Incorporating Serial Dependence using Markov Models for Studies of Vegetation Change

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Abstract
In this paper we re-examine data from a salt-marsh recording changes through 14 years. We use a method that explicitly accounts for possible temporal dependency between successive observations. This method employs first-order Markov models. We compare this with other methods used to explore these data, and also introduce a test for higher order. Although a salt-marsh has strong gradients, which might suggest continuous change, the results suggest that, in terms of major changes, 2 distinct communities are present with relatively weak linkages between them.

Introduction
In a previous paper [14] we used an approach derived from Williams et al. [44; see also 11,15] to investigate temporal changes in the vegetation of a salt-marsh which had been modified for mosquito control. Williams et al.’s analysis comprises 3 steps:

• Clustering the several site-time observations to define states for the system.
• Rewriting the original sequences as strings of states and forming a transition matrix between states for each sequence.
• Clustering the transition matrices, using the method of Dale et al. [15].

The first part is simply a process for defining states, and for this purpose we employed the Minimum Message Length clustering procedure of Wallace & Dowe [43]. This has the advantages of providing a fuzzy assignment of things to clusters and of estimating an optimal number of clusters. However, the analysis ignores any dependency between things. Such dependence is almost certainly present in our data, since they involve sequential observations
through time. It is important, therefore, to determine the effects of this neglect. The most likely effect is an increase in the number of clusters. (Edgoose and Allison 23).

A second way of introducing dependency would be to use k-tuples (q-grams) of states when developing the transition matrices (Claverie et al., 7). Renaming the combinations provides a new set of states for which a transition matrix can be derived, at the expense of a large increase in the number of states and hence in the quantity of data required for any analysis. Further extensions of this approach are possible using variable length subsections of the observed sequences and permitting variable length gaps in these subsections. These are variously known as motifs, events and episodes (see Dietterich and Michalski, 20; Viswanathan et al., 42). It would also be possible to allow hierarchical relations between states (Srikant and Agrawal, 39) or to use context-dependent weighting schemes with Levenshtein metrics (Dale and Barson, 13).

However, using k-tuples introduces a problem. As k increases, we introduce more historical information, and the extent of this has to be determined. If k is too large then we are using noise, if it is too small then we are losing information useful for prediction. It is possible of course that the value could vary because of variation in rates of development, a situation considered by Myers and Rabiner [31] and more recently by Tino and Dorffner [41]. A third alternative, more in the spirit of Williams et al.’s [44] analysis, is to incorporate potential dependency into the state definition itself. This is possible if we modify the initial

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1 Much work on sequences has been done in studies of proteins and nucleic acids. There is a general distinction between global matching where the matching is over the entire sequence and local matching where small subsections are identified as common to all sequences in the comparison. A second area where sequences have been studies is speech processing where variation in rates of production has led to the use of time-warping methods. Sankoff & Kruskal (1983) provide a good general introduction.

2 Motifs (Cockwell and Giles, 1989) are repeating substrings, events (Ronkainen, 1998) are subsequences which may include gaps, while episodes (Mannila et al., 1995; Mannila and Toivonen, 1996) are recurrent combinations of events satisfying certain conditions. See Morris et al. (1995) for temporal interpretation of such scenarios.
stage of clustering the site-time data. Edgoos e and Allison [23] reported a Minimum Message
Length method that does exactly what we wish, using a first order Markov model to capture
the dependency. It is this method we shall explore here. The advantages of the method are
that it estimates the number of clusters (states) and that it permits a test to determine if the
additional complexity of models incorporating dependency is really necessary.
Edgoose (pers. comm.) has recently extended his method to allow higher order Markov
models to be used and in this case we can test if the additional complexity is necessary.
Higher order processes are needed if the system has memory, so that the prediction of
subsequent stages requires knowledge of the history of the process over more than 1 sampling
interval. The determination of the length of the ‘memory’ of a vegetation system is important
because it determines if snapshots (observations taken at one time only) are useful for
predicting the future course of the system. If a higher order process is required, then
snapshots are inadequate for making such prediction of the course of future changes in the
system. In assessing environmental impacts we rarely have the opportunity for long term
observations and evidence to indicate whether snapshots are sufficient is obviously highly
desirable.
There are other possibilities for comparing sequences which rely on sequences of symbols
(strings). Thus there are Minimum Message Length procedures available for aligning
sequences (Allison et al., 3; Powell et al. 32; Allison, 2; Yee and Allison, 46) which have
been used estimating evolutionary relationships for proteins and nucleic acids. These might
be appropriate for situations such as those examined by Wildi and Schütz (45). Dale and
Barson (13) have tried to capture common structure using a context-free grammar formalism.
While useful, such procedures do not seem to be appropriate for the present problem.

**Minimum Message Length Methodology**
Dale (12) has examined practical methods for induction based on the notion of Kolmogorov
complexity and the trade-off of model complexity against fit. In effect we are selecting the
simplest explanatory model consistent with our observations, because it provides the most
probable prediction. Minimum message length methods implement this procedure by
calculating the length of an optimal 2-part message, which both states a model and assesses
the likelihood of the data assuming the correctness of that model. In the present case we need to cluster the site-time observations, incorporating possible dependence between consecutive observations in the same series. The dependence itself is represented by a first order Markov process with as many states as there are clusters in the data. We also require the message length of the optimal model ignoring dependence since we do not wish to enforce the assumption unnecessarily. Minimum message length permits us to make this choice rationally. Incidentally, we shall also obtain the message length for a single cluster; this represents the null hypothesis of 1 cluster and no dependence between samples.

The coded message must contain the following information:

1. The estimated number of clusters
2. The relative abundance of each cluster
3. The distribution parameters for each cluster of all significant attributes which, if dependence is present, will include information on the relative abundance of the next class conditional on being preceded by this cluster.
4. For each observation an assigned cluster and the attribute values given this cluster.

The first 3 represent our hypothesis, while the fourth represents the encoding of the data conditional on the hypothesis.

Attributes can be of several types - multistate (Bernoulli), numeric (Gaussian), non-negative numeric (Poisson) or angular von Mises and each of these has a particular set of appropriate parameters. The initial observation in any sequence has to be treated separately as it has no known preceding cluster member. Missing values are permitted in the data, but intra-cluster correlation of attributes is not permitted. For the present analyses all attributes were regarded as having Gaussian distributions within clusters.

There are in effect 2 sub-problems: 1) estimating the number of cluster and 2) estimating the parameters of those clusters. Given these, the likelihood of the data given the hypothesised model can be calculated. The search space is large and increases rapidly with the number of clusters. The Minimum Message Length principle keeps this expansion to a minimum. The program tSnob combines an EM algorithm for estimation with split, reallocate and join heuristics to determine the necessary values and calculate the message length. The estimates
used for the transition matrices are known to be conservative since they include information on all states.

**Data and Analyses**

Dale et al. (17, 18) provide a description of the area investigated, which is on Coomera Island, Queensland (S27° 51', E153° 33') (Figure 1). The area is a major breeding site for mosquitoes, particularly *Ochlerotatus vigilax* (Skuse) which is a vector for alphaviruses such as Ross River Fever and Barmah Forest virus. Part of the area has been treated by runnelling to reduce mosquito numbers. Runnelling consists of linking isolated mosquito larval habitats to the tidal source via shallow (<0.30 m deep) channels or runnels, which do not drain the marsh. Field research and remote sensing has indicated that the marsh becomes wetter in the runnelled area (Dale et al. 17, 18).

The data consist of 30 sites sampled 4 times a year for 14 years. The analysis was done on 4 plant variables. These were the density and size of Marine Couch (*Sporobolus virginicus* (L. Kunth) and *Sarcornia quinqueflora* (Bunge ex Ung-Stern). Grey Mangrove (*Avicennia marina* (Forsk) occurs along inlets but not in our samples. Other data which were included in the results, but not as part of the cluster analysis, included substrate moisture, pH and salinity, water table depth and salinity and the presence of crab holes and mangrove pneumatophores.

The questions we wish initially to address are:

• is there evidence of clusters of observations or is the area to be considered uniform?
• is there evidence of dependence between the sequential observations?
• is there evidence of ‘memory’ in the system if dependence is confirmed?

We shall also examine the results in order to illuminate the processes which are active.

Mike. To compare classes from the classifications we clustered on the 4 plant variables using Ward’s method in JMP. [36]

**Results**

*Independent v. Dependent*

The 1-cluster solution (ie the whole data set treated as a single population) yields a message length of 61142.56 bits. In contrast, the ‘independent’ analysis yields 10 clusters and a message length of 41408.87, a considerably shorter message from which it is clear that the 1-
cluster solution cannot be accepted. The ‘dependent’ analysis also yields 10 clusters but the message length is still further reduced to 39157.00, a difference of 2251.87. The introduction of dependency has clearly produced a better solution; the odds are 22251.87:1 in favour of the first order dependency model when compared to the ‘independent’ model!

However, when one looks at the results, the dependent and independent analyses produced almost identical class descriptions as is shown in Table I. This tends to be confirmed by the Ckluster analysis results in which the classes matched one to one from both analyses (Figure 2). For most states in either analysis there exists a similar state in the other. The biggest difference appears to be class 5 in both: there \textit{Sporobolus} is denser and taller in the dependent analysis than in the independent one. Other differences are small: compared to the independent analysis there is more \textit{Sporobolus} in class 0 in the dependent analysis, taller \textit{Sarcocornia} in class 1, more \textit{Sporobolus} in class 7, taller \textit{Sporobolus} in class 9 and fewer and smaller \textit{Sarcocornia} in classes 8 and 9.

This fig is just for us Data are Dep minus Independent
Thus the reduction in message length appears to be almost entirely due to the use of the transition probabilities to improve prediction of the next stage rather than to differences in the definitions of states.

This repeats the para below a bit In terms of class abundance the independent analysis identified classes 0 (tall dense *Sporobolus*, no *Sarcocornia*) and 4 (moderate density and size *Sarcocornia*, no *Sporobolus*) as most abundant, with relative abundances 41% and 17% respectively The dependent analysis was similar with classes 0 and 4 most abundant (36% and 17%) (Table 1).

If a higher order process is assumed to be active, the message length required is 39196.76. This is less than the message length for the independent analysis but greater than that for the first order analysis. The odds are roughly 240:1 in favour of the first order model compared to a higher order model. While a higher order model would be preferable to a model ignoring dependence completely, it is unnecessarily complex, and for these data the first order model suffices. This means that a snapshot sample taken at a single time is an acceptable record of the state of the system. The first-order dependency analysis results will be used from here on to describe the system and its processes of change.

*The Dependent Analysis: Abundance and Transitions*

See above Focussing on the states from the preferred ‘dependent’ analysis, we find the commonest are pure stands of *Sporobolus* (state 0, freq 0.364 and state 5, freq 0.108) and of *Sarcocornia* (state 4, freq 0.174). A state representing bare ground is also present but this is less common (state 2, freq. 0.035). Of interest is the transition matrix shown in Table II and in
diagrammatic form in Figures 3 and 4. From Table II there is a considerable degree of diagonal dominance, which indicates that most states are relatively stable. Thus 7 out of the 10 states have a 70% or greater chance of staying in the same state. The major exception is state 1, which is usually transient, changing mainly to state 6. States 3 and 9 also have reasonable probabilities of changing to other states.

States 0, 4 and 7 are almost absorbing states; once entered they are rarely left. Figure 3 shows that the transitions can be organised into 2 disjoint series at the P<= 0.10 level. The states are (0, 7, 9) and (1, 2, 3, 4, 5, 6, 8). The former is dominated by dense *Sporobolus*, although state 7 includes moderately dense *Sarcocornia*. The latter series is more complex, with variable amounts of both species and also including bare ground (state 2), sparse tall *Sporobolus* and the absorbing state 4 with pure *Sarcocornia*. In this series *Sporobolus* is always sparse in all states and the pure state 5 shows transitions only towards bare ground.

Figure 4 takes a lower probability of changing (0.08) and shows that there are some linkages across the ‘disjoint’ series. Thus state 1 may change to state 7 and vice versa. At this level the bare ground (state 2) now shows transitions to *Sporobolus* in state 0, as well as to *Sarcocornia* at the 0.1 level. So we have a peculiar situation where both species can invade independently, but not apparently together. This may be due to some environmental controlling variable or variables, which determines the actual direction. However, the most likely explanation seems to be that the relative location of the sample is critical. If it is in drier areas (usually high on the marsh) *Sporobolus* is the invader, if wetter (usually low on the marsh) *Sarcocornia* is the invader.

Figure 4 also shows a lower probability of changing (0.05) and this adds complexity, with state 7 bypassing state 9 and losing its *Sarcocornia* to become tall dense *Sporobolus* (state 0); this state can now be reached by state 5 (*Sarcocornia*). State 5 can be reached by state 6 (a

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3 Fig 2 P 0.10
Fig 3 P 0.08
Fig 4 P 0.05
mixture of tall *Sporobolus* and *Sarcocornia*) and this represents a loss of the *Sporobolus*. It seems that there is an outer ‘circle of change’ in which *Sarcocornia* declines and *Sporobolus* takes over (States 7 to 6 to 5 to 0, the latter being quite stable, with the probability of not changing = 0.930).

It is recognised that marsh vegetation sequence is related to tidal flooding and that *Sporobolus* tends to occupy higher marsh positions (Adam 1988). In this analysis there was no discernible relationship between state and distance from the tidal source (non-parametric correlation), although the bare ground state was closest to the water and also had the highest water table (closest to the surface), one of the lower salinities and most pneumatophores (mangrove ‘roots’).

*Effects of habitat modification (runnelling)*

In terms of the modification the runnelled sites contain a disproportionate amount of class 5 (*Sporobolus*, which is most likely to remain the same or go to bare ground) than do the control sites. A similar relationship exists for classes 9 (*Sporobolus* and *Sarcocornia*, but relatively unstable) and 7 (*Sporobolus* and *Sarcocornia*), both of which are part of the relatively discrete series (0,9,&7). Class 2 (bare ground) also has a large proportion of runnelled sites. These observations are consistent with field observations (Dale unpublished data).

**Discussion**

As in other analyses (eg Dale & Dale 14) the tall dense *Sporobolus* class dominates: it is most common and is most stable. The apparently odd bare ground state 2, which can change to states with either of the other two species, may be explained in terms of its other characteristics. It is wetter and closer to the tidal source than the other states and this would be likely to favour *Sarcocornia*. However state 2 also has low salinity, perhaps related to the increased flushing which runnelling may cause. Lower salinity tends to favour *Sporobolus* (which otherwise tends to occupy the higher marsh which receives less tidal flooding).
The analytic procedure has some deficiencies that need brief attention. As noted earlier, the transition matrix is encoded in a conservative manner, since we should be able to save the coding of 1 row. This, we believe, is unlikely to affect our results. The estimation of $k$, the number of clusters, may be somewhat biased because it is not sampled properly from the appropriate posterior distribution. Richardson & Green (33) describe a reverse jump Markov chain approach which avoids this problem but the program does not implement this nor any other unbiased search. It is therefore possible that the estimate of the number of clusters is inaccurate. However the same form of search is used for both independent and dependent analyses.

The analysis has used a crisp assignment of things to clusters, which is likely to produce inconsistent estimates of cluster parameters. Partial assignment of things to clusters can be used to reduce the message length and improve the consistency of parameter estimates. This may make an alternative search procedure, such as simulated annealing, more effective. None of these, we feel, is likely to have a major effect. It is possible, of course, that our data cover too small a period to identify nonstationarity in the processes such as responses to long-term changes in the climate. Trends of this kind could be detected, given sufficient data, although our 14 year records are long in ecological studies. It is possible that Wildi and Schütz’s (45) approach, based on combing short sequences may be useful for this problem.

We need also to consider the possibility that other models may be more appropriate than a first order Markov model. Alternatives in the literature include generalised Lévy processes\(^4\) (Staley et al., 40), and Ristad’s (35) use of finite state models in a supervisory role. Since we do not have evidence here of higher order Markov processes, these extensions are probably not needed for our present analyses. A further complication has been addressed by Liebovitch (26). He considered a situation where the state boundaries were themselves

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\(^4\) The Lévy process allows a period after entry to a state during which a state makes NO transitions. The period for which this restriction is held true is itself a random variable. This might, for example, reflect a period of maturation after establishment.
labile. Ecologically this might be appropriate if the conditions for colonisation and for survival once present differed, as is quite likely.

We must also consider that the restriction to a single Markov process for each cluster may be inappropriate. Is a single model optimal? It is known that for prediction, model uncertainty may be very large and that some form of model averaging provides better predictions. (Chatfield, 6). Yee & Allison (46) and Eddy (22) have already employed multiple models when attempting to identify similarity in remotely related nucleic acid sequences, and similar procedures may be appropriate for ecological studies.

Finally the relationship of pattern, complexity and modelling is subject to discussion. The usual approaches to induction have relied, as here, on estimating Kolmogorov complexity in some manner (Dennett, 21) which is equivalent to accepting randomness is the most complex situation. Crutchfield and Shalizi (10) argue for a different definition which, they claim, is preferable. Their argument seems to centre on which operations can be regarded as primitive for the simulating machine, and their assumption of a random generator as a primitive seems suspect.

**Substantive**

**Sampling, Scale and Description**

We have so far assumed that our data collection is necessarily meaningful, that is that both the scale and the describing attributes are appropriate for identifying patterns. It is obvious that changes in scale reflecting changing size of sampling units could certainly change the nature of the patterns we recognise, and that in some cases, inappropriate choice could vitiate the entire analysis. Crutchfield (9) indicates that distortion introduced by the measurement process can lead to drastic consequences for an observer’s ability to infer structure in the environment. Daley (1977) has considered how optimal descriptions might be inferred and Dale, Salmina and Mucina (16) has shown that species may not be univocal in their message concerning environmental controls.

There is a second point to consider. Even if we can infer structure it may not be the kind of structure we desire. Consider Antonelli’s (5) example of an ant moving across a landscape. Teleologically the ant may be returning home, but a search for patterns could well identify
sequences of behaviour representing ways of overcoming local barriers to movement. We would learn, perhaps, that ants go over, under or around obstacles in particular ways and can apply these episodes recursively, but this may not represent the kind of knowledge we seek.

**Gradients and Boundaries**

The present results are unlike those of Anand and Heil (4) or Dale (11) who both demonstrated a progression towards some kind of attractor. Here we seem to have reached one of several attractors within which change is largely random. This is somewhat surprising. The saltmarsh can reasonably be regarded as being a gradient associated with tidal inundation. While largely periodic, the amplitude and frequency is subject to considerable contingent variation as well as more predictable changes of a seasonal nature. Local topography and local weather can modify the tidal inundation amplitude and frequency. So we might expect that we should recover a somewhat fuzzy gradient. In fact, at one level we seem to have at least 2 disjoint processes in operation. One is associated with the high marsh and *Sporobolus* communities while the other, more dynamic, is associated with the low marsh and *Sarcocornia* communities, although this was not related to distance from the tidal flooding source (and hence elevation). However it has previously been suggested position in the local drainage network at the micro scale is more important in determining patterns that actual elevation (Dale et al 1986) Note that if you insert this reference you will have to renumber ALL subsequent references accordingly!!!!

There is a limited amount of interchange and uncertainty between these two parts, but no more than might be expected given the potential effects of contingent variation. Our gradient seems to be broken into 2 distinct communities! A single example is insufficient to establish this as a general rule, of course; indeed there may be no general rule. But it is thought provoking that in a situation where a gradient seems a priori to be a likely model, a disjoint community model, albeit with a fuzzy boundary, seems indicated.
References


Table I.
Class characteristics for the Dependent and Independent analyses

Dependent analysis

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<th>Class</th>
<th>Abundance</th>
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<th>Sporobolus height (mm)</th>
<th>Sarcocornia # SD</th>
<th>Sarcocornia size (mm)</th>
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Independent analysis

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Table II

Transition Matrix for Dependent Analysis

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Figure Headings

Figure 1. Location of study area.

Figure 2. Cluster analysis of the classes from each analysis (D – Dependent analysis; I Independent analysis).

Figure 3. Linkages in terms of change at the P => 0.10, dependent analysis.

Figure 4. Linkages at the > 0.08 and >0.05 level, dependent analysis (key as in Figure 3).
Figure 1. Location of study area
Figure 2. Differences between the Independent and Dependent analyses (Values are mean values in the Dependent analysis minus the mean values in the Independent analysis (data as in Table I).
Figure 3. Linkages in terms of change at the $P \geq 0.10$, dependent analysis.

Sporobolus: tall medium, short
Sarcocornia: large, medium, small
Density high, medium, low:
No of symbols 3,2,1

P of remaining in same state
$P \Rightarrow .25$
$P > .10 < .25$

State 7

State 6

State 1

State 8

State 9

State 0

State 2

State 4

State 5

State 3

$P \Rightarrow .25$
$P > .10 < .25$
Figure 4. Linkages at the >0.08 and >0.05 level, dependent analysis