection, Figure 12.1(b & c). When two species occupy the same position, they are located in the same niche, it is assumed that they are in direct competition with each other and hence the fitness of both of these species is decreased - which effects a depression of the fitness landscape.

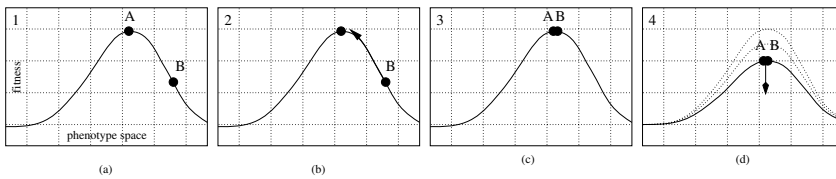


Fig. 12.1 Two species are located on the same fitness landscape. (a) Species *A* has reached a local fitness peak. (b) Species *B* is adapting to the same local optimum, i.e. is adapting to the same niche. (c) Species *A* and *B* are co-located at the same ecological niche. (d) The presence of species *B* in the same niche has an impact on the fitness of species *A*. The fitness of both species is reduced.

Before describing how we apply this basic mechanism in a multi-species model, we will briefly discuss how a two-species system might result in an arms race or Red Queen dynamics.

12.2 The Red Queen Hypothesis

A classic example of coevolutionary selective pressures is found in the predator-prey scenario. Individuals from the predator population need to catch prey in order to survive, and prey need to escape from predators. Such a scenario may lead to an arms race where both sides try to out-compete their opponent [5] in terms of, say running ability or maneuverability. Note that, usually, predator-prey models assume instantaneous interaction between the predator and prey population. A more accurate model might involve some delay between the adaptation of one population and the effect of this evolution on the other population [11].

The idea that a particular trait may be continually changing as a result of selective pressures even though the fitness of both coevolving species remains constant over

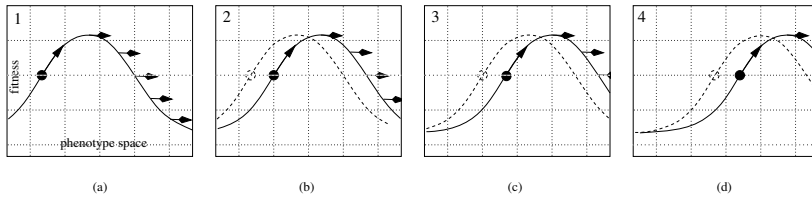


Fig. 12.2 According to the Red Queen hypothesis, the fitness of coevolving species may remain at the same level over evolutionary time even though some particular trait is evolving in response to a selective pressure. Here, it is assumed that as the species adapts to its local optimum, the fitness landscape is deformed by the presence of that species. (a)–(c) The local maximum in the fitness landscape is effectively shifted to the right by this deformation. Thus even though the species has been continually adapting to its local optimum it still has the same fitness over time. In other words, the species is moving through phenotype space even though its fitness remains constant.

time has been called the Red Queen hypothesis after a figure from Lewis Carroll's novel *Through the Looking Glass* [8, 34, 36, 41]. In the novel Alice and the Red Queen have to run but apparently do not get anywhere since the ground moves backward underneath them at an equal rate. The Red Queen explains: “Now here, you see, it takes all the running you can do, to keep in the same place” [2].

Figure 12.2 visualizes the Red Queen effect. A species is assumed to be driven towards a local optimum by the selective pressure. Initially, it is located on one side of a local optimum. As the species climbs towards the top, the landscape changes. Due to this change of the landscape, it appears as if the species has not succeeded in climbing the hill despite being driven to follow the local adaptive gradient. Measuring progress in coevolutionary scenarios can therefore be problematic [3, 21]. In open-ended evolutionary systems, e.g. self-reproducing programs [1, 7, 31, 32], we might hope that continued evolutionary change results in continued progress or improvement. But, it is not guaranteed that coevolutionary interactions that lead to continued change, i.e., Red Queen dynamics, will necessarily result in continued improvement, i.e., as implied in the term ‘arms race’. Over-specialisation and intransitive relationships may result in continual cycling through trait space that fails to produce improvement in any absolute sense [44].

The conditions that lead to either Red Queen dynamics or conversely conditions that produce a stable attractor where no further change (let alone progress) is possible, are therefore of great interest. Van Valen [41] originally suggested that species may exhibit Red Queen dynamics, producing continuous evolutionary change, without any extrinsic changes in environment. Maynard Smith [38] pointed out, however, that Van Valen's model depends on the assumption of a zero-sum game where an evolutionary change in one species that improves its fitness necessarily results in an equal decrease in fitness in total over all other species. Stenseth and Maynard Smith [39] argue that Van Valen's assumption of a zero-sum game does not necessarily follow from the assumption of a fixed amount of total resources. Their approach separates the notions of a fitness interaction between two species from the notion of

how a change in one species affects the 'lag load' of another species. The lag load is a measure of how far a species is from a local adaptive peak - and the presence of a non-zero lag load implies continued evolutionary change. Crucially, they argue that a genetic change conferring a fitness increase in one species may produce either a net increase or a net decrease in the lag-load of all species taken together. In other words, even with constant total resources, there are ways to utilise resources efficiently and ways to utilise them inefficiently, and this means that the underlying game is not zero-sum. Then, for non-zero-sum games there remains the possibility that, for linear interactions, the resulting dynamics may be either contractive leading to stable coexistence with each species at a local peak, or divergent where some species may lag increasingly far behind the local peak, possibly leading to extinctions. However, in the case where the relationship between lag load and change in lag load is non-linear then, as before, a Red-Queen dynamics of stable change is possible. Intuitively, this would be the case if, when lags are small and species are near local optima, most evolutionary changes in one species produce large increases in the lags of other species (this follows from geometric arguments - i.e., from a point near a local optima, most directions lead down) whereas, when lags are large most evolutionary changes in one species produce relatively little increase in the lags of other species. In this case, a stable but non-zero amount of total lag is expected, thereby conferring continued evolutionary change.

As Stenseth and Maynard Smith suggest, whether a coevolutionary scenario has the necessary conditions for Red Queen dynamics or for stasis is ultimately an empirical matter. But here we introduce a relatively simple mechanistic model of inter-species interactions to investigate contributing factors. In this model, different arrangements of species utilise resources with different degrees of efficiency; e.g., in an efficient arrangement, each species utilises a niche that has as little overlap as possible with other species, whereas if all species attempt to utilise the same resource this is relatively inefficient. The underlying evolutionary game implicit in this model therefore has non-zero-sum properties. Our model also has the potential to exhibit the non-linear relationship between lag load and change in lag load described by the geometric intuition above. It therefore seems plausible that Red Queen dynamics might occur in accord with the arguments of Stenseth and Maynard Smith. However, we observe that under some conditions our model nonetheless results in evolutionary stasis - or at least, exhibits qualitatively different modes of behaviour with very different amounts of evolutionary change. We investigate which parameters of the model determine these distinct modes of behaviour and we find that which of these modes is observed depends on the latency between the movement of a species in trait space and its effect on available resources. Specifically, if ecological change is nearly instantaneous compared to evolutionary change, stasis results; but conversely, if evolutionary timescales are closer to ecological timescales, such that ecological resource depletion is not instantaneous on evolutionary timescales, then Red Queen dynamics result. We also observe that in the stasis mode, the overall utilisation of resources by the ecosystem is relatively efficient, with diverse species utilising different niches, whereas in the Red Queen mode the organisation of the ecosystem is such that species tend to clump together competing for overlapping

resources. These models thereby suggest a link between the issues of change and stasis discussed by Stenseth and Maynard Smith and matters of ecological diversity and organisation. In the same way, these models also suggest some basic conditions that influence the organisation of inter-species interactions and the balance of individual and collective adaptation in ecosystems, loosely corresponding to the opposites of cooperative and competitive approaches to artificial coevolution.

In the next section, we describe the details of our modelling approach, and the various conditions and parameters that we investigate.

12.3 A Dynamically Deforming Fitness Landscape

We model the mean phenotype of a species as a point in an n -dimensional continuous trait space. An n -dimensional vector is used to represent the position of each population. For example, $n = 1$, describes a one-dimensional fitness landscape [9] and each species is represented using a single scalar value or quantitative trait. Natural selection moves the population mean in the direction that climbs the local gradient in the fitness landscape. Here this is modeled abstractly as a gradient ascent or hill climbing process (see Figure 12.3) on a fitness landscape [46].

This approach simplifies the evolutionary dynamics of each species making it easier to focus on the evolutionary interaction between many species and the interaction between evolutionary and ecological dynamics in a complex ecosystem. This

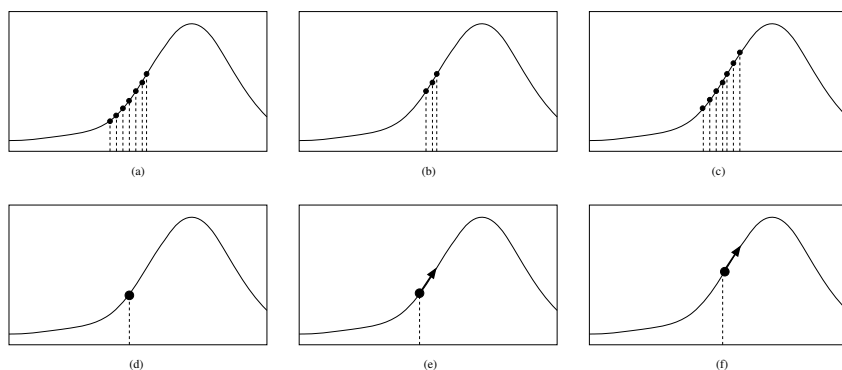


Fig. 12.3 Modeling the evolutionary process. (a), (b), and (c) show a population climbing towards a local optimum on a one-dimensional fitness landscape. (a) Initially, a population of individuals is located on the side of an incline. (b) only highly fit individuals survive (c) the remaining individuals then produce offspring and the new population is now located at a higher position in fitness space. (d), (e), and (f) show the same population represented as the population average. (d) a single point represents the population of individuals (e) gradient of the fitness landscape (f) the population average is moved up the incline depending on the measured gradient. The population average is now located at a higher position in fitness space.

approach is justified on the assumption that the genetic diversity within any one species is insignificant (at least, compared to the genetic diversity between species), and that the distribution of genetic variation remains unimodal (speciation is excluded), as for example, under ‘strong selection weak mutation’ assumptions [14]. Intuitively, we might imagine that the exact relationship between the local fitness gradient and the rate of adaptation of the species could be important in affecting the type of dynamics we observe in the ecosystem of multiple interacting species. Below we define three different methods that we investigated for updating the position of a species. In all cases the direction of change is determined by the direction of increasing fitness in each dimension of the fitness landscape - but the different methods affect the rate of evolution: 1) constant rate evolution, 2) rate of evolution linearly proportional to fitness gradient, 3) rate of evolution determined by rate of change of fitness gradient.

The first of these, constant rate, is appropriate where evolution is mutation limited. That is, regardless of how steep the fitness gradient is, the maximum rate of evolution is limited by the availability of variation that can respond to it, and the generation of genetic variation is unaffected by the selective pressure. Suppose that a species is located at position $x(t)$ at time step t . If $f(x, t)$ denotes the height of the fitness landscape at position x at time step t , then the simple update rule would be

$$\dot{x}(t) = \begin{cases} -1 & \text{if } \frac{\partial}{\partial x} f(x, t) < 0, \\ 0 & \text{if } \frac{\partial}{\partial x} f(x, t) = 0, \\ 1 & \text{if } \frac{\partial}{\partial x} f(x, t) > 0 \end{cases} \quad (12.1)$$

where $\dot{x}(t)$ is the velocity of the species. Thus, using update rule (12.1), fitness only controls the direction of movement.

In more general conditions the rate of evolution in a population will be sensitive to the magnitude of the selective coefficients. Our second, linearly proportional, update method thus sets the velocity of the species proportional to the gradient of the fitness landscape in Equation (12.2). This is consistent with a conventional population genetic model where the rate of change is proportional to fitness variance.

$$\dot{x}(t) = \alpha \frac{\partial}{\partial x} f(x, t) \quad (12.2)$$

Here α is the factor of proportionality.

The third update model is a logical extension. Specifically, Equation (12.3) integrates the fitness gradient over time such that the rate of evolution is a function of the second differential of fitness rather than the first differential or a constant. Hence the population responds to the gradient of the current position as well as to the gradient of the previous time step.

$$\dot{x}(t) = \alpha \left(\frac{\partial}{\partial x} f(x, t) \right) + \beta \dot{x}(t-1) \quad (12.3)$$

A momentum term such as this is known to have interesting effects on many kinds of dynamical systems. In an evolving population this type of dynamic could result if recent selection altered the ability of the population to respond to subsequent selection. For example, Pavlicev et al. [27] show that the action of past selection can alter the evolvability of the population by increasing genetic variation in the direction of selection.

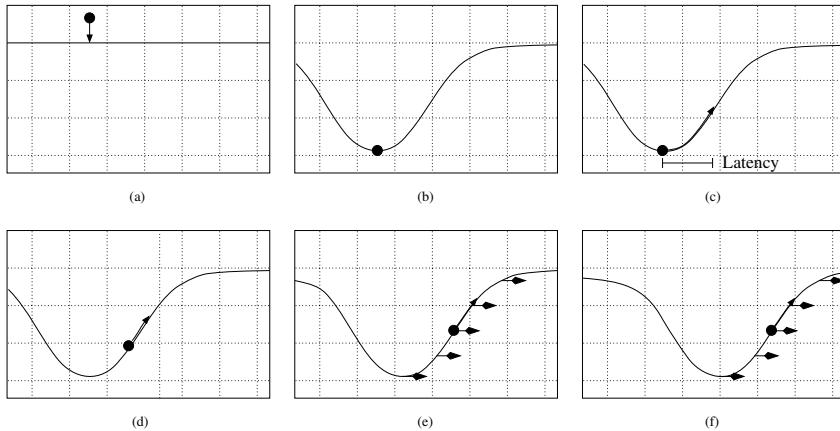


Fig. 12.4 Deformation of the fitness landscape. (a) Initially, a flat fitness landscape represents a uniform distribution of resources. (b) Each species placed on this landscape deforms the landscape in its vicinity as if by depleting available resources. This is similar to the deformation of a rubber sheet by a point mass. (c) Natural selection moves each species up the local fitness gradient. (d) In general, the ecological depletion of resources caused by the species is not necessarily immediate. (e) The deformation of the landscape caused by the species thus follows the position of the species with a latency period of several time steps. (f) As the position of the species moves away from the depression in the fitness landscape, and the deformation of the landscape responds to the position of the species, this leads to a condition of stable evolutionary change (Red Queen dynamics).

In our model all species coexist in a shared fitness landscape. The fitness landscape represents, abstractly, the availability of resources in a continuous niche space and the height of each point in the landscape is thus modified dynamically in response to the location of species. Each species thus has an impact on the shape of the fitness landscape in its local vicinity. Intuitively, each species deforms the landscape much like a point mass placed on a rubber sheet. In principle, the shape of this deformation reflects the distribution of phenotypes around the population mean. Here we assume a Gaussian population distribution and hence a corresponding Gaussian deformation. More generally, our model could be extended to investigate a positive effect on the fitness landscape, but here we assume only negative effects as if by competition for resources. (This negative impact on fitness is similar to fitness sharing or crowding methods which are used in evolutionary algorithms to promote

diversity [15].) We assume that the shape of the population distributions and the resource depletion that they confer is equal for all species, but the more species that occupy a certain point on the fitness landscape the larger the deformation.

If ecological dynamics are very rapid compared to evolutionary change then the effect of a species on its environment is effectively immediate. This assumes, in effect, that resources are always at equilibrium before the next evolutionary change occurs. This might be appropriate when modelling physical resources such as space or light. More generally, the ecological response of a niche to the intrusion of a new species may not be immediate. A latent effect on local fitness might be appropriate when modelling biotic resources (species of the lower trophic level) that are themselves subject to nonlinear growth and decay. Rather than model the dynamic behaviour of resources explicitly, here we simply investigate the effect of a delay or latency term in the effect that each species has on the depression of the fitness landscape. A latent effect takes some time steps before it becomes apparent. Hence, in our model, we basically have two different modes. The deformation is either placed at the same position as the species (immediate effect) or it is placed at the position where the species was located some time steps ago (latent effect). For simplicity, we assume the same latency value for all species/locations in trait space.

In the latent as well as the non-latent model each species climbs the local fitness gradient. However, in the latent model, it takes a certain time before a local optimum is depressed by the presence of the species. Once this happens, the fitness of the species is no longer optimal and it needs to adapt to a new optimum. Figure 12.5 illustrates what happens if two species climb towards the same local optimum.

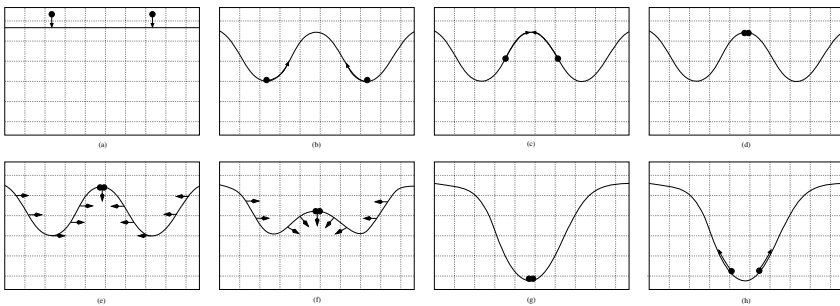


Fig. 12.5 (a) Two species are placed next to each other. (b) Initially, they deform the landscape surrounding them which causes a local optimum which is located in between the two species. (c) Both species are climbing towards the same local optimum. (d) If the latency is rather long, then both species are able to reach this optimum before the landscape deforms. Once they have reached this optimum, they have to stay put. (e-f) After a while the deformation caused by the exploitation of local resources follows them. This significantly reduces their fitness. (g-h) From the bottom of the valley, they may climb up again to either side of the valley they created.

12.4 Experimental Results

Experiments were performed on a one-dimensional and on a two-dimensional fitness landscape with circular boundary conditions. We will see below that interesting behavior emerges as we switch from a one-dimensional to a two-dimensional world. The source code for these experiments can be downloaded from the second author's web page¹. The experiments are also available as MPEG as well as AVI movies.

12.4.1 Experiments on a One-Dimensional Landscape

First we investigated the dynamics of competitive coevolution on a one-dimensional landscape. We have varied the update rule, the latency period and the type of environment used. The parameters for these experiments are shown in Table 12.1. The different settings illustrate interesting qualitative features of the dynamics. In particular, there are three different dynamic regimes that these experiments exhibited - static, cyclic, and races - as we shall discuss.

Table 12.1 Nine different experiments were carried out on a one-dimensional fitness landscape. We have varied the update rule, the latency period and the type of environment. The most important parameter determining the behavior of the species is the latency period.

Experiment	Species	Update Rule	Latency	Hills	Observed Behavior	Figure
1	10	Equation (12.1)	0	0	cyclic (stasis)	12.7
2	10	Equation (12.1)	50	0	clumped shift	12.8
3	10	Equation (12.2)	0	0	stasis	12.9
4	10	Equation (12.2)	50	0	cyclic or arms race	12.10 & 12.11
5	10	Equation (12.3)	0	0	stasis	same as 12.9
6	10	Equation (12.3)	3	0	cyclic	12.12
7	10	Equation (12.3)	50	0	arms race	12.13
8	10	Equation (12.3)	0	25	stasis	12.14
9	10	Equation (12.3)	50	25	arms race	12.15

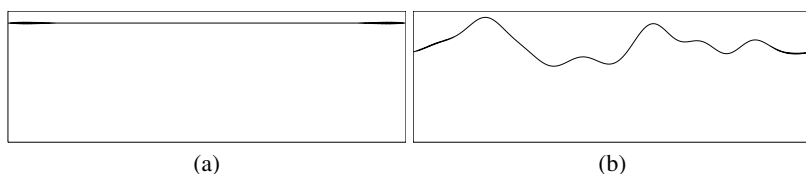


Fig. 12.6 (a) Flat fitness landscape. (b) Non-flat fitness landscape with random variations.

¹ <http://stubber.math-inf.uni-greifswald.de/~ebner/>

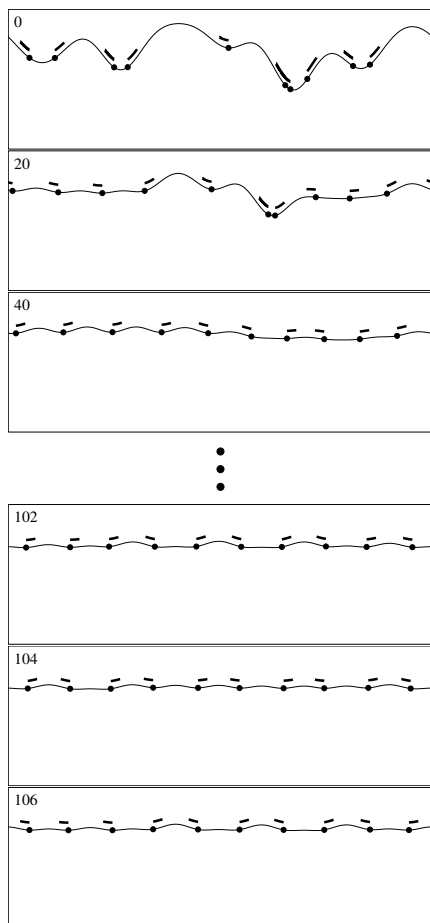


Fig. 12.7 Experiment 1: The velocity is determined by the sign of the environment's gradient (constant evolution rate). The parameters (shown in Table 12.1) lead to small cyclic behavior. The species keep oscillate back and forth. The species' current velocity is illustrated by the lines directly above the species. The number in the upper left corner shows the current time step.

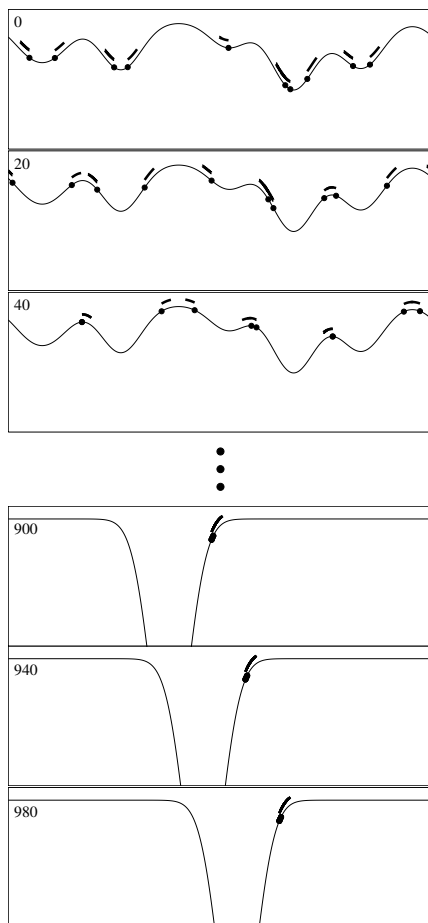


Fig. 12.8 Experiment 2: Velocity is set according to the sign of the landscape's gradient (proportional rate). The parameters (shown in Table 12.1) lead to a 'clumped shifting' behavior.

We have used 10 species throughout our experiments on the one-dimensional fitness landscape. Experiments were carried out using different environments, specifically, a uniform distribution of resources creating an initially completely flat landscape (Figure 12.6(a)) and a non-uniform distribution of resources where some Gaussian ‘hills’ were distributed randomly over the landscape (Figure 12.6(b)).

We experiment with all three update rules and vary the latency period. We observe that the latency period is the crucial parameter in determining the different modes of behaviour that the ecosystem exhibits. Specifically, an arms race only results if we have a non-zero latency period.

For Experiment 1, update rule (12.1) was used to update the direction of the species’ evolution (with constant rate). A completely flat environment and no latency was used, i.e. the depletion of resources happens immediately. The resulting behavior is shown in Figure 12.7. The species spread over the landscape and keep moving back and forth because the best place to be is the point that is most distant from other species at the current time. However, as soon as a species moves in the direction the best place to be is behind it in the other direction. Basically, evolution has come to a halt. The species no longer move over the landscape.

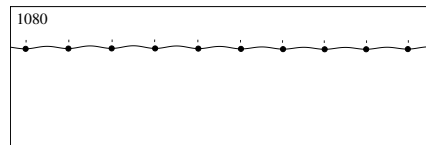


Fig. 12.9 Experiment 3: For this experiment, we use a velocity update rule where velocity is directly proportional to the gradient of the environment. As we can see from the small dots located directly above each species, the species are almost stationary. As a result, no further evolutionary change or improvement is possible and evolutionary space is only partially explored.

When we set the latency to 50 (Experiment 2), we observe the clumped shifting behavior as shown in Figure 12.8. First, the species climb towards a local optimum. Then the deformation increases. Eventually several or even all of the species end up very close together. The clump of species causes a large depression on the fitness landscape and continually moves in one direction. The entire evolutionary landscape is explored. Note that at any point in time there are many areas of the fitness landscape where resources are not being utilised at all (i.e., there are no species in those locations and no depression of the landscape).

For Experiment 3 we used the update rule (12.2) to update the velocity of the species. The parameter α was set to 10. No latency, i.e. the depletion of resources is immediate, and a completely flat environment was used. As a result, the species spread over the entire landscape utilising all areas of niche space equally. This leads to an almost stationary state with little movement as shown in Figure 12.9. Once the species are spread over the entire fitness landscape, no further evolution or improvement is possible. This can also be viewed as each species having found a niche where they do not interfere very much with the other species.

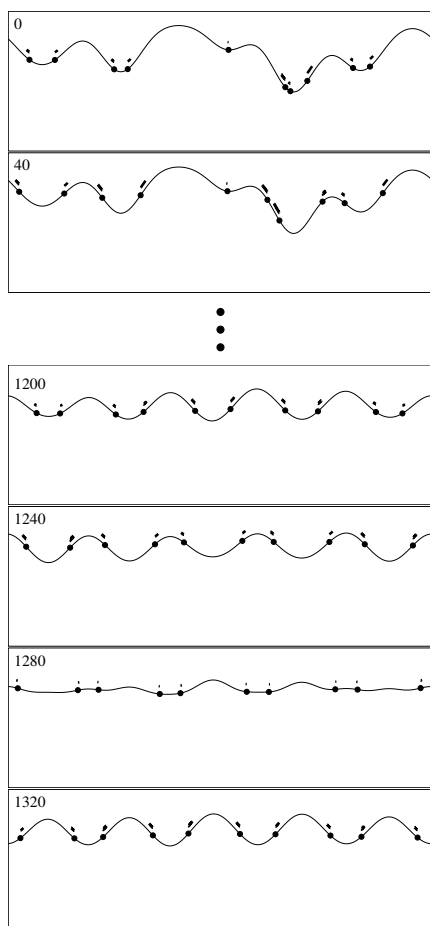


Fig. 12.10 Experiment 4(a): Here, we use a velocity update rule where velocity is always equal to the gradient of the environment. The parameters of this experiment (as shown in Table 12.1) may lead to a cyclic behavior as is shown here.

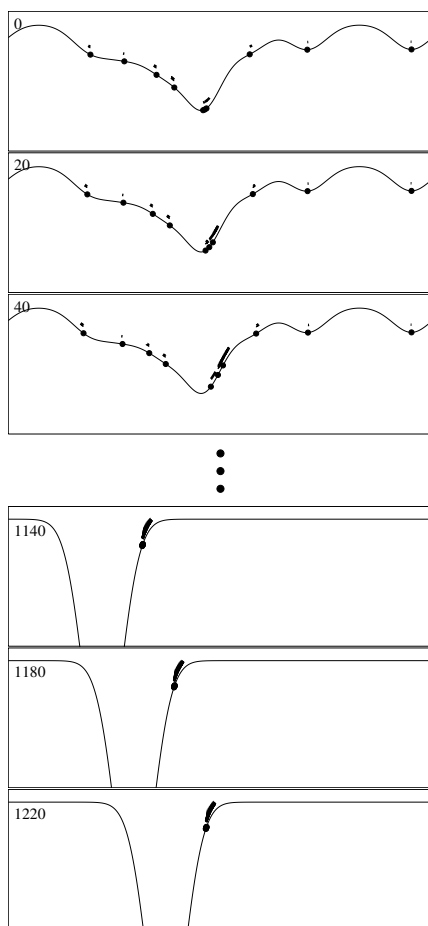


Fig. 12.11 Experiment 4(b): The parameters of Experiment 4 may also lead to an arms race

For Experiment 4 we used update rule (12.2). The latency parameter was set to 50, i.e. the depletion of resources does not happen immediately. We have used a completely flat landscape/uniform environment for this experiment. Two qualitatively different behaviors were observed. One outcome of this experiment, a cyclic behavior, is shown in Figure 12.10. First, the species spread out over the landscape. Local optima are created in between two species due to the delayed impact on the fitness landscape. The species try to climb towards these optima. However, once they have reached them, the depletion of resources sets in and the species are moved

to a lower position on the fitness landscape. New local optima have formed and the species again have to climb towards these optima. This process repeats indefinitely. Evolution essentially has come to a halt. Depending on how the species are distributed initially over the fitness landscape, we also observed an arms race (see Figure 12.11). This happens if several species are located very close to each other. As they sweep over the landscape, they collect more and more species in their arms race until eventually all species are included.

Update rule (12.2) as well as update rule (12.1) result in a rather slow movement of the species. Update rule (12.3) results in a much faster movement of the species. Experiment 5 is the first to use update rule (12.3) with parameters $\alpha = 9$ and $\beta = 0.9$. No latency and an initially flat landscape was used. We again observe the behavior which was observed in Experiment 3 (see Figure 12.9). The species spread-out over the landscape and remain almost stationary. Evolution has come to a halt.

For Experiment 6 we only changed one parameter slightly. Specifically, here a latency of 3 is introduced. This leads to a cyclic behavior as is shown in Figure 12.12. Initially, the species spread out over the entire landscape. We then observe groups of two species which are located next to each other. Both of them try to climb towards the local optimum located in between them. Due to the non-zero latency parameter, the deformation follows the species with a little delay. This causes the depression of the optimum to which they have climbed and the creation of new local optima at the exact same position where they started out. This leads to cyclic behavior because the species now try to climb these optima and they end up in the exact same position where they had started. Once this state has been reached, no further improvement is possible and the evolutionary space is only partially explored.

Experiment 7 examines a latency of 50. Here we observe an arms race between the species. Figure 12.13 shows the results obtained for a typical run. From their initially random distribution, two species that happen to lie on the same side of a deformation try to climb towards the same local optimum. After a while the deformation follows them. As they try to escape from the local valley, more and more species are caught by this deformation. Eventually an arms race results in which all species are involved.

We also experimented with a non-uniform distribution of resources creating an initial fitness landscape that is not flat. For this environment, 50 Gaussian peaks are distributed over the fitness landscape and summed (Figure 12.6(b)). As before, the landscape is then deformed by the positions of the species. This landscape was used for Experiments 8 and 9.

Experiment 8 uses the same parameters as Experiment 5 except that the initial fitness landscape is not flat. The species again spread out over the entire landscape. Due to the fact that the latency factor was set to 0, the influence of a species on their environment happens immediately. Hence, the non-flat landscape is deformed slightly by the species. The species nevertheless adapt to their environment and an almost stationary state as shown in Figure 12.14 results. Once this attractor has been reached, evolution comes to a halt. Note that the non-uniform distribution of species matches the availability of resources in the initial fitness landscape resulting in an ecosystem organisation where no resources are left unused.

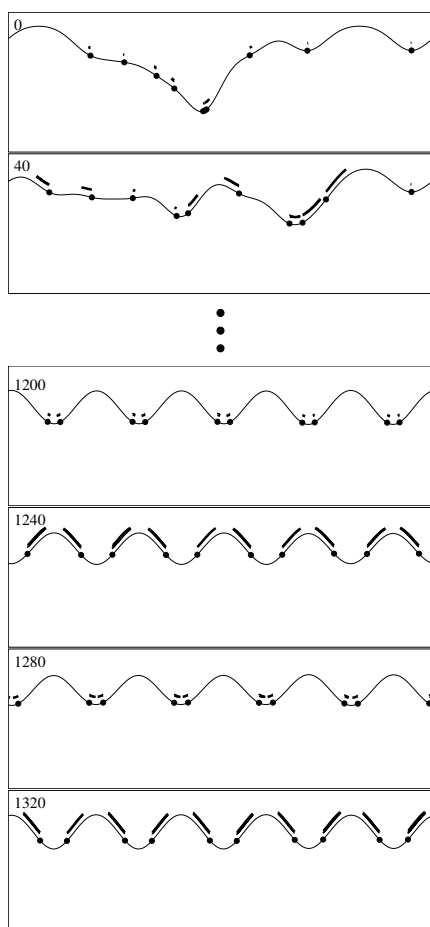


Fig. 12.12 Experiment 6: The cyclic behavior shown here is the attractor of Experiment 6. The species spread out over the landscape. Groups of two species try to climb towards the local optimum which is located in between them. Due to the latency, the depletion follows the species after a delay. The species then find themselves with low fitness and new fitness gradients, but this returns them to a position they have been to before. Once this attractor is reached, no further improvement is possible.

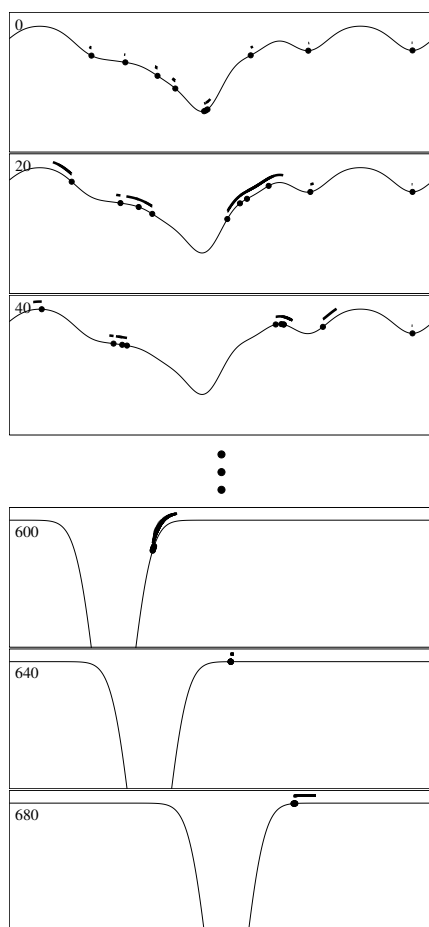


Fig. 12.13 Experiment 7: The parameters of Experiment 7 (as shown in Table 12.1) lead to an arms race

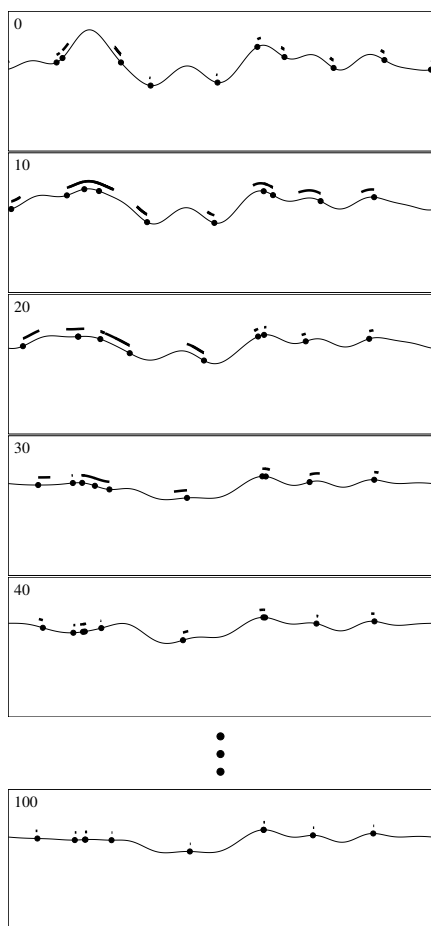


Fig. 12.14 Experiment 8: A non-flat fitness landscape was used. The shape of this fitness landscape can be seen in Figure 12.6(b). Initially, the species spread out over the fitness landscape. They try to climb towards a local optimum avoiding the negative influence of other species. After some time a stable attractor is reached. All species become stationary. Once this has happened, no further improvement is possible.

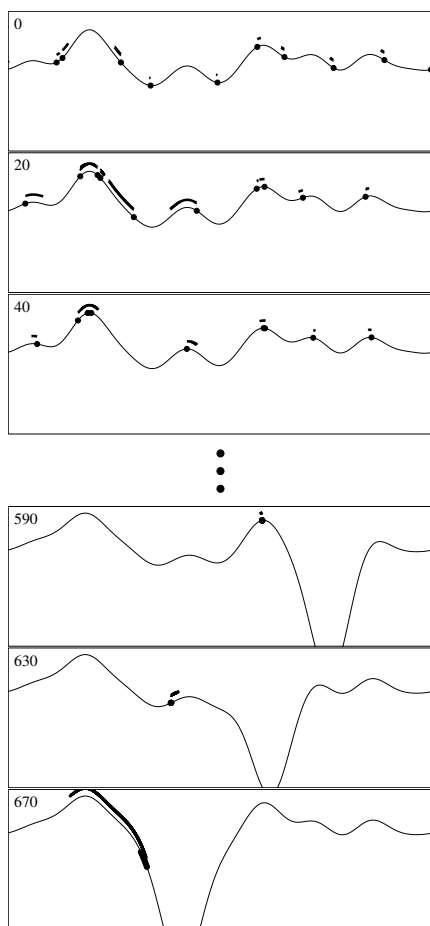


Fig. 12.15 Experiment 9: This experiment uses the same parameters as Experiment 7 except that a non-flat fitness landscape was used. Due to the large latency, the species clump together setting up an arms race. The species explore the entire fitness landscape despite the non-uniform distribution of resources, but at any one point in time, many niches are left unused.

For Experiment 9 we have increased the latency to 50. All other parameters were exactly the same as for Experiment 7. We observe that the species first adapt to their environment by climbing towards a local optimum. However, once this optimum has been reached, depletion of the resources kicks in and the species are no longer located on the optimum. They have to adapt and climb towards a new optimum. An arms race sets in where the entire evolutionary space is explored. The species move over the entire landscape, i.e. all local optima are explored (Figure 12.15).

We conclude this set of experiments by noting that with latency an arms race is possible. Without latency an arms race does not happen for any of the conditions we tested. This is robust for all update rules, i.e. models of evolutionary rates.

12.4.2 Experiments on a Two-Dimensional Landscape

Conceivably, the results obtained with a one-dimensional landscape, although simple to simulate, might introduce special symmetries that are not representative of trait spaces with dimensionality higher than one. Intuitively, one might put it like this - pushing a ball up an incline with a pointed stick is much easier in a pipe than on a plane. That is, when one species moves away from another species in a

Table 12.2 Parameter settings which were used for the experiments on the two-dimensional landscape.

Experiment	Species	Update Rule	Latency Hills		Observed Behavior	Figure
10	30	Equation (12.1)	0	0	shift	12.17
11	30	Equation (12.1)	50	0	continued motion	12.18
12	30	Equation (12.2)	0	0	stasis with small drift	12.19
13	30	Equation (12.2)	50	0	cyclic with drift	12.20
14	30	Equation (12.3)	0	0	stasis with drift	12.21
15	30	Equation (12.3)	3	0	cyclic with drift	12.22
16	30	Equation (12.3)	50	0	arms race	12.23
17	30	Equation (12.3)	0	100	stasis	12.25
18	30	Equation (12.3)	50	100	arms race	12.26

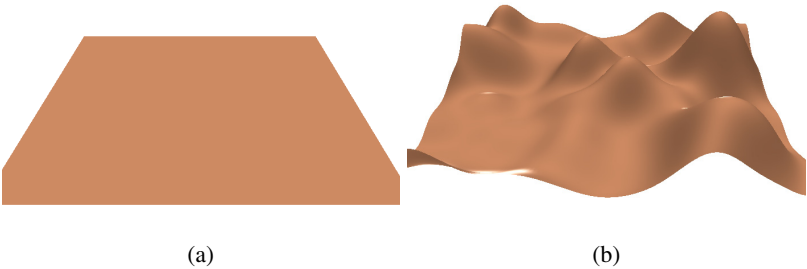


Fig. 12.16 (a) Flat 2D fitness landscape. (b) Non-flat 2D fitness landscape with random variations.

one-dimensional space, the ‘evader’ has no option but to move in exactly the same direction as the ‘pursuer’. This might contribute to a stability in the arms race that is somewhat artificial. In contrast, in a two-dimensional space, the direction of movement of two species may diverge and one species may move ‘past’ another.

We therefore perform the same experiments on a two-dimensional landscape. In the two-dimensional experiments it is even more difficult to convey the dynamics of the experiments using static figures than it is in previous figures using a one-dimensional environment. The interested reader is referred to the movies or the programs which are available for download². Table 12.2 summarizes the parameters that we have used for our experiments in two dimensions. Since the two-dimensional landscape is bigger than the one dimensional landscape, we have increased the number of species to 30. Figure 12.17 shows the results for Experiment 10. Experiments 10 through 16 use a flat two-dimensional fitness landscape shown in Figure 12.16(a). The results for the experiments on the two-dimensional landscape are qualitatively similar to the results which were obtained for the one dimensional case. However, in some cases more complex behavior results due to the fact that additional directions are available in which a species can move. For example, in Experiment 2, on the one-dimensional fitness landscape, we experienced a clumped shifting behavior of all species. For the two-dimensional case (Experiment 11) we experience continued motion because the species are not constrained to move along a single line. The results of Experiment 11 are shown in Figure 12.18. The results of Experiments 12 and 13 are shown in Figures 12.19 and 12.20 respectively. For Experiment 12, we observe a resulting state of stasis as in the one-dimensional case. Experiment 13 results in a mix between cyclic behavior and continued motion.

Experiments 14 through 18 produced the most interesting behaviors. Experiment 14 resulted in a state of stasis with small drift. A snapshot of the resulting state is shown in Figure 12.21. For Experiment 15 the latency was increased to 3. With a latency of 3 we again observed cyclic behavior with drift (Figure 12.22). Because of the two dimensions, the individuals also move through space. When we use a latency of 50 (Experiment 16) we again obtain an arms race similar to the one obtained in Experiment 7 on the one-dimensional fitness landscape. In comparing the two corresponding experiments (Experiment 7 and 16) in one- and two- dimensional spaces we can see how they differ. In both environments, the species climb towards a local optimum, and the landscape responds to the presence of these species, the local optimum has turned into a valley. On a one-dimensional environment the species have only two possible directions in which they can leave this local depression – left or right. However on a two-dimensional landscape, the individuals have an infinite number of directions they can move in. In climbing out of the local depression, the species spread-out across the rim Figure 12.24. If the separation between the species is of sufficient extent, then two separate depressions may be created each of which may result in its own arms race further increasing the separation between them. We expect that this possibility would be further increased in trait-spaces with higher dimensionality than two. It is interesting to note that our model does not involve island

² <http://stubber.math-inf.uni-greifswald.de/~{}ebner/>

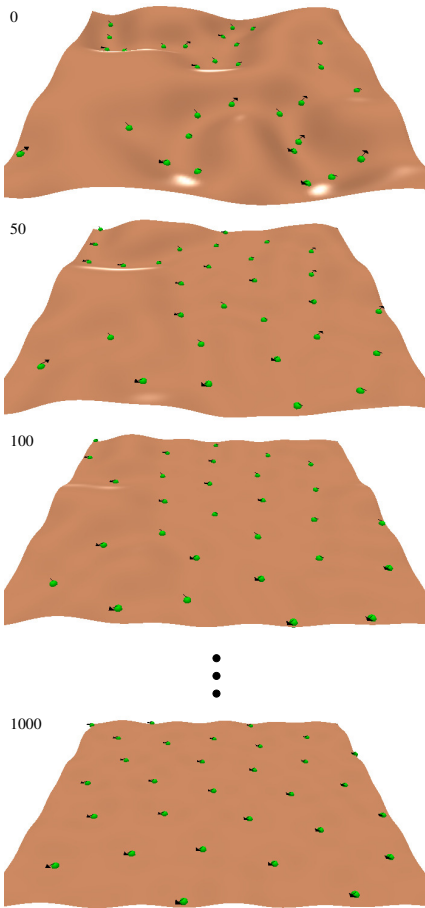


Fig. 12.17 Experiment 10: As in the one-dimensional case one can observe a slow synchronous shift of the species

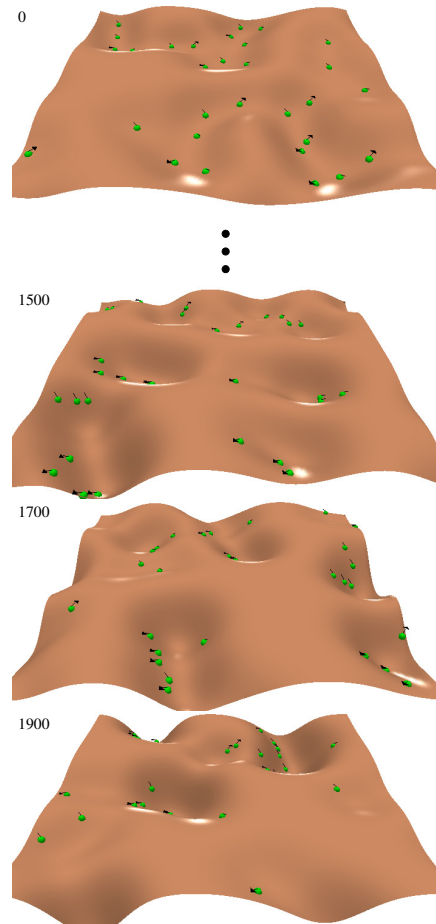


Fig. 12.18 Experiment 11: We observe continued asynchronous motion. The results are again similar to the one-dimensional case. The asynchronous motion results from the increase in the number of directions a species can move.

models or other means of artificially segregating the species, i.e. reproductive isolation [16] or mate preference due to marker traits [6, 35]. Here, sympatric speciation [40], speciation without geographic or physical isolation, is a result of the coupled dynamics of the species [25]. However, this is nonetheless an impoverished form of ecological diversity compared to the results of experiments without latency.

Experiment 17 and 18 use a non-flat fitness landscape shown in Figure 12.16(b) with 100 Gaussian hills distributed randomly over the landscape. A latency of 0 is used for Experiment 17. We obtain a state of stasis with oscillations which is shown

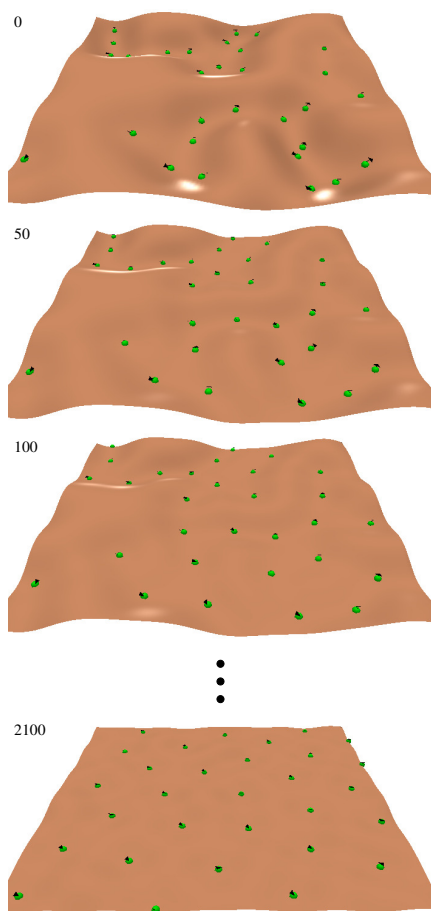


Fig. 12.19 Experiment 12: We again observe stasis with drift as in the one-dimensional case

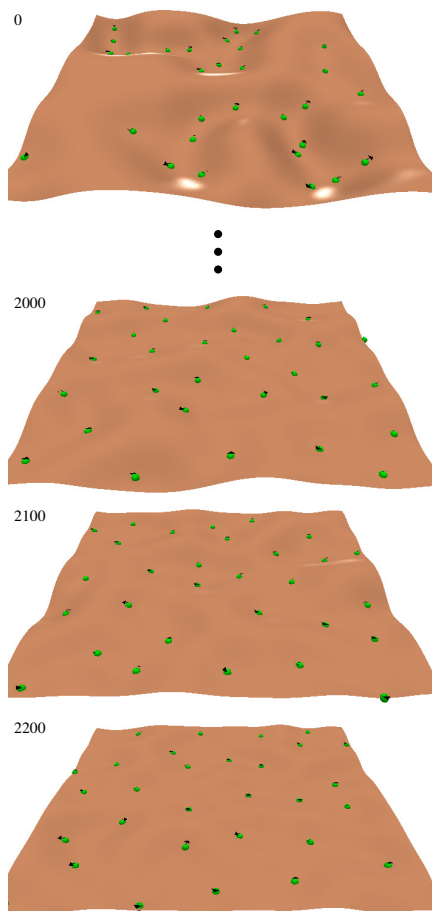


Fig. 12.20 Experiment 13: We observe a mixture between cyclic behavior and continued motion

in Figure 12.25. The species distribute over the entire landscape climbing hills as long as it is advantageous to them and in so doing they equalize the landscape. The ecosystem therefore arrives at an organisation of species which uses the available resources efficiently. In contrast, when we use a latency of 50, we again observe Red Queen dynamics as shown in Figure 12.26. Latency thus causes an ecosystem organisation where resources are not used efficiently - the same resources are being used by many species whilst others are not being used.

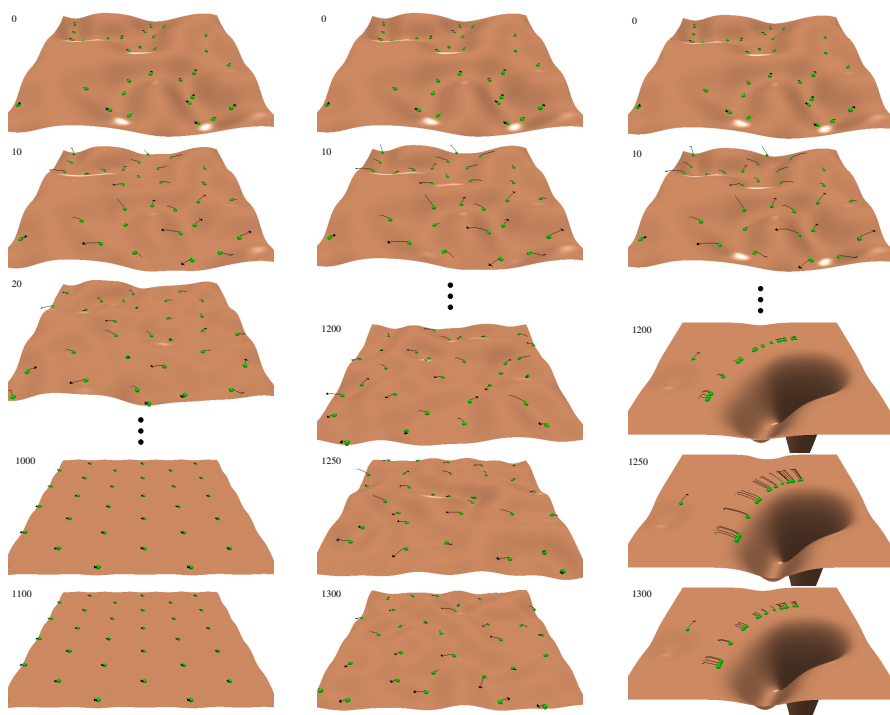


Fig. 12.21 Experiment 14: With a latency of 0 evolution eventually stops and a state of stasis is reached

Fig. 12.22 Experiment 15: A latency of 3 produces cyclic behavior

Fig. 12.23 Experiment 16: With a latency of 50 we obtain an arms race between different species



Fig. 12.24 Spontaneous speciation occurs during Experiment 16. The species spread along the rim of the depression. This causes the creation of two separate sub-sets of species engaged in their own arms races.

12.5 Discussion and Conclusions

12.5.1 Stasis, Change and Improvement

The investigations above have examined a model of an ecosystem where multiple species compete for shared resources. We studied the conditions in this model that produce Red Queen dynamics. The reasoning of Stenseth and Maynard Smith suggests that such a model, having a non-zero-sum game and where the relationship between the lag load (distance from local peaks) and the rate of increase of lag load

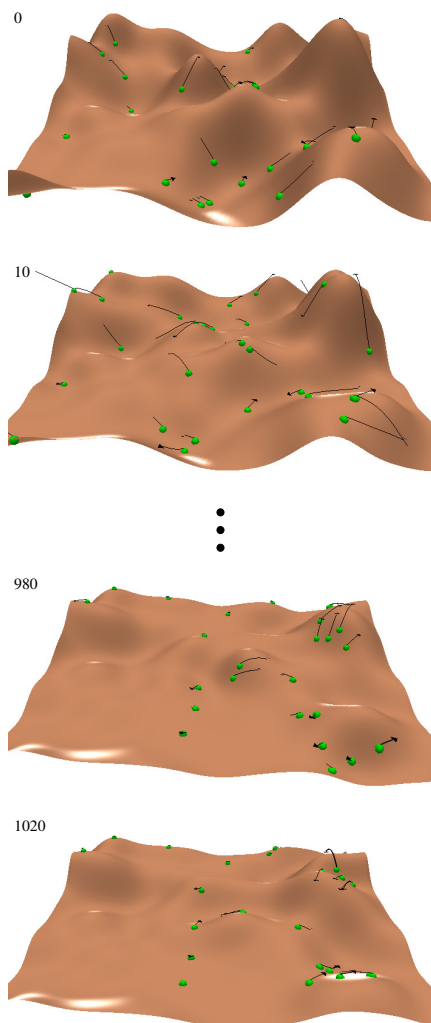


Fig. 12.25 Experiment 17: A non-flat environment and a latency of 0 was used. The species again spread over the landscape to avoid the negative influence of other species and to exploit and fitness advantages present in the landscape.

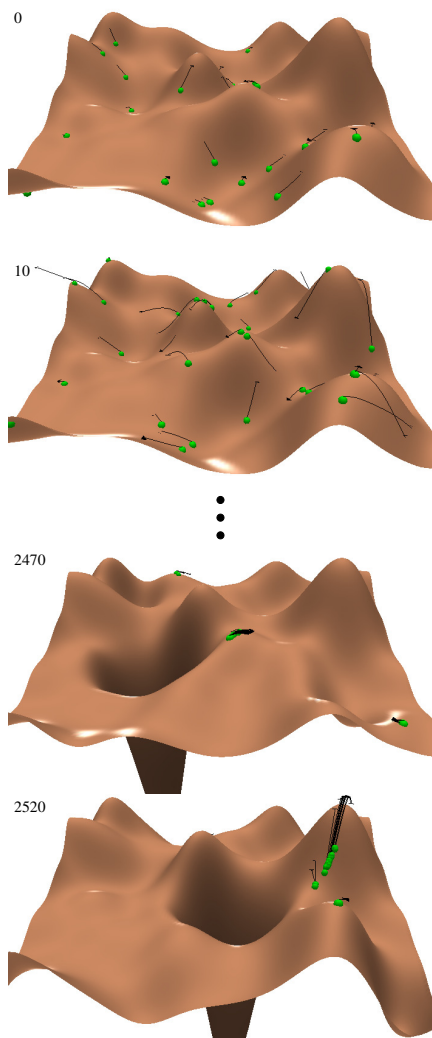


Fig. 12.26 Experiment 18: An arms race occurs. The species eventually sweep over all local optima, but at any one point in time their use of available resources is inefficient.

is non-linear in this manner, can readily produce stable Red Queen dynamics. Our model provides a specific mechanistic illustration of the scenario they describe and our observations indicate that Red Queen dynamics can be readily exhibited. However, we also observe that within these conditions the same model can also produce evolutionary stasis. We find that the critical parameter in determining this distinction is the latency with which evolutionary changes affect ecological resources and thus affect other species. Specifically, if ecological changes are much more rapid than evolutionary changes, such that the ecological response to an evolutionary change is effectively instantaneous, then an evolutionary change in one species has (via its effect on the fitness landscape) an immediate effect on the selective pressure acting on other species and evolutionary stasis is possible. However, if evolutionary timescales are closer to ecological timescales, such that the ecological response to an evolutionary change is not immediate, then we often observe species engaging in Red Queen dynamics.

We investigated several other factors that may affect such dynamics; the relationship between rate of evolution and the slope of the fitness landscape, the dimensionality of the trait/niche space, and whether the intrinsic distribution of resources is uniform or non-uniform. We find that the relationship between latency and the Red Queen dynamics is quite robust to these factors. However, there were some differences between one- and two-dimensional spaces and it seems plausible that higher dimensional spaces would amplify these differences.

In the case of a uniform distribution of resources, we cannot really say that the presence of continued evolutionary change corresponds to improvement – all parts of the trait space have intrinsically equal value. However, it is notable that the continued evolutionary change causes species to explore the entire space. In the case of non-uniform resource distributions, some areas of trait space are intrinsically more valuable than others. In this case, the Red Queen dynamics are capable of pushing species off local optima and forcing them to explore other peaks in the landscape. There is however, no guarantee that any subsequent peak is an intrinsic improvement over the previous peak – it is only a relative improvement at this point in time because of the transient resource depletion. The relationship between continued evolutionary *change* and an arms race that produces continued *improvement* therefore remains problematic.

12.5.2 *Diversity and Efficiency*

Moving beyond the questions of change and stasis as discussed by Stenseth and Maynard Smith, we find that there is a strong link between these different dynamical outcomes and features of ecological diversity and efficiency. The natural result of ecological competition is to produce a selective pressure to diversify – to utilise resources that others are not using. But conversely, when species evolve without competition on the same landscape the tendency is for them to follow the same selective gradients and therefore converge on the same high fitness regions. We observe that when ecological dynamics respond rapidly to evolutionary change

(latency = 0), species diversify onto different resources as expected. But when ecological responses are delayed (latency > 0), species clump together competing for resources in the same or strongly overlapping niches. This is not because competition has been turned off or reduced – species still use the same amount of resource in any one timestep and the total resource available is constant – but the organisation of that competition is different. We can make some intuitive sense of this observation. In an ecosystem of species where competition is latent the organisation of the species with respect to one another is based on out-of-date information – based on the locations that species occupied some evolutionary timesteps in the past. Thus, such an ecosystem is less able to organise itself to utilise resources efficiently than one where the information about the location of other species is up-to-date. In the case of a uniform distribution of resources, the non-latent ecosystem simply spreads out evenly over niche space. In the case of a non-uniform distribution of resources we observe that the distribution of species is correspondingly non-uniform tending to approximately equalise the landscape. In contrast, in the latent dynamics (given either uniform or non-uniform resources), species positions are clumped together leaving many resources under-utilised at any particular point in time. The non-latent dynamics are thereby relatively efficient in their collective use of resources compared to the latent dynamics. Future work could plausibly quantify the efficiency of the resultant resource utilisation and the relationship of these qualitative regimes to the amount of latency.

It also makes intuitive sense that the two modes of diverse-efficient organisation and clumped-inefficient organisation correspond to the two dynamical modes of stasis and Red Queen dynamics, respectively. In order for a species to stop evolving, selective gradients in all directions need to be exhausted. That can be achieved when species are utilising all resources in a diverse manner, but when species are clumped together that naturally leaves some resources under-utilised with non-zero fitness gradients that promote further evolutionary change. This suggests a systematic relationship between ecological organisation and diversity and evolutionary stasis that deserves further attention.

In artificial coevolution, these two modes of behaviour correspond loosely to the two types of coevolutionary set-up – cooperative and competitive. In the diverse organisation, the ecosystem as a whole collectively solves the problem of utilising all available resources. This effectively decomposes the overall problem, dynamically dividing it up into semi-independent sub-problems and avoiding a scenario where multiple species attempt to solve the same part of the problem. But, at the same time, this scenario fails to produce an arms race where continued evolutionary change is observed. Conversely, in the clumped organisation, the species do engage in arms races – each species continually pushing other species to evolve to new areas of the trait space. This means that all species tend to cover all areas of the space, including the highest peaks in the underlying fitness landscape. But, at the same time, in this dynamic the ecosystem as a whole fails to utilise all resources collectively. Accordingly, we can view the non-latent dynamics as producing a cooperative coevolution scenario and the latent dynamics as producing a competitive coevolution scenario. The former effectively solves the problem-decomposition issue of

cooperative coevolution (although the nature of the decomposition problem here is not difficult) whereas the latter effectively solves the arms-race conditions required for competitive coevolution (although continued improvement is a different matter). However, our observations also suggest that finding a balance of the two is non-trivial and perhaps even intrinsically opposed. In the current models the trait space of a species and its fitness dependencies on other species have a direct relationship (i.e., based on distance). For engineering purposes, where the task being performed (collectively or individually) is complex, the relationship between the trait space of an individual and its frequency dependent fitness effects on others will be less straightforward. Nonetheless, further investigation could address the change-over from the diverse-stable mode to the converged-dynamic mode as a function of latency and whether or not the trade-off of competition and cooperation can be usefully controlled.

In summary, our simple evolutionary model allows us to explore the dynamics of coevolution under various conditions. The model is simple and easy to understand and the behaviour of the species can be observed in real time. Our investigations using these models illustrate some important factors which influence the balance of evolutionary stasis and Red Queen dynamics. We find that both outcomes are possible without changing the nature of the underlying game, or the level at which selection is applied, but merely by altering the coupling between ecological and evolutionary timescales. Specifically, if ecological change is nearly instantaneous compared to evolutionary change, stasis results; but conversely, if evolutionary timescales are closer to ecological timescales, such that resource depletion is not instantaneous on evolutionary timescales, then Red Queen dynamics result. We also observe that in the stasis mode, the overall utilisation of resources by the ecosystem is relatively efficient whereas in the Red-Queen mode, the organisation of the ecosystem is inefficient as species tend to clump together competing in overlapping niches. These models thereby suggest a link between the issues of change and stasis discussed by Stenseth and Maynard Smith and matters of ecological diversity and organisation. In the same way, these models also suggest some basic conditions that influence the organisation of inter-species interactions and the balance of individual and collective adaptation in ecosystems.

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