Temporal clustering of tropical cyclones and its ecosystem impacts

Peter J. Mumbya,b,1, Renato Vitolo, and David B. Stephensonc

aSchool of Biological Sciences and Global Change Institute, Goddard Building, University of Queensland, St Lucia, Queensland 4072, Australia; bBioSciences, College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4PS, United Kingdom; and cCollege of Engineering, Mathematics and Physical Sciences, Harrison Building, North Park Road, University of Exeter, Exeter EX4 4QF, United Kingdom

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Tropical cyclones have massive economic, social, and ecological impacts, and models of their occurrence influence many planning activities from setting insurance premiums to conservation planning. Most impact models allow for geographically varying cyclone rates but assume that individual storm events occur randomly with constant rate in time. This study analyzes the statistical properties of Atlantic tropical cyclones and shows that local cyclone counts vary in time, with periods of elevated activity followed by relative quiescence. Such temporal clustering is particularly strong in the Caribbean Sea, along the coasts of Belize, Honduras, Costa Rica, Jamaica, the southwest of Haiti, and in the main hurricane development region in the North Atlantic between Africa and the Caribbean. Failing to recognize this natural nonstationarity in cyclone rates can give inaccurate impact predictions. We demonstrate this by exploring cyclone impacts on coral reefs. For a given cyclone rate, we find that clustered events have a less detrimental impact than independent random events. Predictions using a standard random hurricane model were overly pessimistic, predicting reef degradation more than a decade earlier than that expected under clustered disturbance. The presence of clustering allows coral reefs more time to recover to healthier states, but the impacts of clustering will vary from one ecosystem to another.

The devastating economic, social, and ecological impacts of tropical cyclones are well established (1–3). Estimates of hurricane rates are needed to model the dynamics of many ecological (4–6), social (7), and economic (8) processes. A key implicit assumption of virtually all such models is that cyclones occur randomly in time with a constant rate that can vary geographically. Using a century of cyclone tracks from the Atlantic (9), we begin by testing whether such a model of hurricanes is indeed appropriate. In areas where such models are found to be inappropriate, because hurricane events are in fact clustered in time rather than obeying a constant rate, we then investigate whether this departure from a Poisson process matters when predicting the health of Caribbean coral reefs. Important theories of disturbance ecology originating from coral reefs (2), making them a convenient system to pose this question. It should be noted that clustering of natural hazards such as hurricanes can also have a profound impact on nonecosystem features: For example, clustering can induce a sub-

Climate change | climate variability | multidecadal variability

Impact of Clustered Hurricane Events on Ecosystems. We asked whether the observed levels of hurricane clustering (Fig. 1) are sufficient to cause a significant change in coral reef state. To do this we used a spatial simulation model of a Caribbean coral reef under realistic levels of hurricane disturbance. The model simulates the population dynamics of several growth forms of coral under both chronic and acute disturbance. A detailed model parameterization is given in SI Text, and its predictions have been


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1To whom correspondence should be addressed. E-mail: p.j.mumby@uq.edu.au.

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validate against a long-term empirical dataset from Jamaica during which multiple hurricanes occurred (32).

For three representative rates of annual hurricane incidence (0.05, 0.10, 0.20) we compared the overall health of reefs under four models of temporal dispersion: a null model of random hurricane events, and three representative levels of overdispersion (0.1, 0.3, 0.5). We initialized reefs with a moderately healthy coral cover of 30% and assumed that reefs were well managed with high fish herbivory, high natural algal productivity, and no sedimentation. The long-spined sea urchin, which was decimated by disease in 1983 (33), was assumed to be functionally absent in the reef habitat and depth modeled. Background levels of coral mortality were included, but we ignored ocean acidification and coral bleaching so as to focus specifically on the impact of hurricanes.

Under fairly intense hurricane rates (>0.1 per annum), overall coral cover declined during the century, emphasizing the problems faced by today’s reefs, which often lack a major class of branching corals (34) and experience an undergrazed environment lacking a major group of herbivores (32). However, individual reef trajectories under clustered hurricanes tended to be healthier for longer than those experiencing random hurricane events at the same rate (Fig. 3A). Indeed, average coral cover was always greater under clustered hurricanes and the magnitude of this “mitigation” increased, often nonlinearly, with mounting overdispersion (Fig. 3B and C). Comparing the response across different rates of hurricane, the effects of clustering were also nonlinear; reefs experiencing intermediate rates of disturbance (0.1) responded relatively strongly to modest clustering in disturbance (Fig. 3C). The exceptional response of reefs under intermediate disturbance arises because more frequent events maintain the system in a highly degraded state, thereby attenuating the scope for recovery, and reefs experiencing less frequent events spend so little time in a degraded state that the century-averaged response to hurricanes is minor.

To synthesize our results, we determined the year at which reefs become functionally degraded under a sustained hurricane regime. We loosely define “degraded” as having occurred once at least 95% of the subsequent reef observations remain in a degraded state of <10% cover. Degradation was found only under the higher hurricane rates but clustering delayed the onset of degradation considerably: by 6 y under frequent hurricanes and 14 y under intermediate hurricane rates (Fig. 4).

Although cyclones damage reefs, our results imply that a strongly clustered hurricane regime will allow ecosystems to remain in a later successional state for a greater proportion of the time. If a system has not been struck for some time, the first hurricane event will often have a devastating impact and remove many of the vulnerable organisms (35). If the next hurricane occurs before much recovery has taken place (i.e., as part of a cluster of events), its impact may be relatively weak because few vulnerable individuals remain and ecosystem recovery remains at a nascent stage that limits the addition of new susceptible colonies (36, 37). Indeed, a metaanalysis of hurricane impacts on 286 reefs found that time elapsed since the previous hurricane event was a major positive correlate of subsequent damage (38), which provides supporting empirical evidence that clustered events should, on average, damage the ecosystem less. Comparable variations in hurricane impact during successive events have been reported in other ecosystems including tropical forests (6, 39) and oyster beds (40).

Our conclusions are likely to be conservative in that the “mitigative benefits” of clustered disturbance are likely to be underestimated in our analysis of reef ecosystems, largely because our simple model captures some, but not all, of the vulnerability among individual corals to hurricane damage. In our model,
vulnerability is implemented as a function of coral size, but additional variability is likely among individuals by virtue of their phenotypic expression (e.g., shape) and local microhabitat (e.g., proneness of their underlying substrate to collapse). Our model does not resolve such small-scale effects, but these would tend to increase the disparity of impacts between successive hurricane events and increase the “mitigative effect” of clustered versus Poisson processes.

The reef framework built by living corals underpins several important ecosystem services including coastal protection from storms, reef fisheries, and the generation of sand for building materials and beach tourism. Given that reefs are increasingly disturbed by the El Niño–Southern Oscillation phenomenon, climate change, and overexploitation, most exist in a transient state, rarely reaching a truly late successional community composition. However, the principle remains that a reef in a higher state of recovery will tend to have higher cover, a later successional state, and offer higher levels of reef-based ecosystem services.

Hurricanes are a major structuring force in terrestrial (42, 43), estuarine (44), and aquatic systems (45). The impact of hurricane clustering on ecosystems will depend on their vulnerability to hurricane damage, the consequences of remaining in a damaged state during successive clustered hurricane events (even if followed by an extended recovery phase), and the relative rates of ecosystem recovery and hurricane incidence. For example, an ecosystem experiencing severe Allee effects (46) after a hurricane might be negatively impacted by clustering. The next Intergovernmental Panel on Climate Change assessment will place renewed effort in determining the effects of climate change on cyclone activity. Predictions of climate change in hurricane-prone ecosystems should consider the clustered nature of events as these can have a significant bearing on results. For coral reefs in the Atlantic, hurricanes are sufficiently clustered to alter the predictions of ecosystem degradation by more than a decade.

Methods
We considered cyclones passing over disks of radius 300 km in order to capture the damaging footprint of strong surface winds distributed asymmetrically about the eye of the storms (47). We count the yearly number of impacts of tracks on disks of radius \( R = 300 \) km centered at grid points with spacing 1° on a domain surrounding the North Atlantic. This gives a time series \( Y = (y_1, \ldots, y_{10}) \) of counts for each grid point. The dispersion statistic is defined as \( \varphi = s^2/y - 1 \), where \( y \) is the sample mean and \( s^2 \) is the sample variance of the counts. If the process of cyclone transit is totally random (that is, events are independent of each other) and stationary, then the counts should follow a Poisson distribution and so have \( \varphi = 0 \). Therefore, \( \varphi > 0 \) indicates overdispersion compared to a constant mean Poisson distribution and provides a measure of serial (temporal) clustering of the cyclone transit process (10, 17628 | www.pnas.org/cgi/doi/10.1073/pnas.1100436108 Mumby et al.)
When the maximum wind speed within a disk is larger than 0.2 and comparison of randomly dispersed hurricanes (black) with those clustered events (blue) showed a hurricane rate of 0.2 and comparison of randomly dispersed hurricanes (black) with those at an overdispersion of 0.5 (red).

The same analysis is performed for hurricane impacts, which are counted when the maximum wind speed within a disk is larger than 119 km h⁻¹. For Poisson regression we fitted the model

\[ Y \mid X_1, X_2, \ldots, X_m \sim \text{Poisson} (\mu) \]

\[ \log(\mu) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3. \]

This expresses the rate \( \mu \) as a function of the time-varying covariates, which are used to describe the hurricane characteristics, such as wind speed, size, and location. Following Elsner et al. (2009), for every year in the record we took August-October averages of the monthly values of the AMO and SO indices and May-June pre-hurricane-season averages of the monthly values of the NAO index.

Each coral reef simulation was run for a period of 100 y. Each combination of hurricane rate and dispersion was repeatedly simulated 100 times and the mean response reported in figures. Although the simulation of disturbances was probabilistic, only those disturbance regimes that conformed exactly to the overall long-term disturbance rate (e.g., five events over 100 y for a rate of 0.05) were included, which ensured that comparisons between disturbance regimes were not confounded by minor statistical noise. Statistical analyses were not undertaken because they would have limited meaning.

We could always increase the number of simulations to obtain a significant difference among treatments. Further details of the model are given in SI Text.

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Fig. 3. Impacts of clustered versus random hurricanes after a century of disturbance showing examples of individual reef trajectories (A). Increases in century-averaged coral cover under clustered events are expressed both in absolute units of coral cover (B) and in relative terms where the increase is given as a percentage of the mean-century-averaged cover under random hurricane events (C). Individual trajectories (A) shown for a hurricane rate of 0.2 and comparison of randomly dispersed hurricanes (black) with those at an overdispersion of 0.5 (red).

Fig. 4. Delays to the degradation of coral reef ecosystems under clustered versus random sequences of hurricanes. Degradation was defined as having occurred once coral cover remained below 10% for >95% of subsequent time steps. The earlier the degradation occurs, the longer the reef remains in a degraded state.

11. The same analysis is performed for hurricane impacts, which are counted when the maximum wind speed within a disk is larger than 119 km h⁻¹. For Poisson regression we fitted the model

\[ Y \mid X_1, X_2, \ldots, X_m \sim \text{Poisson} (\mu) \]

\[ \log(\mu) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3. \]
Further Details of the HURDAT Dataset. The Atlantic Basin Hurricane Database (HURDAT), available at http://www.aoml.noaa.gov/hrd/hurdat/Data_Storm.html, contains tropical cyclone tracks in the North Atlantic since 1851. Several authors have noted that this record is not spatiotemporally homogeneous: Until 1943, it is based on ship logbooks and landfall observations, with changes over time in the ship tracks affecting the record (1). The ship and landfall record was complemented by aircraft reconnaissance flights from 1944 and satellite observations have been used since they became available in 1966. Various corrections have been proposed to address the storm undercounts which are likely to have occurred before 1944 (1, 2). However, these corrections are of no use for the purpose of our paper because they aim at correcting the basin-wide yearly numbers of tropical cyclones, whereas our methodology requires the actual tracks. To partially address this issue, following Villarini et al. (3), we only consider HURDAT tracks lasting for more than 2 d. In the figures below, we compare the results obtained by taking all HURDAT tracks versus the results (presented in the main text) which use only tropical cyclones with duration of at least 2 d: There is virtually no change and the same holds for the dispersion of the hurricane tracks. Indeed, only 21 tracks are removed by the 2-d filtering procedure (Fig. S1).

Fig. S1. Comparison of yearly transit rates (A), dispersion for all cyclones (C), and dispersion for hurricanes only (D) using all HURDAT tracks (Left) versus only HURDAT tracks that last more than 2 d (Right). Subpanel lettering (A, C, D) matches that provided in Fig. 1 of the main text to aid comparison. The circles in A have equal radius of 300 km with distances measured along a great circle.
Coral recruitment
Coral growth
Competition between corals and cropped algae
Competition between corals and macroalgae 1:
Effect of macroalgae on corals
Competition between corals and macroalgae 2:
Effect of corals on macroalgae
Grazing by fishes and impact of fishing

Table S1. Contents of individual cells (0.25 m²) within the model

<table>
<thead>
<tr>
<th>Substratum</th>
<th>Range, cm²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brooding coral 1 (e.g., Porites, Agaricia) (BC1)</td>
<td>1 ≤ BC1 ≤ 2,500</td>
</tr>
<tr>
<td>Brooding coral 2 (e.g., Mycetophyllia) (BC2)</td>
<td>1 ≤ BC2 ≤ 2,500</td>
</tr>
<tr>
<td>Spawning coral 1 (e.g., Montastraea cavernosa, Meandrina) (SC1)</td>
<td>1 ≤ SC1 ≤ 2,500</td>
</tr>
<tr>
<td>Spawning coral 2 (e.g., Montastraea annularis) (SC2)</td>
<td>1 ≤ SC2 ≤ 2,500</td>
</tr>
<tr>
<td>Cropped algae (filamentous, coralline red algae, and short turfs (&lt;5 mm height)), 0–6 mo (Aₖ)</td>
<td>0 ≤ Aₖ ≤ 2,500</td>
</tr>
<tr>
<td>Dictyota pulchella (D)</td>
<td>0 ≤ D ≤ 2,500</td>
</tr>
<tr>
<td>Lobophora variegata (L)</td>
<td>0 ≤ L ≤ 2,500</td>
</tr>
<tr>
<td>Ungrazeable substratum (e.g., sand), U</td>
<td>U = 0 or U = 2,500</td>
</tr>
</tbody>
</table>

All substrata represented as area (cm²).

Table S2. Basic parameterization of simulation model for midshelf reefs without significant sediment input and sparsisomid-dominated grazing

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coral recruitment</td>
<td>Corals recruit to cropped algae, Aₖ, and A₁₂, because algal turfs are not heavily sediment laden. Recruit at size 1 cm². Recruitment rate of brooders and spawners (respectively): 2 and 0.2 per 0.25 m² of cropped algae per time interval. Recruitment rate was adjusted for rugosity (ca. 2) and the cover of cropped algae at Glovers Reef (1).</td>
</tr>
<tr>
<td>Coral growth</td>
<td>Coral size is quantified as the cross-sectional, basal area of a hemispherical colony (cm²). BC have a lateral extension rate of 0.8 cm y⁻¹ and SC grow slightly faster at 0.9 cm y⁻¹ (based on median rates for Porites astreoides, Porites porites, Siderastrea siderea, Montastraea annularis, Colpophyllia natans, and Agaricia agaricites) (2–6).</td>
</tr>
<tr>
<td>Coral reproduction</td>
<td>Excluded, assume constant rate of coral recruitment from outside reef (i.e., no stock-recruitment dynamics).</td>
</tr>
<tr>
<td>Colonization of cropped algae</td>
<td>C (i) when macroalga is grazed and (ii) after all coral mortality events (7) except those due to macroalgal overgrowth (see coral–algal competition below).</td>
</tr>
<tr>
<td>Colonization of macroalgae</td>
<td>Macroalgae have a 70% chance of becoming established if cropped algae are not grazed for 6 mo (mostly Dictyota) and this increases to 100% probability after 12 mo of no grazing (mostly Lobophora). Rates acquired from detailed centimeter-resolution observations of algal dynamics with and without grazing (8).</td>
</tr>
</tbody>
</table>
| Macroalgal growth over dead coral (cropped algae) | In addition to arising from cropped algae that are not grazed (above), established macroalgae also spread vegetatively over cropped algae (mostly Lobophora because Dictyota spread shows little pattern with grazing). The probability that macroalgae will encroach onto the algal turf within a cell, P₉₂₅ₕ, is given by P₉₂₅ₕ = M₄ₕₗₗₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜₜ¢...
<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td>Partial-colony mortality of corals</td>
<td>Size-dependent, following empirical observations from Curaçao before major bleaching or hurricane disturbances (19). State variables reported in literature converted to dynamic variables using least squares optimization until equilibrail state in model matched observed data. Implementation uses $P_{pm} = (100 - \sqrt{8.9 + 11.2 \ln(j)})/100$ and $\ln(A_{pm} \times 100) + 1 = -0.5 + 1.1 \ln(x)$, where $P_{pm}$ is the probability of a partial mortality event, $A_{pm}$ is the area of tissue lost in a single event, and $x$ is the size of the coral in squared centimeters.</td>
</tr>
<tr>
<td>Whole-colony mortality of juvenile and adult corals</td>
<td>Incidence of mortality in juvenile corals (60-250 cm²), 2% per time interval (ca. 4% pa). Halved to 1% (2% pa) for mature colonies (&gt;250 cm²) (20). These levels of mortality occur in addition to macroalgal overgrowth. Algal overgrowth and predation affects juvenile corals (see above and below).</td>
</tr>
<tr>
<td>Predation on coral recruits</td>
<td>Instantaneous whole-colony mortality occurs from parrot fish predation at a rate of 15% each 6-mo iteration of the model (11). Predation is confined to small corals of area ≤5 cm², based on Meesters et al. (19), where between 60% and 95% of bite-type lesions were of this size.</td>
</tr>
<tr>
<td>Hurricane impact on juvenile corals (&gt;60 cm²): Whole-colony mortality</td>
<td>Whole-colony mortality of larger corals is represented using a quadratic function (5) where $x$ is the cross-sectional basal area of colony (20, 21). Small colonies avoid dislodgement due to their low drag, intermediate-sized corals have greater drag and are light enough to be dislodged, whereas large colonies are heavy enough to prevent dislodgement $P_{pm} = -0.0000003x^2 + 0.0007x + 0.0551$.</td>
</tr>
<tr>
<td>Hurricane impact on mature corals (&gt;250 cm²): Partial-colony mortality</td>
<td>The extent of partial mortality, $M_{pm}$, is modeled using a Gaussian distribution with mean of 0.30 and standard deviation of 0.20. Each value of $M_{pm}$ represents the percentage of original colony tissue that is lost due to the hurricane. If $M_{pm} ≤ 0$, there is no mortality. If $M_{pm} ≥ 1$, the entire colony is lost (though this is a rare event) (22).</td>
</tr>
<tr>
<td>Hurricane impact on juvenile corals (1-60 cm²)</td>
<td>Scouring by sand during a hurricane may cause 80% whole-colony mortality in juvenile corals (1).</td>
</tr>
<tr>
<td>Hurricane impact on macroalgae</td>
<td>Hurricanes reduce the cover of macroalgae to 10% of its prehurricane level (23).</td>
</tr>
</tbody>
</table>

**Parameter Details**

- **BC**: brooding coral
- **SC**: spawning coral
- **pa**: per annum
- **CL**: confidence level