

Periodic polymorphisms with density-dependent selection

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(Received 11 April 1996 and in revised form 12 March 1997)

Summary

It is known that genetic polymorphisms can be maintained in populations without superiority of the heterozygote subject to constant but non-linear selection through periodic and higher-order behaviour. In this paper we explore evolutionary paths from single equilibria to higher-order attractors and the existence of polymorphisms that do not arise from equilibria. We explore whether there is a continuous range of allelic types that can create such polymorphisms. We use a single-locus genetic model with exponential density-dependent fitness functions and show that there are large parameter ranges in regions of both overdominance and partial dominance where polymorphic attractors exist.

1. Introduction

The maintenance of genetic polymorphisms in populations subject to constant but non-linear selection has been studied and complex dynamics have been revealed (Hastings, 1981). With density- and frequency-dependent selection, non-linearities are known to produce irregular dynamics without random perturbations (Auslander *et al.*, 1978). Single-locus genetic models have shown that a wide range of polymorphic behaviours can be generated that do not depend on heterozygote superiority in carrying capacity (Asmussen & Feldman, 1977; Asmussen, 1979).

Recently, Ferriere & Fox (1995) have speculated that genotypes with lower fitness than any resident genotypes may be able to invade populations due to the existence of regions of attraction that are sufficiently complex that 'less fit' mutants may succeed. Analyses of plant growth models have shown that the effects of density on individual survival and reproduction can lead to optimum fitness strategies that can cause population densities to behave with periodic fluctuations (Bishir & Namkoong, 1992). In these analyses, the optimum allocation of energy among seed and vegetative plant parts is density dependent and population growth is dependent on seed production such that the replacement rates of the seedling generation lead to such non-linear dynamics that periodic population behaviour results. Appar-

ently the population growth rate potential can become so high that the carrying capacity equilibrium is destabilized. If genotypes differ in either energy gathering efficiency or the efficiency of energy allocation among plant parts, then periodic behaviour can be generated jointly in population sizes and allele frequency polymorphisms (Namkoong *et al.*, 1993) without heterozygote superiority in carrying capacity fitness.

While it may be clear that genetic polymorphisms can exist in the form of periodic and higher-order behaviour with and without heterozygote superiority, the purpose of this paper is to explore whether there are simple evolutionary paths from single, attracting equilibria to such higher-order behaviour. We consider that mutations of alleles affecting density-dependent fitness can be favoured by selection if they increase either the population growth rate or the carrying capacity. Then if stepwise mutations generate small increments in those population parameters, is it also feasible to suspect that selection can lead populations from single stable equilibria into periodic behaviour? We investigate models of density-dependent selection in which a continuous series of allelic effects on population parameters may exist (but for which no heterozygosity superiority exists in the parameter effects). While previous investigations have shown that period behaviour can be generated, no studies have explained how such behaviour may evolve from single stable equilibria into periodicity. Similarly, no previous studies have examined whether the parameter

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levels and hence the types of allelic effects must lie within very small ranges for periodic behaviour to exist. We wish to determine whether a range of parameters exists that can create such polymorphisms, and whether there is a continuous set of parameters within that range such that there can be a continuous evolution into that set. We use single-locus genetic models of non-frequency-dependent density responses.

2. Model equations

Suppose we have a single population and two alleles, A_1 and A_2 . At time t the population size is denoted by N_t and the frequency of allele A_1 is denoted by p_t . We assume discrete generation intervals for diploid, random mating organisms with viability selection occurring after zygote formation but before reproduction and with the population censused before density-dependent selection and reproduction. The fitness of genotype A_iA_j ($i, j = 1, 2$) at time t is denoted by w_{ij}^t . The marginal fitness of A_i is thus

$$w_i^t = p_t w_{i1}^t + (1 - p_t) w_{i2}^t \quad (i = 1, 2)$$

and the mean population fitness is

$$\bar{w}^t = p_t w_1^t + (1 - p_t) w_2^t.$$

Differences in fitness among genotypes may be interpreted as the result of different responses to ecological pressures. Following Asmussen (1979) and Namkoong *et al.* (1993), exponential density-dependent fitness functions of the form

$$w_{ij}^t = \exp(a_{ij} - b_{ij} N_t) \quad a_{ij}, b_{ij} > 0, (i = 1, 2) \quad (1)$$

are used in this paper. Such monotonic decreasing functions of population density are often used to model the detrimental effects of population crowding (Selgrade & Namkoong, 1992).

If Hardy–Weinberg frequencies are assumed at each time t , then the recursion equations for p and N are

$$p_{t+1} = p_t \frac{w_1^t}{\bar{w}^t} \quad (2a)$$

$$N_{t+1} = \bar{w}^t N_t \quad (2b)$$

where the region of practical significance is $0 \leq p \leq 1$, $N > 0$. With the above equations the carrying capacity K_{ij} for genotype A_iA_j acting alone is given by

$$K_{ij} = \frac{a_{ij}}{b_{ij}}.$$

For a more detailed description of the model see Namkoong *et al.* (1993).

To study the effects of varying relative carrying capacities separately from the effects of the growth

rates of the genotypes, we added an additional multiplicative factor to the fitness functions to give

$$w_{ij}^t = \exp(c_{ij}(a_{ij} - b_{ij} N_t)) \quad a_{ij}, b_{ij}, c_{ij} > 0, (i = 1, 2). \quad (3)$$

Varying c_{ij} has no effect on carrying capacities ($K_{ij} = a_{ij}/b_{ij}$) but does affect the growth rate ($c_{ij} * a_{ij}$) of the A_iA_j genotype. Conversely, varying b_{ij} affects the carrying capacity but not the growth rate for genotype A_iA_j . These are the variables that will be varied in the model analysis. The methods of analysis and the results are discussed in the next section. For clarity we will use p_1 instead of p to indicate the frequency of the A_1 allele in the remainder of the paper.

3. Model analysis

(i) Approach

Equilibria and their associated stability properties have been studied analytically for models such as the one described above. These theoretical results help predict the conditions under which stable equilibria can be expected (see, for example, Asmussen, 1979; Roughgarden, 1979). However, periodic dynamics (particularly polymorphic cycles) are more difficult to study (Asmussen, 1979; Namkoong *et al.*, 1993). Fortunately, various dynamical systems computer packages have been developed which can help us with such analyses. We used DSTOOL (Back *et al.*, 1992) and XPPAUT (Ermentrout, 1996) to solve the system of equations over time and to find fixed points. The initial parameters we use are for populations that exhibit stable equilibria. With heterozygote superiority a stable equilibrium exists with $0 < \rho < 1$. In the absence of heterozygote superiority, the only attracting equilibrium is stable at fixation of the allele conferring the highest carrying capacity. Any mutations of alleles that confer higher carrying capacities for populations with stable equilibria would ultimately fix those mutants and hence evolution would drive populations to possess only those alleles with highest carrying capacities, as long as they exhibit a single, stable, attracting equilibrium. However, many populations are often also subject to selection for high growth rate. Simultaneous selection would be expected to increase both parameters to the extent that is physiologically possible. If such selection were to destabilize any previously existing equilibrium then population dynamics may induce periodic behaviour that limits evolution before physiological limits become constraining.

At any level of carrying capacity, the rate parameter ($c_{ij} * a_{ij}$) can be increased without affecting population dynamics to the point of destabilizing the equilibrium. Just beyond that level ($c_{ij} * a_{ij} > 2 \cdot 0$) the equilibrium changes from an attracting to an unstable point and other fixed-point attractors can appear. The location of the attractors can be diagrammed in relation to the

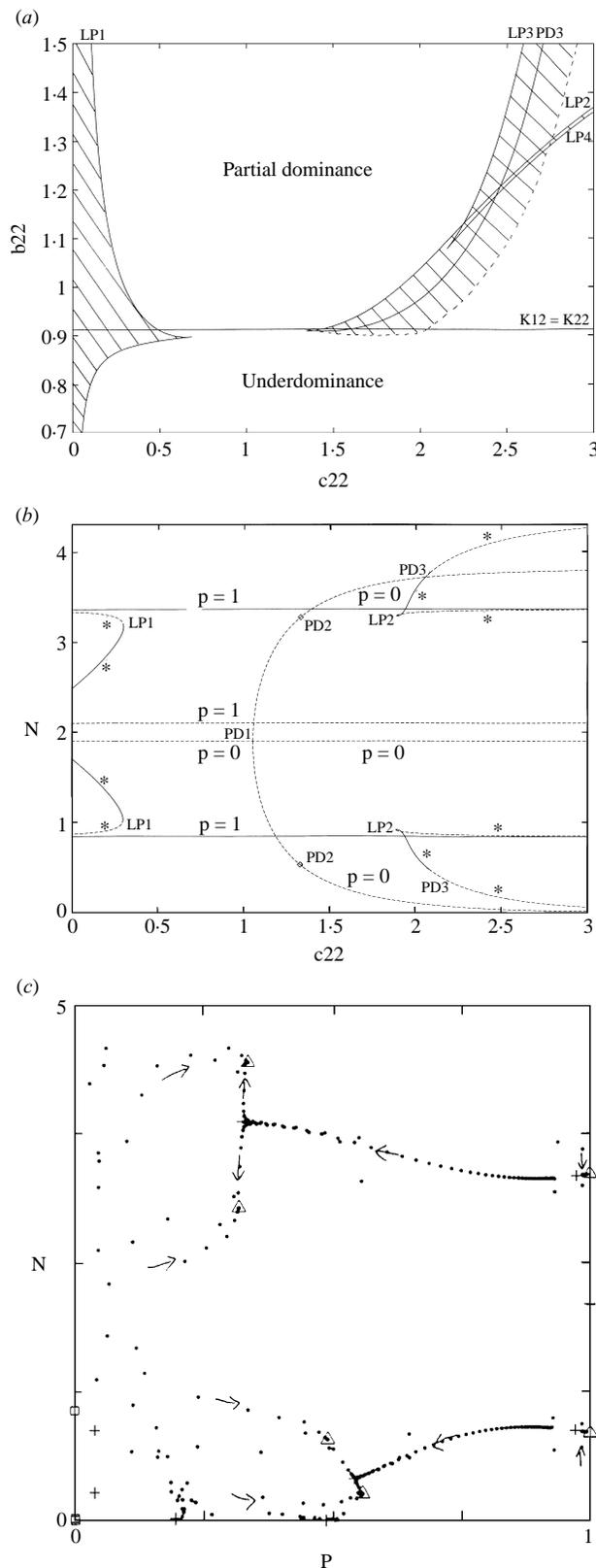


Fig. 1. (a) Two-parameter space of b_{22} versus c_{22} for $a_{11} = 2.1$, $b_{11} = 1.0$, $c_{11} = 1.1$, $a_{12} = 2.0$, $b_{12} = 0.96$, $c_{12} = 1.0$, $a_{22} = 1.9$. With these values $K_{11} = 2.1$ and $K_{12} = 2.083$. K_{22} decreases as b_{22} increases. The curves denote boundaries where fixed points bifurcate. The hatched regions denote parameter combinations which give rise to genetic polymorphisms. (b) One-parameter bifurcation diagram for $b_{22} = 1.0$ in (a). Continuous curves indicate attracting fixed points and dashed curves indicate

parameters using XPPAUT's output for AUTO (Doedel, 1981). We use the continuous interface package of AUTO to explore the effects of simultaneous and continuous variations in two parameters.

With this combination of analytical and graphical packages we can follow the development of period-doubling bifurcations to delimit the parameter space for qualitative changes in periodic behaviour. For higher than period-2 behaviour we used the second iterate of the model in which a period-2 attractor is a single point equilibrium, and found the bifurcation points that generate the period-4 attractors.

(ii) Analyses

We consider a homozygote genotype which has a rate parameter ($c*a$) that would endow it with period-2 behaviour if growing as a monomorphic population, and examine the kinds of alleles with which it could coexist. At rate parameters below 2.0, allelic polymorphisms can be maintained only if heterozygotes are superior in carrying capacity. We arbitrarily set the b parameter near 1.0 for convenience, but it can be scaled appropriately for any carrying capacity since $K = a/b$. We assume that rate constants are increased above 2.0 for at least one genotype. Specifically, we assume that an A_1A_1 genotype has a rate constant greater than 2.0. The initial parameter values we use are $a_{11} = 2.1$, $b_{11} = 1.0$, $c_{11} = 1.1$, $a_{12} = 2.0$, $b_{12} = 0.96$, $c_{12} = 1.0$, $a_{22} = 1.9$ so that the heterozygote has a lower carrying capacity than the A_1A_1 genotype ($K_{11} = 2.1$, $K_{12} = 2.083$).

(a) Partial dominance – underdominance

We first examine the range of conditions for the A_2A_2 genotype that create either underdominance or partial dominance in carrying capacity to determine whether genetic polymorphisms can persist in the absence of an attracting equilibrium. Fig. 1a is a two-parameter bifurcation diagram of b_{22} versus c_{22} showing the parameter combinations which give rise to a persistent genetic polymorphism (hatched regions). The horizontal line at $b_{22} = 0.912$ corresponds to $K_{12} = K_{22}$ and divides a region of partial dominance ($K_{11} > K_{12} > K_{22}$) above the line from a region of heterozygote inferiority or underdominance below the line.

On the upper portion of the figure where the A_2A_2 genotype has lower carrying capacities than either A_1A_1 or A_1A_2 , there are A_2A_2 genotypes with either

repelling fixed points. The asterisks mark branches having $0 < p < 1$. LP stands for a limit point or saddle-node bifurcation. PD stands for period-doubling bifurcation. Only period-1 and period-2 fixed points are shown. (c) A phase plane diagram at $b_{22} = 1.0$, $c_{22} = 21.5$, with a polymorphic period-4 attractor and a period-2 attractor at $p_1 = 1$. The triangles mark attracting points, and the crosses mark saddle nodes.

very high or very low rate parameters which allow coexistence with large domains of attraction. However, the lower the carrying capacity (and hence the higher b_{22}), the more extreme the rate parameter for the A_2A_2 genotype has to be for it to persist. It can also be noted that under conditions of underdominance in carrying capacity (lower part of Fig. 1a) only alleles with very low rate parameters can be maintained in a polymorphism.

Over most of the parameter space the general rule for genetic polymorphisms with density dependence holds true: the homozygote with the highest carrying capacity excludes an allele with a lower carrying capacity. It thus seems that the period-2 dynamics of the A_1A_1 genotype can only maintain a polymorphism with a limited variety of alternative allelic types under conditions of partial dominance and underdominance. Nevertheless, examination of the types of attractors that exist indicate that several forms of polymorphism can be generated.

The behaviour of attractors within the shaded regions of Fig. 1a can be examined by considering the one-parameter (c_{22}) bifurcation diagram (Fig. 1b) for N where the genotype ordering of carrying capacities is $K_{11} > K_{12} > K_{22}$. This diagram illuminates the dynamics that correspond to different values of c_{22} in the range $[0, 3]$ in Fig. 1 along the line where $b_{22} = 1$. Continuous curves are the locus of attractors in N and dashed curves represent the locus of repellers. Curves marked with asterisks denote the locus of interior fixed points, where $0 < p_1 < 1, N > 0$.

For $c_{22} < LP1$ there is also an interior period-2 attractor. At the left-hand edge of Fig. 1b where $c_{22} = 0$, and continuing to the right, a saddle point as well as a period-2 attractor at $p_1 = 1$ persists at constant values N of approximately 2.1, 0.8 and 3.3, respectively. This interior attractor disappears at LP1 through a limit point or saddle-node bifurcation. At this point an interior period-2 saddle and an interior period-2 sink collide and disappear. The repelling equilibrium at $p_1 = 0$ also persists at a constant N of approximately 1.9. This bifurcates at PD1 into a period-2, and at PD2 into a period-4 and subsequently into chaotic behaviour.

For $LP1 < c_{22} < LP2$ the general rule holds for allelic displacement by homozygotes with superior carrying capacity as there is no interior attractor – the period-2 attractor at $p_1 = 1$ is now globally attracting. At LP2 another saddle-node bifurcation occurs which introduces a second region of interior attractors. For $LP2 < c_{22} < PD3$ this attractor is period-2 and at PD3 a period-doubling bifurcation occurs giving rise to a period-4 interior attractor (see Fig. 1c for a phase plane diagram of N and p_1 for $c_{22} = 2.15$). Fig. 1a shows how the position of this period-doubling point varies with b_{22} as well as c_{22} . As c_{22} is increased beyond PD3 further period-doublings occur resulting in higher-order interior attractors and finally a chaotic attractor. This period-doubling route to chaos is well

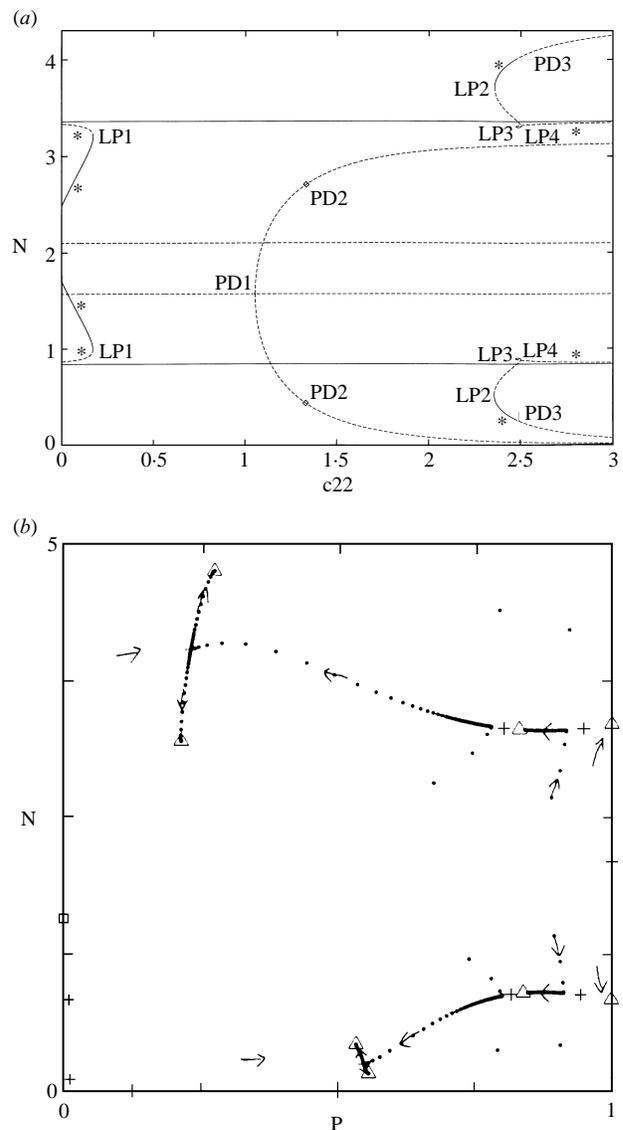


Fig. 2. (a) One-parameter bifurcation diagram for $b_{22} = 1.21$ in Fig. 1. The notation is as in Fig. 1b. (b) A phase plane diagram at $b_{22} = 1.21, c_{22} = 2.5$ and the remaining parameter values as in Fig. 1a with two regions of attraction for genetic polymorphisms.

known (May, 1976; Devaney, 1992; Selgrade & Roberds, 1996 and the references therein). However, in this case the initial bifurcation is a saddle-node bifurcation and not a period-doubling from an equilibrium to period-2 behaviour as in most documented cases. The dashed curve in Fig. 1a approximates the boundary of the region of interior attractors. Beyond this curve there is a global (chaotic) attractor which includes part of the $p_1 = 0$ and $N = 0$ axes even though the A_1A_1 homozygote has a superior carrying capacity.

Other regions in Fig. 1a can also be illuminated using one-parameter bifurcation diagrams and phase portraits. For example, if we shift b_{22} to 1.21, Fig. 2a shows the various dynamics that occur for different values of c_{22} . There are two additional limit points in

this diagram, LP3 and LP4, which delimit a small loop in the interior period-2 branches. Between these values of c_{22} there are two interior attractors (see Fig. 2*b* for phase plane diagram at $c_{22} = 2.5$).

(*b*) *Overdominance – partial dominance*

If we now consider the situation where the heterozygote (A_1A_2) carrying capacity is greater than that of A_1A_1 , the endurance of the A_1 allele can be examined for cases of heterozygote superiority or partial dominance in carrying capacities. The upper part of Fig. 3*a* corresponds to a carrying capacity of A_1A_2 that exceeds that of both homozygote and thus illustrates the fate of polymorphism for heterozygote superiority. (The parameter values for this figure are the same as for Fig. 1 except for b_{12} which now has the value 0.94 so that $K_{12} = 2.128$.) As might be expected, a large range of A_2A_2 types can coexist with the A_1A_1 genotype, but even heterozygote superiority cannot maintain a polymorphism since a chaotic A_2A_2 genotype can exclude the A_1A_1 genotype (region to the right of the dashed curve).

We can use one-parameter bifurcation diagrams to clarify the different regions in Fig. 3*a*. Fig. 3*b* corresponds to conditions where $b_{22} = 1.0$. For $c_{22} < 0.208$ (PD1) there is a polymorphic equilibrium and a period-doubling bifurcation at $c_{22} = 0.208$, which gives rise to a period-2 interior attractor. This becomes period-4 at PD2 ($c_{22} = 2.098$), which can be seen in the phase diagram of Fig. 3*c* and *d* respectively. It can be shown that a rapid succession of period-doubling bifurcations occurs as c_{22} is increased further, leading to a chaotic interior attractor. Beyond $c_{22} = 2.3$ the chaotic attractor can be seen in the phase diagram of Fig. 3*e* to contain an L-shaped region on the $p_1 = 0$ and $N = 0$ axes for $c_{22} = 2.31$.

The one-parameter bifurcation diagram for $b_{22} = 1.3$ (Fig. 3*f*) shows how the regions marked A and B in Fig. 3*a*, which correspond to two interior attractors, arise. At $c_{22} = 2.637$ (LP1) the interior period-2 branches reach a limit point and bend back on themselves. A second limit point is reached at LP2 = 2.435 and the branches regain stability and double back once again (this is known as hysteresis) giving rise to a range of c_{22} values where two separate interior period-2 attractors exist, each with large domains of attraction. At $c_{22} = 2.575$ (PD2) a period-doubling bifurcation occurs leading to an interior period-4 attractor together with an interior period-2 attractor. As c_{22} is increased, further period-doubling bifurcations occur until a period-2 attractor coexists with a chaotic attractor. At the dashed curve the interior chaotic attractor is replaced by a chaotic attractor which includes an L-shaped region on the axes $p_1 = 0$ and $N = 0$. High levels of $c_{22} * a_{22}$ can therefore maintain the A_2 allele in polymorphic state or can displace A_1 alleles even if the heterozygote (A_1A_2) carrying capacity is superior to both homo-

zygotes. This further confirms that heterozygote superiority is not a necessary condition for maintaining polymorphisms.

Thus, if an allele can generate periodic behaviour in the homozygous state it can maintain or be maintained in a genetic polymorphism by competing genotypes with wide variations in effect. Allelic coexistence as well as allelic exclusion can exist for cases of underdominance, partial dominance and overdominance in carrying capacity.

The above results were obtained for an A_1A_1 genotype with a rate parameter of $c_{11} * a_{11} = 2.31$. Rates closer to 2.0 show similar qualitative behaviour but on a smaller, less easily visualized scale. At higher values, such as when the rate parameter of the A_1A_1 genotype is $c_{11} * a_{11} = 2.64$, we can see that larger ranges of parameters can maintain polymorphisms for A_2A_2 genotypes that are either superior to or inferior to the A_1A_1 carrying capacity (compare Figs. 4 and 1*a* and Figs. 5 and 3*a*). The ranges of rate and carrying capacity parameters are much larger and indicate, at least in this range of behaviour, that many allelic polymorphisms can exist. At this higher rate parameter, the dynamics for the A_1A_1 genotype existing alone are period-4. Thus in Fig. 5 there is an additional curve PD# (when compared with Fig. 3*a*) delimiting a region of interior period-4 attractors.

In both Fig. 4 and Fig. 5 a curve of period-doublings from an interior period-2 to an interior period-4 attractor (marked PD*) dips below the horizontal line which divides the regions where $K_{22} < K_{12}$ and $K_{22} > K_{12}$. Using DSTOOL we found that a small region of interior attractors exists below this dividing line in both figures as shown by the dashed curve. This region also exists in Figs. 1 and 4 but it is smaller. Thus A_2A_2 genotypes can coexist under any condition of heterozygote superiority, intermediacy or inferiority. It is possible for alleles with marginally higher carrying capacities and acting with partial dominance to maintain a genetic polymorphism with a resident allele but only if its rate parameter is within a limited range. Thus, if small increases in carrying capacity are obtained by genotypes at the expense of increased rate parameters, polymorphisms can evolve.

In these cases of competition among genotypes with high rate parameters, the coexistence of three alleles would seem to be possible though the parameter ranges and domains of attraction may not be at all similar. We have investigated three-allele dynamics from the range of allele types which could coexist pairwise with A_1A_1 genotypes. Using a three-allele, single-locus model and choosing parameter values from Fig. 4 in the range where all gene actions are in the partial dominance range, and where those for A_1 and A_2 alone and for A_1 and A_3 alone give rise to polymorphic period-2 attractors, it can be shown that A_2 and A_3 can also coexist when A_1 is not present. In one case there was no attractor at which all three alleles coexist but we did find a parameter set at which

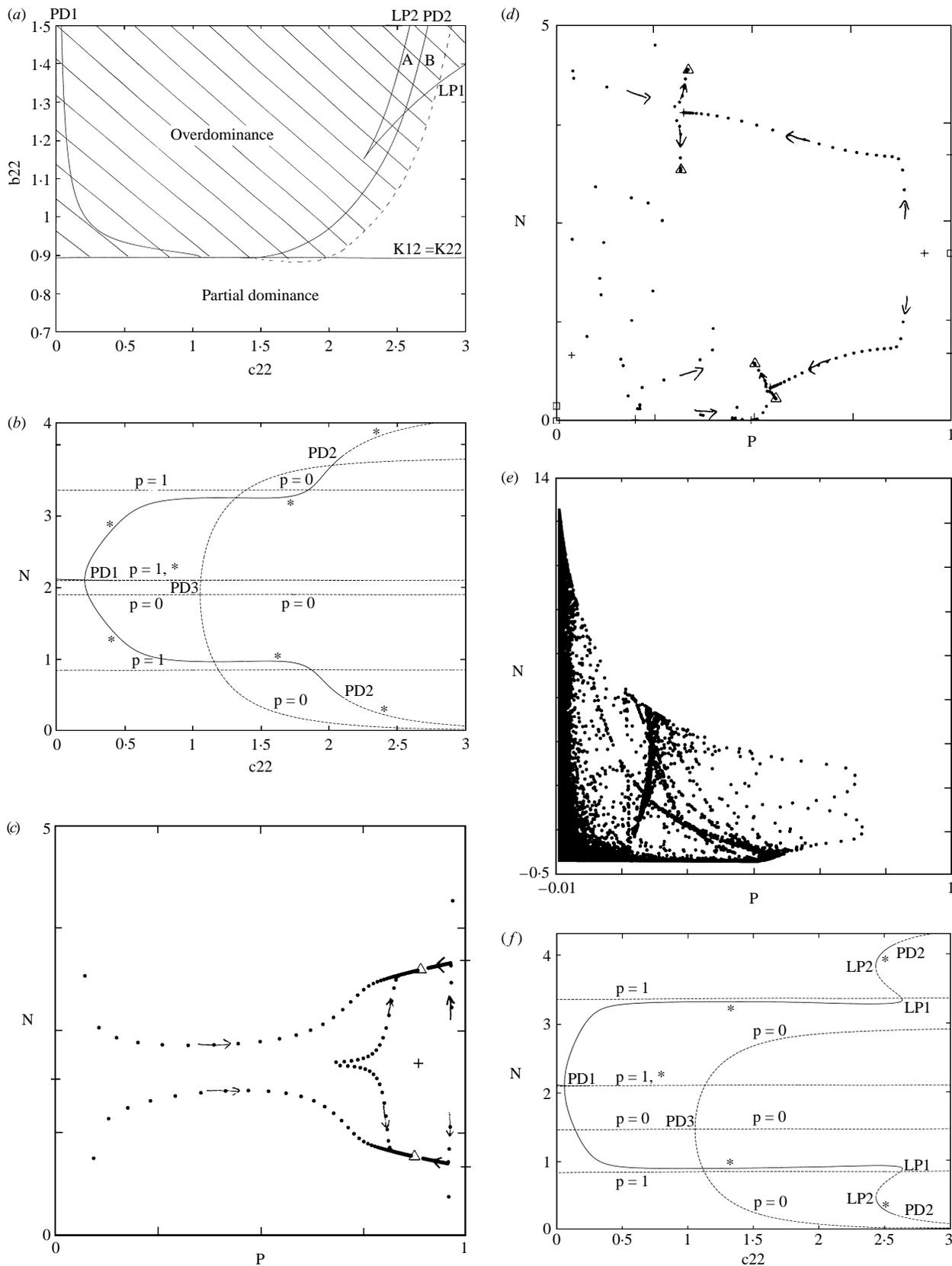


Fig. 3. (a) Two-parameter bifurcation diagram of b_{22} versus c_{22} parameter space for $a_{11} = 2.1$, $b_{11} = 1.0$, $c_{11} = 1.1$, $a_{12} = 2.0$, $b_{12} = 0.94$, $c_{12} = 1.0$, $a_{22} = 1.9$. With these values $K_{11} = 2.1$ and $K_{12} = 2.128$. K_{22} decreases as b_{22} increases. The hatched regions denote parameter combinations which give rise to polymorphic attractors. (b) One-parameter bifurcation diagram for $b_{22} = 1.0$ in (a). Notation as in Fig. 1b. (c) A polymorphic period-2 attractor for $b_{22} = 1.0$, $c_{22} = 1.0$ in (a). (d) A polymorphic period-4 attractor for $b_{22} = 1.0$, $c_{22} = 2.15$ in (a). (e) 80000 points on the attractor when $b_{22} = 1.0$ and $c_{22} = 2.31$ in (a). Note the different scale on the axes so that the boundary of the attractor at $p = 0$ and $N = 0$ can be seen with greater clarity. (f) One-parameter bifurcation diagram for $b_{22} = 1.3$ in (a). The notation is as in Fig. 1b.

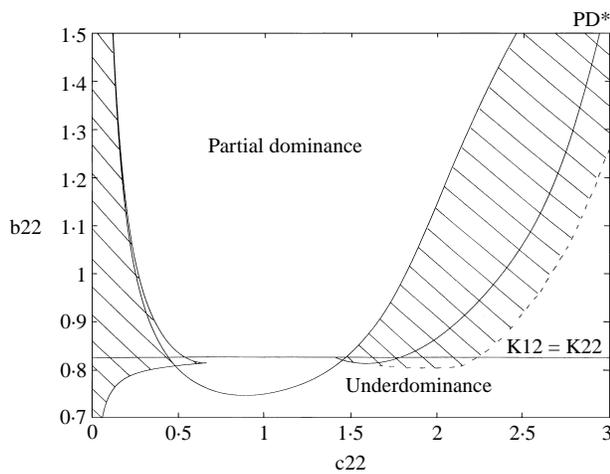


Fig. 4. Two-parameter bifurcation diagram of b_{22} versus c_{22} parameter space for $a_{11} = 2.2$, $b_{11} = 1.0$, $c_{11} = 1.2$, $a_{12} = 2.0$, $b_{12} = 0.917$, $c_{12} = 1.0$, $a_{22} = 1.8$. With these values $K_{11} = 2.2$ and $K_{12} = 2.181$. K_{22} decreases as b_{22} increases. The hatched regions denote parameter combinations which give rise to polymorphic attractors.

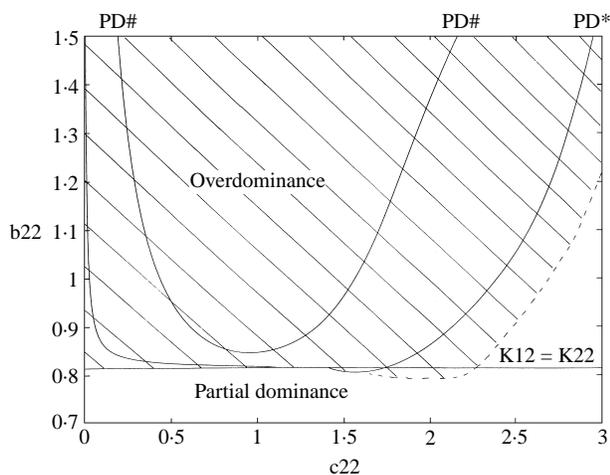


Fig. 5. Two-parameter bifurcation diagram of b_{22} versus c_{22} parameter space for $a_{11} = 2.2$, $b_{11} = 1.0$, $c_{11} = 1.2$, $a_{12} = 2.0$, $b_{12} = 0.9048$, $c_{12} = 1.0$, $a_{22} = 1.8$. With these values $K_{11} = 2.2$ and $K_{12} = 2.210$. K_{22} decreases as b_{22} increases. The hatched regions denote parameter combinations which give rise to polymorphic attractors.

such a three-allele attractor exists. With that set of genotypes removing any one of A_1 , A_2 or A_3 resulted in an attractor at which the other two alleles coexisted.

4. Conclusions

For the types of parameter variations examined in these exponential density-dependent models, the maintenance of genetic polymorphisms in single-locus models can be seen often to follow the familiar rules in that overdominance of carrying capacity is both necessary and sufficient. However, there are also very large parameter ranges where overdominance is

neither necessary nor sufficient and which lie in continuous sets. Hence, once entering the set, it is possible that several allelic types could coexist, at least in pairs and sometimes in larger sets. Alleles with higher-order behaviour also seem capable of creating larger sets for coexistence, with some of the pairs of alleles creating several domains of attraction for different types of polymorphisms. Hence, the invasion of monomorphic populations by alleles with either higher or lower carrying capacity can lead to periodic and higher-order genetic polymorphisms.

We would like to thank Don Ludwig, Wayne Nagata and Jim Selgrade for their helpful suggestions and for interesting discussions. The research was undertaken as part of the project entitled The Impact of Disturbance on Species and Genetic Interactions, and was partly funded by Forest Renewal B.C.

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