Simulation models for educational purposes: an example on the coexistence of plant populations

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Introduction

An understanding of the basic principles of population ecology is essential for anyone concerned with the management of natural resources. A theoretical framework is important from both the basic and the applied viewpoints. It improves understanding of the behaviour of the system, enabling appropriate management techniques to be developed.

It is difficult to demonstrate just from bibliographic examples how environmental heterogeneity or disturbances can affect plant or animal population dynamics. The type of experiments or observations needed for such purposes are difficult to perform. The cost in time, labour, and space is high, especially if students are supposed to be actively involved in each stage. Assembling simple simulation models for a microcomputer or a programmable calculator, discussion of their assumptions, progressive elaboration, and 'numerical experimentation' in the classroom may replace *in vivo* experiments in the learning process (Geyer, 1983). Development of a conceptual model of a complex system, its representation as a diagram and a set of algorithms, and finally its translation into computer language trains students in logical reasoning and helps them to understand the system and generate new hypotheses (Hall and Day, 1977).

The objective of this paper is to introduce a simple model and its computer program designed for teaching. The model describes the competitive relations between two populations on the basis of the Lotka–Volterra equations and allows students to assess the influence of environmental heterogeneity and disturbances on the behaviour of populations.

In the following sections the influence of environmental heterogeneity and disturbances on the classical plant species coexistence theory is briefly reviewed and the Lotka–Volterra model and computer program are described. As an example, two numerical experiments are presented which explore the influence of different precipitation and disturbance regimes on the coexistence of a mesophytic and a xerophytic plant population in Patagonia (Argentina). Finally, other possible questions and program modifications are suggested.

Abstract

A solid background in population ecology is valuable for anyone concerned with natural resources management. However, without the opportunity of field experience, it may be difficult for students to become familiar with some of the principles of population biology. Microcomputers and programmable pocket calculators allow the construction of simple simulation models, making it possible to carry out some 'numerical experiments' in the classroom which may play the same role in the learning process as in vivo *experimentation.*

This work introduces a mathematical model based on the Lotka–Volterra equations and a computer program developed for a programmable calculator. They can be used to assess the influence of environmental heterogeneity and disturbances on the results of competitive relationships between two plant populations. As an example, the interaction between two tussock grass species of the Patagonian steppe, Stipa speciosa *Trin. et Rupr. and* Festuca pallescens *(St Yves) Parodi (the second being less xerophytic than the first one), is analysed.*

Plant species coexistence

According to Gause's competitive exclusion principle, two species can coexist in a stable environment only if their ecological niches do not overlap, that is, if they have different requirements and tolerances[1] (Vandermeer, 1981). The lack of empirical evidence supporting Gause's principle seems to be partly associated with its assumption of environmental stability and homogeneity (Wiens, 1977). The intensity of competition between two species may be the result of the response of each one to environmental factors, which under natural conditions vary both in space and time (Begon and Mortimer, 1986, pp. 89–90).

The occurrence of a disturbance modifies com-

[1] See Begon and Mortimer (1986, pp. 101–102) for a discussion on the role of realized niches in the coexistence of potentially competing species.

petitive interactions between populations in the plant community, thus preventing them from reaching a competitive equilibrium (Pickett, 1980). Huston (1979) stated that most communities exist in a state of non-equilibrium. Competitive equilibrium does not occur because there are periodic population reductions due to disturbances of moderate intensity, such as fire, grazing, or pests.

The inclusion of these two elements, environmental variability and periodic disturbances, in a model could allow students to understand coexistence situations which the competitive exclusion principle fails to explain.

The model

The model used here is based on Lotka–Volterra's logistic equation (Silvertown, 1982; Begon and Mortimer, 1986, p. 91) defined by:

$$dX/dt = r_x * X_{i-1} * [(K_x - X_{i-1} - \alpha_{xy} * Y_{i-1})/K_x] \quad (1)$$
$$dY/dt = r_y * Y_{i-1} * [(K_y - Y_{i-1} - \alpha_{yx} * X_{i-1})/K_y] \quad (2)$$

in which:

X: population size (number of individuals or density) of species 'x'
Y: population size (number of individuals or density) of species 'y'
r_x: intrinsic growth rate for the 'x' population
r_y: intrinsic growth rate for the 'y' population
K_x: carrying capacity of the system for the 'x' population
K_y: carrying capacity of the system for the 'y' population
α_{xy}: competition coefficient on species 'x' of species 'y'
α_{yx}: competition coefficient on species 'y' of species 'x'
$_i$: subscript specifying the year (or, more broadly, the generation).

This model predicts the coexistence of 'x' and 'y' in a stable equilibrium only if:

$$K_x - (K_y/\alpha_{yx}) < 0 \quad \text{and} \quad (3)$$
$$K_y - (K_x/\alpha_{xy}) < 0 \quad (4)$$

Under these conditions, it is possible to calculate equilibrium population sizes (X_{eq} and Y_{eq}) as follows:

$$X_{eq} = (K_x - \alpha_{xy} * K_y)/(1 - \alpha_{yx} * \alpha_{xy}) \quad (5)$$
$$Y_{eq} = (K_y - \alpha_{yx} * K_x)/(1 - \alpha_{yx} * \alpha_{xy}) \quad (6)$$

To assess the effect of environmental variability, it is assumed that K, r, and α are linear functions of the precipitation of the current year. The influence of disturbances is simulated by modifying population size at different frequencies.

The program

The program was developed for a Casio FX-702 P calculator and has three subprograms (see Appendix):

Subprogram 1 (P1). This defines for each population the y-intercept and the slope of the linear equations relating K, r, and α with precipitation.
Subprogram 2 (P2). This calculates the size of populations for consecutive years. With this subprogram it is possible to change the starting population sizes, the number of years under consideration, and the precipitation for each period. To avoid meaningless results, it is assumed that $X \geqslant 0$, $Y \geqslant 0$, and $K \geqslant 1$.
Subprogram 3 (P3). This calculates the equilibrium conditions under fixed precipitation values. It solves equations (3), (4), (5), and (6) using information generated by P2.

This modular structure was adopted in order to shorten the program since not all the subprograms have to be used every time. Once the precipitation functions are defined in P1, the other two modula, P2 and P3, can be used for each combination of initial sizes, number of years, and precipitation level. In turn, if the precipitation level is not changed, results of P3 remain unchanged and only P2 can be used.

Using the program: an example

The model allows us to evaluate hypotheses concerning different pairs of species, such as a crop–weed system, two range grasses, two forage species, and so on. In this example we analyse the competitive relations between two tussock grasses in the Patagonian steppe (Argentina): *Stipa speciosa* Trin. et Rupr. and *Festuca pallescens* (St Yves) Parodi, the latter being less xerophytic than the former. In relation to our objective, the following general hypothesis is proposed:

'The competitive relationship between the populations is controlled by resource availability and the occurrence of disturbance.'

For both populations, K and r are assumed to increase with precipitation and always to be positive. We assume that, with low precipitation, the more xerophytic *Stipa speciosa* (species 'y') will outcompete the more mesophytic *Festuca pallescens* (species 'x') and that the opposite will occur under high precipitation conditions. Thus, the steepest slope and the lowest y-intercept are assigned to the more mesic species in the linear regressions of K and r with precipitation (table 1). Competition coefficients (α) have slopes of opposite sign (table 1), leading to competitive advantage for the xerophytic species under conditions of scarce rainfall and competitive disadvantage under conditions of high water availability.

Annual precipitation was chosen to represent resource availability, and frequency of disturbance as the main disturbance regime descriptor (White and Pickett, 1985). To discriminate between the effects of each of these factors, the behaviour of populations was considered (a) in the absence of disturbance

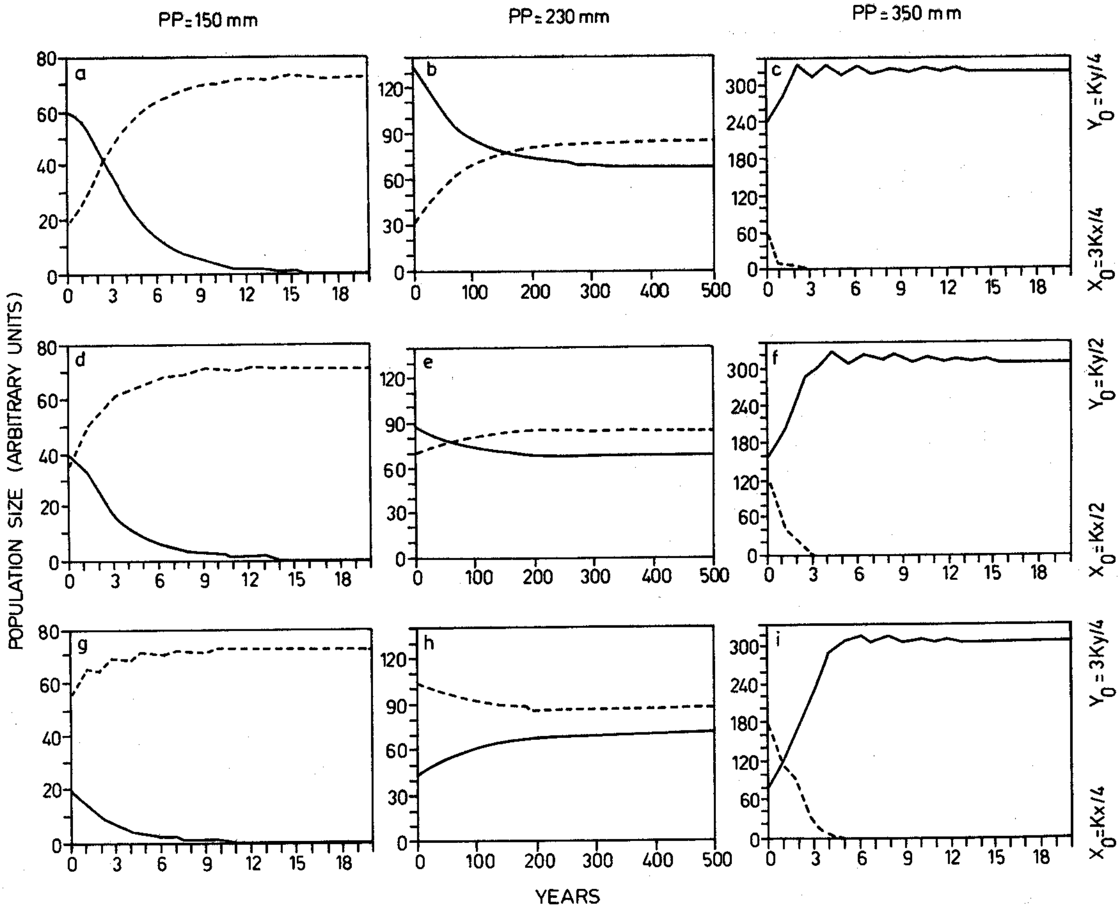

Figure 2 Competitive outcome in the absence of disturbance for the two populations under three precipitation regimes: 150 mm (a,d,g); 230 mm (b,e,h), and 350 mm (c,f,i), and with three pairs of starting population sizes: $X_o = 3K_x/4$ and $Y_o = K_y/4$ (a,b,c); $X_o = K_x/2$ and $Y_o = K_y/2$ (d,e,f); and $X_o = K_x/4$ and $Y_o = 3K_y/4$ (g,h,i).
x (more mesophytic population): ———
y (more xerophytic population): --------

Using the program: other possibilities

The model allows the exploration of alternatives related to the postulated hypotheses which are not considered above. An important example is the influence of the intensity and the type of disturbance. The following questions could be valuable teaching tools: 1. How are the results affected when disturbances are applied simultaneously on the two populations? 2. How are the results affected when the two populations are subjected to different disturbances? For example, the more xerophytic species could be reduced to 10 per cent every 5th year and the more mesophytic one reduced to 50 per cent every year. 3. What are the effects of such disturbance regimes at each rainfall level? If the teacher thinks it appropriate, results could be discussed in relation to the concepts of resilience (Holling, 1973) or diversity (Huston, 1979).

Other hypotheses or questions can also be explored. Some interesting possibilities are: 1. The simulation of sequences of dry and wet years. 2. The effect of changes in one variable keeping the others unchanged. 3. The consequences of modifying the shape of precipitation-dependent functions or the inclusion of functions using other environmental factors (e.g. nitrogen, see Berendse *et al.*, 1987). 4. The coexistence of two populations which have the same degree of xerophytism. 5. The analysis of unstable equilibrium conditions when equation 3 and equation 4 are not valid.

Interesting modifications may be incorporated in the program which require diagrammatic representation of the program and its manipulation by the students, a fruitful exercise in logical reasoning. They could range from the addition of a printing subroutine to an increase in the number of species modelled or the inclusion of randomness in the determination of pluviometric values.

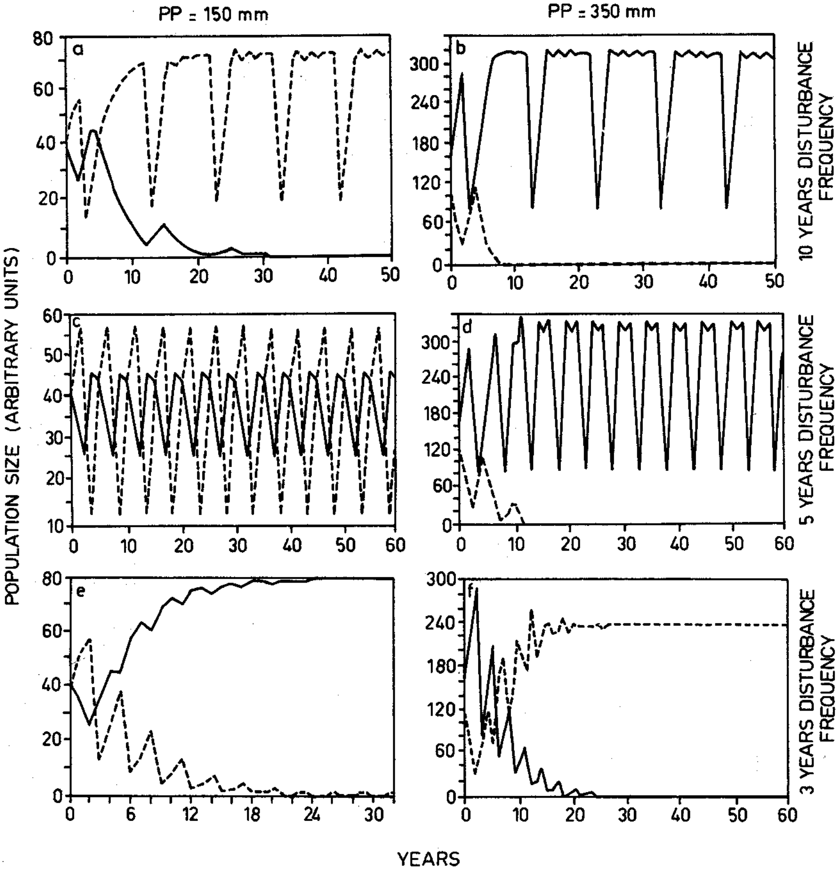

Figure 3 Competition outcome for the same populations under two precipitation levels: 150 mm (a,c,e) and 350 mm (b,d,f), and three disturbance frequencies: every 10th year (a,b); every 5th year (c,d), and every 3rd year (e,f).

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Appendix: Programs

Subprogram 1 (P1)

```
10 INP "AKX", B
20 INP "AKY", C
30 INP "BKX", D
40 INP "BKY", E
50 INP "A ALPHAYX", F
60 INP "A ALPHAXY", G
70 INP "B ALPHAYX", H
80 INP "B ALPHAXY", J
90 INP "ARX", K
100 INP "ARY", L
110 INP "BRX", O
120 INP "BRY", Q
```

Subprogram 2 (P2)

```
10 INP "XO", A
20 INP "YO", I
30 INP "#year", N
40 INP "PRECIPITATION", P
160 R=B+D*P
170 IF R<1; R=1
180 T=C+E*P
190 IF T<1; T=1
200 U=F+H*P
210 V=G+J*P
220 W=K+O*P
230 X=L+Q*P
240 Y=W*A*((R-A-(V*I))/R)
250 Z=X*I*((T-I-(U*A))/T)
260 A=A+Y
270 I=I+Z
280 IF I<0; I=0
290 IF A<0; A=0
300 A1=A1+1
310 PRT "X"; A1; "="; RND (A,-1)
320 PRT "Y"; A1; "="; RND (I,-1)
330 PRT "PP"; A1; "="; RND (P,-1)
340 IF A1>=N THEN 370
360 GOTO 160
370 A1=0
380 END
```

Subprogram 3 (P3)

```
10 PRT "KX="; R
20 PRT "KY="; T
30 PRT "ALPHA YX="; U
40 PRT "ALPHA XY="; V
50 PRT "RX="; W
60 PRT "RY="; X
70 PRT "XEQ="; (R-T*V)/(1-U*V)
80 PRT "YEQ="; (T-U*R)/(1-U*V)
90 PRT "KX-KY/ALPHAYX=";R-T/U
100 PRT "KY-KX/ALPHAXY="; T-R/V
```

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