Past states of continuous-time Markov models for ecological communities

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Abstract

Discrete-time Markov chains are often used to model communities of sessile organisms. The community is described by a set of discrete states, which may represent species or groups of species. Transitions between states are modelled using a stochastic matrix. A recent study showed how the time-reversal of such a Markov chain can be used to estimate the distribution of time since the last occurrence of some state of interest (such as empty space) at a point, given the current state of the point. However, if the underlying process operates in continuous time but is observed at regular intervals, this distribution describes the time since the last possible observation of the state of interest, rather than the time since its last occurrence. We show how to obtain the distribution of time since the last occurrence of a state of interest for a continuous-time homogeneous Markov chain. The expected time since the last occurrence of an initial state can be interpreted as a measure of the successional rank of a state. We show how to distinguish between different ways in which a state can have high successional rank. We apply our results to a marine subtidal community.

Key words: Continuous time Markov chains, community ecology, first passage time, marine subtidal, time reversal

1 Introduction

Markov chains are often used to model the dynamics of communities of sessile organisms [1–4]. It is assumed that a point in space can be in one of a finite number of states $1 \ldots s$, such as different species or groups of species, and free space. In most cases, the dynamics of the system are assumed to be described by a temporally homogeneous, ergodic discrete-time Markov chain. Temporally homogeneous means that the conditional probability of each state one unit of time in the future, given the current state, does not depend on time. Ergodic means that any state is eventually reachable from any other state, the expected return time to any state is finite, and the probability of returning to any state i in n time steps is non-zero for all sufficiently large n. Let $\mathbf{P}(t)$ be an s-by-s matrix of transition probabilities , whose entries $p_{ij}(t)$ are the conditional probabilities that a point in state i at time τ will be in state j at time $\tau + t$ (note that in much of the ecological literature, the transition probability matrix is transposed relative to this definition). We will sometimes refer simply to the transition probability matrix $\mathbf{P}$, when the time step t is fixed. If $\mathbf{x}(\tau)$ is an s-by-1 vector of state probabilities at time τ, then

$$\mathbf{x}^{\mathrm{T}}(\tau + t) = \mathbf{x}^{\mathrm{T}}(\tau)\mathbf{P}(t) \tag{1}$$

where $\mathbf{x}^{\mathrm{T}}$ denotes the transpose of $\mathbf{x}$. $\mathbf{P}(t)$ is a stochastic matrix, with rows summing to 1. Under the above assumptions, there is a unique vector of stationary probabilities $\boldsymbol{\pi}$ such that $\boldsymbol{\pi}^{\mathrm{T}} = \boldsymbol{\pi}^{\mathrm{T}}\mathbf{P}(t)$, to which the state probabili-

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ties will converge [5, Theorem 1.8.3].

Applications of Markov chains in community ecology have mainly addressed questions such as quantifying the effects of species removals [4,6,7], comparisons of transition probabilities across communities [3,4], turnover rates and recurrence times [4], effects of hypothetical modifications of transition probabilities [3,8], and identification of keystone species [2]. [9] is an excellent review of both discrete- and continuous-time Markov models in ecology. Recently, [10] showed how Markov chains can be used to make inferences about past states. Specifically, they calculated the distribution of times T_j since the last observation of some state j at a point, given the present state of that point. In this paper, we briefly review the results presented in [10]. We show how the distribution of times since the last observation of some state at a point in a discrete-time chain, conditional on the present state, depends on the observation interval, and therefore may not tell us about the most recent occurrence of a given state in the past. We then describe analogous results for a time-homogeneous continuous-time Markov chain. If this is an appropriate model, then the resulting distribution of first passage times in the time-reversed chain can be interpreted as the distribution of times since the last occurrence of a given state at a point in space, conditional on the current state. This distribution is independent of the intervals between observations of the chain. We suggest that the expected first passage time to an initial state (such as empty space) in the time-reversed version of a Markov model for an ecological community provides a way to rank states by successional level. We show how the jump chain corresponding to a continuous-time Markov model can be used to calculate the expected number of events at a point since the last occurrence of a given state j, given the current state of the point. This allows us

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to distinguish between states which have high successional rank because they persist for a long time, and states which have high successional rank because they are likely to be separated from an initial state by a long series of transitions between intermediate states. All our results are based on well-known theory concerning the transient behaviour of Markov chains, for which [11] is excellent source.

2   Biological background

Throughout this paper, we use a model of a subtidal community from the Gulf of Maine [4] as an example. Permanent quadrats were located on a rock wall at 30-35 m depth, and photographed annually. A rectangular grid of points was superimposed on each photograph, ensuring that the points represented corresponding spatial locations each year. The organism present at each point each year was identified. The community consists of 14 species/groups of species of sponges, sea anemones, ascidians, bryozoans and polychaetes. [4] counted the frequencies of transitions among states (species/groups of species and bare rock), and estimated transition probabilities from the time-aggregated counts. Markov models are often used to gain quantitative insight into successional processes [4]. [10] suggested that knowing the expected time since the last occurrence of an initial state, given the current state at a point, is potentially useful in estimating the time since the establishment of suitable habitat, for example the appearance of a hydrothermal vent or the death of a corpse supporting an insect community. Here, we focus on the ways in which inferences about past states can be used to refine our understanding of the successional process. Specifically, we show that time since the last occurrence of an initial

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state, conditional on the current state, can be used to distinguish between

states that are usually associated with early stages of succession, and states

that are usually associated with later stages.

3 First passage times in time-reversed discrete-time Markov chains

To obtain the distribution of time since the last occurrence of some given state j at a point in space with a known current state, [10] first obtained a time-reversed transition probability matrix $\mathbf{P}^R$ under the assumption that state probabilities are stationary:

$$\mathbf{P}^R = \mathbf{\Pi}^{-1}\mathbf{P}^{\mathrm{T}}\mathbf{\Pi} \tag{2}$$

[11, Definition 2.7], where $\mathbf{\Pi}$ is a diagonal matrix of stationary probabilities. [10] then obtained the distribution of first passage times to state j in the time-reversed chain. Without loss of generality, we will assume that the state of interest in the past is $j = 0$. We write

$$\mathbf{P}^R = \begin{bmatrix} p_{00}^R & (\mathbf{p}_0^R)^{\mathrm{T}} \\ \mathbf{r} & \mathbf{T} \end{bmatrix} \tag{3}$$

We define an absorbing state as a state from which no other state can be reached. We construct a chain in which state 0 is absorbing, with transition probability matrix

$$\mathbf{P}_0^R = \begin{bmatrix} 1 & \mathbf{0}^{\mathrm{T}} \\ \mathbf{r} & \mathbf{T} \end{bmatrix} \tag{4}$$

Then the cumulative distribution function for T_0 given current state i is

$$F_{i0}^d(t) = P_i(T_0 \leq t) = [\mathbf{P}_0^R]_{i0}^t \quad t = 1, 2, \ldots \tag{5}$$

[11, p. 80], where the superscript d in $F_{i0}^d(t)$ indicates that this is the cumulative distribution for the discrete-time chain, and the subscript i in $P_i(T_0 \leq t)$ indicates that the distribution is conditional on the current state being i. Equation 5 gives us the cumulative distribution for T_0 in the original chain because we have not changed the probability of entering state 0 from any other state, but once we have entered state 0 we never leave it. [10] applied this method to the Markov model of a rocky subtidal community in the Gulf of Maine developed by [4].

4 Interpretation of the first passage time in the time-reversed discrete-time chain

If $\mathbf{P}(t)$ is the transition probability matrix for a discrete-time Markov chain with time step t, then the transition probability matrix for a chain observed at time intervals of length nt, where n is a positive integer, is $[\mathbf{P}(t)]^n$ [11, p. 16]. We can apply the method described in the previous section to calculate $F_{ij}^d(t)$ for chains with different intervals between observations. For example, in the system studied by [4], state 14 is the polychaete *Spirorbis spirorbis*, and state 15 is bare rock. Figure 1 shows the cumulative distributions $F_{14,15}^d(t)$, with time steps of one, two and five years. Even though the system is undergoing the same dynamics in each case, as the interval between observations increases, the value of $F_{14,15}^d(t)$ for any fixed, finite integer time t decreases. In other words, as the interval between observations increases, so does the apparent

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time since the last occurrence of some given state j at a point. If there may be multiple events at a point in space between two observation times, then we should interpret $F_{ij}^d(t)$ as giving us the cumulative distribution of time since the last possible observation of state j given the current state i, not necessarily the last occurrence of state j.

5   First passage times in time-reversed continuous-time Markov chains

We would like to know the distribution of time since the last occurrence of state j, given that a point is currently in state i. If we suppose that events can occur at any time, and that the rate of events is constant, then we may be able to find a matrix $\mathbf{Q}$ such that

$$\mathbf{P}(t) = e^{\mathbf{Q}t} = \sum_{k=0}^{\infty} \frac{(\mathbf{Q}t)^k}{k!} \tag{6}$$

for any non-negative real time t [5, Theorem 2.1.1]. We assume here that such a matrix exists, and that it is unique. The conditions under which this is true are given in [12]. More details of estimating a suitable $\mathbf{Q}$ matrix for real data are given in the Appendix. We refer to $\mathbf{Q}$ as the generator or rate matrix for a time-homogeneous continuous-time Markov chain. The off-diagonal elements q_{ij} of $\mathbf{Q}$ are the rates (non-negative, real, with dimensions time^{-1}) of transitions from state i to state j. The diagonal elements q_{ii} are defined as $-\sum_{j \neq i} q_{ij}$, so $-q_{ii}$ is the rate of leaving state i.

Using the homogeneous continuous-time model, we can calculate the distribution of times since the last observation of some state j given current state i as the interval between observations becomes arbitrarily small. The methods are

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similar to the discrete-time case. Let q_{ij} be the instantaneous rate of transitions from state i to state j in a stationary finite-state ergodic continuous-time homogeneous Markov chain, and let π_i be the stationary probability of state i. Then the instantaneous rate of transitions from j to i in the corresponding stationary time-reversed chain is $q_{ji}^R = (q_{ij}\pi_i)/\pi_j$ [5, Theorem 3.7.1]. Thus we can find a time-reversed generator matrix $\mathbf{Q}^R$:

$$\mathbf{Q}^R = \mathbf{\Pi}^{-1}\mathbf{Q}^{\mathrm{T}}\mathbf{\Pi} \qquad (7)$$

Assuming without loss of generality that $j = 0$, and writing $\mathbf{Q}^R = \begin{bmatrix} -q_0^R & (\mathbf{q}_0^R)^{\mathrm{T}} \\ \mathbf{r} & \mathbf{T} \end{bmatrix}$,

we construct a chain in which state 0 is absorbing,

$$\mathbf{Q}_0^R = \begin{bmatrix} 0 & \mathbf{0}^{\mathrm{T}} \\ \mathbf{r} & \mathbf{T} \end{bmatrix} \qquad (8)$$

Now the cumulative distribution of first passage times to state 0 in the time-reversed chain is given by

$$F_{i0}(t) = [e^{\mathbf{Q}_0^R t}]_{i0} \quad t \geq 0 \qquad (9)$$

Let T_j be the first passage time to state j. Without loss of generality we assume $j = 0$. Then the probability density of the first passage time to state 0 from initial state i is given by

$$f_{i0}(t) = \mathbf{e}_i e^{\mathbf{T}t}\mathbf{r} \qquad (10)$$

95   for $t \geq 0$, where $\mathbf{e}_i$ is a vector with 1 in position i and 0 elsewhere [11, p. 213].

96   The first passage time T_0 to state 0 from initial state i in a stationary finite-

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state ergodic continuous-time homogeneous Markov chain has mean $E_i[T_0] = \mathbf{e}_i(-\mathbf{T})^{-1}\mathbf{1}$ [9,11, p. 212] and variance $V_i[T_0] = 2\mathbf{e}_i(-\mathbf{T})^{-2}\mathbf{1}) - (\mathbf{e}_i(-\mathbf{T})^{-1}\mathbf{1})^2$ [13], where the subscripts i in $E_i[T_0]$ and $V_i[T_0]$ indicate that they are conditional on initial state i. We estimated the generator matrix (Table 1) for the system studied by [4] as described in the Appendix. Figure 2 shows the cumulative distributions of first passage times to state 15 (bare rock) from each other state, calculated from the discrete-time model with observation interval one year (solid lines) and the continuous-time model (broken lines). It is easy to show that the cumulative distributions from the continuous-time model will always lie above those for the discrete-time model. This is because if we observe the system continuously, we will see all occurrences of state j that occurred at observation times in the discrete-time chain, in addition to the occurrences between observation times. Then, using the result that for a random variable X with density $f(x) = 0$ for $x < 0$ and distribution function F, $E[X] = \int_0^\infty (1 - F(x))dx$ [14, Lemma 4.3.4], we can show that the expected first passage time for the continuous-time chain will be less than that for the discrete-time chain. The difference between the continuous- and discrete-time distributions may be large. For example, with current state 14 (*Spirorbis spirorbis*), the probability that the last occurrence of state 15 (bare rock) was no more than 10 years ago is 0.81 (from the continuous-time model). However, the probability that an occurrence of bare rock would have been observed in the last 10 years if we made observations at one-year intervals is only 0.55.

6 Expected first passage time in the time-reversed chain as a measure of successional rank

Table 2 gives the mean ($E_i[T_{15}]$) and variance ($V_i[T_{15}]$) of first passage time to bare rock (state 15) in the time-reversed continuous-time chain based on data in [4], conditional on each other current state i. Points currently in states for which $E_i[T_{15}]$ is small are likely to have been bare rock more recently than points currently in states for which $E_i[T_{15}]$ is large. Since bare rock is the initial stage of a successional process, $E_i[T_{15}]$ tells us how far from this initial stage a point in space is likely to be, given its current state. This information is difficult to obtain in other ways when succession is stochastic and many alternative pathways are possible. However, Table 2 also shows that the variance of time since the last occurrence of bare rock is large for all states. The difference between the smallest and largest values of $E_i[T_{15}]$ among current states is 7.93 years, but for any given current state $V_i[T_{15}]$ is at least 70. We are quite uncertain about the past states of a point in space, given its present state.

For the continuous-time model based on data in [4], there is little relationship between the stationary probability of a state and the expected time since the last occurrence of bare rock (Figure 3a, Pearson correlation 0.21: we do not test the statistical significance of this and other correlations, because we have sampled the entire population of states). However, there is quite a strong negative relationship between the rate of leaving a state and the expected time since the last occurrence of bare rock (Figure 3b, Pearson correlation -0.74). In other words, if we observe a highly persistent species (as measured by low leaving rate: -1 times the diagonal element of the $\mathbf{Q}$ matrix) such as the sea anemone *Urticina crassicornis* (other species in this genus are known to live

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at least 20 years [15]) or the sponge *Mycale lingua*, it is unlikely that the point was bare rock recently (95th percentiles of T_{15}: 35 years for *Urticina*, 34 years for *Mycale*). If we observe a species such as *Spirorbis spirorbis* that is less likely to persist at a point for a long time, the point is likely to have been bare rock more recently (95th percentile of T_{15}: 23 years). The relationship between the stationary probability and rate of leaving a state is negative but relatively weak (Figure 3c, Pearson correlation -0.37). Species that are relatively poor at persisting may be able to maintain moderately high abundance by colonizing bare rock.

7   The number of events since the last occurrence of a given state

The negative relationship between the rate of leaving a state and the expected time since the last occurrence of bare rock (Figure 3b) suggested that states with high successional rank tend to be highly persistent. This could mean that states with different succesional rank differ mainly in the length of time it takes for them to colonize bare rock (Figure 4a). However, it is also possible for a state to have high successional rank if it is likely to be separated from the initial state by a long series of transitions among intermediate states (Figure 4b). In order to see which of these patterns occurs in a continuous-time Markov chain, we need to calculate the expected number of events (changes of state) since the last occurrence of the initial state for each current state at a point in space.

The jump matrix $\mathbf{S}$ associated with a continuous-time Markov chain is a stochastic matrix whose entries s_{ij} are the probabilities of each state j being the new state when a transition occurs, given that the current state is

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i:

$$
s_{ij} = \begin{cases} -q_{ij}/q_{ii} & j \neq i, q_{ii} \neq 0 \\ 0 & j \neq i, q_{ii} = 0 \end{cases}
$$
$$
s_{ii} = \begin{cases} 0 & q_{ii} \neq 0 \\ 1 & q_{ii} = 0 \end{cases}
$$
(11)

[5, p. 87]. We can calculate $\mathbf{S}$ for the time-reversed chain $\mathbf{Q}^R$. As before, we assume without loss of generality that the state of interest in the past is $j = 0$, and define the absorbing jump matrix

$$
\mathbf{S}_0 = \begin{bmatrix} 1 & \mathbf{0}^{\mathrm{T}} \\ \mathbf{r} & \mathbf{T} \end{bmatrix}
$$
(12)

Let J_0 be the number of jumps from state i to state 0 in the absorbing jump chain for $\mathbf{Q}^R$. J_0 has expectation $E_i[J_0] = \mathbf{e}_i \mathbf{N} \mathbf{1}$ [9] and variance $V_i[J_0] = 2\mathbf{e}_i \mathbf{N}^2(\mathbf{N} - \mathbf{I})\mathbf{r} + E_i[J_0] - (E_i[J_0])^2$, where $\mathbf{N} = (\mathbf{I} - \mathbf{T})^{-1}$ and $\mathbf{e}_i$ is a vector with a 1 in position i and 0 elsewhere [11, pp. 80-81].

Table 3 gives the mean ($E_i[J_{15}]$) and variance ($V_i[J_{15}]$) of the number of jumps since the last occurrence of bare rock (state 15) given the current state, for the continuous-time chain based on data in [4]. The Pearson correlation between the time since the last occurrence of bare rock ($E_i[T_{15}]$) and the number of jumps since the last occurrence of bare rock ($E_i[J_{15}]$) is 0.87 (Figure 5). In other words, states for which the expected time since the last occurrence of bare rock is longer are also expected to be separated from bare rock by a larger number of intermediate states. However, the differences among states in the expected number of jumps since the last occurrence of bare rock are small relative to the variance in number of jumps for any given state. From Table 3,

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the difference between the largest and smallest values of $E_i[J_{15}]$ is 1.48, while $V_i[J_{15}]$ is at least 16.54 for all states.

8 Conclusions

Markov models for communities are usually formulated in discrete time. In many ecological communities, it is reasonable to assume that some events such as mortality can occur at any time, and many other events such as reproduction may occur over quite long time periods. If this is the case, then a continuous-time model might be more appropriate for inferences about some kinds of properties than a discrete-time model, which predicts the state of the system only at discrete observation points. If the underlying dynamics of the system are in continuous time, a discrete-time model will miss many events that occur between observation intervals. Here, we showed that the expected time since the last occurrence of some past state (estimated from a continuous-time model) will be less than the expected time since the last observation of this state (estimated from a discrete-time model of the same system). Elsewhere, we showed that inferences about the complexity of interaction networks [16] and the consequences of changing interspecific interaction parameters [17] from discrete-time models may also be misleading if the true dynamics are in continuous time.

One important caveat is that we assumed homogeneity in time. This may not be true, especially in temperate habitats such as the one we studied, where it is likely that survival, reproduction and interspecific interactions will vary seasonally. There is also statistically significant interannual variability in transition probabilities in this system, although the biological consequences

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of this variability may not be major [18]. We did not consider models with temporal variability here because such models cannot be identified from time-averaged data such as those presented in [4]. However, temporal variability could potentially have large effects on inferences about past states. If the sequences of states at points in space are available, these effects could be checked by direct comparison of the calculated and observed distributions of first passage times. Both time-averaged discrete-time models and homogeneous continuous-time models are potentially useful caricatures of the dynamics of a community, but it is important to remember their limitations.

A central idea in the concept of ecological succession is that some states in a community tend to appear soon after an initial state such as empty space, while others do not occur until much later. However, when the sequence in which states occur is not deterministic, it is not immediately obvious how we should identify early- and late-succession states. The approach we describe here is one way to do this. We refer to states for which the expected time since the last occurrence of an initial state (such as bare rock) is long as having high successional rank. We can also learn something about why a state has high or low successional rank. For the Gulf of Maine subtidal data set we analyzed, states with high successional rank tended to be good at persisting at a point, and to be separated from bare rock by longer sequences of events than states with low successional rank. However, other relationships might occur in other communities. Comparative studies of Markov models from a range of communities [3,4] will be the best way to address this.

Inferences about past states could also be useful for estimating the age of a habitat [10]. However, for the community we analyzed, the variance in time since the last occurrence of bare rock given the current state was large relative

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to the differences in expected time since the last occurrence of bare rock among current states. In other words, for this community, knowing the current state does not give us much information about the past. We did not consider the consequences of uncertainty in transition probabilities [10], but such uncertainty would be likely to further reduce the amount of information available about the past.

Several other studies have examined related problems, such as first passage times in flow-balanced ecological networks describing food webs and hydrodynamic compartments [19], and the estimation of event times in chain-of-events models for the progression of HIV, where data are observed at discrete intervals [20]. In the latter case, the problem differs from ours in that the sequence of events is known but their timings are unknown, and that a semi-Markov model was used. There are other potential applications to disease modelling. For example, hidden Markov models can be used to describe the occurrence of drug-resistance mutations in HIV. Given parameter estimates for these models [21], it might be of interest to estimate the probability distribution of mutation times given the current mutational state.

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Appendix: estimating the continuous-time model

Assume that each of a set of independent fixed points in space has a state determined by the same finite-state homogeneous Markov chain. If the interval between observations is t for all points, the maximum likelihood estimate of a transition probability p_{ij} is $\hat{p}_{ij} = n_{ij}/n_i$, where n_{ij} is the number of points in state j at time $\tau + t$ that were in state i at time τ, and n_i is the number of points in state i at time τ [22, p. 135].

We used data from Table 2 in [4], derived from annual photographic observations of a rocky subtidal community over nine years. Including bare rock, there were $s = 15$ distinguishable states, labelled 1 to 15. Note that in [4], the transition probability matrix is transposed with respect to our notation. The rows of the matrix in Table 2 of [4], which we refer to as $\tilde{\mathbf{P}}(t)$, did not exactly

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sum to 1, presumably because of rounding errors. We therefore rescaled all elements by the row sums to obtain the estimate $\hat{\mathbf{P}}(t)$:

$$\hat{p}_{ij} = \tilde{p}_{ij} / \sum_{k=1}^{s} \tilde{p}_{ik} \qquad (13)$$

If $\mathbf{P}(t) = e^{\mathbf{Q}t}$, an obvious estimate of the continuous-time rate matrix $\mathbf{Q}$ is $\tilde{\mathbf{Q}} = 1/t \log \hat{\mathbf{P}}(t)$, where log is the matrix logarithm. This is the maximum likelihood estimate if $\mathbf{P}(t)$ was generated by a homogeneous continuous-time Markov chain [23]. However, this estimate often has negative off-diagonal entries, either because of sampling error or because the transition probabilities were not generated by a homogeneous continuous-time Markov chain. If $\tilde{\mathbf{Q}}$ has negative off-diagonals, there will be some time intervals for which $e^{\tilde{\mathbf{Q}}t}$ also has negative entries, so this cannot be a valid rate matrix. If the original data are available, constrained maximum likelihood [24,16] or Markov Chain Monte Carlo [23] methods can be used. However, if only $\hat{\mathbf{P}}(t)$ is available, as in this case, we could set any negative off-diagonal entries in $\tilde{\mathbf{Q}}$ to zero and adjust the diagonal elements to maintain zero row sums, giving the estimate $\hat{\mathbf{Q}}$:

$$\hat{q}_{ij} = \begin{cases} \max(\tilde{q}_{ij}, 0) & i \neq j \\ \tilde{q}_{ii} + \sum_{k \neq i} \min(\tilde{q}_{ik}, 0) & i = j \end{cases} \qquad (14)$$

[25]. Other approaches are possible when only $\hat{\mathbf{P}}(t)$ is available, such as finding a rate matrix whose eigenspectrum matches that of the transition probability matrix as closely as possible [26]. However, for the data we used, $e^{\hat{\mathbf{Q}}t}$ was very close to $\hat{\mathbf{P}}(t)$, and gave almost indistinguishable results for the distribution of first passage times to bare rock. $\hat{\mathbf{Q}}$ is therefore a satisfactory estimate of the continuous-time rate matrix for our purposes. All the discrete-time results we report are based on $e^{\hat{\mathbf{Q}}t}$, so that differences between discrete- and continuous-

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time results are not artefacts of the estimation method for the continuous-time

model. Table 1 shows the estimate $\hat{\mathbf{Q}}$.

Table 1

Generator matrix **Q** for a continuous-time Markov chain estimated from the data in [4], as described in the Appendix. States are (1) *Hymedesmia* sp. 1, (2) *Crisia eburnea*, (3) *Myxilla fimbriata*, (4) *Mycale lingua*, (5) *Filograna implexa*, (6) *Urticina crassicornis*, (7) *Ascidia callosa*, (8) *Aplidium pallidum*, (9) *Hymedesmia* sp. 2, (10) *Idmidronea atlantica*, (11) coralline algae, (12) *Metridium senile*, (13) *Parasmittina jeffreysi*, (14) *Spirorbis spirorbis*, (15) bare rock. All rates are years^{-1}.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	-0.2925	0.1206	0.0170	0.0030	0.0137	0	0.0423	0.0193	1.54e-04	0.0279	0.0012	0.0011	0.0081	0.0069	0.0312
2	0.1821	-0.5889	0.0391	0.0128	0.0332	0.0052	0.0479	0.0599	0.0147	0.0275	0.0172	0.0103	0.0071	0.0062	0.1260
3	0.0537	0.0216	-0.3553	0.0032	0.0202	0.0043	2.52e-06	0.0078	0.0361	0	0.0051	0.0081	0.0016	0.0281	0.1655
4	0.0098	0.0510	0.0049	-0.1776	0.0010	0	7.61e-04	0.0084	0.0100	0.0042	0.0076	0.0148	0	0.0086	0.0565
5	0.1290	0.3239	0.0455	2.59e-04	-0.9734	0.0093	0.0941	0.0834	0.0177	0	9.51e-04	0.0017	0.0083	0.0031	0.2561
6	0.0039	0.0105	0.0131	0	0.0219	-0.1595	0	0.0117	0.0212	0.0032	0.0048	0.0088	0	0	0.0603
7	0.5416	0.3596	0.1207	0.0326	0.2628	0.0645	-2.5204	0.2331	0.0263	0.1729	0.0804	0	0.0644	0.1467	0.4147
8	0.3483	0.4066	0.0609	0.0327	0.2681	0.0075	0.2215	-2.0042	0.0278	0.0966	0.0317	0.0530	0.0218	0.0522	0.3754
9	0.0346	0.1750	0.0305	0.0122	0.0169	0.0068	5.70e-04	0.0612	-0.5435	0.0472	0.0053	0.0036	0	0.0133	0.1364
10	0.6604	0.4312	0.0428	0.0123	0.0049	0.0065	0.2063	0.1055	0.0149	-1.8940	0.0205	0.0111	0.0370	0.0090	0.3316
11	0.0245	0.3324	0.0315	0.0077	0.0500	0	0.0601	0.0349	0.0060	0	-0.6977	0	0.0068	0	0.1438
12	0.0201	0	0.0213	0.0420	0	0	0	0.0169	5.94e-04	0	0	-0.8073	0	0	0.7063
13	0.6096	0.2839	0.0230	0	0.1546	0	0.0936	0.0347	0	0.0540	0.0342	0	-1.4746	0	0.1870
14	0.2815	1.9948	0	0.0488	0.4633	0.0075	0.0938	0	0.0547	0.2226	0	0	0	-3.9231	0.7561
15	0.0281	0.6355	0.0191	0.0060	0.1204	0.0015	0.2224	0.0980	0.0177	0.1023	0.0285	0.0365	0.0298	0.0962	-1.4418

Table 2

Mean ($E_i[T_{15}]$) and variance ($V_i[T_{15}]$) of first passage time in years to state 15 (bare rock) from each other current state i in the time-reversed stationary continuous-time Markov chain based on the data in [4].

Current state i	$E_i[T_{15}]$	$V_i[T_{15}]$
1 (*Hymedesmia* sp. 1)	10.60	90.33
2 (*Crisia eburnea*)	7.49	78.09
3 (*Myxilla fimbriata*)	10.54	91.08
4 (*Mycale lingua*)	13.00	112.38
5 (*Filograna implexa*)	7.04	76.04
6 (*Urticina crassicornis*)	13.34	117.97
7 (*Ascidia callosa*)	6.32	74.63
8 (*Aplidium pallidum*)	7.13	78.49
9 (*Hymedesmia* sp. 2)	9.48	89.84
10 (*Idmidronea atlantica*)	6.98	78.89
11 (coralline algae)	7.67	78.40
12 (*Metridium senile*)	7.18	79.47
13 (*Parasmittina jeffreysi*)	7.09	78.28
14 (*Spirorbis spirorbis*)	5.41	70.31

Table 3

Mean ($E_i[J_{15}]$) and variance ($V_i[J_{15}]$) of number of state changes (dimensionless) separating each other current state i from state 15 (bare rock) in the time-reversed stationary continuous-time Markov chain based on the data in [4].

Current state i	$E_i[J_{15}]$	$V_i[J_{15}]$
1 (*Hymedesmia* sp. 1)	5.42	17.64
2 (*Crisia eburnea*)	4.35	17.38
3 (*Myxilla fimbriata*)	5.45	17.91
4 (*Mycale lingua*)	5.35	17.80
5 (*Filograna implexa*)	4.63	17.54
6 (*Urticina crassicornis*)	5.42	17.68
7 (*Ascidia callosa*)	4.41	17.41
8 (*Aplidium pallidum*)	4.86	17.76
9 (*Hymedesmia* sp. 2)	5.23	18.13
10 (*Idmidronea atlantica*)	4.68	17.79
11 (coralline algae)	4.68	17.50
12 (*Metridium senile*)	4.26	17.12
13 (*Parasmittina jeffreysi*)	4.73	17.83
14 (*Spirorbis spirorbis*)	3.97	16.54

Fig. 1. Cumulative distributions of first passage time (T_{15}, years) to state 15 (bare rock) from state 14 (*Spirorbis spirorbis*) in the time-reversed stationary discrete–time Markov chains based on the data in [4], with observation intervals 1 (solid line), 2 (broken line) and 5 (dash-dot line) years.
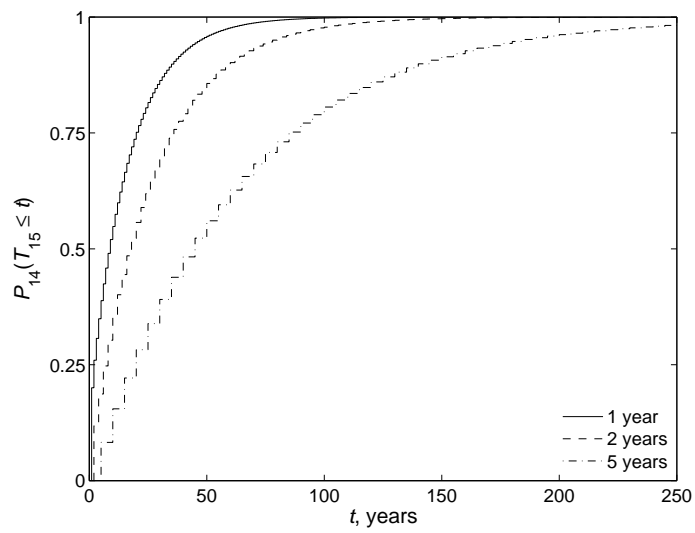
Fig. 2. Cumulative distributions of first passage time (T_{15}, years) to state 15 (bare rock) from each current state i (panel numbers) in the time-reversed stationary continuous-time (broken lines) and discrete-time (solid lines) Markov chains based on the data in [4]. See Table 2 for state names.
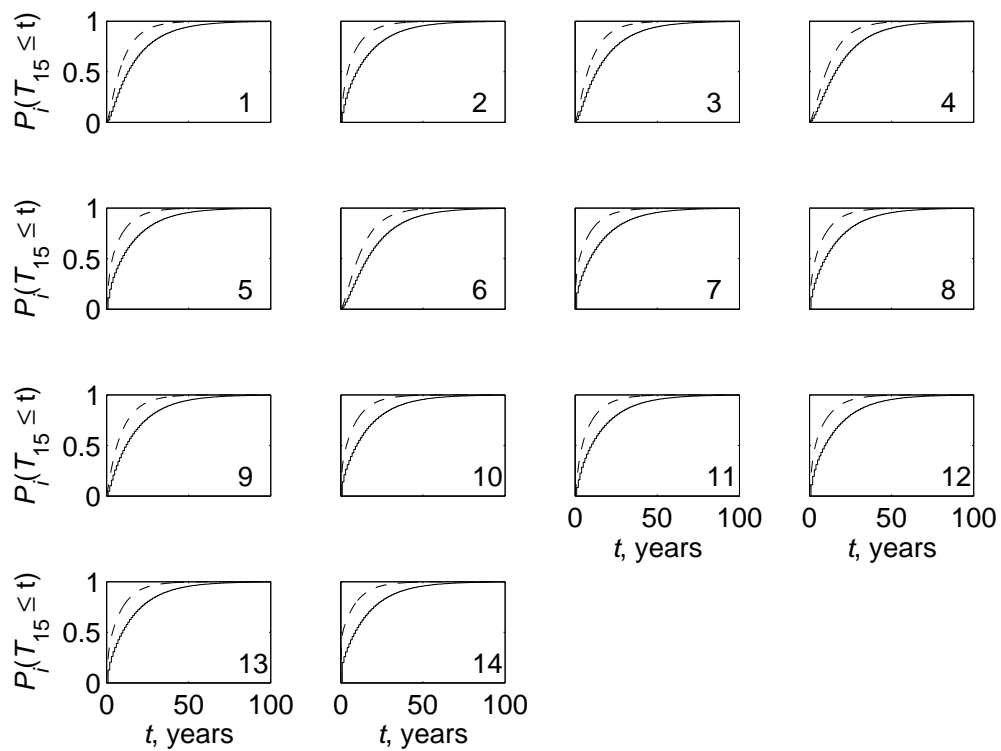
Fig. 3. Relationships between (a) stationary probability (π_i, dimensionless) and expected first passage time ($E_i[T_{15}]$, years) to state 15 (bare rock), (b) rate of leaving ($-q_{ii}$, years^{-1}) and expected first passage time to state 15, (c) stationary probability and rate of leaving, for all states i other than bare rock in the time-reversed stationary continuous-time Markov chain based on the data in [4].
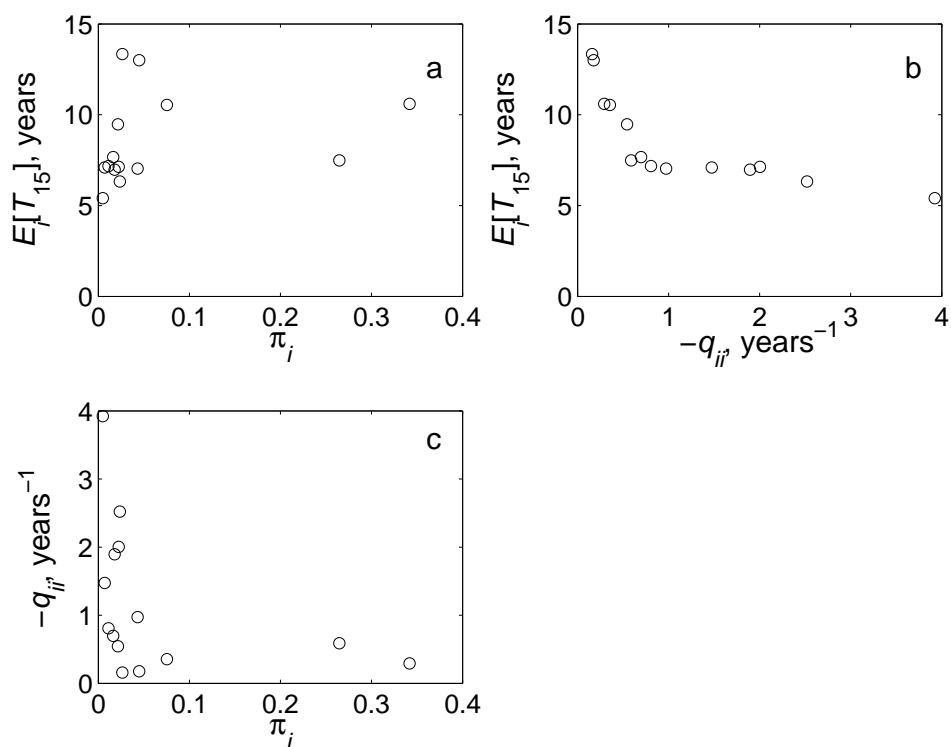
Fig. 4. Successional patterns where: (a) differences in successional rank result only from differences in the rate of colonization of bare rock (state j); and (b) differences in successional rank result from differences in the number of events separating a state from bare rock.
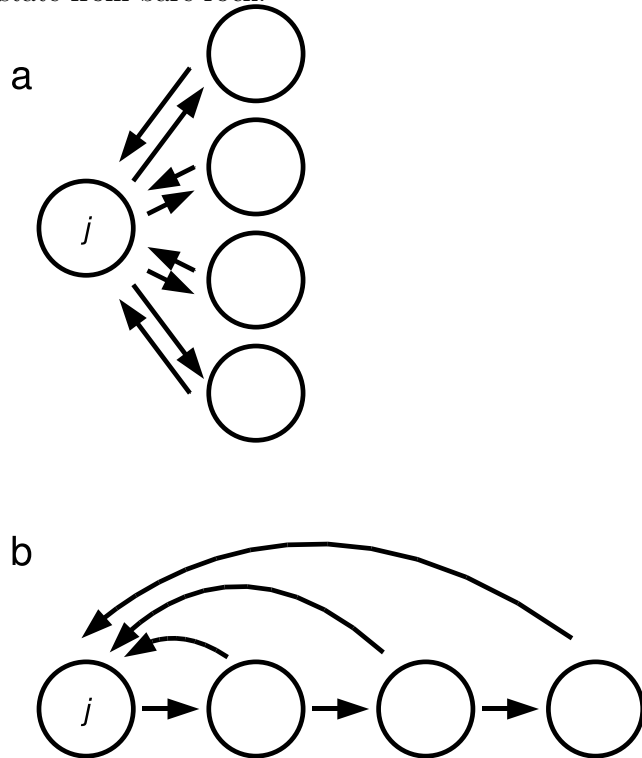
Fig. 5. Relationship between expected number of jumps ($E_i[J_{15}]$, dimensionless) and expected time ($E_i[T_{15}]$, years) to state 15 (bare rock), for all states i other than bare rock, in the time-reversed continuous-time Markov chain based on data in [4].