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MARKOVIAN APPROACHES TO ECOLOGICAL SUCCESSION

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SUMMARY

(1) Analysis of published studies generally indicates that ecological succession can be considered as a non-random process.

(2) Two examples are discussed in detail, termite succession on baitwood blocks in Ghana (Usher 1975) and predator–prey dynamics of mites in a complex universe of oranges (Huffaker 1958), and both indicate that succession is a non-stationary Markovian process.

(3) The discussion considers that complex non-random or Markovian processes are likely to characterize ecological successions, the transition probability matrix elements not being constant but being functions either of the abundance, or of the rate of change of abundance, of a recipient class.

(4) Tests of various hypotheses, using χ^2 criteria, are given.

INTRODUCTION: SUCCESSION AS A MARKOVIAN PROCESS

If a community of plants or animals, or more accurately a portion of space, is inspected at two separate points in time, observational data tend to show that there has been a change in the species complement. This can be represented by

collection $A \rightarrow$ collection B,

where the word 'collection' is used in a neutral sense so as not to imply changes from one community to another, nor to imply clearly recognizable suites of species at two points in time, etc. Such observational evidence, of which there is plenty in the ecological literature, tends to demonstrate three features of this process. First, in general the longer the time period between the repeated observations the more dissimilar are collections A and B. Secondly, series of observations on similar pieces of land tend to show a sequence

$\ldots$ collection $I \rightarrow$ collection $J \rightarrow$ collection $K \rightarrow \ldots$,

where I, J and K are usually referred to as seral communities or seral stages. Unlike A and B above, in this instance I, J and K are assumed to be different from each other, and to be characterized by a few species usually subjectively selected for descriptive or classificatory purposes by the research worker. Thirdly, there is some collection of species, say M, after which there appears to be no further change in species composition so that the time sequence becomes

$\ldots$ collection $L \rightarrow$ collection $M \rightarrow$ collection $M \rightarrow \ldots$.

Time scales are usually judged in human terms, and hence 'no further change' is usually measured in terms of decades or a century or two, and not in longer periods that would be influenced by climatic cycles. Also, it has to be remembered that studies tend to look at portions of space that are large compared to the space taken up by an individual plant

or animal, and hence 'no further change' implies an averaging of species over the whole portion and not the species covering a particular point. The collection M has been referred to as 'the climax', sometimes qualified by an adjective indicating that the composition of the collection has been influenced, from that of the broader geographical unit, by the soil conditions, by the degree of pollution, by the management imposed, etc. Whether a collection M does exist, and the characteristics of its component species, is not of concern in discussing succession as a Markovian process.

In considering this subject, it is desirable to define the term 'Markov process' since there is a certain amount of disagreement in the literature about this. Quoting the definition of Bartlett (1955, p. 24), a Markov process is 'a stochastic process for which the values of X_r at any set of times t_r ($r = 1, 2, \ldots, n$) depend on the values X_s at any set of previous times t_s ($s = 0, -1, \ldots, -j$) only through the last available value X_0'. Since the dependence is on the single and last available value, X_0, this definition implies that a Markov process is a first order process. This narrow definition, although usually adhered to in the literature on stochastic processes, is often broadened for practical applications. In the statistical literature Anderson & Goodman (1957) provide tests for the hypothesis that a Markov chain is uth order against the alternative hypothesis that it is rth order and not uth order, where u and r are non-negative integers. This wider definition, which might be equated to a statement that the values in the sequence of X_t are non-independent or non-random, is used in this paper. This is consistent with the use of the word 'Markov' in the recent ecological literature, though it has to be appreciated that it is not necessarily consistent with the use of the word 'Markov' in the stochastic processes literature. It does, however, accord with Bailey's (1964, p. 39) definition which encompasses higher order processes than first order, though he does not pursue that generalization in his book.

The nature of the sequence of observations on a community of plants or animals,

$$\ldots \text{collection } x_{i-1} \rightarrow \text{collection } x_i \rightarrow \text{collection } x_{i+1} \ldots,$$

has attracted considerable attention during the last half century. Slatyer (1977) and Connell & Slatyer (1977) have reviewed the literature, and have concluded that there are three intrinsically different conceptual models of succession. In the historically older, termed the 'facilitation model', it is assumed that collection x_{i-1} makes the microenvironment less favourable for its own existence but more favourable for collection x_i to invade and become dominant. The lengths of time in the states having collections x_{i-1}, x_i, etc., are undefined, and hence any pair of samples of the same community (or same piece of space) might indicate that the same collection of species has been retained or that the community or space has moved to a collection further along the sequence. Formally, the community has changed thus:

$$\text{collection } x_i \rightarrow \text{collection } x_{i+c},$$

where $c \geqslant 0$. If this were to be represented as a Markovian process the transition probability matrix would have the form

$$
\begin{bmatrix}
P_{11} & P_{12} & P_{13} & \ldots & P_{1m} \\
0 & P_{22} & P_{23} & & P_{2m} \\
0 & 0 & P_{33} & & P_{3m} \\
\vdots & & & & \vdots \\
0 & 0 & 0 & \ldots & 1
\end{bmatrix},
$$

where P_{jk} represents the probability that a community with collection j would change to collection k over one period of time ($k \geqslant j$). All elements below the main diagonal of the matrix are zero (or near zero if the data are estimated in the field).

A second model proposed by Connell and Slatyer is the 'tolerance model' in which it is assumed that the presence of collection x_i either increases or decreases the rates of recruitment, establishment and growth to maturity of other collections of species. Species that are generally associated with being later in a successional sequence might either have arrived later, or have had their germination inhibited, or have had their growth suppressed. A Markovian representation of this model would be

$$\begin{bmatrix} P_{11} & P_{12} & P_{13} & \cdots & P_{1m} \\ P_{21} & P_{22} & P_{23} & & P_{2m} \\ P_{31} & P_{32} & P_{33} & & P_{3m} \\ \vdots & & & & \vdots \\ P_{m1} & P_{m2} & P_{m3} & \cdots & P_{mm} \end{bmatrix},$$

where it is possible to move backwards in the sequence, although for the development towards a 'climax' it will be seen that $P_{jk} > P_{kj}$ ($k > j$) in the majority of comparisons. In both the 'facilitation' and the 'tolerance' models the interpretation of transitions is wider than that used by Slatyer (1977): this is due to the time interval being here undefined whilst Slatyer assumed a time interval which was at least as short as the minimum period of time spent with one of the collections of species. Thus, during one time interval Slatyer assumed that the only change to occur is collection $x_i \rightarrow$ collection x_{i+c} ($c = 0$ or 1), whilst here it is assumed that a community can move through more than one collection of species.

The third model proposed by Connell and Slatyer occurs where there is a truncation of the successional process at an intermediate stage: the model is termed the 'inhibition model'. This is essentially the same as the tolerance model outlined above, except that one of the intermediate states is an absorbing state, i.e. for some j ($1 < j < m$), $P_{jj} = 1$. The system requires a perturbation, such as a fire, etc., to jolt it out of the jth state into another state so that the successional process can re-commence. It is possible to generalize this concept from an absorbing state j to a set of absorbing states, say j, k and l, such that the system, once it reaches any one of the states in this set, can move between states in the set but is unable to move to any state outside the set.

Despite the apparent ease with which successional phenomena can be translated into probabilistic terms, it appears that ecologists have generally avoided consideration of succession as a non-random process. However, data analysed in this manner are those of a mixed hardwood forest succession in Connecticut (Stephens & Waggoner 1970; Waggoner & Stephens 1970), mixed hardwood forest succession in New Jersey (Horn 1975a, b), termite succession on baitwood blocks (Usher 1975; Usher & Parr 1977) and *Eucalyptus* forest in Australia (the data are described by I. R. Noble and R. O. Slatyer, unpublished). There are also some studies of forest tree development which rely on the use of probability matrices. Perhaps the first of these matrix approaches was used for modelling the growth of a *Pinus sylvestris* stand by Usher (1966), but they have subsequently been used for modelling other forest tree species (see, for example, the review of techniques by Peden, Williams & Frayer (1973)). In all of these studies where a transition matrix is used, except that of Usher & Parr (1977), the process is assumed to

be of first order, i.e. Markovian in the strict sense, without there being any critical assessment of whether or not this assumption is justified.

A test for independence in a matrix of transition probabilities has been proposed by Anderson & Goodman (1957). The null hypothesis, that successive steps in the sequence are statistically independent, is tested against the alternative hypothesis that the steps are not independent and therefore that they could form a first order Markov chain. Anderson and Goodman show that $-2 \ln \lambda$ is distributed asymptotically as χ^2 with $(m-1)^2$ degrees of freedom, where

$$-2 \ln \lambda = 2 \sum_{i=1}^{m} \sum_{j=1}^{m} n_{ij} \ln(P_{ij}/P_j) \qquad (1)$$

and where P_{ij} is the probability of transition from state i to state j $(i, j = 1, 2, \ldots, m)$, P_j is the marginal probability for the jth column (i.e. $P_j = \sum_{i=1}^{m} n_{ij} / \sum_{i=1}^{m} \sum_{j=1}^{m} n_{ij}$) and n_{ij} are the frequencies of transition from state i to state j in the original data matrix. The lack of testing of ecological data probably stems from the fact that the test is not widely known, although it has been used for geological sequences by Harbaugh & Bonham-Carter (1970). Testing the published data on succession using probability transition matrices, Table 1, shows that the null hypothesis of statistical independence can be rejected in all cases except those of the zooplankton at seven sampling stations in Kingston Harbour, Jamaica (and a child selecting coloured 'Smarties' blindfold from a box of these sweets). It would therefore seem appropriate to experiment further with Markov models, in the broad sense, as a basis of studying and modelling ecological succession.

Another interesting property of some Markov processes is known as the ergodic property. This means that there is a convergence towards a limiting probability distribution among the states of the system irrespective of the starting state of the system. Bailey

TABLE 1. The asymptotic χ^2 criterion (eqn 1) for testing the null hypothesis of statistical independence of events in a sequence. In all cases, except those of the plankton in Kingston Harbour and a blindfold child selecting coloured sweets, the null hypothesis is rejected. The data quoted for Grahame (1976) and Huffaker (1958) were not treated as Markovian processes in the original publications

Organisms	Reference	χ^2	d.f.	Significance
'Smarties' selected blindfold by a child	—	48·8	36	$P > 0.05$
Predator–prey relations of orange mites	Huffaker (1958)	325·4	25	$P \ll 0.001$
Mixed hardwoods in Connecticut	Stephens & Waggoner (1970)	467·6	16	$P \ll 0.001$
Termites on baitwood in Ghana	Usher (1975)			
Complete data		609·7	36	$P \ll 0.001$
Wood aged 4–8 weeks		609·1	36	$P \ll 0.001$
Wood aged 8–16 weeks		202·0	36	$P \ll 0.001$
Wood aged 16–32 weeks		62·2	36	$P = 0.004$
Mixed hardwoods in New Jersey	Horn (1975a)	2428·0	100	$P \ll 0.001$
Zooplankton in Kingston Harbour, Jamaica	Grahame (1976)			
Complete data		84·6	81	$P > 0.05$
Station 1		0·09	1	$P > 0.05$
Station 3		3·6	4	$P > 0.05$
Station 4		6·2	9	$P > 0.05$
Station 6		39·4	49	$P > 0.05$
Station 8		52·3	49	$P > 0.05$
Station 9		23·5	25	$P > 0.05$
Station 10		0·86	1	$P > 0.05$

(1964) quotes a theorem stating that the Markov process is ergodic if there is a finite number of states and if the process is aperiodic and irreducible. In ecological applications, there is a finite number of states, and the process is aperiodic. However, irreducibility is not guaranteed. Reverting to Connell & Slatyer's (1977) conceptual models, the tolerance model is irreducible, whilst the facilitation and inhibition models are reducible since both have an absorbing state ($P_{mm} = 1$ in the former) or an absorbing set of states. Irreducibility occurs when it is possible to move from any one state to any other state of the system (not necessarily in one move). The implications of an ergodic process are ecologically important. With an ergodic process, such as all the data matrices listed in Table 1, the limiting probability distribution is given by the dominant eigenvector of the probability transition matrix, and this shows to what the system will converge given sufficient time. This concept is very close to that of the ecological climax, collection M above. It might therefore be appropriate to define the climax in terms of the elements of the dominant eigenvector of the matrix of probabilities.

CHANGES IN BIOLOGICAL DATA WITH TIME

A Markov process is defined as a stationary process if during the passage of time the transition probabilities, P_{ij}, do not change. Although simple Markov models assume that such changes do not take place, there is no *a priori* reason why ecological succession should be a stationary process. Horn (1974) reviewed some of the dynamic processes of succession, indicating that productivity, diversity and stability (however defined) might change during a successional sequence, but he subsequently (Horn 1975a, b) seems to have pooled all his data on mixed hardwood stands and treated them as if they were stationary. It is clearly important to know if the transition possibilities, P_{ij}, are independent of time or if they are functions of time, $P_{ij}(t)$. In the latter case the nature of the functional relationship is important, since for all i at any given time t the functions are constrained by

$$\sum_{j=1}^{m} P_{ij}(t) = 1. \tag{2}$$

The form of a possible functional relationship will be explored in the next two sections, in which there is an analysis of long runs of data. It is interesting to note that succession has traditionally been studied by plant ecologists, but the development of near climax plant communities takes so many years that long runs of botanical data do not exist in the literature. However, repeated sampling of animal populations has produced data which can be used to investigate the stationarity of such successional processes.

A test of stationarity was suggested by Anderson & Goodman (1957), and is discussed by Harbaugh & Bonham-Carter (1970). The null hypothesis tested is that $P_{ij}(t)$ is constant and is a specified number, P_{ij}. Again it is shown that $-2 \ln \lambda$ is distributed asymptotically as χ^2 with $m(m-1)(T-1)$ degrees of freedom, where T is the number of time intervals, and

$$-2 \ln \lambda = 2 \sum_{i=1}^{m} \sum_{j=1}^{m} \sum_{t=1}^{T} n_{ij}(t) \ln\{P_{ij}(t)/P_{ij}\}, \tag{3}$$

and $P_{ij}(t)$ and $n_{ij}(t)$ are respectively the probability and frequency of transition from state i to state j in time interval t.

GHANAIAN TERMITE DATA

An experiment at Fumesua, Ghana (6°40′N, 1°35′W), was carried out to monitor the change in a termite community following clearance of a farm scrub community. The site has been described by Usher (1975). The data concern 826 locations at each of which a baitwood block of *Triplochiton scleroxylon* sapwood had been inserted in the ground. Baitwood blocks were removed from the ground every 4 weeks during a 48-week period, inspected, assessed for termite activity and either re-inserted in the ground or replaced by a new baitwood block according to the following rules: so that termite genera that reached a block could be identified with a reasonable degree of confidence, after even-numbered inspections (second, fourth, sixth, etc.) all damaged baitwood blocks were replaced by new blocks; and all blocks which had been in the ground for eight periods (32 weeks) were replaced. Thus, the length of time that a baitwood block had been in the ground at any inspection could be 4, 8, . . . , 28 or 32 weeks (hereafter referred to as ages). For analysis, blocks have been grouped into three age classes, 4 and 8 weeks, 12 and 16 weeks and 20 to 32 weeks.

Although a total of twenty-five species of termites were recorded during the twelve inspections of the baitwood blocks, some species were extremely rare (single or double occurrences) and hence some grouping of the data has taken place. The following seven states were therefore recognized.

(1) No termite activity.

(2) *Ancistrotermes*. A block was assigned to this state if termites in this genus were seen on the baitwood block, or if the runways were found on the block, or if there was eating of the block which could be recognized as being due to this genus. Although the termites of the three species, *A. crucifer*, *A. cavithorax* and *A. guineensis*, could be told apart, it was impossible to distinguish runways or feeding of the different species, and hence they have been lumped together.

(3) *Macrotermes*. Similarly a block was assigned to this state if termites, runways or damage could be assigned to this genus. Two species, *M. bellicosus* and *M. subhyalinus*, occurred on the site. Although all castes of the termites are simple to distinguish, it was not always possible to distinguish their artefacts, and hence they have been grouped together.

(4) *Microtermes*. Only one species, *M. subhyalinus*, was known to occur on the site. Blocks showing this species, or its very characteristic runways or damage, were assigned to this state.

(5) *Pseudacanthotermes*. Similarly there was only one species, *P. militaris*, and blocks with it, its runways or damage, were assigned to this state.

(6) Other termites. A total of eighteen other species were found, though all of them occurred less frequently than the genera listed above.

(7) Unknown termites. Sometimes it was impossible to assign either a runway or damage to a species or genus with any degree of certainty: this state includes all such observations, and could therefore include species which are otherwise unknown from the experiment.

Aspects of the ecology of this termite community are further discussed by Usher (1975), who illustrates the changes in the number of baitwood blocks in the first five classes above during the total inspection period.

Stationarity of the termite succession on baitwood blocks can be investigated with these data from two points of view, time and baitwood age. Is the process stationary

through time? This can be investigated for blocks in each of the three age classes: using eqn (3) it can be seen that the null hypothesis is rejected in two of the three analyses (Table 2). This indicates that, at least with baitwood that has not been subjected to massive fungal decay, the process was not stationary (in Table 1 it is shown that the process is not independent). Since through time the process was not stationary, it is appropriate to divide the time scale into subunits, and then to test for stationarity between the baitwood ages. The results of these analyses are also shown in Table 2: in the majority of cases the null hypothesis would be accepted and the process assumed to be stationary. These results imply that changes in transition probabilities through time, rather than with baitwood age, need to be further investigated.

TABLE 2. Analyses of the stationarity of the Markovian process of termite colonization of baitwood blocks

Process analysed	χ^2	d.f.	Significance
Through time			
Baitwood aged 4 and 8 weeks	348·2	168	$P \ll 0{\cdot}001$
Baitwood aged 12 and 16 weeks	304·5	168	$P \ll 0{\cdot}001$
Baitwood aged 20 to 32 weeks	130·6	126	$P > 0{\cdot}05$
Through the baitwood ages			
Up to the 4th inspection	58·3	42	$P = 0{\cdot}05$
4th to 6th inspections	126·2	84	$P < 0{\cdot}001$
6th to 8th inspections	102·2	84	$P > 0{\cdot}05$
8th to 10th inspections	75·6	84	$P > 0{\cdot}05$
10th to 12th inspections	79·3	84	$P > 0{\cdot}05$

Transition probabilities can be considered from two points of view. First, they can be considered as the set of probabilities from one class to all other classes, in which the relation

$$\sum_{j=1}^{m} P_{ij} = 1 \tag{4}$$

holds for all donor classes i. Secondly, the set of probabilities into the recipient class j can be considered, but for this set there is no strict relation equivalent to eqn (4). Since the class *Ancistrotermes* was the most abundant, the transition probabilities from this class to other classes over time are shown in Fig. 1. Also in Fig. 1 is shown the number of baitwood blocks on which *Ancistrotermes* spp. were found. It appears that none of the transition probabilities from the donor class are correlated with the abundance of this donor class. Similar illustrations for the other six donor classes also indicate that there is no close correspondence between the abundance of the class and the transition probability to any other class. In Fig. 1 four of the graphs of transition probabilities through time show a trend: thus the transition to *Pseudacanthotermes* increases from close to zero to approximately 0·07, and the transition probability to *Microtermes*, after an initial small decrease, increases to approximately 0·1. Due to the relation in eqn (4) there is a decrease in the transition probabilities to *Ancistrotermes* and to 'no termites', though these two probabilities tend to fluctuate, the fluctuations complementing each other.

The transition probabilities into a recipient class, *Pseudacanthotermes*, are shown in Fig. 2. This recipient class was chosen for illustration since it was the one that increased most markedly during the sampling period. It will be seen that the transition probabilities of all other classes into this class increased. Similar results were obtained for transitions
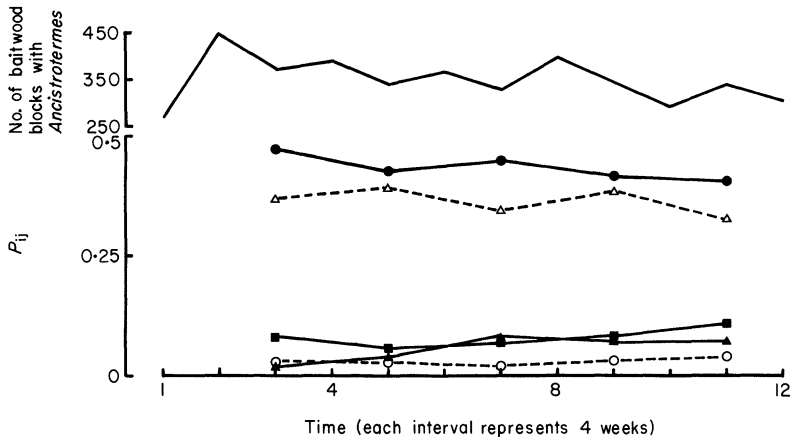
FIG. 1. The transition probabilities from class *Ancistrotermes* to the other classes. The upper continuous graph indicates the number of baitwood blocks on which *Ancistrotermes* was found, or inferred to have visited, at each of the twelve inspections. The continuous lines represent transitions to *Ancistrotermes* (●—●), *Microtermes* (■—■) and *Pseudacanthotermes* (▲—▲), and the dashed lines transitions to *Macrotermes* (○---○) and 'no termites' (△---△). For clarity, transitions to the classes 'other termites' and 'unknown termites' have been omitted.
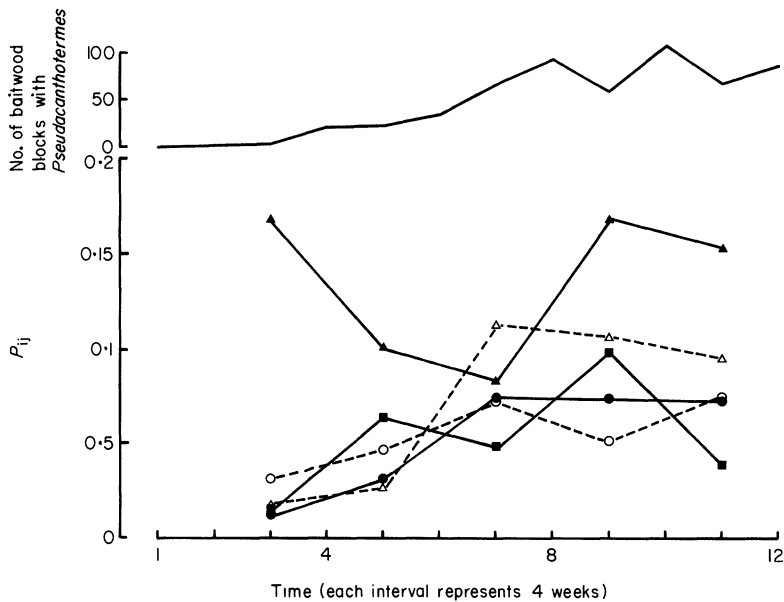

FIG. 2. The transition probabilities from other classes to class *Pseudacanthotermes*. The upper continuous graph indicates the number of baitwood blocks in which *Pseudacanthotermes* was seen or inferred to have been present at each of the twelve inspections. The continuous lines represents transitions from *Ancistrotermes* (●—●), *Microtermes* (■—■) and *Pseudacanthotermes* (▲—▲), and the dashed lines transitions from *Macrotermes* (○---○) and 'no termites' (△---△). For clarity, transitions from the classes 'other termites' and 'unknown termites' have been omitted.

into class *Microtermes*, a species that also increased in abundance during the period of observation. It would therefore appear that the transition probability at time t from state i to state j is a function of the abundance of class j at that time. There are insufficient data to investigate the form of this function, but it seems intuitive that a sigmoid function would be appropriate (cf. the transition probability from class *Ancistrotermes* to class *Pseudacanthotermes* in Fig. 2).

HUFFAKER'S PREDATOR–PREY MITE DATA

Huffaker (1958) described an experiment in which the orange-feeding six spotted mite, *Eotetranychus sexmaculatus*, was preyed upon by *Typhlodromus occidentalis*. The experiment was conducted in a complex universe, consisting of a grid of 120 oranges arranged in a square lattice of ten oranges by twelve oranges. The 8 months during which the experiment was conducted were divided into 18 equal periods (lettered A to R inclusive), and for each of these periods Huffaker published a plan to show the density of both predator and prey species. Thus, for each of the 120 oranges there is a record of the seventeen transitions from and to various prey and predator density classes. Although this experiment could not be described as an ecological succession, it nevertheless provides an example of a time-dependent ecological process.

TABLE 3. The frequencies of transitions between classes of prey and predator abundance in Huffaker's (1958) data. Prey density nil means 0–5, density low is 6–25 and density medium to high means 26 or more; predator density is divided into only two classes—predators absent and one or more predators present

Donor class	Recipient class					
	A	B	C	D	E	F
A: Prey density nil, no predators	1300	50	88	25	81	18
B: Prey density nil, predators present	83	10	3	0	3	0
C: Prey density low, no predators	53	13	17	5	37	12
D: Prey density low, predators present	35	10	0	2	1	0
E: Prey density medium to high, no predators	54	9	28	11	25	18
F: Prey density medium to high, predators present	37	8	0	2	1	1

Huffaker divided the prey abundance (mites per orange) into four classes, 0–5, 6–25, 26–75, and 76 and over, and he also divided the predator abundance into four classes, giving a total of sixteen potential classes of prey and predator abundance (some of these potential classes do not exist). Pooling some of Huffaker's classes gives the data in Table 3, which, when dividing by row totals, gives the transition matrix

$$
\begin{bmatrix}
0\cdot832 & 0\cdot032 & 0\cdot056 & 0\cdot016 & 0\cdot052 & 0\cdot012 \\
0\cdot838 & 0\cdot101 & 0\cdot030 & 0 & 0\cdot030 & 0 \\
0\cdot387 & 0\cdot095 & 0\cdot124 & 0\cdot036 & 0\cdot270 & 0\cdot088 \\
0\cdot729 & 0\cdot208 & 0 & 0\cdot042 & 0\cdot021 & 0 \\
0\cdot372 & 0\cdot062 & 0\cdot193 & 0\cdot076 & 0\cdot172 & 0\cdot124 \\
0\cdot755 & 0\cdot163 & 0 & 0\cdot041 & 0\cdot020 & 0\cdot020
\end{bmatrix}.
$$

This is not independent (Table 1). These data from the whole experiment lump together three cycles of prey abundance followed by predator abundance, and it seemed appropriate to question if the predator-prey process was stationary. The first cycle of prey and predator abundance consisted of Huffaker's periods A to E, a second cycle of periods E to J and a third cycle of periods J to P (see Fig. 18 in Huffaker's paper; periods Q and R have been omitted since both the prey and predators were at their lowest levels, and these periods did not appear to be part of the third or of a fourth cycle). A test of stationarity gave $\chi^2_{60} = 89\cdot02$ ($P = 0\cdot01$), indicating that the process is not stationary. If the three cycles are divided into three categories—those periods when the prey density was increasing, those when the prey density was decreasing and those when the prey density was more or less stable at a low density—the process is also not stationary ($\chi^2_{60} = 303\cdot83$, $P \ll 0\cdot001$). Similarly, dividing into those periods when the predator density was increasing, when the predator density was decreasing and when the predator density was more or less stable at a low level, also indicated that the process was not stationary ($\chi^2_{60} = 136\cdot30$, $P \ll 0\cdot001$). From these results it seems appropriate to consider in more detail the stationarity of the process when prey population density is the dividing factor.

The data for transitions from only one of the classes, no predators and the 'nil' prey density, to all other classes are shown in Table 4. With the division of the data according to the change in the prey population it is perhaps to be expected that the transition probabilities reflect the abundance of the prey species to some extent. It will be seen,

TABLE 4. Transition probabilities from the class of nil prey density (0–5 mites per orange) without predators to the six classes used in Huffaker's (1958) data

Overall situation in experiment	Prey nil density		Prey low density		Prey medium to high density	
	No pred.	With pred.	No pred.	With pred.	No pred.	With pred.
Prey abundance increasing	0·705	0·027	0·106	0·022	0·120	0·019
Prey abundance decreasing	0·849	0·068	0·030	0·021	0·016	0·016
Prey at low density	0·955	0·007	0·024	0·006	0·007	0

however, that it is the recipient class, rather than the donor class, which seems to influence the transition probability to the greater extent. Once again it would appear that there is a functional form of P_{ij} which depends either upon the numerical abundance of the recipient class j or upon the rate of change of the abundance of the recipient class (dn_j/dt).

DISCUSSION

Two simple conclusions can be drawn from these analyses. First, the majority of successional processes can be considered as non-independent sequences in character, and by implication Markovian, in the broad sense, and not merely random (strictly, sequences of statistically independent events). Secondly, in the two cases where there are sufficient data to test for stationarity, neither process is stationary. The first of these statements would appear to be reasonably robust and this can be generalized to the statement that *ecological successions are not independent processes in character*, and by implication are Markovian. On the strength of only two examples the second statement would appear not to be a

generalization; however, there are some theoretical considerations which lead to the generalization that *most ecological successions are non-stationary processes.*

In considering the models for succession proposed by Connell & Slatyer (1977) there was a separation into the facilitation and tolerance models: in the former, one collection gives way to another collection, the collections following each other in sequence; whilst in the latter, it was essentially the speed of development and the degree of inhibition of some collections which were important. In either case some of the states in a successional sequence are going to be either absent or very rare at any one point in time. Transition probabilities to these states are thus zero or close to zero, whilst transition probabilities from these states cannot be defined. However, as soon as one of these states either becomes present or begins to increase from extreme rarity the probabilities of transition to that state will take non-zero values and the probabilities from that state to other states will be defined. Thus, the models of ecological succession assume that, if succession is Markovian, then it is non-stationary. It therefore seems appropriate that transition matrices describing ecological processes should have elements that are functional rather than constant. The two forms proposed above, where the probabilities are functions of either the abundance of the recipient class or the rate of change of abundance of the recipient class, would both appear to have some advantages: perhaps the former best describes the process of ecological succession whereas the latter more closely approximates cyclical phenomena such as predator–prey oscillations.

This, however, raises two further areas for discussion. The first is the mathematical area of the properties of Markov models and their applicability. The second is the practical area of the use, as opposed to the theory, of describing succession in terms of a non-independent or Markovian process.

Mathematically, the examples quoted are usually of first order processes, but it is not necessary for all processes to be of this order. Thus, a higher order process would imply that the state of the system at two previous points in time would determine the future course of the system, thus

$$s_{t-b} \to s_{t-a} \to s_t,$$

where s_t is the state at time t, and a and b are both positive integers such that $b > a$. Taking $a = 1$ and $b = 2$, and pooling all of the Ghanaian termite data for both baitwood age and time, gives a $7 \times 7 \times 7$ matrix of transition probabilities of the form P_{ijk} (the probability of transition from state i at time $t - 2$ to state j at time $t - 1$ to state k at time t). A test of the order of the process, using the probabilities P_{ijk}, is given by Anderson & Goodman (1957). Again, the test criterion is $-2 \ln \lambda$, which is distributed asymptotically as χ^2 with $m(m - 1)^2$ degrees of freedom, and is given by

$$-2 \ln \lambda = 2 \sum_{i=1}^{m} \sum_{j=1}^{m} \sum_{k=1}^{m} n_{ijk} \ln(P_{ijk}/P_{jk}),$$

where n_{ijk} are the number of observed transitions from state i at time $t - b$ to state j at time $t - a$ to state k at time t, and $P_{jk} = \sum_{i=1}^{m} n_{ijk} / \sum_{i=1}^{m} \sum_{k=1}^{m} n_{ijk}$. Using this test gives $\chi^2_{252} = 1170.8$ ($P \ll 0.001$), which leads to the rejection of the null hypothesis of a first order process. The generality of higher order processes in ecological succession is unknown. However, it seems intuitively obvious that higher order processes are likely to occur. Consider a system in state i which remains in state i during a period of time, and assume that state i is not an absorbing state. Since observations on non-climax ecosystems

indicate that change occurs, the probability of the system remaining in state i would decrease for every time period that it does not move. Ecologically, there therefore seem to be good reasons for suggesting a process is of a higher order than first order.

For an ergodic transition probability matrix the dominant eigenvector is of interest since this vector indicates the 'eventual' state of the system after repeated applications of the transition matrix. The eigenvector has been considered as being the climax state of the system (see, for example, Usher 1973). However, a greater interest might lie in the eigenvalues. The dominant eigenvalue is 1 since, by the extension of the Perron–Frobenius theorems to non-negative matrices, all the row sums of the transition matrix are 1. The ratio $|\lambda_1|/|\lambda_2|$ (where $\lambda_1 = 1$ and λ_2 is the eigenvalue of next largest modulus) indicates the speed with which the system will approach the 'climax' state: the larger this ratio the faster the approach. The ratios for the various transition matrices of ecological succession are shown in Table 5, where it can be seen that the ratios for processes involving animals are larger than the ratios for forest succession. Whether this is a true reflection of the difference between plant and animal successions is unknown: it might purely reflect the time step in the collection of the data, implying that the steps in animal communities are longer compared to the time taken for the whole successional process than the steps in plant communities. It is also of interest to note that non-independent processes have values of $|\lambda_1|/|\lambda_2|$ which span the two values of random processes (3·41 for Grahame's (1976) zooplankton data and 4·49 for a 'Smarties' experiment).

TABLE 5. The ratio of the dominant eigenvalue to the modulus of the next largest eigenvalue, $|\lambda_1|/|\lambda_2|$, of the transition matrices of ecological successions

Organisms	References	$|\lambda_1|/|\lambda_2|$
Mixed hardwoods in Connecticut	Stephens & Waggoner (1970)	1·34
Mixed hardwoods in New Jersey	Horn (1975a)	1·57
Zooplankton in Kingston Harbour (complete data)	Grahame (1976)	3·41
Termites in Ghana (complete data)	Usher (1975)	3·82
'Smarties' selected by a child	—	4·49
Predatory and prey mites on oranges (complete data)	Huffaker (1958)	5·60

Practically, there appear to be four sets of difficulties in the application of Markovian processes in studies of ecological succession. First, there is the effort required in gathering sufficient data on which to build the model. With a model of m states, there are a total of m^2 transition probabilities to estimate. If the process is going to provide a reasonably close correspondence with the ecological process each one of the P_{ij} will have to be estimated with a reasonably small standard error: this implies the collection of a large amount of field data. The amount of data required is even greater if stationarity is to be investigated and included in the model; and if higher orders than first order are to be investigated there are at least m^3 elements P_{ijk} to estimate. The amount of data required to construct such a transition matrix has probably deterred ecologists from a wider acceptance and application of the model.

Secondly, much ecological data consists of small fragments of sequences in the successional process, often collected over a geographically large area. Methods are required for the use of such fragmental data in constructing an overall Markovian model: the approach of Morgan (1976) in the behavioural sciences commends itself in the ecological sciences.

Thirdly, the time step between observations needs to be considered critically. The

apparent differences between studies of animal and plant communities shown in Table 5 might relate more to the method of sampling rather than to intrinsic differences in the communities. Also, there is much evidence to suggest that successional processes slow down as the succession proceeds; thus the mean passage time from state i to state $i + 1$ may be much longer when i is large than when i is small. This slowing down in the passage time might account for the differences in stationarity through time in Table 2. Since both baitwood ages were assessed by the same time step, this might account for the 'young' baitwood being clearly non-stationary whilst 'old' baitwood was assumed to be stationary.

Fourthly, there is the vexed question of what to consider as states when building a model. In this paper, succession was defined as the change from collection I to collection J in a defined space (volume or area); however, all examples of the application of the transition probability matrix model have relied upon the name of a single species such as big-toothed aspen or *Pseudacanthotermes* or of rag-bag categories such as 'other species'. The problem of developing an objective system of classifying the stages in an ecological succession is one that is receiving some attention, but as yet no wholly acceptable system exists. It is likely that the statistical ecologist will have to use methods of successive approximation to the modelling of field successional processes: multivariate statistical procedures to define the stages and to indicate the data to include in a Markovian model, and a Markovian model to approximate to the successional process and to refine the stages.

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