



Transient dynamics mask the resilience of coral reefs

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Abstract

Coral reefs are model systems for studies of ecological resilience, with communities generally exhibiting multiple stable states and more resilient regions trending towards a single, coral-dominated, regime. We expand the theory of ecological resilience beyond the concepts of distinct stable states to integrate emerging ideas from transient dynamics as long-term intermediate states with no pronounced trend towards equilibria. We show that low coral abundance, together with stochastic larval supply and disturbance, can trap otherwise resilient reefs in a persistent intermediate state whose long-term outcome is difficult to predict. Common metrics, such as the ecosystem slowing down before crossing tipping points and using historical coral cover trends, may become unreliable predictors of future behaviour. Helping reefs out of transient states requires agile management that allows for short-term, targeted interventions after which natural ecological feedbacks can take over.

Keywords Coral reefs · Transient dynamics · Resilience · Ecological tipping point · Regime shift · Coral-algal competition

Introduction

Theories of regime shifts have explored how ecosystems converge towards stable asymptotic states that persist in the absence of major perturbations (Holling 1973; Scheffer et al. 2001a, b; Scheffer and Carpenter 2003; Folke et al. 2004; Mumby et al. 2007; Fabina et al. 2015). In systems with more than one stable state, a regime shift occurs when the system exhibits a change in qualitative behaviour, e.g., a switch

from recovery to decline, often as a result of a change in an environmental parameter (Scheffer et al. 2001a, b; Carpenter et al. 2011; Hastings et al. 2018). This shift, also known as a ‘tipping point’, can be quite sudden and dramatic and associated with a narrow range of environmental conditions. In coral reefs, the ecosystem state is commonly described as either coral-dominated with high biodiversity, including fish and other organisms, or macroalgal-dominated with low biodiversity. Because coral reefs have undergone persistent flips between these two states (Schmitt et al. 2019), they have become one of several canonical systems, like shallow lakes and savannahs (Scheffer and Jeppesen 2007; Carpenter et al. 2011; Scheffer et al. 2015), which transition between alternative regimes. Qualitatively, a shift in system dynamic can be observed as trajectories that used to recover towards a coral-dominated attractor switch and decline towards a coral-depleted state often dominated by macroalgae (Mumby et al. 2007; Graham et al. 2013, 2015; Fabina et al. 2015; Schmitt et al. 2019). In some coral reefs, such shifts can be quite abrupt and also exhibit putative tipping points, with the loss of herbivory as the most often cited cause (Mumby et al. 2007; Hughes et al. 2010). Much of the theory on coral reef regime shifts has developed from models of Caribbean ecosystems (Hughes and Tanner 2000; Hughes et al. 2003; Mumby et al. 2007; Fung et al. 2011; Fabina et al. 2015). However, reefs in this region have lower biodiversity and

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resilience than most other locales, raising questions of the theories' relevance to broader bio-geographic application (Roff and Mumby 2012).

Conventional theory posits that post-disturbance recovery is inevitable in resilient systems that only possess a single coral attractor or in bistable systems that have not approached a tipping point. Yet an emerging theory on transient dynamics argues that this theory is incomplete and that systems may remain in long transient states during which limited recovery might occur (Hastings et al. 2018; Morozov et al. 2020). While much of the current theory concerns the behaviour of the systems in terms of early warning signals (van Nes and Scheffer 2007; Scheffer et al. 2009, 2012), such as potential slowing down of ecosystem dynamics before reaching the tipping point, the system may also continue to exhibit slow dynamics after it crosses the tipping point (Hastings 2016). That is, although the rate of recovery from perturbations may slow down right before a catastrophic regime shift, the rate of change may continue to be slow even after the regime shift has occurred and the system transitioned into a different basin of attraction, a phenomenon called a ghost attractor (Hastings et al. 2018). Such ongoing slow dynamic post-regime shift may mask the fact that, over longer time periods, the system will tend to exhibit qualitatively different asymptotic behaviour and thus complicate the identification that such shift has already occurred. At the same time, slow dynamics that characterises the transient state after the shift would not only prevent runaway change in ecosystem state but also provide a window of opportunity for the shift to be reversed, either through natural processes or potential management interventions (Francis et al. 2021). Similar processes may already be manifesting in reefs with low coral cover found around the world (Graham et al. 2014; Guest et al. 2016; Edmunds 2018; Gilmour et al. 2019). We extend the theory of transient dynamics to coral reef models by considering the roles of broad-scale acute disturbances and highly variable larval supply on system behaviour. We then reveal circumstances that would lead to such non-intuitive behaviour and potentially misleading patterns of resilience and propose new interpretations of the slow recovery of coral trajectories as well as some major challenges for coral reef management.

To this end, we used a simple model with demonstrated efficacy for representing coral reef dynamics (Mumby et al. 2007; Elmhirst et al. 2009; Blackwood et al. 2011; Fung et al. 2011; Fabina et al. 2015) to explore potential drivers and consequences of transient dynamics (see 'Materials and methods' for mathematical details). In the model, corals are recruited into the system annually through local retention and external supply of larvae from outside sources, and then mature and grow to cover available space. Macroalgae compete for larval settlement space, as well as overgrowing

settled coral recruits and, to a limited extent, adult corals. Coral provides habitat for herbivorous fish which reduce macroalgae through the disruptive aspects of their feeding behaviour. This model predicts non-linear dynamics (Fig. 1). We then employ this model to investigate the emergence of transients in this system across three ecological scenarios centred on potential interpretation dilemmas in the monitoring and management of coral reefs. The first scenario focuses on the effects of non-linear dynamics on system trajectories around potential tipping points, essentially buffering against expectation of rapid state transitions. The second and third scenarios add environmental stochasticity and investigate how transients could buffer the expected efficacy of management efforts (scenario 2), or affect predicted future recovery dynamics that relies on the historical trajectories (scenario 3).

Materials and methods

Model definition

To determine the features that lead to the emergence of transient dynamics, we adapted and extended a well-established framework for modelling coral-macroalgal dynamics (Mumby et al. 2007; Elmhirst et al. 2009; Blackwood et al. 2011; Fung et al. 2011; Fabina et al. 2015). In our current model, the ecosystem is simplified and represented by a three-state model in which fractions of the seabed can be covered by coral recruits (R), adult coral (C), or macroalgae (M), all expressed as the proportion of cover (unitless, ranging from 0 to 1). The rate at which the seabed can be colonised by coral recruits is given by the following:

$$\frac{dR}{dt} = k(wC + e)(1 - R - C - M) - aR - sRM - nR \quad (1)$$

Both self-recruitment, expressed as larval saturation due to current coral cover (wC), and external supply (e) contribute to coral recruitment as recruits colonise a portion of available free space ($k(1-R-C-M)$). The inclusion of external supply in particular allowed us to consider the stochastic nature of drivers, as well as to investigate the dependence of local population on the state of the wider system. For simplicity, we assume that coral recruitment to the seabed is not density-dependent. Recruits grow and contribute to the coral cover ($-aR$), but a fraction of recruits will either get overgrown by algae ($-sRM$) or die from other causes ($-nR$). The rates of change for the coral (C) and macroalgal (M) covers were defined as follows:

$$\frac{dC}{dt} = aR + gC(1 - R - C - M) - bCM - mC \quad (2)$$

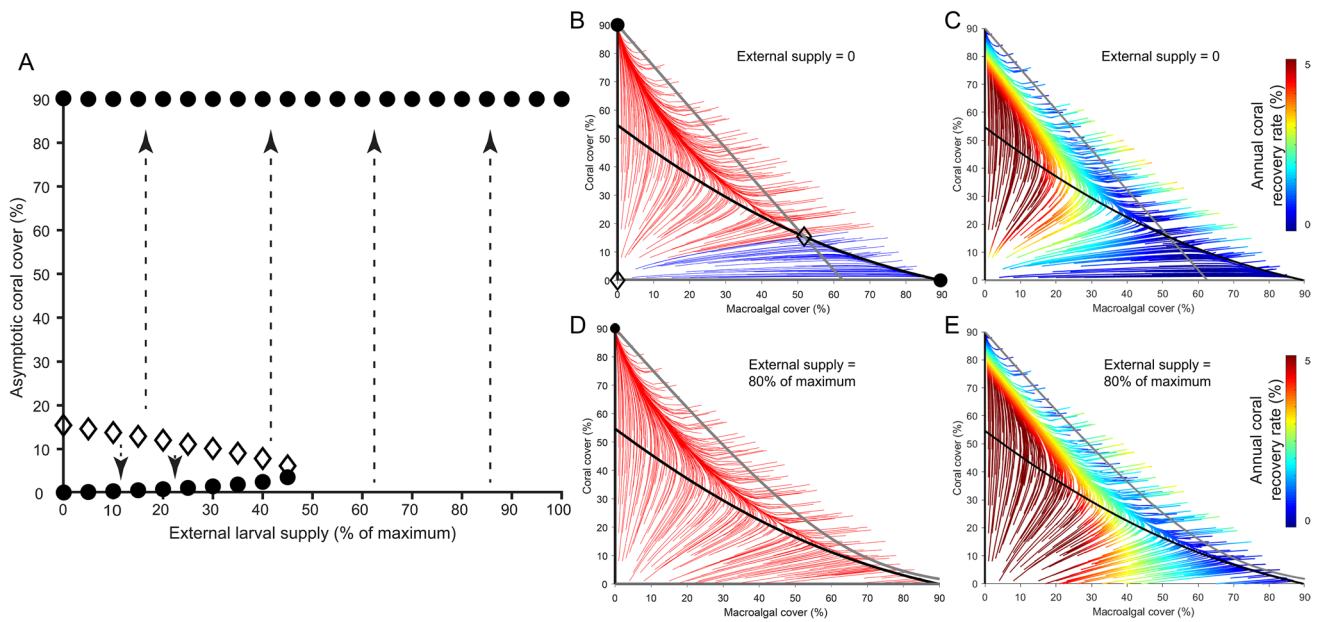


Fig. 1 Non-linear dynamics in a coral reef model. **A** Hysteresis diagram obtained from the deterministic coral reef model by varying levels of external supply. Arrows on dashed lines show the direction of asymptotic behaviour but not the rate of change. Circles, stable equilibria; diamonds, unstable equilibria/saddle; grey lines, coral cover that corresponds to given levels of external larval supply in subsequent panels. **B** Phase plane of a bistable system with no external supply ($e=0$) and two basins of attraction. System trajectories move either towards a coral-dominated stable state (red) or towards an algal-dominated stable state (blue). Grey lines, coral zero-growth isoclines; black lines, algal zero-growth isoclines; equilibria arise where the zero-growth isoclines intersect. **C** The same phase plane as in **B**, but with trajectory colours showing the annual increase in coral cover

(from blue/slow recovery to red/fast recovery; zero-growth isoclines shown; equilibria symbols not shown). Coral cover changes slowly around all equilibria (a ‘crawl-by’). **D** Phase plane of a more resilient system with up to 80% of maximum available recruitment provided by external larval supply ($e=0.8$). The system exhibits a single basin of attraction, and zero-growth isoclines no longer intersect in the phase plane removing all equilibria except the coral-dominated one. **E** The same phase plane as in **D**, with trajectory colours showing the yearly rate of coral recovery (zero-growth isoclines shown; equilibria symbols not shown). The system continues to exhibit slow dynamics at high macroalgal cover and low coral cover where the unstable equilibrium once existed (‘ghost attractor’)

$$\frac{dM}{dt} = sM(1 - C - M) + bCM - zM\left(\frac{oC}{1 + oC}\right) - hM \quad (3)$$

Coral cover increases either by recruits growing to become adults (aR) or by adult corals overgrowing free space ($gC(1-R-C-M)$), but can also decrease either by being overgrown by macroalgae ($-bCM$) or due to other forms of coral mortality ($-mC$). As in Fabina et al. (2015), macroalgae overgrow free space ($sM(1-R-C-M)$) and coral recruits over the first year after settlement (sRM) at the same rate s , and we combine these two terms and reduce them into a single cumulative growth term $sM(1-C-M)$. Macroalgae can also overgrow adult coral, but at a lower rate (bCM). The model did not include any external supply of macroalgae, and thus increase in macroalgal cover is considered to arise from local recruitment processes. Macroalgal cover decreases either due to grazing by coral-mediated herbivores like parrotfish ($-zM(oC/(1+oC))$, where z represents the rate of decrease in macroalgal cover due to coral-mediated herbivores and o represents herbivore habitat provisioning from coral cover), or due to other causes of macroalgal mortality ($-hM$), such

as herbivory that is independent of coral cover or disturbances that reduce the macroalgal cover. As in Fabina et al. (2015), but unlike Blackwood et al. (2011), population dynamics of parrotfish and other coral-mediated herbivores were not modelled explicitly and were instead implemented indirectly via increased herbivory/algal mortality that was dependent on coral cover habitat.

Numerical simulations

Coral reef systems undergo fluctuations and often marked seasonality in parameter values, such as larval supply across different spawning seasons (Hock et al. 2019), but also major disturbances that periodically disrupt the system (Graham et al. 2013, 2015; Hughes et al. 2018). To capture ecosystem fluctuations and noise, the model was discretised and then analysed as a system of difference equations. Discretisation on its own was not found to have introduced irregular behaviour around equilibria such as overcompensation (e.g., in deterministic outputs of Scenario 1 that do not include

stochasticity; see also Fig. S1) and also occurred at different time scales (single time step) from the proposed transient dynamics (multiple time steps). The transient dynamics obtained from the numerical simulations were thus not the by-product of discretisation but rather emerged from the intrinsic model dynamics.

Numerical simulations tracked changes in coral and macroalgal cover in discrete yearly time steps. In order to simplify the model analysis and presentation, we assumed that annual increase in coral cover from coral recruits will be equal to an equilibrium value, that is, the processes that affect dR will converge to a stable value of R within a time step before this R is added to the next year's value of C . This also helps to account for the fact that the processes affecting coral recruits often occur at sub-annual scale (Doropoulos et al. 2015). We also assumed that each year's recruits will either measurably increase the coral cover in the next generation or die (R does not carry over between years). The value of R_t which represents the increase in coral cover in the next year C_{t+1} has been obtained by setting $dR/dt=0$ and solving Eq. (1) for the equilibrium value of R :

$$R_t = -\frac{k(wC_t + e_t)(C_t + M_t - 1)}{a + n + sM_t + k(wC_t + e_t)} \quad (4)$$

This term is then incorporated into the difference equations derived from Eqs. (2) and (3) as follows:

$$C_{t+1} = C_t + [aR_t + gC_t(1 - R_t - C_t - M_t) - bC_tM_t - m_tC_t] \quad (5)$$

$$M_{t+1} = M_t + \left[sM_t(1 - C_t - M_t) + bC_tM_t - zM_t \left(\frac{oC_t}{1 + oC_t} \right) - h_tM_t \right] \quad (6)$$

Model parameterisation

Values for individual parameters were derived from several published model parameterisations (Mumby et al. 2007; Blackwood et al. 2011; Fung et al. 2011; Doropoulos et al. 2015; Fabina et al. 2015), as none of these models has considered the entire range of the parameters implemented here. As such, the parameter values used to derive the outputs in figures are not meant to represent a geographically or ecologically specific coral reef, but rather provide a framework to demonstrate the emergent transient dynamics that can arise from an ecologically plausible range of parameter values. For the model examples shown, all parameters were held constant unless otherwise noted, with figures generated using the following values: $k=0.25$, $w=0.4$, $a=0.2$, $s=0.95$, $n=0.5$, $g=0.4$, $b=0.2$, $m=0.05$, $z=0.64$, $o=4$, $h=0.1$, while values of e varied across scenarios. Additional parameter descriptions and rationales for the employed parameter values are provided in Table S1.

Stochasticity in the numerical models (Scenarios 2 and 3) was derived from two sources: disturbance-induced mortality (denoted with m_t and h_t) and connectivity fluctuating annually over spawning seasons (e_t). The model included the impacts of both storms/cyclones and bleaching as increased mortality. We simulated storm and bleaching years at intervals using two independent Poisson processes that both had $\lambda=7$. In a storm year, mortality increased for both coral and macroalgae ($m_t=m_S \sim U[0.05,0.5]$, instead of $m_t=0.05$; $h_t=h_S \sim U[0.1,0.8]$, instead of $h_t=0.1$) (Mumby et al. 2005). Bleaching years only increased coral mortality ($m_t=m_B \sim U[0.05,0.8]$, instead of $m_t=0.05$). If both a storm and bleaching occurred in the same year, the effect was not cumulative as such events can be potentially antagonistic (Carrigan and Puotinen 2014), and therefore, a higher value between m_S and m_B was used as m_t . Potentially increased mortality of coral recruits due to disturbances (Mumby 1999) was not explicitly modelled at this stage.

We simulated the stochastic nature of marine connectivity by adding white Gaussian noise to the external supply of coral larvae e_t with a signal-to-noise ratio of 5 and values of e_t bounded between 0 and 1. Thus, when $e_t=1$, contribution from external sources saturated coral recruitment and rate of increase in coral cover from supply coming from external sources was equal to the proportion of free space available for recruitment $k(1 - C_t - M_t)$. In contrast, when $e_t=0$, the system was entirely dependent on self-recruitment wC_t . Otherwise, recruitment was a sum of external and local larval supply.

A thousand stochastic realisations/Monte Carlo simulations were performed for each scenario. While in each simulation we explored a broad range of combinations for the initial system conditions (i.e., C and M values), we illustrated system dynamics with the help of several example trajectories (initial conditions in Fig. S2). For consistency, system trajectories in both phase plots and recovery plots for all figures were derived from first-order numerical integration derived from the simulations rather than by solving Eqs. 1–3 analytically. For conciseness, stochastic simulation examples in figures show outputs from a single realisation which has been found to exhibit transient dynamics. In this study, a simulation was considered to have exhibited transient dynamics if a coral attractor existed, and at least for some system trajectories, the coral cover did not deviate more than $\pm 5\%$ over a period of 15 years, provided that the total level of coral cover also neither dropped below 5% during this period nor increased to within the 10% of the coral attractor. We note that this is simply an operational definition that we used in our current study to interpret the results of Monte Carlo simulations, while acknowledging that any quantitatively explicit definition of what constitutes a 'transient state' will be inherently system- and purpose-specific. As such, by defining transient states in

this way, we are neither trying to be prescriptive nor imply that this exact definition should be used in the real-world coral reef systems.

We also performed sensitivity analysis (parameter value ranges provided in Table S1) to ensure that the results of the numerical simulations were robust and that the presence of transients is not confined to a small part of the total parameter space. We found that around 50% of the simulations exhibited transient dynamics as defined (Fig. S3). We have also found that the transients tended to appear across the simulated parameter space rather than being characteristic of a specific combination of parameter values (Fig. S4). However, given that the ranges of parameter values in the current study were not all derived from the same coral region, we opted not to do an in-depth analysis to determine the specific parameter combinations that will be more likely to generate transient dynamics. While an analysis that highlights the conditions, i.e., parameter value combinations, when transients emerge would be intriguing, we believe the derived parameter combinations may not be indicative of a real-world coral reef while risking that a reader may interpret them as such. We therefore limit this study to the effects of transients, and the exact conditions for their emergence will be explored in future studies with (eco)system-specific parameters.

Stability analysis

Stability analysis was performed using Symbolic Math Toolbox in Matlab, following the procedure for a coral reef model described in Fabina et al. (2015). The zero-growth isoclines in Fig. 1 were calculated by setting Eqs. 2 and 3 to zero and using Matlab to solve for C and M . For presentation clarity, zero-growth isocline with values below zero is not shown in Fig. 1 (unlike in Elmhirst et al. (2009)). In the numerical simulations, the unstable equilibrium represents a putative ‘tipping point’—conditions when the system changes qualitative behaviour, e.g., from recovery to decline and vice versa. In models with no stochasticity (Scenario 1), this unstable equilibrium/tipping point remained constant during the time series as long as the parameters remained constant as well. To illustrate the extent to which the equilibria can vary over time with inherently stochastic inputs (Scenarios 2 and 3), we calculated the equilibria for each time step using a timestep-specific set of parameter values (i.e., incorporating time-sensitive values of larval supply and mortality). This provided the stability structure that was dynamic and unique for every time step and allowed us to illustrate that in a stochastic system, a ‘tipping point’ where the regime shift occurs is not a unique set of fixed conditions but rather a fuzzy and dynamic region in which unstable equilibria could be located and thus demonstrate the effect of this phenomenon on transient dynamics.

Results and discussion

Ecological scenario 1: crossing a tipping point does not result in rapid decline

Coral reefs can have rapid dynamics in both decline and recovery, so it seems reasonable to assume that crossing a tipping point could result in rapid reef decline (Mumby et al. 2007). However, a system in proximity of the equilibria can exhibit long transient dynamics on both sides of a tipping point (Hastings et al. 2018). In the model, as a system approaches a tipping point, its dynamics can slow down because the competitive abilities of the coral and macroalgae are nearly balanced, which weakens reinforcing feedbacks that drive rapid approach to the attractors (Fig. 1). The system can exhibit very slow dynamics and ‘crawl by’ a tipping point (Hastings 2016; Hastings et al. 2018), yet appear to be experiencing stable coral cover over ecological time scales, i.e., years, and only exhibiting decline far later (Fig. 2). In such an example, we may incorrectly infer that the system remains stable and resilient when it has actually embarked on a slow trajectory of collapse that is difficult to ascertain when system is observed over short reference time windows, e.g., a few years in our example (Fig. 2A). Likewise, the system just above the tipping point may also be on a recovery trajectory that is equally challenging to detect and could lead observers to conclude it lacks resilience. Slow dynamics resulting in a long transient state can also occur when only one attractor is present, e.g., in a resilient system with temporarily abundant macroalgae (Fig. 1E), which behaves as if it has an additional, ‘ghost’ attractor (Hastings et al. 2018). It is thus essential to recognise that, even though a system may consistently move towards one of the attractors, the rate of this behaviour may change (Fig. 1C, E) which may affect the ability to detect whether the system gravitates towards a stable state over a relatively short monitoring period.

Ecological scenario 2: management interventions appear to be losing their efficacy

Scenario 1 involved transients emerging from non-linear deterministic dynamics; however, transients can also arise from stochasticity in system drivers, including disturbances and larval supply. To study the effects of noisy environmental processes on transient dynamics (Hastings et al. 2018), we extended our model to include stochastic coral bleaching and cyclone disturbances, as well as inter-annual fluctuations in larval supply. These extensions are relevant in the context of climate change, not only because of intensifying disturbances (Frieler et al. 2012) that can

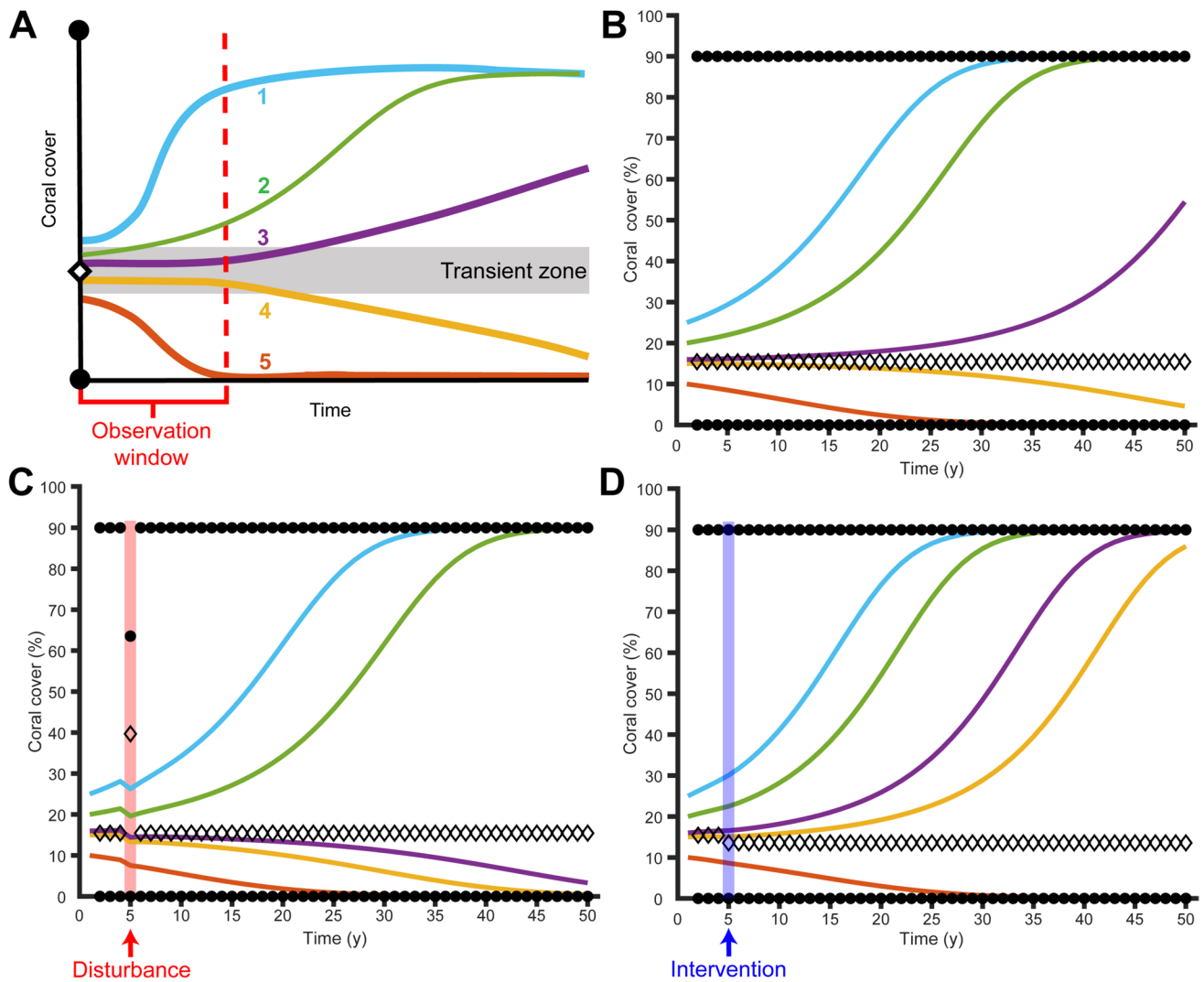


Fig. 2 Transients arise from non-linear dynamics due to macroalgal competition. **A** Graphical model of a system with bistability showing the emergence of transient dynamics on both sides of unstable equilibrium. As in Fig. 1, circles denote stable equilibria, diamonds denote unstable equilibria/saddle, and the coloured lines denote example trajectories of changes in coral cover. For a sufficiently short observation window, trajectories 3 and 4 that start at either side of the unstable equilibrium could be indistinguishable. **B** Example system trajectories obtained from a coral reef model showing transient dynamics above and below the unstable equilibrium in the absence

of disturbances. **C** Although a disturbance impact at $t=5$ (that is, $m(t_5)=0.15$) pushes trajectory 3 below a tipping point, rather than undergoing a rapid collapse the system declines slowly due to slow dynamics around the tipping point. **D** While an intervention, such as increased herbivory (value of z increase from $z(t_1, \dots, t_4)=0.64$ to $z(t_5, \dots, t_{50})=0.7$), may improve the conditions and permanently lower the tipping point and set trajectories 3 and 4 on path of recovery, the system may still respond slowly due to transient dynamics. Initial conditions for the example trajectories are defined in Fig. S2

delay recovery processes (Hughes et al. 2019), but also because recovering coral populations will be increasingly dependent on the supply of larvae from less damaged areas (Nystrom and Folke 2001; Hock et al. 2017) or sources that have become degraded as well (Hughes et al. 2019). For simplicity, here we examine the system under variable but not escalating disturbance.

We can imagine a scenario where management maintains a reef in a favourable environment—such as moderately good water quality—but increasing rates of disturbance are

impacting neighbouring reefs and interrupting the external supply of larvae. In a system that cannot exclusively sustain itself through local retention of larvae, an increasingly stochastic external larval supply creates temporary bistability and a reef may experience attraction to a coral-depleted state when external larval supply is low (Fig. 3; see Fig. S2 for initial conditions of trajectories). This occurs because the overall larval supply is now insufficient to facilitate recovery if local population gets depleted, such as after disturbances. In contrast, when external larval supply is plentiful, there

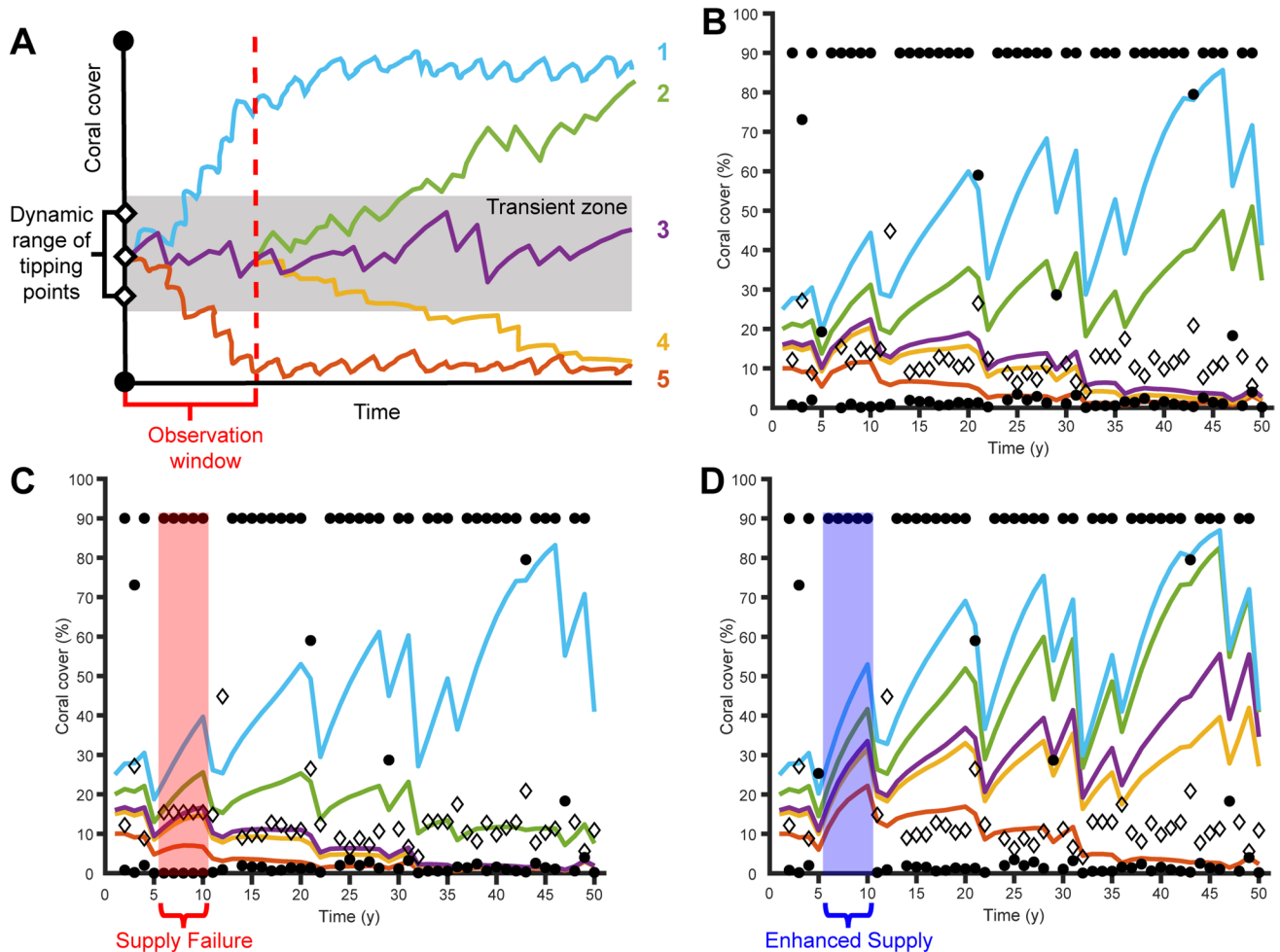


Fig. 3 Transients arise due to stochastic larval supply and disturbance impacts. **A** Graphical model of a system with stochastic perturbations showing the emergence of transient dynamics over a range of states. Circles denote stable equilibria, diamonds denote unstable equilibria/saddle, and the coloured lines denote example trajectories of changes in coral cover. **B** The stability structure (stable equilibria, filled circles; unstable equilibria, empty diamonds) changes at every time step due to environmental stochasticity (variable supply of coral larvae) and disturbance impacts. At low coral cover, an otherwise resilient system exhibits long transient dynamics because of slow growth and dynamic tipping points. **C** A series of years with inadequate external larval supply ($e(t_6, \dots, t_{10}) = 0$) may shift the future system trajectories,

trapping previously resilient systems (trajectory 2) in the transient zone that buffers their recovery and pushing some systems (trajectory 3) outside of the transient zone towards persistent decline. **D** A series of years with enhanced external larval supply (e.g., due to natural causes or intervention; $e(t_6, \dots, t_{10}) = 1$) can engender recovery in systems that would otherwise be trapped in the transient zone (trajectories 2, 3, and 4) and prevent rapid decline of other systems (trajectory 5) that are now trapped in and buffered by the transient zone. Initial conditions for the example trajectories are defined in Fig. S2. All reefs shown here have exactly the same disturbance regime with the same relative disturbance impacts

is sufficient coral recruitment for population recovery even when local coral cover is low, there is little self-recruitment, and coral-mediated grazing intensity is at its weakest. This effectively traps the community in an intermediate state instead of a clear trend towards either coral or macroalgal attractor. In such system, there is no single ‘tipping point’—an unstable equilibrium that clearly delineates a regime shift. Instead, the variability in location of the unstable equilibria due to constantly changing environment creates a fuzzy ‘transient zone’, a region in which these dynamic tipping points can be located probabilistically. With such dynamic

tipping points, systems at a given state can sometimes be above and at other times below the unstable equilibrium, with potentially rapid changes in qualitative behaviour and a tendency towards slow quantitative change in either direction due to constant proximity to the unstable equilibrium. In a system exhibiting transient dynamics due to environmental stochasticity, monitoring may record little net change in state over time (Fig. 3A, trajectory 3; Fig. 3B). Without information on variability in larval supply and its effect on system trajectory, the observers may therefore incorrectly blame the poor performance of the reef on a lack of improvement

in water quality management as a factor that consistently keeps the reef from exhibiting strong net recovery, or even conclude that the system permanently lacks resilience rather than that it is in a temporary and reversible state of flux. The key difference here is that a system exhibiting transient dynamics may need less input to escape the transient zone, as it may be more feasible to reduce environmental stochasticity than to restore lost feedback mechanisms (Mumby and Steneck 2008).

Reducing stochasticity and skewing it towards more deterministic behaviour by shifting or shrinking the transient zone could occur either due to natural causes or through deliberate management intervention (Rice 2001). Since system behaviour will become more deterministic outside the transient zone, temporal clustering of factors that results in short periods of predictable net trends will be important for escaping the transient zone. For example, consecutive years of poor larval supply could shift the balance of a system and either trap a heretofore recovering system in a transient state with little net recovery or alternatively shift many of the system trajectories away from the transient zone and towards a macroalgal-dominated state (Fig. 3C). Conversely, a sequence of years with high larval supply could cause temporary bout of recovery that will eventually allow system trajectories to escape from the transient zone and

towards higher coral cover states and more predictable net recovery (e.g., trajectories 3 and 4 in Fig. 3D). However, if enhanced supply in Fig. 3D was spread across several years rather than focused on a contiguous period, the effect would be less drastic as the system would have less of a chance to break out from transient dynamics (Fig. S5). From the management perspective, it would be more efficient to focus interventions in time in order to increase the short-term likelihood of system escaping the transient zone towards the parameter space where intrinsic positive feedbacks can take over and continue to drive the system towards recovery, after which management actions can de-escalate. The specific timing of interventions to counter specific disturbance regimes in this context will be explored in future work.

Ecological scenario 3: historical patterns of resilience become poor predictors of future performance

The emergence of transient dynamics can also mask the potential resilience, or the loss of resilience, of ecosystems. In a hypothetical example, consider two highly resilient reefs in a system that has only a single attractor (Fig. 4A). A reef that never approaches the transient zone continues to show rapid recovery (Fig. 4A, trajectory 1). In contrast, a reef that starts with a lower initial coral cover, perhaps because

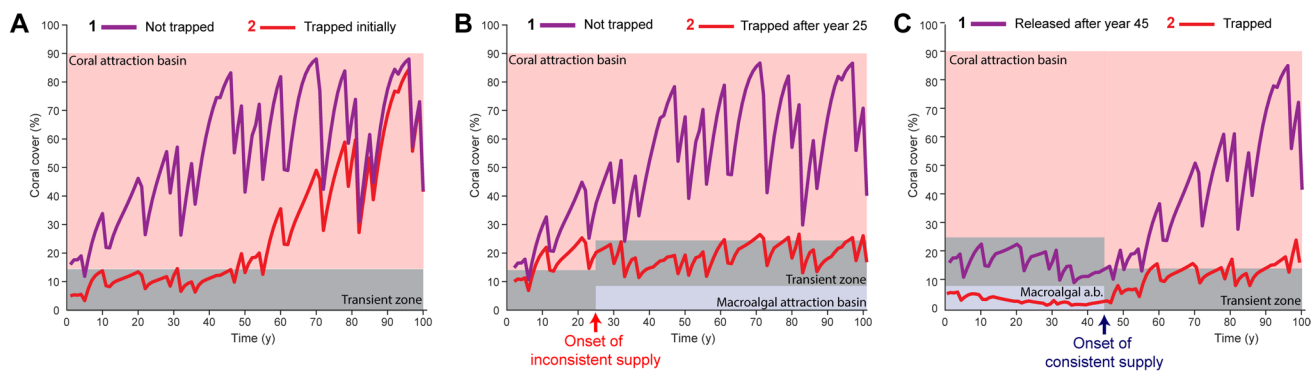


Fig. 4 Transient dynamics can mask reef resilience by trapping the system in a state with a low recovery rate. **A** In a system with a single coral attractor, a system that escapes the transient zone can recover rapidly (trajectory 1), whereas a system experiencing exactly the same conditions but starting at a lower initial level of coral cover (trajectory 2) can become trapped in a transient zone at low coral cover (‘ghost attractor’). The external supply remains high throughout the simulation ($e(t_1, \dots, t_{100}) \sim N(0.75, 0.01)$). **B** When external larval supply becomes inconsistent ($e(t_1, \dots, t_{25}) \sim N(0.75, 0.01)$, and after that e alternates between 6 years of $e \sim N(0.1, 0.01)$ and 4 years of $e \sim N(0.75, 0.01)$) and generates dynamic bistability, the transient zone will shift as well. A system that is already outside the transient zone can continue to recover (trajectory 1), whereas a system that happened to be in the newly formed transient zone can become trapped (trajectory 2) due to proximity to dynamic unstable equilibria (‘crawl-by’ with dynamic tipping points). The trapped system will not necessarily collapse, but will be trapped in a long-term transient

behaviour with little net change in coral cover despite not losing feedback mechanisms. **C** A shift from bistability to a single attractor due to consistent external larval supply (e alternates between 6 years of $e \sim N(0.1, 0.01)$ and 4 years of $e \sim N(0.75, 0.01)$ for the first 45 years, and after that $e(t_{45}, \dots, t_{100}) \sim N(0.75, 0.01)$) will also shift the transient zone. Response to the change may be rapid in some systems that were previously trapped (e.g., due to ‘crawl-by’ effect), but are now outside of the newly formed transient zone (trajectory 1). However, even though this resilient system now has only a single, coral-dominated attractor, recovery may not be immediately apparent for systems that become trapped in the newly formed transient zone (e.g., ‘ghost attractor’ effect on trajectory 2). Shaded background areas approximate the basins of attraction with red, coral attraction basin; blue, macroalgal attraction basin; grey, fuzzy transient zone. Initial conditions for the example trajectories are defined in Fig. S2. All reefs shown here have exactly the same disturbance regime with the same relative disturbance impacts

it experienced greater initial mortality after some disturbance, gets arrested by transient dynamics and shows little net recovery (Fig. 4A, trajectory 2). Both reefs experience the same disturbances, as well as having the same resilience and feedback mechanisms, yet the transient dynamics, due to increased overgrowth by algae at low coral cover and continued disturbance, slows the recovery of the second reef for four decades (Fig. 4, trajectory 2). The slow recovery here occurs because of a transient zone emerging due to nonlinear dynamics and environmental stochasticity resulting in a ‘ghost attractor’ effect (Fig. S6) and not simply because of Allee effects at low population size. In this case, the reef eventually escapes the transient zone and sets on a path of a more consistent recovery after two chance events that happen a few years apart—storm impacts around year 55 that both reduced macroalgal cover but only slightly impacted coral cover—provide a temporary release from competitive pressure from macroalgae. Such sudden shocks to the system, e.g., perturbations due to the storms, have been suggested as one of the mechanisms that can help with the recovery of coral reefs (Graham et al. 2013). Importantly, simply monitoring system performance in the 40 years prior to its sudden recovery would likely lead to this site being considered a relatively poor performer, even though it had the potential to recover rapidly with little warning all along.

A second set of reefs shows the emergence of transient dynamics because larval supply was disrupted by disturbance impacts elsewhere that made the external larval supply inconsistent, with alternating periods of four good years of larval supply followed by six poor years (Fig. 4B). This produced a system that exhibits bistability and shifted the transient zone towards moderate coral cover levels. While a reef that was already outside this newly formed transient zone was able to continue to recover rapidly (Fig. 4B, trajectory 1), a reef that was previously recovering but by chance has not yet recovered sufficiently before the shift to escape the new transient zone now gets trapped (Fig. 4B, trajectory 2). Environmental stochasticity now keeps the second reef in the transient zone with little net recovery, due to dynamic even though the trapped reef has the same ability to recover as the one that has clearly recovered. Notably, the temporarily trapped reef can continue to recover if, by another sequence of favourable chance events, it manages to escape the transient zone. However, observing historical patterns and the divergence of the trajectories a monitoring programme could incorrectly conclude that these two reefs have notably different resilience.

The final set of reefs in this scenario involves a system that shifts from dynamic bistability to a resilient system with a single coral attractor, possibly due to the recovery of larval sources elsewhere in the system (Fig. 4C). Prior to this shift, monitoring may have observed two reefs that were not recovering and conclude that both lacked resilience,

even though under the same disturbance regime and feedbacks one of them was essentially trapped in a transient zone due to dynamic tipping points (Fig. 4C, trajectory 1) and the other was slowly declining to a heavily degraded state (Fig. 4C, trajectory 2). While the reef that was previously trapped in a transient zone may now suddenly show a marked improvement as external larval supply becomes consistent (Fig. 4C, trajectory 1), the other reef that was also not recovering may stop degrading but remains trapped in a newly emergent transient zone where macroalgal attractors used to be located (Fig. 4C, trajectory 2). Monitoring could therefore fail to notice the change in resilience and instead conclude that the historical pattern of (non-)recovery and (non-)resilience continues.

Overall, transient dynamics that impair clear and rapid shifts in qualitative behaviour towards stable attractors imply that historical patterns of resilience may be poor predictors of future recovery patterns. In such cases, the outcome may come as a surprise to the observer—either in a form of sudden onset of recovery or continued lack of notable net change. Early warning signs that use time series analysis and interpolation from past trends (Dakos et al. 2015, 2019) may therefore not be able to predict the changes in system trajectory or the underlying resilience. However, such surprises could be better anticipated if the underlying mechanisms are considered and the apparent lags and qualitative uncertainty are viewed from the perspective of transient states. Shifting the focus from trends in ecosystem state, which tend to be the domain of much monitoring (Lam et al. 2017), to field assessments on the processes generating resilience will be key to avoid the sorts of interpretative errors identified here for resilience-based management (McLeod et al. 2019).

Conclusions and future directions

Conventional resilience theory increasingly recognises that critical thresholds are fuzzy and shift with environment (Hillebrand et al. 2020), yet many studies explicitly or implicitly assume a single underlying stability landscape (Scheffer and Carpenter 2003; Mumby et al. 2007), as did we in our introductory examples (Fig. 1). However, rather than simply being a gradual monotonic transition during an inevitable regime shift, which observers can then perceive as being either slow or rapid (Hughes et al. 2013), transients arise as a consequence of dynamic yet short-term shifts in stability structure affected by both non-linear dynamics and stochastic drivers, which ultimately characterise a system in flux. Notably, in contrast to systems that are either slow or fast, the rate of change in system state will change with the proximity to the tipping point, and this rate may continue to be slow after the tipping point has been crossed until the system moves further away from the

tipping point, thus potentially masking the critical transition as no sudden transition occurs after regime shift. In such systems, both recovery and collapse are still possible, and the eventual outcome is uncertain and subject to vagaries of stochastic drivers, while remaining possibly amenable to the right set of interventions.

Building on recent theory on transients in ecological systems (Hastings et al. 2018; Francis et al. 2021), we here use a simple model of coral-algal competition to illustrate how alternating attractions arising from a combination of stochastic disturbance regimes and larval connectivity can trap a system in a long transient state, during which the system stays in proximity to dynamically oscillating equilibria. Even a resilient ecosystem that has a single coral attractor can undergo periods of slow recovery and behave as if it had multiple equilibria (Fig. 1D, E) and can also develop temporary bistability due to environmental fluctuations (Fig. 3). Indeed, the disruptions brought on by climate change, which include (i) reducing coral growth and ability to compete for space (Jones and Berkelmans 2010), (ii) intensifying the disturbance regimes (Frölicher et al. 2018), and (iii) reducing the reliability of larval supply (Hughes et al. 2019), may all increase the likelihood of long transient states even in the formally resilient systems, such as the coral reefs far from human population centres that are thought to have high resilience with little risk of a regime shift. Recognising the role of transients in not only stressed ecosystems but also those that may serve as resilience standards may become increasingly important as most coral reefs will likely at least periodically exhibit low, degraded coral states in the future (Hoegh-Guldberg et al. 2007).

We have demonstrated for an important particular system, as suggested by Francis et al. (2021) in an abstract setting, that understanding the role and importance of transients is key to the management of ecological systems. An important novel aspect of our work here compared to earlier efforts (Francis et al. 2021; Hastings et al. 2021) has been to incorporate realistic considerations of the effects of stochasticity on transients in a management setting. Thus, we have both demonstrated the importance of transients in a specific system and extended our understanding of the importance of transients in general, providing a guide for management in the face of realistic consideration of stochasticity.

Our ability to interpret and predict the dynamics of coral reefs in isolation is likely to weaken as the degradation of these ecosystems continues. A priority for the future management approaches is thus to distinguish between systems with persistent low resilience due to systemic causes and essentially resilient systems with long-transient dynamics that retain the potential to escape transient zone and recover. Unlike systems that have lost their ability to recover and may need substantial long-term effort to prop them up and restart ecological feedbacks, systems with transients likely

still possess the necessary resilience and feedback mechanisms which can more readily take over once the system is outside the zone of transient dynamics. Recovery support in transient systems may also need more modest interventions, but only if such investment is targeted and timed well to help push the system out of the ‘slow’ zone of uncertainty towards more deterministic behaviour. Realising the ‘true resilience potential’ of future reefs will likely require a more nuanced integration of trends in physical, biological, and ecological processes, while also shifting to larger, meta-population scales: a considerable challenge for field programmes. Reefs identified as exhibiting transient dynamics will require agile management, capable of applying short-term intense interventions that target and support the right ecological processes, to help them break out and unmask their resilience potential.

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Author contribution K.H., A.H., and P.J.M. conceived and designed the study and wrote the manuscript; K.H. adapted and designed the models and simulations (with inputs from A.H. and P.J.M.), implemented the simulations, analysed the outputs, and produced the figures; P.J.M. performed sensitivity analysis and model comparison and produced corresponding figures; and all authors provided inputs to the study and scenario design and contributed substantially to manuscript revisions. All authors gave final approval for publication.

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Data availability The Matlab code used for the simulations and analyses, as well as the simulation outputs used to generate the figures, are available at <https://github.com/khock1/TransientDynamics> and <https://zenodo.org/record/4708653>. Additional materials are available from K.H. and P.J.M. upon reasonable request.

Declarations

Competing interests Alan Hastings is Editor-in-Chief of *Theoretical Ecology*.

Conflict of interest The authors declare no competing interests.

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