



## Evidence for and against the existence of alternate attractors on coral reefs

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Synthesis

Coral reefs are widely thought to exhibit multiple attractors which have profound implications for people that depend on them. If reefs become 'stuck' within a self-reinforcing state dominated by seaweed, it becomes disproportionately difficult and expensive for managers to shift the system back towards its natural, productive, coral state.

The existence of multiple attractors is controversial. We assess various forms of evidence and conclude that there remains no incontrovertible proof of multiple attractors on reefs. However, the most compelling evidence, which combines ecological models and field data, is far more consistent with multiple attractors than the competing hypothesis of only a single, coral attractor. Managers should exercise caution and assume that degraded reefs can become stuck there.

Testing for the existence of alternate attractors in ecosystems that possess slow dynamics and frequent pulse perturbation is exceptionally challenging. Coral reefs typify such conditions and the existence of alternate attractors is controversial. We analyse different forms of evidence and assess whether they support or challenge the existence of multiple attractors on Caribbean reefs, many of which have shown profound phase shifts in community structure from coral to algal dominance. Field studies alone provide no insight into multiple attractors because the non-equilibrium nature of reef dynamics prevents equilibria from being observed. Statistical models risk failing to sample the parameter space in which multiple attractors occur, and have failed to account for the confounding effects of heterogeneous environments, anthropogenic drivers (e.g. fishing), and major disturbances (e.g. hurricanes). Simple and complex models all find multiple attractors over some – though not all – regions of a system driver (fishing). Tests of model predictions with field data closely match theory of alternate attractors but a forward-leaning monotonic curve with only a single attractor can also be fitted to these data. Deeper consideration of the assumptions of this monotonic relationship reveal significant ecological problems which disappear under a model of multiple attractors. To date, there is no evidence against the existence of multiple attractors on Caribbean reefs and while there remains no definitive proof, the balance of evidence and ecological reasoning favours their existence. Theory predicts that Caribbean reefs do not exhibit alternate attractors in their natural state but that disease-induced loss of two key functional groups has generated bistability. Whether alternate attractors becomes a persistent element of reef dynamics or a brief moment in their geological history will depend, in part, on the ability of functional groups to recover and the impacts of climate change and ocean acidification on coral growth and mortality.

The concept of alternate attractors of community state first emerged in marine ecosystems during the late 1960s (Lewontin 1969), and has formed a core theme of ecology ever since (Holling 1996, Gunderson 2000, Beisner et al. 2003). Interest in alternate attractors has been driven, in part, by the profound management implications of ecosystems getting trapped in potentially undesirable states. If a system exhibits alternate attractors, there is likely to be a hysteretic dynamic that makes reversal or restoration of an ecosystem increasingly difficult as the system degrades (Suding et al. 2004, Suding and Hobbs 2009).

Much of the fundamental theory of alternate attractors developed in the 1970s (Holling 1973, Sutherland 1974,

May 1977), yet despite more than three decades of subsequent study, their existence continues to be contested in a number of ecosystems including rangelands (Oliva et al. 1998, Briske et al. 2003), inter-tidal rocky shores (Bertness et al. 2002, Petraitis and Dudgeon 2004), and coral reefs (Bruno et al. 2009). Controversy over the existence of alternate attractors has three principal sources. The first occurs because a diversity of approaches have been taken to test for alternate attractors yet few are capable of providing an equivocal test. Schröder et al. (2005) reviewed 35 experimental tests of alternate attractors yet considered 14 of them to be inadequate, mostly because the time series were too short. Controversy also tends to arise when a given set

of empirical observations are considered to support alternative interpretations (Connell and Sousa 1983). Lastly, if alternate attractors do occur they are often restricted to specific parts of a system's parameter space (Chase 2003). Therefore, a pair of studies may genuinely find opposing evidence for the existence of alternate attractors if they sample different environments.

Most successful demonstrations of alternate attractors have been undertaken under experimental laboratory conditions, typically using organisms with high population turnover (Schröder et al. 2005). However, testing for the existence of alternative attractors in larger ecosystems is often problematical (Scheffer and Carpenter 2003) and many of the challenges are exemplified when considering the case of coral reefs. First, the dynamics of the main state variable, coral cover, occur slowly on time scales of years to decades (Halford et al. 2004, Adjeroud et al. 2009) that do not lend themselves to experimental observation. Second, because coral reefs are disturbance-driven ecosystems, with frequent cyclone impacts (Connell 1978), it is rare that their stable equilibria can be observed in situ. Third, many coral reefs face so much anthropogenic disturbance that large-scale manipulations of coral would not be permitted (Petraitis and Dudgeon 2004).

Although manipulative experiments will usually provide the greatest certainty in testing for alternate attractors, other approaches may still provide important insights where experiments are infeasible. Thus, field studies, statistical models, and mechanistic models all have a role to play in evaluating the existence and form of ecosystem stability (Carpenter 2003, Scheffer and Carpenter 2003). Here, we consider the evidence for and against the existence of alternate attractors on coral reefs. By taking each type of evidence in turn, we aim to clarify some of the misconceptions that have arisen in the coral reef literature while also attempting to reconcile the apparent disagreement between evidence derived from models versus the field. While we draw heavily on published evidence we also undertake new analyses. We conclude that definitive proof of alternate attractors remains lacking but 1) there is no compelling evidence against the existence of alternate attractors and 2) that the balance of evidence supports a nuanced view in which alternate attractors are a recent phenomenon for coral reefs that are context-specific and potentially ephemeral.

## Coral reef phase shifts and the role of alternate attractors

We begin by reviewing the theory of alternate attractors as it pertains to phase shifts on coral reefs. The term phase shift was introduced to describe a marked change in the community structure of a coral reef (Done 1992). The most common phase shift is a switch from coral to algal dominance but other outcomes are possible including urchin barrens (Bellwood et al. 2004), soft corals, or sponges (Norstrom et al. 2009). Phase shifts can be caused by many drivers but those that are relevant for alternate attractors must sit outside the system and be either independent of the system's state or only weakly coupled to it (Beisner et al. 2003, Scheffer and Carpenter 2003). Thus, the primary drivers of an algal bloom are either fishing of herbivores (McManus et al. 2000) or eutrophication (Banner 1974). Here we will focus on fishing. Note that corals usually have to experience mortality from an external event, such as a cyclone, before an algal bloom will occur (Mumby and Steneck 2008).

The existence of a phase shift makes no assertion about stability and a continuum of possible relationships could occur between ecosystem state (coral cover) and the external driver (fishing), which is also referred to as the 'conditions' (Scheffer and Carpenter 2003) or 'environmental parameter' (Petraitis and Dudgeon 2004). At one extreme is a simple linear relationship between coral and fishing (Fig. 1a). Note that rather than plotting fishing intensity, which is difficult to quantify, we plot the outcome of fishing, which is the grazing potential of herbivorous fish (a measure of grazing potential is the proportion of reef area maintained in a grazed state). Grazing potential increases with a higher abundance of herbivores and is therefore inversely related to fishing. The mechanism behind the increase in coral with grazing is competition for space between corals and algae (McCook et al. 2001); as grazing levels increase, the abundance of fleshy algae decrease which favours a higher abundance of coral.

A more complex, threshold relationship might emerge if the influence of the driver is non-linear, albeit retaining a monotonic increase (Fig. 1b). There are two important implications of this monotonic function. First, for any level of the driver (fishing/grazing) there is only a single attractor or equilibrium state (phase). Second, a decline of

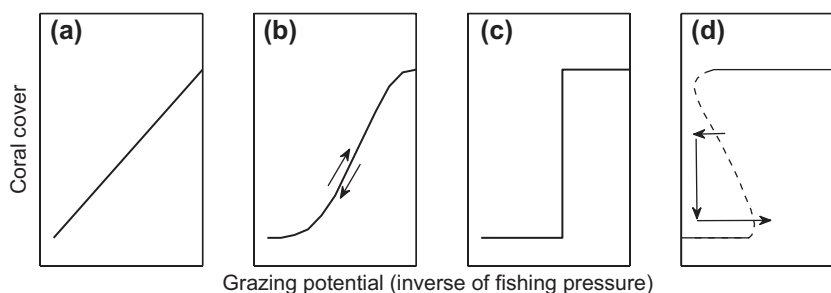


Figure 1. Extremes from a continuum of possible relationships between ecosystem state (coral) and an external driver (grazing potential) from linear (a), threshold monotonic increase (b), severe threshold with alternate states (c), and alternate states with hysteresis (d). Arrows indicate that reversals of state are simple in (b) but complex in (d) where a small decline in grazing can shift the system into decline but a much larger increase in grazing is needed to restore the system. Dashed line denotes unstable equilibrium.

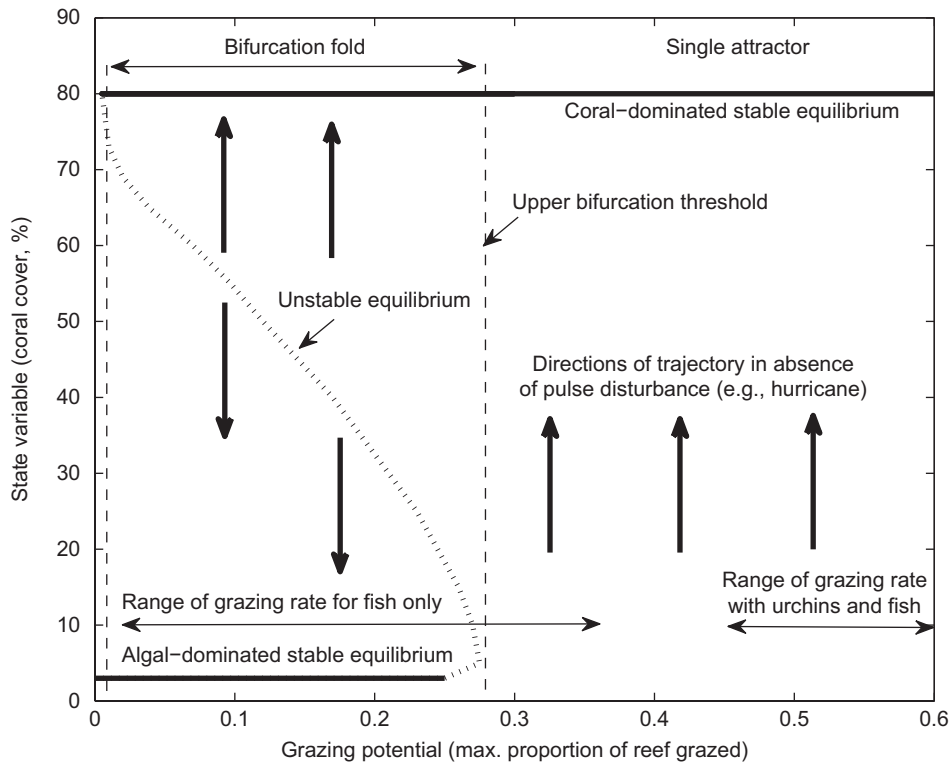


Figure 2. Theoretical framework for the ecological resilience of a Caribbean coral reef in the absence of the branching coral *Acropora cervicornis*. Note that range of grazing potential for fish does not reach zero and subsequent figures do not display the left side of the bifurcation fold.

ecosystem state can be reversed ‘simply’ by returning the driver back to a previous level (Fig. 1b). In principle, a threshold relationship can be so acute that a system can exhibit more than one attractor across a very narrow range of the driver (Fig. 1c, Dudgeon et al. 2010). More commonly, however, alternate attractors are predicted to occur over a range of fishing levels (Fig. 1d). So, at some fixed intermediate level of grazing potential, the trajectory of coral can follow one of three paths (Fig. 1d). It can 1) exhibit growth/recovery such that the combined effects of colonisation and growth outweigh mortality (a coral-dominated attractor), 2) it can remain constant, or 3) it can exhibit decline such that mortality rates exceed the capacity for recovery (coral-depauperate or algal-dominated attractor). To understand these dynamics we have to consider the ecology of the system and we focus here on Caribbean coral reefs because many have experienced a phase shift in recent decades (Gardner et al. 2003).

A little terminology is required to discuss alternate attractors and this is illustrated using a modelled representation of coral cover versus grazing potential (Fig. 2). The two attractors are theoretically stable equilibria representing absolute coral dominance or algal dominance (coral-depauperate). Note that reefs rarely reach a stable coral dominated state because of periodic disturbance. The range of grazing in which both attractors coexist is called the bifurcation fold and this is bounded by a threshold at either side (May 1977). Locations outside of the bifurcation fold only have a single attractor. Thus, a grazing potential of 0.5 implies that corals will always attempt recovery and be

attracted towards coral dominance, although they may not get far before being interrupted by the next disturbance. The attractors are separated by an unstable equilibrium, so called because even a minor displacement of a reef away from the unstable equilibrium will result in attraction towards the nearest stable state. Unstable equilibria are combinations of reef state and grazing potential in which processes of coral recovery are balanced by mortality.

As in many other systems, the mechanism driving alternate attractors is density dependence (Berryman 2002). A negative trajectory begins once a bottleneck in recruitment prevents adequate replenishment of coral populations. The bottleneck occurs because competition with fleshy algae reduces the settlement and survival of juvenile corals (Box and Mumby 2007, Arnold et al. 2010). This trajectory is then reinforced by a negative feedback as coral cover declines. For a given grazing potential (abundance of herbivores), a reduction in coral cover will reduce the intensity of grazing because fish have more area in which to forage. This dilution of grazing intensity occurs rapidly and has been demonstrated experimentally (Williams et al. 2001). A reduction in grazing intensity permits a rapid increase in the cover of fleshy algae which then reinforces the competitive exclusion of juvenile corals (Mumby et al. 2007a). These processes can occur in reverse when coral recruitment is high enough to allow net growth of the population. Here, increases in coral cover enhance grazing intensity, deplete algal cover and elevate coral recruitment rates until space becomes limiting (Mumby and Steneck 2008). The diagonal shape of the unstable equilibrium reflects the independent interactions

of coral cover (ordinate) and herbivore abundance (abscissa) on grazing intensity and it logically implies that fewer herbivores are needed to maintain intense grazing when coral cover is high.

There is some confusion in the literature about whether consumers – in this case herbivorous fish – can be placed on the abscissa because of their postulated dependence on the ordinate (coral cover). Dudgeon et al. (2010) incorrectly conflate herbivore abundance with grazing intensity to assert that herbivore abundance should not be placed on the abscissa. Herbivore abundance directly influences grazing rate which is measured in bites per unit time (which determines grazing potential in our plots). Grazing intensity is the density of grazing rate in space and is measured in bites per unit time per unit area. It is only grazing intensity that is directly dependent on coral cover because herbivore abundance is maintained below carrying capacity by fishing. We point out, however, that a long-term feedback may occur between herbivore abundance and coral cover in which the bioconstruction of reefs creates a more complex habitat that facilitates higher herbivore abundance. These slow processes are rarely considered explicitly in models of alternate attractors (but see Blackwood et al. 2011).

The key outcome of plots like figure 1d is that the system exhibits hysteresis (Scheffer et al. 2001). A reef can cross an unstable equilibrium because of a modest reduction in grazing potential (Fig. 1d). If the system is then allowed to degrade, because it is now attracted towards the coral-depauperate state, it will require ever larger increases in grazing in order to shift the system back across the unstable equilibrium (Fig. 1d). Thus, the system becomes progressively harder to restore as it degrades suggesting that remediative action should occur sooner rather than later (Mumby et al. 2007b).

### **Evidence for and against alternate attractors on Caribbean reefs**

Historically, the null model of ecosystem dynamics has been one of a single attractor. Thus, the evidentiary onus has been placed on proving the existence of multiple attractors rather than proving the presence of only a single attractor. The logic of this requirement has rightly been questioned (Scheffer and Carpenter 2003), particularly given the predisposition of marine ecosystems to multiple attractors (Knowlton 1992). However, we follow convention and ask what evidence, if any, provides support for the hysteresis model (Fig. 1d, 2) versus simpler monotonic relationships (Fig. 1a–b). We do not consider the multiple attractors model that lacks hysteresis (Fig. 1c) because distinguishing it from alternatives will be extremely difficult. Scheffer and Carpenter (2003) identify three principal types of evidence for the possible existence of alternate attractors. We consider each in turn.

#### **Field data alone**

The first reported evidence that purported to counter the existence of alternate attractors on Caribbean reefs was a collation of data on recent reef state from various locations and sampling dates (Bruno et al. 2009). The authors rejected the existence of alternate attractors on the grounds that, ‘Surprisingly, our results indicate that few of the world’s reefs fall into either of the classically defined coral reef stable

points of coral or macroalgal dominance’. In essence, this was a test of multimodality in the frequency distribution of states. If reefs were equilibrational systems then the lack of bimodality would indeed detract from the support for alternate attractors. However, it has long been realised that pulse perturbations are an integral part of reef dynamics (Connell 1978) and many reefs are far from equilibrium. Thus, the authors’ test of bimodality in present reef state does not constitute a test of alternate attractors; it simply reveals that many reefs are far from a coral-dominated equilibrium. Moreover, Mumby (2009b) demonstrated theoretically that the pattern observed by Bruno et al. (2009) – a highly variable relationship between coral and macroalgae – can be generated from stochastic perturbations to a system that exhibits alternate attractors. Thus an absence of bimodality in reef state cannot be used as evidence against alternate attractors as claimed by Dudgeon et al. (2010).

In general, it is almost impossible to comment meaningfully on the existence of alternate attractors when only confronted with field data on an observed phase shift. For example, Dudgeon et al. (2010) described the creation of an algal phase shift when sewage entered a bay in Hawaii. The phase shift reversed many years later when the sewage was redirected. This system might well constitute a monotonic function as asserted by Dudgeon et al. (2010), but alternate attractors cannot be discounted without a good time series on external drivers; in this case nutrient concentration. In theory, multiple attractors might occur over a range of intermediate nutrient levels but the original sewage impact (high nutrients) and subsequent restoration activity (low nutrients) might have kept the system outside the bifurcation fold, meaning that the parameter space with multiple attractors was never encountered. However, a modest increase in nutrients might yet push this system into the bifurcation fold and generate alternate attractors.

#### **Statistical models driven by field data**

A more sophisticated test for multimodality in system state was carried out by Zychaluk et al. (2012). Many, short time series of data on reef state were used to parameterise a stochastic Markovian model based on the Dirichlet distribution. Data were sourced from a wide range of locations, time intervals, and sampling methodologies. Each dataset in a region was used as an independent replicate from which to model the trajectory of reef state for each biogeographic region over time. The authors rejected the existence of alternate attractors because the distribution of projected equilibria did not bifurcate into coral and algal-dominated equilibria. However, the statistical approach makes a number of unrealistic assumptions.

1) Assumption of a constant environment over space and time. The authors implicitly assume that reefs in each region obey the same equilibrational model. That is, they ignore any environmental or ecological heterogeneity among reefs, treating individual reefs as replicates, even when separated by thousands of kilometres. This assumption contravenes a fundamental principle of alternate attractors; that alternate attractors occur within the same environment. We demonstrate the problem graphically, by comparing the difference in interpretation of reef trajectories depending on whether they inhabit the same physical environments or not. In

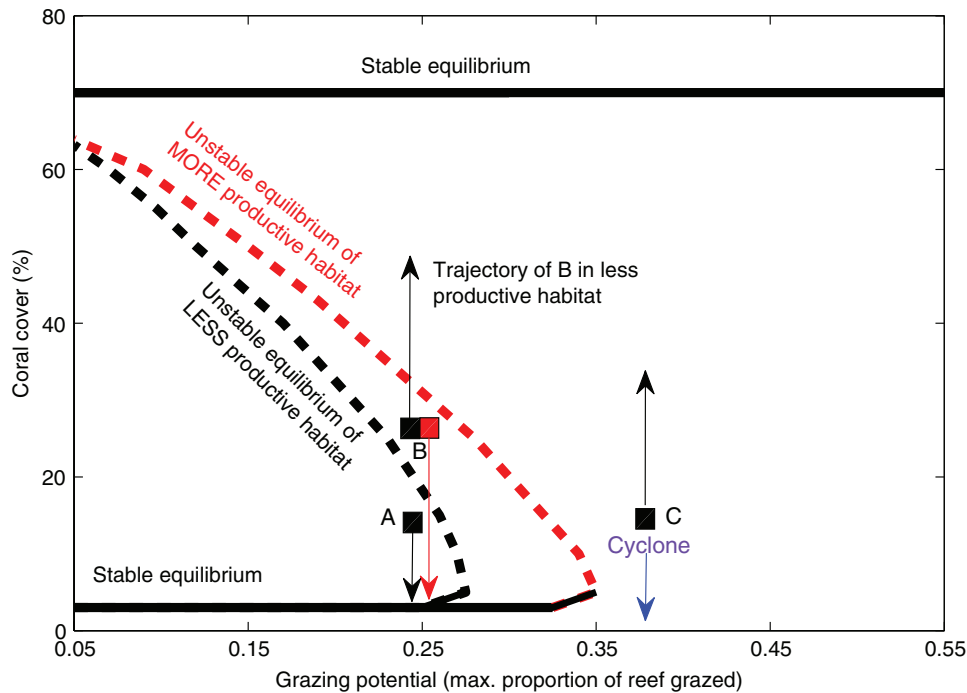


Figure 3. Confounding effects on the interpretation of trajectories in the state variable. Reefs A and C are located in the environment with black dotted unstable equilibrium. The trajectory of reef B depends on its environment. If it is assumed that A and B share the same environment but B really exhibits a more productive environment (red dotted line), then the common downward trajectories appear (misleadingly) to imply a lack of alternate attractors. If a cyclone strikes reef C its trajectory will reverse to becoming negative (blue). If knowledge of the cyclone was ignored then the common negative trajectories of A and C appear (misleadingly) to argue against the existence of alternate attractors.

theory, the existence of alternate attractors can be demonstrated for a single physical environment by finding divergent reef trajectories either side of a putative unstable equilibrium (opposing trajectories of reefs A and B that share the same unstable equilibrium, denoted by a black line in Fig. 3). This is a test of path-dependence (Scheffer and Carpenter 2003, Kuznetsov 2004). We now consider a situation where reef A is unchanged but reef B lies in a more productive environment and obeys the red (dashed) unstable equilibrium (Fig. 3). The trajectories of both reefs are now negative (coral decline) because they both sit below their respective unstable equilibria. However, had we assumed that both reefs obeyed the same equilibrium model, as Zychaluk et al. (2012) do, we would incorrectly conclude that alternate attractors does not exist because we did not detect a divergence of trajectory.

The assumption of a single equilibrium model for a region prevents the interpretation of trajectories which need to be made with reference to context-specific unstable equilibria. Pooling of trajectories across the region will confound interpretation as the sample of reefs will inevitably incorporate a wide range of unstable equilibria because of differences in connectivity, productivity, sedimentation stress, chronic mortality rates, species composition, and so on.

## 2) Assumption that field data represent the full range of parameter space

If multimodal frequencies are to be used to provide insight into alternate attractors then it is important that an adequate range of parameter space is sampled (see also comments

about use of field data alone). In the case of Zychaluk et al. (2012), all field data were collected after 1996 by which time many reefs were heavily degraded. An argument could be made that most reefs in their dataset had already slipped below an unstable equilibrium giving the false impression of a single attractor. A longer time series might yield a different outcome.

## 3) Absence of data on drivers

The approach taken by Zychaluk et al. (2012) is based purely on observations of the state variables without any consideration of a driver of resilience such as grazing potential. Yet it is changes in the driver that are hypothesized to be responsible for the occurrence of alternate attractors and ignoring differences in grazing potential among reefs can lead to a misinterpretation of observed trajectories. Returning to Fig. 3, we see that the initial state of reefs A and C have identical coral cover but that C has a considerably higher grazing potential (i.e. less fishing). Note that algal cover in the two reefs could be similar if reef C had higher productivity. The approach used by Zychaluk et al. (2012) would conclude that both reefs had the same initial condition but divergent trajectories. Thus, there would be an equal likelihood of positive and negative trajectories and alternate equilibria could, in principle, emerge. However, if we now assume that many of the field data were collected at sites with modest fishing, placing them nearer reef A, then the stochastic model would now predict an overall regional trajectory downwards because these trajectories would dominate the dataset. From a statistical viewpoint, this provides



an accurate representation of the average trajectory of the population of reefs considered. However, by ignoring the position of reefs along the abscissa, the conclusion for alternate attractors is in fact incorrect. The approach effectively averages away the real evidence for alternate attractors because the single positive trajectory for C should not have been pooled with the negative trajectories for A even though they all shared the same initial coral cover.

#### 4) Confounding effects of disturbance on trajectories

Sudden disturbances, such as cyclones, are an integral part of coral reef dynamics but their impact can conceal the divergent, underlying trajectories associated with alternate attractors. Although Zychaluk et al. (2012) allow stochastic disturbance to be incorporated implicitly into the analysis (e.g. as large vectors of a state change), this exacerbates the difficulty in interpreting observed trajectories. Tests for path dependence should identify alternate trajectories that represent internal feedbacks of opposing direction. In other words, trajectories need to be measured in the absence of confounding external disturbance such as cyclones. The problem can again be demonstrated by referring to reefs A and C in Fig. 3. Reefs A and C share the same environment but sit on opposite sites of a common unstable equilibrium. In the absence of disturbance, their trajectories would move in opposite directions. However, if reef C was struck by a cyclone, both trajectories would follow the same negative trajectory (Fig. 3). Without explicit knowledge of the existence and impact of the cyclone event, the observation of two negative trajectories either side of the putative unstable equilibrium would falsely appear to disprove the existence of alternate attractors. The reality, however, is that the system does exhibit alternate attractors but the cyclone masked their detection. The statistical approach taken by Zychaluk et al. (2012) cannot distinguish whether an observed negative trajectory occurs because of a genuine failure of recruitment to replenish the population (the proposed driver of reinforcing feedbacks) or merely reflects the transient impact of a cyclone on adult coral cover.

#### Use of mechanistic ecological models

Scheffer and Carpenter (2003) distinguished three forms of models; qualitative reasoning, simple analytic models and complex simulation models. All three provide some insight into alternate attractors although none provide a definitive test.

##### 1) Qualitative reasoning

Qualitative ecological reasoning can provide some assessment of the validity of the monotonic relationship versus multiple attractors. The monotonic curve (Fig. 1b, 4) makes superficial intuitive sense in that higher equilibrium levels of coral are associated with higher levels of grazing potential and less algae. However, this continuous, forward-leaning curve is at odds with our current understanding of reef ecology. Consider two reefs, A and B, that initially sit on the equilibrium curve (Fig. 4). Reef A<sub>1</sub> experiences a reduction in fishing and the grazing potential increases to point A<sub>2</sub>, placing the reef beneath the equilibrium where it recovers to A<sub>3</sub>. In contrast, reef B experiences an increase in fishing so it moves from B<sub>1</sub> to B<sub>2</sub>. The subsequent trajectory of B<sub>2</sub> is

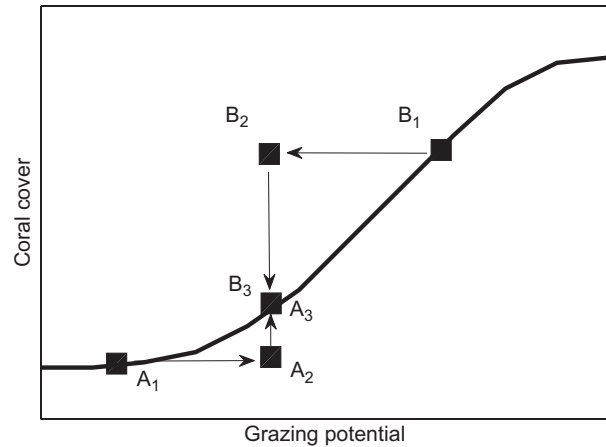


Figure 4. Ecological difficulties with the threshold model of phase shifts on coral reefs. Reef A<sub>1</sub> experiences an increase in grazing to A<sub>2</sub> after which its coral increases to A<sub>3</sub>. Reef B<sub>1</sub> experiences fishing and grazing levels drop to B<sub>2</sub> after which the reef declines to B<sub>3</sub>. Note that the healthier reef, B<sub>2</sub>, exhibits decline whereas the less healthy reef, A<sub>2</sub>, experiences recovery.

one of decline towards B<sub>3</sub>. Observe that reefs A<sub>2</sub> and B<sub>2</sub> have the same grazing potential but that A<sub>2</sub> has low coral cover and B<sub>2</sub> is 'healthier' with high coral cover. The problem with this scenario is that the 'healthier' reef, B<sub>2</sub>, exhibits decline whereas the historically degraded coral population, A<sub>2</sub>, exhibits recovery. As both reefs have the same herbivore community, we would expect algal cover to be lower in B<sub>2</sub> because the grazing intensity would be high and there is limited space for algal colonisation. Yet, despite fewer algal competitors, reef B<sub>2</sub> exhibits decline whereas reef A<sub>2</sub> shows recovery in the face of more intense competition. The implication, therefore, is that algal competition is unimportant in driving coral recovery. Moreover, these putative dynamics require that negative density-dependence is so extreme that the coral assemblage B<sub>2</sub> is unsustainable at lower grazing potential. As far as we can tell, the only reported process that increases the risk of total coral mortality as population size increases a density-dependent epizootic (Bruno et al. 2007). However, to explain the occurrence of epizootics at B<sub>2</sub> (low grazing – Fig. 4) rather than B<sub>1</sub> (high grazing), there needs to be a putative link between density-dependent epizootics and lower grazing potential.

Mumby (2009a) hypothesized that intense parrotfish grazing, which also causes corallivory, could open corals to infection and facilitate epizootics. However, this process would operate in the opposite direction to that required to explain Fig. 4: lower rates of infection would be expected at B<sub>2</sub>, because of its lower grazing potential, yet this is where epizootics would need to be more likely. Further, available evidence finds no effect of parrotfish abundance on the rate of corallivory (Roff et al. 2011). An alternative hypothesis might link higher algal cover in B<sub>2</sub> (compared to B<sub>1</sub>) to increased probability of epizootics. There is some evidence that one coral disease is positively associated with algal contact (Nugues et al. 2004) though no demonstration yet that epizootics are more likely on reefs with higher algal cover. More importantly, even if the density-dependent epizootic scenario does prove to be feasible, a monotonic

increase in coral with grazing implies that the impact of the epizootic mechanism outweighs the negative impacts of fleshy algae on coral recovery and growth which have been documented extensively in many reef ecosystems (Tanner 1995, McCook et al. 2001, Jompa and McCook 2002, Nugues and Bak 2006, Box and Mumby 2007, Hughes et al. 2007, Foster et al. 2008, Arnold et al. 2010, Ferrari et al. 2012).

A hysteresis curve (Fig. 1d) still has the intuitive property that coral recovery is generally more likely and faster under higher levels of grazing potential, but it does not require the troublesome disassociation between coral recovery and algal competition that is required by the forward-leaning monotonic curve.

## 2) Simple mathematical models

A very simple analytic model of a coral community was proposed by Mumby et al. (2007b) to ask whether the complex behaviour of a simulation model could be characterised by a few simple mechanisms. Alternate attractors occurred across a range of fish grazing. Since then, the model has been extended in various ways and for different oceans (Elmhirst et al. 2009, Anthony et al. 2011, Fung et al. 2011, Blackwood et al. 2012), yet all find multiple attractors over some parameter space. The implication, therefore, is that some reefs might have multiple attractors and others not.

## 3) Complex simulation models

One advantage of simulation models is that the ecology of the system does not have to be greatly simplified in order to achieve analytical tractability. A spatial simulation model was created of Caribbean reefs with an extensive parameterisation that included five coral species, three algal species, and 19 ecological processes (Mumby et al. 2007b, Edwards et al. 2011). The model drew parameters from more than 50 empirical studies and was found to fit an independent time series of data from Jamaica that covered nearly 20 years and incorporated many of the major disruptions to Caribbean systems (Mumby et al. 2007b). The model predicts the existence of alternate attractors throughout a limited range of parameter space (Fig. 2).

The resilience of Caribbean reefs has been shaped strongly by two regional epizootics. Both epizootics occurred within the last 40 years and each removed a key functional group from the ecosystem. The first was massive depletion of the only genus of large-bodied branching corals, *Acropora*, (Bythell and Sheppard 1993) whose growth rates exceed that of all other coral species. The second was functional extinction of the urchin *Diadema antillarum* (Lessios et al. 1984) which massively reduced grazing rates upon reefs (Carpenter 1990). The model predicts that alternate attractors only became an issue once *Acropora* and *Diadema* were lost from the system (Mumby et al. 2007b, Roff and Mumby 2012). *Acropora* grows so quickly that it overwhelms the ability of macroalgae to constrain its population dynamics, creating a single coral-dominated attractor. In the case of *Diadema*, once its density exceeds approximately  $1 \text{ m}^{-2}$ , it maintains sufficient grazing intensity that macroalgae are unable to cause a bottleneck in coral recruitment, again leading to a single coral attractor. In the absence of

both species, fishing is predicted to maintain the grazing of parrotfishes at levels that allow alternate attractors.

Complex simulation models allow integration of all available ecological data and make no implicit assumptions about alternate attractors. Yet multiple attractors are an emergent property of the model. That said, evidence from complex models alone does not prove the existence of alternate attractors in situ (Scheffer and Carpenter 2003, Mumby 2009b). There has, however, been some criticism of models in studying alternate attractors. Dudgeon et al. (2010) point out that models generate their parameterisation from multiple studies which were likely conducted in different physical environments. They argue that this contravenes the assumption of multiple attractors in a single environment. This is a weak argument for two reasons. First, most modellers will seek parameters from the appropriate physical environment. For example, growth rates of corals are usually extracted for the depth represented by the model. Second, to guard against uncertainty or real variability in parameter values almost all models undertake a sensitivity analysis. In the case of coral reef models, the existence of alternate attractors was found to be highly robust to changes in the parameterisation (Mumby et al. 2007b).

## 4) Complex models and field data

When considering evidence for multiple attractors in large ecosystems, Scheffer and Carpenter (2003) conclude that, '... our best hope is a combination of multi-interpretable records of past behaviour with 'plausible models' of the system'. They also argue that '...the best strategy is to use multiple models in parallel'. To date, analytic and simulation models of a Caribbean system have given quantitatively similar behaviour (Mumby et al. 2007b). The simulation model has also been able to reproduce faithfully, the observed trajectory of forereefs in Jamaica at a depth of 10 m over nearly 20 years. Here, we combine the predictions of a simulation model with field data to seek evidence for or against multiple attractors. Two case studies are presented with one replicated over space and the other over time.

Our first case study explores the subtlety of crossing the upper bifurcation threshold in the absence of sea urchins, such that changes in grazing rate lie within the realm of fishing impacts (Fig. 2). To explore this scenario, we use a non-planned experiment of fishing pressure from the Bahamas in which four sites have been protected from fishing within a successful marine reserve and six sites were located in exploited areas either side of the reserve. The full dataset is described elsewhere (Mumby and Harborne 2010) but in brief, all ten sites were located on a single stretch of reef within a similar physical environment. Surveys of benthos and grazing were carried out 2.5 years apart during which time the region was not perturbed by a major external disturbance. Most sites had low coral cover (~7%) because of a major bleaching perturbation six years before the study began. Sites varied in their grazing rate because of fishing (Mumby et al. 2006). The reserve location was established in 1959 on the grounds of opportunities for terrestrial conservation and the reef quality within the reserve was not systematically different to that outside the reserve (Ray 1961). Thus, spatial patterns of reef trajectory along the

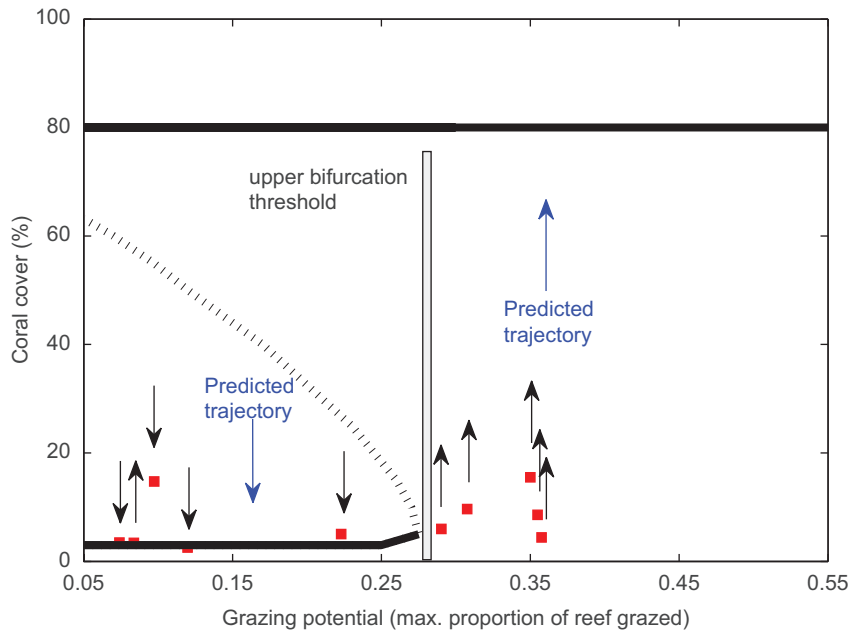


Figure 5. Test for discontinuity across the upper bifurcation threshold using empirical data from 10 sites in the Exuma Cays, central Bahamas (Mumby and Harborne 2010). Points (red squares) denote the initial state and grazing rate of reefs in 2004 and arrows denote the direction of change by 2007 in the absence of pulse perturbation. Coral and algal-dominated stable equilibria shown with horizontal lines and black solid squares. Unstable equilibrium marked using line and open squares. Upper stable equilibrium occurs across top of plot.

fishing gradient are unlikely to be confounded by reserve locations being inherently more resilient.

Superimposing the direction of trajectories upon the modelled unstable equilibrium for a productive, moderately-exposed reef environment, we find that 9/10 of sites fit the

predicted trajectory (Fig. 5). These alternate trajectories were observed within one physical environment, from comparable levels of the state variable, but where anthropogenic differences in grazing rate placed the sites on either side of a hypothesized bifurcation fold.

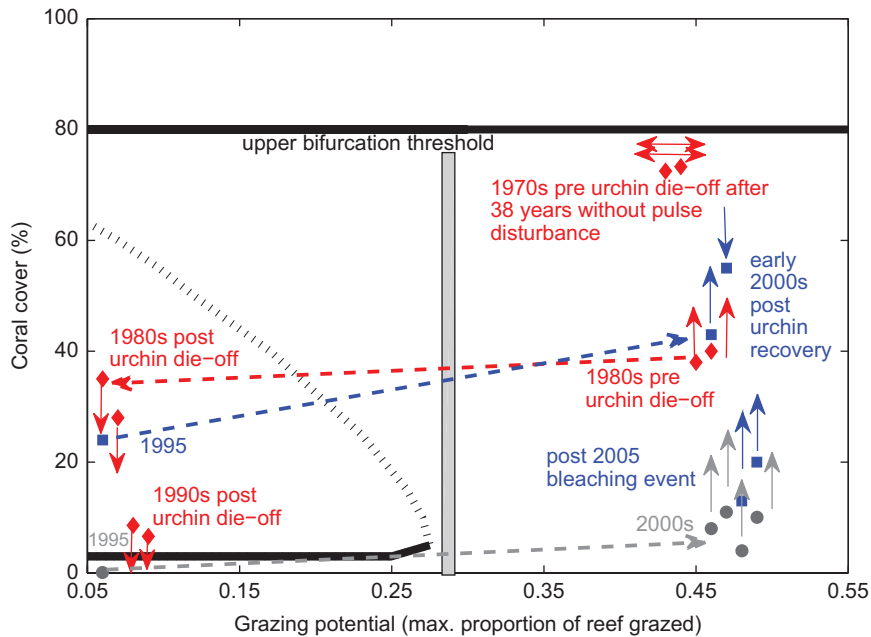


Figure 6. Test for discontinuity across the upper bifurcation threshold using empirical data from near Discovery Bay, Jamaica (red diamonds) and Dairy Bull, Jamaica (total coral cover with blue squares, *Acropora cervicornis* grey circles). Long dotted arrows denote direction of threshold transgression using the same colours as each dataset. Arrows on points denote the trajectory direction before the next pulse disturbance event. Algal- and coral-dominated stable equilibria shown with solid black lines. Unstable equilibrium marked using dotted black line.



Our second case study also examines discontinuity across the upper threshold but differs from the first in that it occurs over time, spans a greater range of grazing rates, and crosses the threshold in both directions (loss of urchins and recovery of urchins). This case study also provides evidence of a lack of recovery on crossing the threshold. Shortly before the loss of urchins in 1983, Discovery Bay in northern Jamaica had experienced a severe cyclone. After the cyclone reefs began to recover towards a coral-dominated attractor (Fig. 6). However, once the urchins died out, Hughes (1994) found a continued trajectory of decline until the end of his observations in 1993. Although this decline was punctuated by another hurricane and bleaching event, no trajectories of recovery were found between successive events. Given that this period extended for a decade, which constitutes multiple turnover events of macroalgal populations (Hoyt 1907, de Ruyter van Steveninck and Breeman 1987), this constitutes a modest test of non-recovery and crossing of a bifurcation threshold.

In the mid 1990s signs of a partial urchin recovery were observed in some shallow Jamaican reefs (author observations in Edmunds and Carpenter 2001). Subsequent surveys at a reef that had escaped the worst hurricane impacts, described an increase in coral cover by 2003 and reduction of macroalgae (Idjadi et al. 2006). Part of this coral recovery included the reappearance of *Acropora cervicornis* from functional obsolescence in 1994 (cover of 0.6%). Despite a large perturbation event in 2005, caused by coral bleaching, coral recovery continued once again (Crabbe 2009), implying that the system followed a coral-dominated attractor as predicted by the model (Fig. 6).

Although Dudgeon et al. (2010) considered the recovery of corals after urchin recovery as evidence against the existence of alternate attractors, we find that these events are entirely consistent with the model-based hypotheses 1) loss of urchins in the functional absence of *Acropora* reverses the system's attractor from that of coral to macroalgae, and 2) that recovery of urchins to functionally significant densities ( $\geq 1 \text{ m}^{-2}$ ), removed the macroalgal basin of attraction. The precise contribution of the acroporid recovery is difficult to elucidate though the chronology implies that its effect was secondary to the urchin recovery.

Both case studies provide a close match between model predictions and observed trajectories of the ecosystem. In each case, the test of path dependence on either side of a bifurcation fold is consistent with multiple attractors. However, it would also be possible to fit a forward-learning monotonic curve to both datasets (Fig. 5, 6). Therefore, the combinations of models with field data provide results that are consistent with a variety of relationships.

## Conclusions

A variety of approaches have been used to investigate the resilience of coral reefs. To date, none have provided evidence against the existence of alternate attractors. Field data are unlikely to provide insight into alternate attractors on their own. Thus, large, coarse-resolution datasets on system state are useful for meta-analyses but have little bearing on the existence of alternate attractors. Statistical approaches should attempt to sample the full range of an external driver

and include the covariables needed to make an informed interpretation of trajectory. Simple and complex models both find alternate attractors across a limited – but important – range of parameter space. The predictions of complex models are consistent with the observed response of ecosystems to fishing, urchin die-off, and urchin recovery. Here, the evidence is consistent with multiple attractors but a forward-learning monotonic curve, that lacks multiple attractors, could also be fitted to these data. However, the ecological implications of a forward-leaning curve are problematical, requiring acceptance of an untested mechanism and rejection of a wealth of evidence about coral-algal competition. To conclude, while there is as yet no definitive empirical test of the existence of alternate attractors in coral reef ecosystems, the balance of evidence favours multiple attractors, at least under certain external control.

The studies of system behaviour presented here mostly focus on detecting discontinuity either side of a system bifurcation. Further study of alternate attractors would test for divergent trajectories at a fixed grazing potential but where the initial conditions of the state variable fall either side of a putative unstable equilibrium. However, because system dynamics slow down near an unstable equilibrium (Hastings 2010), it is advisable to select contrasting levels of state that do not fall too close to the unstable equilibrium. This is because measurement of alternate trajectories near an unstable equilibrium will require high sampling precision and longer observation periods, which increases the risk that the time series will be interrupted by external perturbations that can mask the inherent trajectory of interest.

Temporal context is important. Our results imply that Caribbean reefs in their natural state – with all functional groups of herbivores and corals – do not exhibit alternate attractors. Indeed, geological evidence suggests that coral-dominated states were maintained for millennia in the absence of anthropogenic disturbance (Pandolfi and Jackson 2006). That the loss of urchins can cause alternate attractors is supported by the combination of theory and empirical studies from Jamaica (although as noted, a monotonic curve also fit the data). The role of *Acropora* has not yet been tested empirically and remains theoretical at this stage. If we take the long-term view, then appearance of alternate attractors – if correct – might have been confined to only a few decades of geological time. It is tempting to argue that a recovery of urchins or *Acropora* could banish alternate attractors into history once again. However, rising stress from global warming and ocean acidification may act in concert to reduce coral growth rates and increase the susceptibility of reefs to multiple attractors (Hoegh-Guldberg et al. 2007, Anthony et al. 2011). Given the profound management implications of reefs becoming entrained within an algal-dominated reinforcing feedback, it is perhaps prudent to adopt the risk-averse view that Caribbean reefs will continue to exhibit multiple attractors.

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