

Data-driven models for regional coral-reef dynamics

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Abstract

Coral reefs have been affected by natural and anthropogenic disturbances. Coral cover has declined on many reefs, and macroalgae have increased on some. The existence of alternative stable states with high or low coral cover has been widely debated, but not clearly established. We evaluate the evidence for alternative stable states in benthic coral-reef dynamics in the Caribbean, Kenya, and Great Barrier Reef (GBR), using stochastic semi-parametric models based on large numbers of time series of cover of hard corals, macroalgae, and other components. Only the GBR showed a consistent short-term regional decline in coral cover. There was no evidence for regional increases in macroalgae. The equilibrium distributions of our models were close to recently-observed distributions, and differed among regions. In all three regions, the equilibrium distributions were unimodal rather than bimodal, and thus did not suggest the existence of alternative stable states on a regional scale, under current conditions.

Introduction

Coral reefs have been affected by natural and anthropogenic impacts including overfishing, nutrient and sediment pollution, global climate change, and disease outbreaks (Hughes *et al.* 2003). For example, some Caribbean reefs shifted from high coral and low algal cover in the 1970s to high algal and low coral cover in the 1990s (Hughes 1994). In Kenya, the 1998 El Niño caused large, transient changes in reef composition (McClanahan 2008). In the Great Barrier Reef (GBR), average coral cover declined between 1986 and 2004 (Sweatman *et al.* 2011). The long-term consequences of these changes remain unclear. It has been suggested that coral reefs from all three regions can have alternative stable states, with either high or low coral cover under the same environmental conditions (e.g. Hatcher 1984; Knowlton 1992; McClanahan 1995; Mumby *et al.* 2007). The existence

of such states has important practical implications. If low-coral states are stable, disturbed reefs may not recover without changes in management (Hughes *et al.* 2010).

Although coral-reefs are often used as examples of ecosystems with alternative stable states (e.g. May 1977; Scheffer *et al.* 2001), direct evidence is scarce (Petraitis & Dudgeon 2004; Dudgeon *et al.* 2010). Several mathematical models have indicated that such states are possible. Some of these models are very abstract, and are not intended as realistic descriptions of natural reef dynamics (e.g. Knowlton 1992). Others are fully-specified, in the sense of assuming particular functional forms for biological processes such as growth, competition, and mortality (e.g. Mumby *et al.* 2007; Fung *et al.* 2011). If the assumed forms are inappropriate, or the parameter values are inaccurate, the models may not have the same equilibrium states as the real system. Thus, existing models tell us what is possible, rather than what actually occurs.

Here, we describe a new approach to modelling community dynamics, and apply it to benthic cover data from quantitative coral-reef surveys. Our model is partially specified (Wood 2001): rather than assuming a functional form for next year's reef composition given this year's, we estimate this form from the data in a flexible way. Although partially-specified models have a long history in ecological theory, their use as models of data has been limited. To obtain parameter estimates, we combine information from many short time series, which we treat as realizations of the same stochastic process. We fit our model to large databases of coral-reef benthic dynamics from the Caribbean, Kenya, and GBR, and show that it captures regional patterns. We use our model to estimate the regional equilibrium distributions of reef states if environmental conditions (including human impacts) remain as they were during the observation period. The resulting distributions tell us whether alternative stable states are likely under these conditions. We also find little evidence for consistent short-term trends in reef composition in the Caribbean and Kenya, but an apparent reduction in coral cover in the GBR over the observation period.

Material and methods

Data

We used monitoring data from the benthos of 138 reefs: 69 Caribbean, 14 Kenyan, and 55 on the GBR (Supporting Information, section S1.1). Each reef was surveyed in two or more consecutive years (Caribbean 1997-2006, Kenya 1991-2009, GBR 1996-2006) to quantify the proportion of the seafloor covered by living scleractinian corals ('coral' from here on), macroalgae ('algae', excluding turf, microscopic algae, and encrusting coralline algae) and 'others' (everything other than corals and algae). Thus we have compositional data with three categories (coral, algae, others), summing to 1 for any given observation. These data lie within the 2-simplex (Aitchison 1986, pp. 26-28), an equilateral triangle with compositions $[1, 0, 0]$, $[0, 1, 0]$, and $[0, 0, 1]$ at the vertices, and can be represented on a ternary plot. We define the state of a reef at any time as its composition (the proportions of coral, algae, and others), and the fate of a reef in a given state at a given time as its state the following year.

Model-free summaries

To obtain an overall picture of dynamics, we plotted all time series in each region on ternary axes. We then constructed model-free summaries as follows. For compositional data with three components, an appropriate measure of location is the centre $[g_1, g_2, g_3]/(g_1 + g_2 + g_3)$, where g_i is the geometric mean of the i th component (Aitchison 1989). We divided the 2-simplex into a grid of equilateral triangles, within each of which we calculated the centre of the states of those observations with known fate, and the centre of the corresponding fates. We plotted a vector from

the centre of the states to the centre of the fates for each triangle. We excluded one outlying observation with zero algal cover from the plot for the Kenyan data, because if any observation has a zero component, the centre has a corresponding zero component.

In addition, we used a simple numerical summary of year-to-year change in each region. For a reef with state \mathbf{x} and fate \mathbf{y} , we define the perturbation $\mathbf{v} = C(y_1/x_1, y_2/x_2, y_3/x_3)$, where

$$C(\mathbf{w}) = \mathbf{w} / \sum_i w_i \text{ (Aitchison 1986, p. 42). The vector norm } \|\mathbf{v}\| = \sqrt{\frac{1}{3} \sum_{i < j} \left(\log \frac{v_i}{v_j} \right)^2} \text{ (Pawlowsky-}$$

Glahn & Egozcue 2001) of the perturbation measures the amount of year-to-year change. We calculated the mean and standard deviation of the norms of year-to-year perturbations for each region, excluding two pairs \mathbf{x}, \mathbf{y} from the Kenyan data which contained the observation with zero algal cover (for which this norm is not defined).

To visualize regional changes over time, we plotted time series of the annual centres of the compositions (again, excluding the one Kenyan observation with zero algae).

Model

Assumptions

We assume that the sequence of observations on each reef within a region is an independent realization of the same stochastic process. We ignore spatial autocorrelation arising from dispersal and autocorrelated environmental conditions (e.g. Ninio *et al.* 2000). In the Supporting Information, section S1.2, we review the reasons why spatial autocorrelation may be fairly weak, and would increase our ability to detect alternative stable states if they existed. We have too few observations from each reef to model among-reef heterogeneity.

We also assume that the future states of reefs are conditionally independent of past states, given the current state. This Markovian assumption greatly simplifies the modelling, but is unlikely to be strictly true because, for example, community composition for given coral cover may depend on the length of time for which that cover has been maintained, and may affect future dynamics (Connell 1997).

In addition, we assume that the stochastic process generating observations on a reef is time-homogeneous, in the sense that the statistical properties of chance events such as storms are constant. Thus, we can model pairs of state and fate without regard to year. We further assume that we can predict the fate of a reef in a given state from the fates of reefs with similar states.

Finally, we ignore measurement error. To check whether this is reasonable, we developed a model of measurement error based on literature data (Supporting Information, section S1.13), and showed that our results do not have the characteristics of high measurement error (Supporting Information, section S2.8). Some of our data (Caribbean: 68/100 pairs of fate and state, GBR: 10/374 pairs) came from the Reef Check volunteer programme, which uses relatively low effort. Excluding these data had little effect on our main results (Supporting Information, section S2.8).

The justifications for these assumptions are discussed further in the Supporting Information, Section S1.2.

Model structure

Our model is based on a single discrete-time transition equation that updates the probability density function f_t of reef states at time t on the simplex to a new distribution f_{t+1} the next year:

$$f_{t+1}(\mathbf{q}) = \int k(\mathbf{q} | \mathbf{p}) f_t(\mathbf{p}) d\mathbf{p}. \quad (1)$$

The integral is over the entire set of possible compositions. The transition kernel $k(\mathbf{q} | \mathbf{p})$ describes the contribution of a reef in state \mathbf{p} at time t to the density of reefs with fate \mathbf{q} at time $t+1$. This is an integral equation, with the same form as integral projection models for size-structured populations (Easterling *et al.* 2000), except that reef state is a vector rather than a scalar. The simplest distribution for fate is a Dirichlet distribution (Supporting Information, section S1.4) with three components:

$$k(\mathbf{q} | \mathbf{p}) \sim \text{Dirichlet}(\boldsymbol{\alpha}(\mathbf{p})) \quad (2)$$

where $\boldsymbol{\alpha}(\mathbf{p})$ is a vector of three parameters, whose values depend on the state \mathbf{p} . These values are allowed to vary over the simplex in an arbitrary but smooth way, and are estimated using a local linear method (Fan & Gijbels 1996), with reef state as the explanatory variable. We describe the method graphically here (Fig. 1), and give technical details in the Supporting Information (sections S1.3 to S1.6). Matlab code is available as Supporting Information and from <http://www.liv.ac.uk/~matts/coralsimplex.html>.

For any focal point \mathbf{p} (Fig. 1a, large blue circle), we define a local neighbourhood using the half-taxi distance described in the Supporting Information, section S1.3 (Miller 2002, Fig. 1a: the local neighbourhood is hexagonal due to the geometry of the distance). The size of this neighbourhood is chosen by cross-validation to avoid overfitting (Supporting Information, section S1.6). We find all observations in the neighbourhood with known fates (Fig. 1a, blue circles observations, red dots fates). We estimate the transition kernel (probability distribution of fate of the focal point, Fig. 1b, shading) from the fates of these nearby observations, giving more weight to points closer to the focal point (Fig. 1a: hexagonal contours are equally spaced with respect to weight). In this case, there was an observation at the focal point (Fig. 1b, large blue circle), and its fate (Fig. 1b, red dot) is in the region of high probability density under the estimated transition kernel. However, we can construct a transition kernel estimate without an observation at the focal point.

Long-term equilibrium

We can find an approximate solution to the transition equation (Equation 1) by numerical integration (Supporting Information, sections S1.7-S1.8). In particular, we can estimate the equilibrium distribution which will be approached in the long term if conditions remain constant. If there are alternative stable states, we would expect an equilibrium distribution with two modes, separated by an area of low density. Such a bimodal distribution does not necessarily imply the existence of alternative stable states, because it could also arise from environmental heterogeneity. We return to this in the Discussion.

We also report summary statistics for equilibrium distributions (Supporting Information, section S1.9). We measure centre in the same way as for the empirical data, and add it to the time series plots of annual centres. We measure spread by the square root of the generalized variance of the log-ratio covariance matrix (Aitchison 1986, pp 76-78). We use a jackknife to estimate the standard error of the equilibrium distribution (Supporting Information, Section S1.11).

Equation 1 has a well-defined damping ratio (Rees & Ellner 2009, Appendix C), the ratio of the largest to second-largest absolute eigenvalues of the transition equation, which measures the rate of convergence to the equilibrium distribution. Higher values mean more rapid convergence (Caswell 2001, pp. 95-96).

Finally, iterating the transition equation, starting from the current distribution, shows us what trajectory to expect as the system approaches its equilibrium distribution. We used the empirical distribution function, with point masses of $1/n$ at the most recent observation on each of the n reefs, as an estimate of the current distribution.

Model checking

We used graphical and numerical checks on the behaviour of the model. First, we estimated the transition kernel for the centres in the model-free summary above. We drew vectors from each of the centres to the centres of their predicted fates. If the model is appropriate, this summary should look like the model-free summary. Second, we simulated data under the estimated model by sampling from the transition kernel for each observation with known fate. The resulting one-step trajectories should look like the real data if the model is appropriate. Third, we examined the distribution of standardized residuals between observed and predicted fates (Gueorguieva *et al.* 2008), as described in the Supporting Information (section S1.10).

Analysis of simulated data

To determine whether we could detect alternative stable states if they exist, we simulated 100 data sets with the same size and initial values as the Caribbean data (the smallest data set) under a stochastic differential equation model (Supporting Information, section S1.12) based on the ordinary differential equation model in Mumby *et al.* (2007). We used parameter values for which the ordinary differential equation model had two stable equilibria. We analyzed each simulated data set in the same way as the real data. We also checked that our methods are robust to measurement error by repeating these analyses after adding plausible levels of simulated measurement error (Supporting Information, section S1.13).

Results

Regional time series patterns

Most Caribbean reefs (Fig. 2a) have low to moderate cover of coral and algae. Most of their trajectories lie parallel to the others-algae or others-coral edges, implying that on the one-year timescale, simultaneous changes in coral and algal cover are rare. Instead, an increase in coral cover is usually balanced by a decrease in the cover of others, and vice versa. Similarly, an increase in algal cover is usually balanced by a decrease in the cover of others, and vice versa. In Kenya (Fig. 2b), reef composition is more equitable than in the other two regions. Trajectories that are not parallel to one of the edges, implying simultaneous change in all three components, are more common than in the other regions. In the GBR (Fig. 2c), most observations have very low algal cover and low to moderate coral cover. As in the Caribbean (Fig. 2a), simultaneous changes in coral and algal cover in the GBR are relatively rare (Fig. 2c).

There is little evidence of consistent short-term temporal trends in the Caribbean or Kenya (Fig. 3a and b). The centres of the annual distributions in these regions differ little between the start and end of the time period, although there are unusual years with large transient changes in composition. In the Great Barrier Reef, coral cover appears to decline over time, but there is no consistent increase in algal cover (Fig. 3b).

Model-free summaries

In all three regions, the model-free summaries (Fig. 2d-f) suggest convergence towards a single area of the simplex, but the lengths of the vectors and the location of the area to which they point differ between regions. In the Caribbean (Fig. 2d), the mean perturbation norm is large (Table 1), suggesting high year-to-year change. However, excluding Reef Check data reduces the mean perturbation norm for the Caribbean (Table 1), suggesting that some of this apparent change may be due to relatively low sampling effort in Reef Check. The vectors in the Caribbean (Fig. 2d) point towards low coral cover and moderate algal cover. In Kenya (Fig. 2e), the mean perturbation norm is larger than for the Caribbean without Reef Check (Table 1) and the vectors point towards an area

with more even composition than the other two regions. In the GBR (Fig. 2f), the mean perturbation norm is larger than for either the Caribbean without Reef Check or Kenya, and is little affected by excluding Reef Check data (Table 1). Vectors in the GBR are generally parallel to the others-algae edge (Fig. 2d), except when algal cover is very low, where they are very short. This suggests convergence towards a long, thin area with very low algal cover and low to moderate coral cover. The standard deviation of the perturbation norms (Table 1) is smallest for the Caribbean without Reef Check and largest for the GBR, suggesting greatest heterogeneity among reefs within the GBR.

Model-based results

Model-based mean vectors (Fig. 2g-i) look similar to the model-free summaries (Fig. 2d-f), and simulated fates (Supporting Information, Fig. S8) are similar to the observed data. Thus, our model captures the qualitative patterns in the data. The equilibrium distributions (Fig. 2j-l) differ between regions, and reflect the areas to which the model-free summaries suggested convergence. In the Caribbean (Fig. 2j), the equilibrium distribution has its centre close to the others-algae edge, with moderate algal cover and low coral cover (Table 1, centre of equilibrium). This centre has slightly lower coral cover and higher algal cover than annual centres for most years (Fig. 3a). In Kenya (Fig. 2k), the equilibrium distribution has highest density in a diagonal band of moderate to low coral cover and low algal cover. Its centre has moderate coral cover (Table 1) and is not atypical of the annual centres (Fig. 3b). In the GBR (Fig. 2l), the equilibrium distribution has most of its density near the others-coral edge, with a centre at moderate coral cover and low algal cover (Table 1). This centre has lower coral cover than the centres of all but the three most recent annual centres (Fig. 3c), but is not atypical in its algal cover. We do not know whether the observed trend in the GBR is associated with a change in the location of the equilibrium, although the absence of temporal trends in the residuals (Supporting Information, Fig. S14) suggests that it might not be.

Excluding Reef Check data for the Caribbean and GBR had little effect on the general appearance of the equilibrium distributions (Supporting Information, Fig. S32) or on their centres (Table 1). None of the regions have multimodal equilibrium distributions. The square roots of the generalized variances for the equilibrium distributions (Table 1, root generalized variance) are ranked GBR (with or without Reef Check) > Caribbean including Reef Check > Kenya > Caribbean excluding Reef Check. It is slightly counterintuitive that the equilibrium distribution for Kenya, which visually appears the most diffuse (Figure 2k), has a relatively low root generalized variance. This is because the Kenyan distribution has more probability further from the edges of the simplex than the other two regions. When one of the parts of a composition is small, a small absolute spread represents a large proportional spread, resulting in high generalized variance on the log ratio scale. The proportional scale may be more appropriate for the understanding of dynamics, because, for example, a constant per-capita growth rate represents constant proportional change. It has also been argued that the log ratio scale is the appropriate one for analysis of compositional data (Aitchison 1986, section 3.3). The estimated standard errors of the equilibrium distributions for all three regions are relatively small, and provide little support for long-term dynamics other than those presented in Figure 2 (Supporting Information, Figure S25).

The Caribbean including Reef Check has the highest damping ratio, followed by Kenya, the Caribbean excluding Reef Check, and the GBR (Table 1). Thus, we would expect the GBR to converge more slowly to its equilibrium distribution than the other two regions. This may be because algae have relatively fast dynamics (e.g. Jompa & McCook 2003), so that regions with low algal cover (such as the GBR) will change slowly.

Examination of residuals suggested a few unusual years or reefs, and areas in which there is scope for model improvement, but did not reveal any major flaws. Year 2005 was unusual in the Caribbean (Fig. 3a), where fates had unusually high algae and low others (Supporting Information, Fig. S12). In both Kenya and the GBR, the large 1998 El Niño event (Berkelmans & Oliver 1999; McClanahan

2008; McClanahan *et al.* 2008) was associated with unusual patterns of residuals (Fig. 3b and c, Supporting Information, Figs. S13 and S14). Excluding the few reefs with unusual patterns of residuals made little difference to the estimated equilibrium distributions (Supporting Information, Fig. S24).

Analysis of simulated data

Of 100 data sets simulated under a model with alternative stable states, 86 had bimodal estimated equilibrium distributions. One example is shown in Figure 4 (full details: Supporting Information, section S2.7). Thus, for at least some cases, our method can detect alternative stable states. Low sampling effort can affect the estimated locations of modes in the equilibrium distribution, but the real data do not show the characteristics of such problems (Supporting Information, section S2.8).

Discussion

Human activities have affected the composition of the world's reefs over the last three to four decades. Over-harvesting has reduced the abundance of top predators, ocean warming and disease outbreaks have reduced coral cover, and in intensely-fished regions, herbivore depletion (sometimes in conjunction with nutrient and sediment pollution) has facilitated an increase in fleshy macroalgae (Hughes *et al.* 2003). Recent analyses have quantified the effects of such disturbances by combining large numbers of surveys (e.g. Gardner *et al.* 2003; Bruno & Selig 2007; Wilkinson & Souter 2008; Paddack *et al.* 2009; Schutte *et al.* 2010). This has enabled reef scientists to compare impacts within and among regions, to estimate rates of change and temporal trends, and to measure the effectiveness of mitigation strategies such as marine reserves (Selig & Bruno 2010).

In the Caribbean and Kenya, we did not find consistent temporal trends (Fig. 3a and b). In Kenya, the largest annual change was associated with coral bleaching during the 1998 El Niño, followed by partial recovery (McClanahan 2008). In the GBR, there was a gradual reduction in coral cover over

the course of the study (Fig. 3c), although it is not clear whether this pattern is consistent across subregions of the GBR (Hughes *et al.* 2011; Sweatman *et al.* 2011; Sweatman & Syms 2011). We think it important that no regions show a trend towards increasing algal cover, implying that replacement of corals by macroalgae has not been widespread (Bruno *et al.* 2009). Nevertheless, if a region is far from equilibrium, short-term trends may not reveal the full effects of past disturbances. Estimating the equilibrium distribution of reef composition is therefore important.

Our models enabled us to estimate these equilibrium distributions under recent environmental conditions, with few assumptions about the underlying processes. The equilibrium distributions differ between the Caribbean, Kenya, and the GBR, as expected given their different environmental settings and species composition. More surprisingly, all three regions appear fairly close to these equilibrium distributions, with differences between current and equilibrium distributions decaying rapidly over time (Supporting Information, section S2.3). This implies that recent changes in the locations of equilibrium distributions have been slow enough for the current distribution of reef states to track them fairly closely. The rarity of year-to-year changes towards high algal cover (Figs. 2a-c) is also surprising given the widely held assumption that this is the dominant trajectory of modern reefs (Hughes *et al.* 2010).

The state of coral-reef communities has long been known to be highly dynamical. Within a region, coral cover may be increasing on some reefs and decreasing on others, yet the overall system may be close to a dynamic equilibrium (Bythell *et al.* 2000; Bruno & Selig 2007; Schutte *et al.* 2010). Thus, the equilibrium distribution describes the proportion of time we expect an individual reef to spend in each part of the phase space. We do not assume that any particular reef is close to the state to which it would converge in the absence of disturbance.

Our estimated equilibrium distributions are not temporal forecasts of what will happen, but projections of what would happen if environmental conditions remained as they were during the

survey period. It is likely that environmental conditions, including natural or anthropogenic disturbance regimes, will change. As a result, the future distribution of coral-reef states could look different from our estimated equilibria. The same issue affects asymptotic analyses of structured population models, which nevertheless give useful information about current conditions (Caswell 2001, p. 30).

Determining whether coral reefs have alternative stable states is important for both ecological theory and reef management. Restoration of algal-dominated reefs may be difficult if reefs have alternative stable states, because it may require larger changes in environmental conditions than if reefs have a single equilibrium whose location depends on the environment (Hughes *et al.* 2005; Dudgeon *et al.* 2010). We found no evidence for bimodal equilibrium distributions, and thus no evidence for alternative stable states under the conditions prevailing during our sample period. A bimodal equilibrium distribution is expected if a system has alternative stable states. Each state's basin of attraction will correspond to a high-density region or mode in the equilibrium distribution of a stochastic process in phase space, generating the stochastic equivalent of "a dynamical landscape pockmarked with many different valleys, separated by hills and watersheds" (May 1977) It is possible for the deterministic skeleton underlying a stochastic system to have alternative stable states sufficiently close together that they are not separated by low-density regions in the stochastic equilibrium distribution. However, in such cases, the system would not become trapped at one or other of the modes for long periods of time, and would not therefore have alternative stable states in any meaningful sense.

Our result is consistent with recent reviews of the evidence for alternative stable states in coral-reef ecosystems, which concluded that they are uncommon (Petraitis & Dudgeon 2004; Dudgeon *et al.* 2010). Mumby (2009) suggested that the absence of bimodality in regional distributions of recent coral and macroalgal cover (Bruno *et al.* 2009) is due to slow transient dynamics in a system with

alternative stable states. However, neither recently observed data (Bruno *et al.* 2009) nor our estimated equilibria suggest bimodality in benthic cover.

Had we found bimodal equilibrium distributions, their interpretation would have been more complicated. A bimodal estimated equilibrium distribution is necessary but not sufficient for the existence of alternative stable states. It could also be caused by environmental heterogeneity, if there were subsets of reefs with different equilibrium distributions arising from differences in environmental conditions. Such cases should show up as sets of reefs with unusual residuals. The removal of the small number of unusual reefs did not substantially alter our conclusions (Supporting Information, sections S2.4, S2.5), and in any case, our estimated equilibrium distributions were not bimodal. These subsets of unusual reefs were too small to analyze separately, but it is possible that they have different dynamics from the majority of reefs. It is also possible that our sample of reefs may not be representative of the population in each region.

There have been major historical changes in the distribution of reef states in some regions (e.g. Hughes 1994). Since our analysis is based only on data from the 1990s onwards, we cannot draw any conclusions about past declines in coral cover, or past or future alternative stable states. For example, it has been suggested that there were alternative stable states for Caribbean reefs in the 1980s, after overfishing and mass mortality of sea urchins (Mumby *et al.* 2007), although the subsequent recovery of both coral cover and urchins suggest that a phase shift in response to press perturbation is a more plausible explanation (Dudgeon *et al.* 2010). In addition, there can be rapid changes in community structure as environmental conditions change (phase shifts), even in the absence of alternative stable states (Dudgeon *et al.* 2010). Thus, our findings do not conflict with historical data.

The fact that the dynamics of an individual reef might have a time scale of decades (McClanahan 2000; McClanahan *et al.* 2007) would not prevent us from detecting alternative stable states, given

multiple short time series each spanning a small part of the simplex (Fig. 4). Similarly, lack of knowledge about the benthic composition of alternative stable states is not a major problem. Alternative stable states other than those with high coral or high algae may include urchin barrens and compositions dominated by corallimorphians, soft corals, or sponges (Norström *et al.* 2009), all of which represent high abundance of others in our analyses. Since we are using the data rather than a fully-specified model to determine whether alternative stable states exist, these states would not be harder to detect than those with high coral or algal cover. Detecting states with very low others would be difficult, as we have few observations in this part of the simplex, but we are not aware that such states are thought to exist. There could also be alternative states that do not influence benthic cover greatly, or where coral cover is one of the components least and last affected, as found for a broad-scale survey of western Indian Ocean reefs (McClanahan *et al.* 2011).

Apart from a few unusual years, our model describes the data fairly well. The higher than expected algal variance may be a consequence of rapid change in these unusual years, and could be accommodated in two ways. First, there are more flexible distributions than the Dirichlet for compositional data, although they require more parameters (Aitchison 1986, chapter 6). Second, the local linear models we used to estimate the parameters of the Dirichlet distribution contain only reef state as an explanatory variable (Supporting Information, section S1.5), but could include environmental variables such as sea surface temperature, storm occurrences, or sediment loads. This latter approach would allow us to predict equilibrium distributions under environmental conditions different from the current ones. In addition, heterogeneity in environmental conditions among reefs could either mask the existence of alternative stable states in a subset of reefs, or give the appearance of alternative stable states when in fact there is only a single stable state. Modelling the effects of environmental variables would address this problem (Hughes *et al.* 2010).

Other regional models of coral cover (e.g. Wolanski *et al.* 2004; Melbourne-Thomas *et al.* 2010) take a very different approach, with fully-specified differential equation models of reef dynamics coupled

to hydrodynamic larval dispersal models. Such models are far more mechanistically realistic than ours, but involve many more assumptions. Our approach complements these models by providing a summary of dynamics, including the number and type of basins of attraction, which any plausible fully-specified model should be able to reproduce. Our model and these other regional models are relatively simple and general, and therefore provide a different perspective to detailed single-reef models (e.g. Mumby *et al.* 2006).

Our approach is not in principle limited to compositional data. The transition equation (Equation 1) and the local linear method for parameter estimation could be applied to multivariate time series of population densities, given suitable modifications to the transition kernel. In conclusion, semi-parametric modelling of community dynamics complements more conventional approaches, and will become increasingly useful as more long ecological time series become available.

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Literature Cited

- Aitchison J. (1986). *The statistical analysis of compositional data*. Chapman and Hall, London.
- Aitchison J. (1989). Measures of location of compositional data sets. *Math. Geol.*, 21, 787-790.
- Berkelmans R. & Oliver J.K. (1999). Large-scale bleaching of corals on the Great Barrier Reef. *Coral Reefs*, 18, 55-60.
- Bruno J.F. & Selig E.R. (2007). Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLoS One*, 2.
- Bruno J.F., Sweatman H., Precht W.F., Selig E.R. & Schutte V.G.W. (2009). Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology*, 90, 1478-1484.
- Bythell J., Hillis-Starr Z. & Rogers C. (2000). Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series*, 204, 93-100.
- Caswell H. (2001). *Matrix population models: construction, analysis, and interpretation*. Second edn. Sinauer, Sunderland, Massachusetts.
- Connell J.H. (1997). Disturbance and recovery of coral assemblages. *Coral Reefs*, 16, S101-S113.
- Dudgeon S.R., Aronson R.B., Bruno J.F. & Precht W.F. (2010). Phase shifts and stable states on coral reefs. *Mar. Ecol.-Prog. Ser.*, 413, 201-216.
- Easterling M.R., Ellner S.P. & Dixon P.M. (2000). Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81, 694-708.
- Fan J. & Gijbels I. (1996). Local polynomial modelling and its applications. In: Chapman and Hall London.
- Fung T., Seymour R.M. & Johnson C.R. (2011). Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology*, 92, 967-982.
- Gardner T.A., Cote I.M., Gill J.A., Grant A. & Watkinson A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301, 958-960.
- Gueorguieva R., Rosenheck R. & Zelterman D. (2008). Dirichlet component regression and its applications to psychiatric data. *Comput. Stat. Data Anal.*, 52, 5344-5355.
- Hatcher B.G. (1984). A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. *Coral Reefs*, 3, 199-204.
- Hughes T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547-1551.
- Hughes T.P., Baird A.H., Bellwood D.R., Card M., Connolly S.R., Folke C., Grosberg R., Hoegh-Guldberg O., Jackson J.B.C., Kleypas J., Lough J.M., Marshall P., Nystrom M., Palumbi S.R., Pandolfi J.M., Rosen B. & Roughgarden J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929-933.
- Hughes T.P., Bellwood D.R., Baird A.H., Brodie J., Bruno J.F. & Pandolfi J.M. (2011). Shifting baselines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al. (2011). *Coral Reefs*, 30, 653-660.
- Hughes T.P., Bellwood D.R., Folke C., Steneck R.S. & Wilson J. (2005). New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology & Evolution*, 20, 380-386.
- Hughes T.P., Graham N.A.J., Jackson J.B.C., Mumby P.J. & Steneck R.S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution*, in press.
- Jompa J. & McCook L.J. (2003). Coral-algal competition: macroalgae with different properties have different effects on corals. *Mar. Ecol.-Prog. Ser.*, 258, 87-95.
- Knowlton N. (1992). Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.*, 32, 674-682.

- May R.M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269, 471-477.
- McClanahan T.R. (1995). A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.*, 80, 1-19.
- McClanahan T.R. (2000). Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biol. Conserv.*, 94, 191-198.
- McClanahan T.R. (2008). Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia*, 155, 169-177.
- McClanahan T.R., Ateweberhan M. & Omukoto J. (2008). Long-term changes in coral colony size distributions on Kenyan reefs under different management regimes and across the 1998 bleaching event. *Mar. Biol.*, 153, 755-768.
- McClanahan T.R., Graham N.A.J., Calnan J.M. & MacNeil M.A. (2007). Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.*, 17, 1055-1067.
- McClanahan T.R., Graham N.A.J., Macneil M.A., Muthiga N.A., Cinner J.E., Bruggemann J.H. & Wilson S.K. (2011). Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 17230-3.
- Melbourne-Thomas J., Johnson C.R., Aliño P.M., Geronimo R.C., Villaloy C.L. & Gurney G.G. (2010). A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. *Environmental Modelling and Software*, in press.
- Miller W.E. (2002). Revisiting the geometry of a ternary diagram with the half-taxi metric. *Math. Geol.*, 34, 275-290.
- Mumby P.J. (2009). Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs*, 28, 761-773.
- Mumby P.J., Hastings A. & Edwards H.J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, 450, 98-101.
- Mumby P.J., Hedley J.D., Zychaluk K., Harborne A.R. & Blackwell P.G. (2006). Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model. *Ecol. Model.*, 196, 131-148.
- Ninio R., Meekan M., Done T. & Sweatman H. (2000). Temporal patterns in coral assemblages on the Great Barrier Reef from local to large spatial scales. *Mar. Ecol.-Prog. Ser.*, 194, 65-74.
- Norström A.V., Nyström M., Lokrantz J. & Folke C. (2009). Alternative states on coral reefs: beyond coral-macroalgal phase shifts. *Mar. Ecol.-Prog. Ser.*, 376, 295-306.
- Paddack M.J., Reynolds J.D., Aguilar C., Appeldoorn R.S., Beets J., Burkett E.W., Chittaro P.M., Clarke K., Esteves R., Fonseca A.C., Forrester G.E., Friedlander A.M., García-Sais J., González-Sansón G., Jordan L.K.B., McClellan D.B., Miller M.W., Molloy P.P., Mumby P.J., Nagelkerken I., Nemeth M., Navas-Camacho R.I., Pitt J., Polunin N.V.C., Reyes-Nivia M.C., Robertson D.R., Rodríguez-Ramírez A., Salas E., Smith S.R., Spieler R.E., Steele M.A., Williams I.D., Wormald C.L., Watkinson A.R. & Côté I.M. (2009). Recent region-wide declines in Caribbean reef fish abundance. *Current biology : CB*, 19, 590-595.
- Pawlowsky-Glahn V. & Egozcue J.J. (2001). Geometric approach to statistical analysis on the simplex. *Stochastic Environmental Research and Risk Assessment*, 15, 384-398.
- Petraitis P.S. & Dudgeon S.R. (2004). Detection of alternative stable states in marine communities. *J. Exp. Mar. Biol. Ecol.*, 300, 343-371.
- Rees M. & Ellner S.P. (2009). Integral projection models for populations in temporally varying environments. *Ecol. Monogr.*, 79, 575-594.
- Scheffer M., Carpenter S., Foley J.A., Folke C. & Walker B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591-596.
- Schutte V.G.W., Selig E.R. & Bruno J.F. (2010). Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Mar. Ecol.-Prog. Ser.*, 402, 115-122.

- Selig E.R. & Bruno J.F. (2010). A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PLoS One*, 5, e9278.
- Sweatman H., Delean S. & Syms C. (2011). Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs*, 30, 521-531.
- Sweatman H. & Syms C. (2011). Assessing loss of coral cover on the Great Barrier Reef: A response to Hughes et al. (2011). *Coral Reefs*, 30, 661-664.
- Wilkinson C. & Souter D. (2008). Status of Caribbean coral reefs after bleaching and hurricanes in 2005. In. Global Coral Reef Monitoring Network, and Reef and Rainforest Research Centre Townsville, Australia, p. 152.
- Wolanski E., Richmond R.H. & McCook L. (2004). A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. *J. Mar. Syst.*, 46, 133-144.
- Wood S.N. (2001). Partially specified ecological models. *Ecol. Monogr.*, 71, 1-25.

Tables

Table 1. Summary statistics for coral-reef dynamics in the Caribbean, Kenya, and GBR: mean and standard deviation of norms of year-to-year perturbations, centre and square root generalized variance of equilibrium distribution, and damping ratio. For the Caribbean and GBR, figures after the / are without Reef Check data, which contributed 68 of 100 pairs of fate and state in Caribbean and 10 of 374 pairs in GBR.

Dataset	Caribbean	Kenya	GBR
mean perturbation norm	0.93 / 0.58	0.70	0.80 / 0.79
sd perturbation norm	0.68 / 0.41	0.56	0.68 / 0.68
centre of equilibrium	[0.09,0.20,0.71]	[0.27,0.08,0.65]	[0.26, 0.02, 0.71]
/ centre without Reef Check	/ [0.08, 0.24, 0.68]	-	/ [0.27, 0.02, 0.71]
root generalized variance	1.04 / 0.83	0.91	1.57 / 1.56
damping ratio	1.47 / 1.26	1.36	1.09 / 1.10

Figures

Figure 1. Graphical summary of the modelling approach. (a). Focal point (large blue circle), local neighbourhood (hexagonal region, contours equally spaced with respect to the weight given to points), points in local neighbourhood (blue circles), fates of those points (red dots, connected to points by grey lines). (b) Estimated Dirichlet distribution of fate for the focal point (lighter colours are higher probability density). The blue circle is the focal point and the red dot is its actual fate. Data from the Great Barrier Reef, with an arbitrarily chosen focal point.

Figure 2. Observed and modelled reef dynamics. (a-c): observed dynamics of reefs in (a) the Caribbean, (b) Kenya, and (c) the Great Barrier Reef. Each blue circles is the first observation in a set of two or more consecutive years on a single reef. Subsequent observations are black dots connected by black lines, with a red dot for the last observation in the sequence. (d-f): model-free summaries of reef dynamics in (d) the Caribbean, (e) Kenya, and (f) the Great Barrier Reef. The simplex is divided into small triangles. Observations for which there is also an observation on the same reef the following year are shown as grey dots. Blue circles are the centres of all such state observations in each triangle. Red dots connected by black lines are the centres of the corresponding fates. (g-i): Model-based summaries of reef dynamics in (g) the Caribbean, (h) Kenya, and (i) the Great Barrier Reef. Blue circles are the centres of state observations in the small triangles in (d-f). For each of these, the red dot connected by a black line is the centre of the probability distribution of fate estimated as in Fig. 1. (j-l): Estimated equilibrium distributions for (j) the Caribbean, (k) Kenya, and (l) the Great Barrier Reef. Lighter colours are higher probability densities. The upper limit of the scale is at 25 to show detail in the Caribbean and Kenya data, although the density for the Great Barrier Reef goes up to 82 in the white area along the bottom edge.

Figure 3. Annual centres for (a) Caribbean, (b) Kenya, and (c) Great Barrier Reef. The start of each time series is shown as a blue circle, and the end as a red dot. The centres of the estimated equilibria are marked as blue crosses. Years with unusual residuals are labelled (in Kenya, 1999 is the calendar year of the observations immediately following the 1998 El Niño). Only the portion of the simplex bounded by both coral and algal cover no greater than 0.5 is shown.

Figure 4. A simulated data set with alternative stable states (a: symbols as in Figure 2 a-c), and its estimated equilibrium distribution (b: colour scale as in Figure 2 j-l). Initial values and time series lengths in the simulated data set match those for the real Caribbean data.

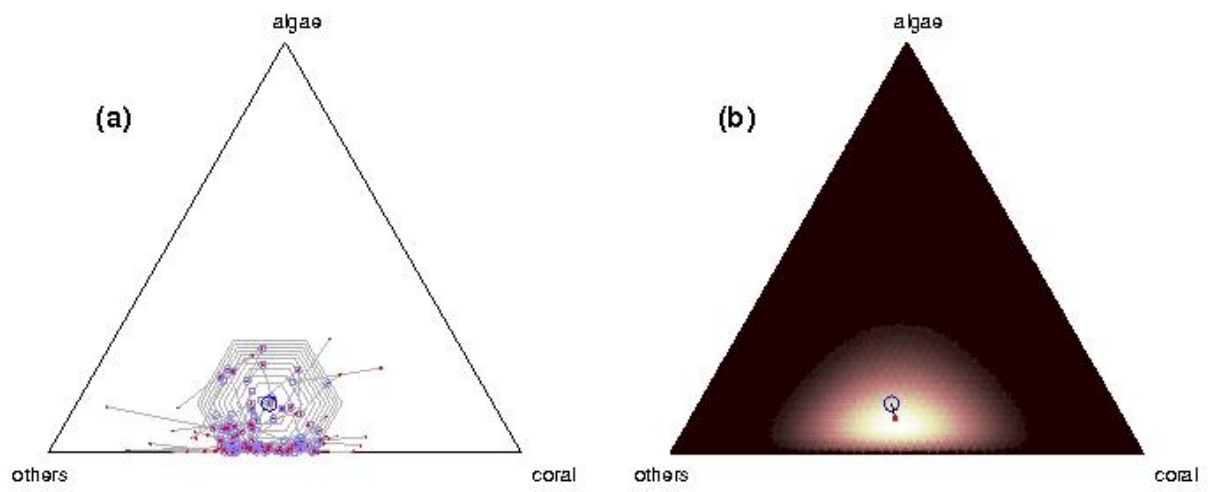


Figure 1

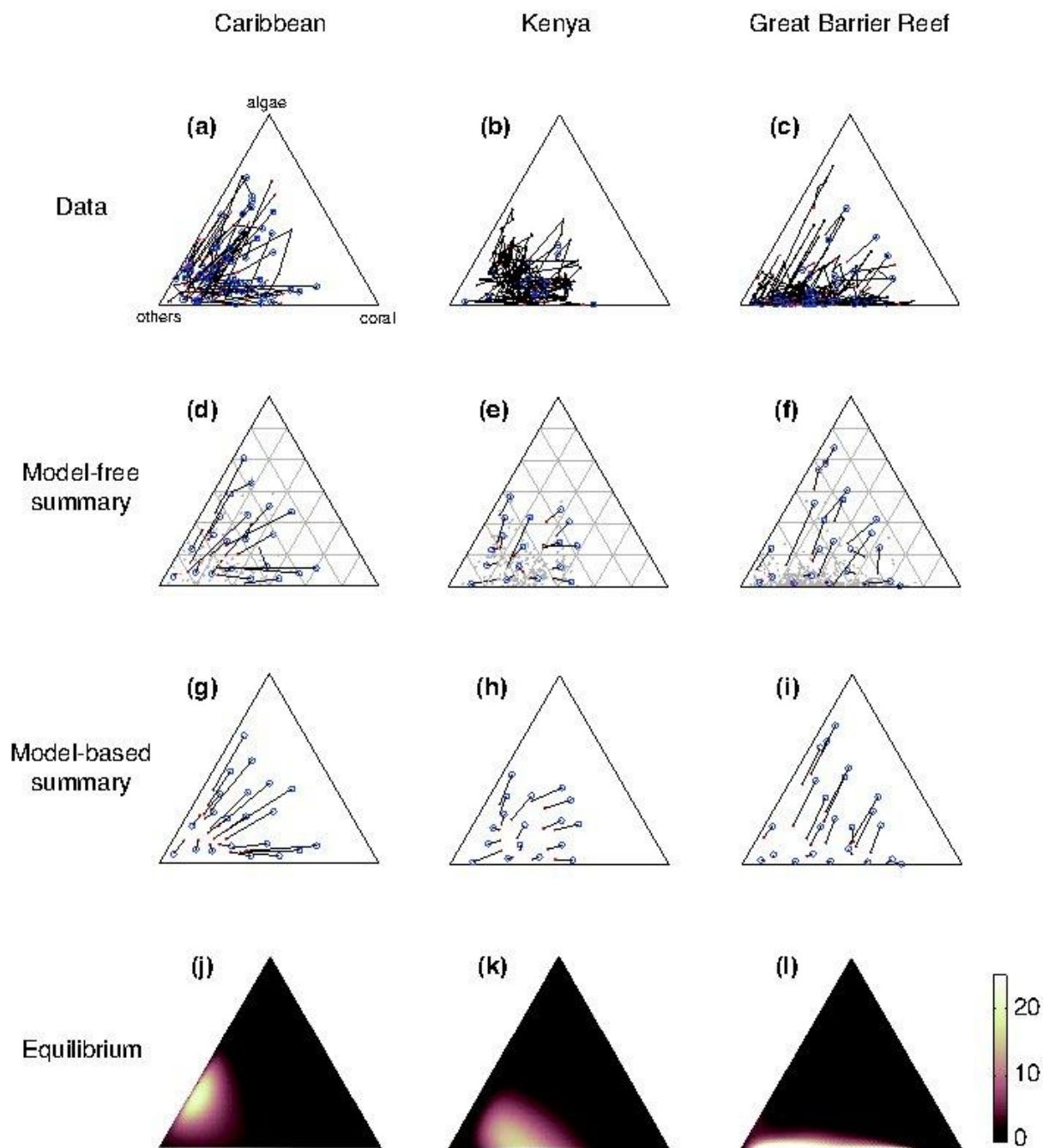


Figure 2

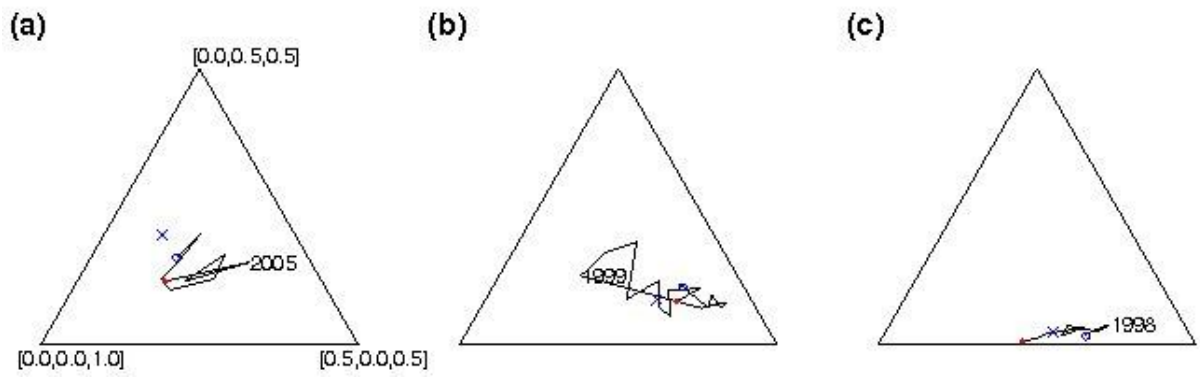


Figure 3

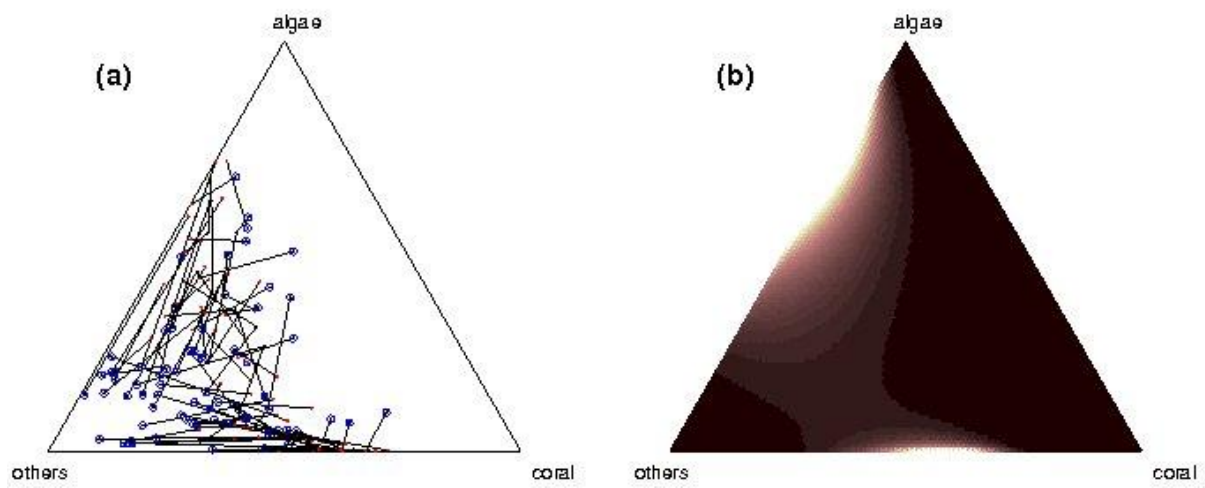


Figure 4