

# Interdependency of tropical marine ecosystems in response to climate change

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**Ecosystems are linked within landscapes by the physical and biological processes they mediate. In such connected landscapes, the response of one ecosystem to climate change could have profound consequences for neighbouring systems. Here, we report the first quantitative predictions of interdependencies between ecosystems in response to climate change. In shallow tropical marine ecosystems, coral reefs shelter lagoons from incoming waves, allowing seagrass meadows to thrive. Deepening water over coral reefs from sea-level rise results in larger, more energetic waves traversing the reef into the lagoon<sup>1,2</sup>, potentially generating hostile conditions for seagrass. However, growth of coral reef such that the relative water depth is maintained could mitigate negative effects of sea-level rise on seagrass. Parameterizing physical and biological models for Lizard Island, Great Barrier Reef, Australia, we find negative effects of sea-level rise on seagrass before the middle of this century given reasonable rates of reef growth. Rates of vertical carbonate accretion typical of modern reef flats (up to 3 mm yr<sup>-1</sup>) will probably be insufficient to maintain suitable conditions for reef lagoon seagrass under moderate to high greenhouse gas emissions scenarios by 2100. Accounting for interdependencies in ecosystem responses to climate change is challenging, but failure to do so results in inaccurate predictions of habitat extent in the future.**

Climate change affects the distribution, extent and functioning of ecosystems<sup>3</sup>. Ecosystems comprise living organisms and the non-living components of their environment in an interacting system. Interactions between distinct ecosystems also occur—for instance, where one ecosystem modifies adjacent environments, allowing other ecosystems to thrive where they otherwise would not exist. At the species level, interdependencies in response to climate change occur when interacting species have different responses to a climate stressor. This can alter interactions such as competition, rates of pathogen infection, herbivory and predation<sup>4–6</sup>. Interdependencies in response to climate change at the ecosystem level may also exist, but have not previously been quantified in a predictive framework.

In shallow tropical seas, coral and seagrass exist in a patchy habitat mosaic, connected by numerous biological, physical and chemical linkages<sup>7,8</sup>. Seagrass supports early life-stages of many reef fish<sup>7</sup>; provides a buffer against low pH (ref. 8); binds sediments to reduce erosion<sup>9</sup> and filters nutrients and sediments from

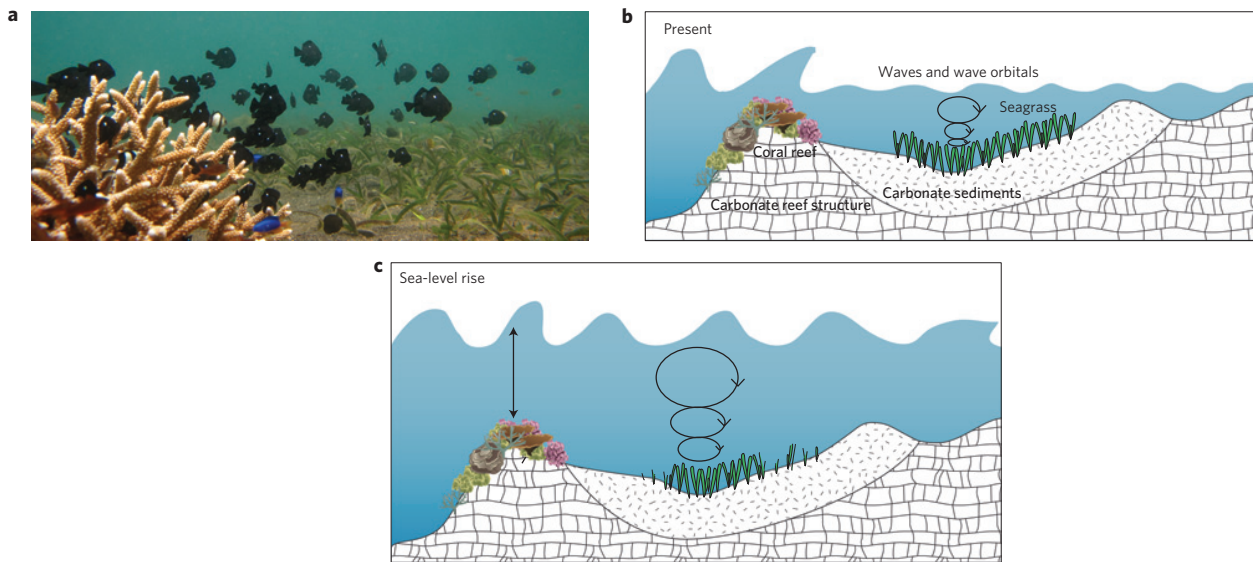
water<sup>9</sup>. In turn, the distribution of shallow seagrass meadows which thrive in low-energy wave environments<sup>9</sup> depends on wave sheltering by coral reefs. Seagrass and coral reefs support the livelihoods of many of the 1.3 billion people who live within 100 km of tropical coasts<sup>10</sup>. Unfortunately, rapid and widespread declines of these habitats are occurring worldwide<sup>11–13</sup>. Accurately predicting effects of climate change on tropical marine ecosystems is essential for developing appropriate management plans to maintain human well-being.

Sea-level rise (SLR) drives changes in the distribution of seagrass<sup>14</sup> and coral reefs<sup>15</sup>. Despite considerable uncertainty, SLR of up to 1 m by 2100 may occur given business-as-usual greenhouse gas emissions scenarios<sup>16–18</sup>. Rising seas result in inland migration of coastal habitats, loss of habitat at the seaward edge, vertical accretion to maintain relative position with sea level, adaptation to new conditions, or a combination thereof<sup>14</sup>. Coral reef growth (carbonate accretion) occurs by calcification of corals and coralline algae, and subsequent in-filling of the reef matrix<sup>19,20</sup>. Sediment accretion in seagrass meadows occurs by the production of roots and rhizomes, and by promotion of high rates of sediment deposition and retention<sup>9</sup>.

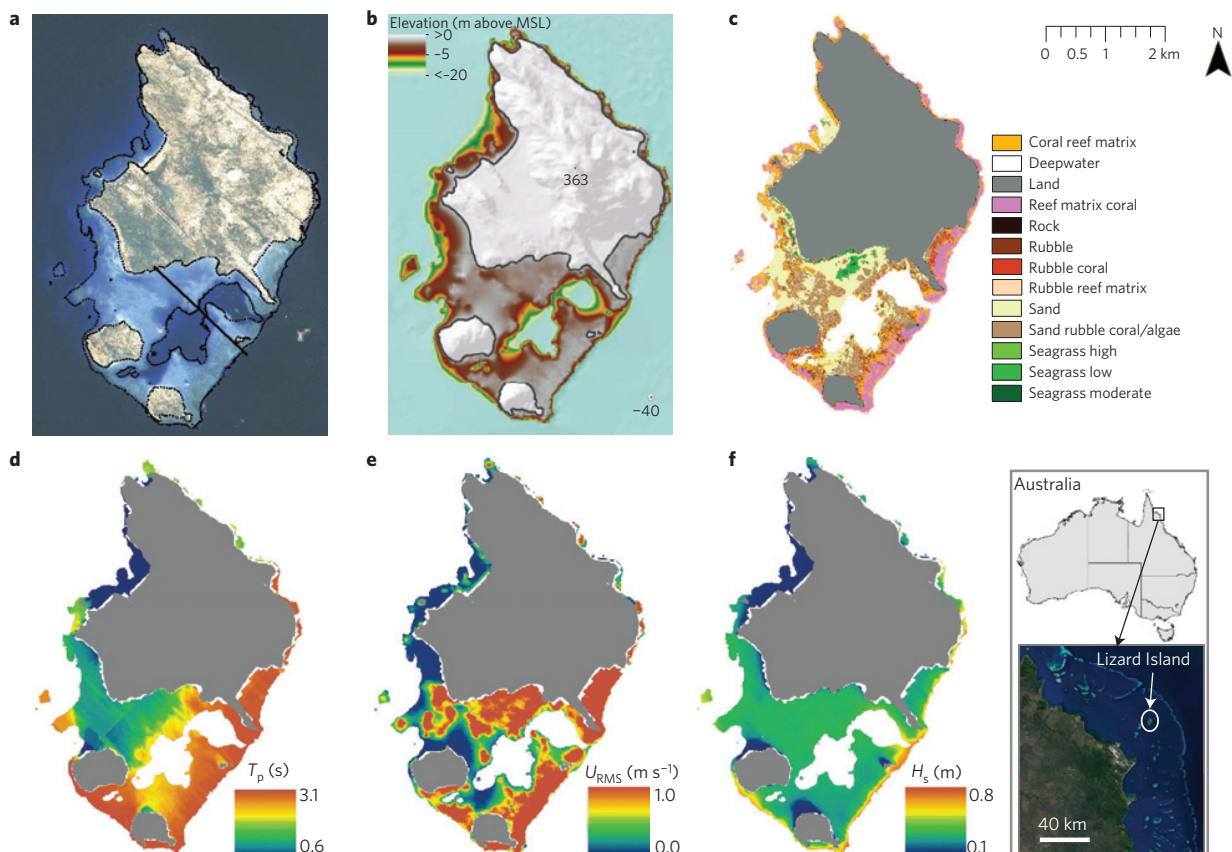
Our aim was to predict the response of seagrass distribution to altered wave conditions resulting from rising seas and the responses of distinct ecosystems (coral reefs and seagrass) to changes in sea level (Fig. 1). We examined this process at an intensively studied coral reef environment at Lizard Island, Great Barrier Reef (Fig. 2a), where there is a gradient of wave exposure over shallow water habitats<sup>15,21,22</sup>.

The first task was to understand the relationship between the wave environment and the distribution of seagrass. To do so, we built a species distribution model (SDM; ref. 23) of shallow water (<5 m) seagrass habitats as a function of the wave environment. Field data on water depth<sup>21</sup> (Fig. 2b) and distribution of benthic habitats (Fig. 2c) were collected and mapped to 5 × 5 m resolution using remote sensing techniques. Synoptic maps of parameters characterizing the wave environment (benthic root mean square wave orbital velocities (m s<sup>-1</sup>, hereafter  $U_{RMS}$ ), peak wave periods (s, hereafter  $T_p$ ), and significant wave heights (m, hereafter  $H_s$ ) (Fig. 2d–f)) at the same locations were generated using bathymetry and wind data as input to the Simulating WAVes Nearshore (SWAN; ref. 24) model. Spatial auto-correlation (SAC) was removed following the residual autocorrelate (RAC) approach<sup>25</sup>.

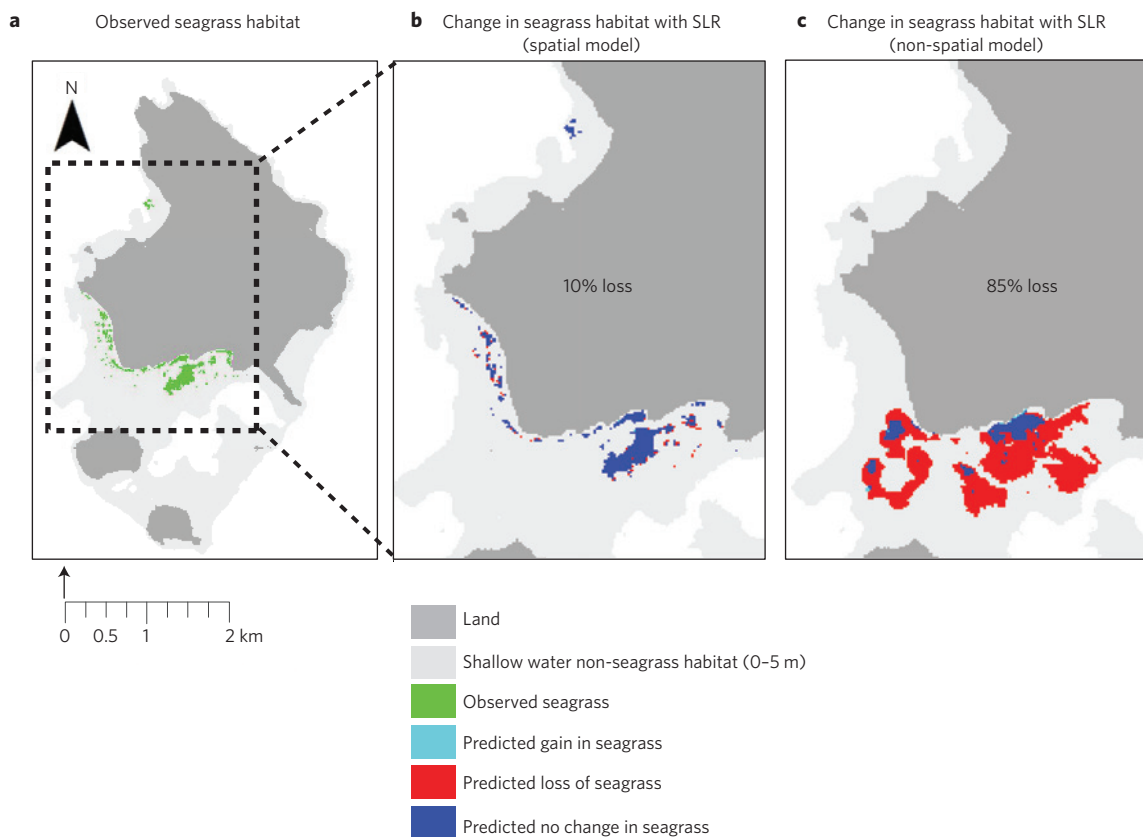
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**Figure 1 |** Seagrass and coral reef ecosystems are connected within landscapes by the physical and biological processes they mediate; in such connected landscapes, the response of one ecosystem to climate change could have profound consequences for neighbouring systems. **a**, Seagrass meadows and coral reefs form distinct ecosystems, yet often live in close proximity in linked tropical marine ecosystems. **b**, Coral reefs block and dissipate wave energy and permit seagrass, which is less wave tolerant, to exist in protected lagoons. **c**, Deepening water from sea-level rise will allow larger, more energetic waves to traverse the reef into the lagoon, reducing habitat suitability for seagrass. Images reproduced with permission from: **a**, M. I. Saunders, **b,c**, Tracey Saxby, Diana Kleine, Catherine Collier, Joanna Woerner; Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/imagelibrary](http://ian.umces.edu/imagelibrary)).



**Figure 2 |** Input data used to examine the effect of sea-level rise and coral reef growth on the distribution of seagrass at Lizard Island, Great Barrier Reef, Australia. **a**, High-resolution Worldview 2 satellite image of the study site at Lizard Island, Great Barrier Reef, Australia, obtained in October 2011. Overlaid are a polygon indicating boundaries of the shallow water (0–5 m) modelled in 2D analyses (dashed black), and a transect line used in 1D analyses (solid black). **b**, Digital elevation model<sup>21</sup> (DEM); **c**, Benthic habitat maps produced using remote sensing techniques and field validation. **d–f**, Upper 90 percentiles of three wave parameters: peak wave period,  $T_p$  (s) (**d**); benthic wave orbital velocity,  $U_{RMS}$  ( $m\ s^{-1}$ ) (**e**); significant wave height,  $H_s$  (m) (**f**). Images reproduced with permission from: **a**, DigitalGlobe Educational Licence 2011, Univ. Wollongong; **b**, ref. 21, Taylor and Francis, [www.tandfonline.com](http://www.tandfonline.com).



**Figure 3 | Results of model simulations examining the response of seagrass to altered wave conditions resulting from sea-level rise and no coral reef growth at Lizard Island, Great Barrier Reef, Australia. a,** Observed seagrass presence mapped using remote sensing and field validation in 2011/2012. **b,c,** Changes in predicted seagrass suitable habitat based on wave parameters resulting from 1 m sea-level rise and no accretion of the benthos. **b,** Present-day spatial dependencies are maintained (10% seagrass habitat loss). **c,** Spatial dependencies are omitted, reflecting the potential for altered spatial relationships in the future (85% seagrass habitat loss).

SAC may represent unmodelled environmental variables or population processes such as dispersal, and it is debatable whether it should be accounted for in SDMs used to predict future scenarios<sup>26,27</sup>. Therefore, predictions of future seagrass distribution (Figs 3 and 4) are presented for two scenarios<sup>27</sup>: the 'spatial model', in which current spatial dependencies, such as limits to colonization, persist into the future; and the 'non-spatial model', in which the present and future distribution of seagrass is not limited by current spatial dependencies. The non-spatial model makes less accurate predictions of present-day distribution, but may more accurately predict seagrass redistribution in the future. This may be more realistic than the spatial model, as the size of the study area is small, thus seagrass is unlikely to be limited by dispersal over multiple decades.

Seagrass presence versus absence was correctly classified by the spatial model in  $99.5 \pm 0.03\%$  of cases (deviance explained = 90%;  $p < 0.01$ ; Supplementary Tables 2 and 4). The probability of seagrass presence declined with increases in each of the wave parameters ( $H_s$ ,  $T_p$ , and  $U_{RMS}$ ) (Supplementary Fig. 8). Increases in erosion, plant breakage, reductions in establishment potential, or a combination of factors may drive this relationship.

The next step was to examine how deeper water resulting from SLR, in the absence of accretion in either habitat, would affect the distribution of seagrass. To do so, we simulated SLR of 1 m by increasing water depth at all locations, re-calculated the wave parameters using SWAN, and predicted seagrass distribution using the SDM based on the revised wave parameters. Using the spatial model, SLR of 1 m reduced the area of habitat suitable for seagrass by 10%, from 6.5 to 5.7 hectares (Fig. 3b). Losses were due to larger, more energetic waves crossing the reef crest, resulting in increases in

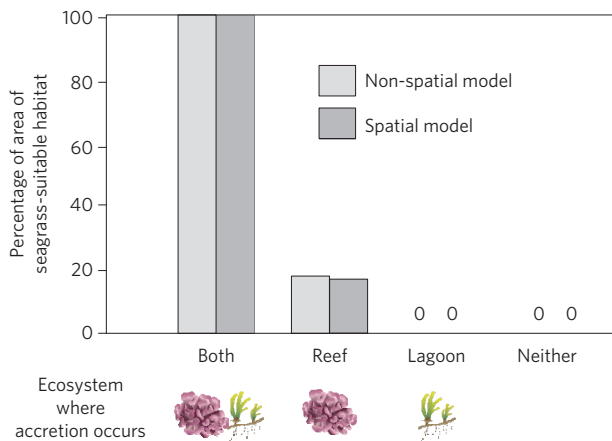
the magnitude of  $U_{RMS}$ ,  $T_p$ , and  $H_s$  in the lagoon. Results for the non-spatial model, in which spatial dependencies in habitat occurrence were omitted, indicated 85% seagrass habitat loss (Fig. 3c).

In reality, bathymetry will be modified by geomorphic and ecological feedbacks during SLR such as sediment accretion and reef growth. To examine the effect of ecosystem-specific response to SLR on the likelihood of seagrass occurring, we factored in habitat-specific accretion to modify the bathymetry concurrently with SLR.

From this point onwards, for computational efficiency, we used only a subset of data occurring along a one-dimensional (1D) transect passing over the reef and through the seagrass (Fig. 2a). Two sets of scenarios were examined: one in which the coral reef platform, and/or the inner lagoon, could accrete to 1 m (or not) by 2100 to keep pace with 1 m SLR; and the second in which SLR magnitudes ranging from 45 to 135 cm by 2100, corresponding to published SLR trajectories<sup>16,17</sup>, and rates of reef growth ranging from 1 to 10 mm yr<sup>-1</sup> (ref. 20), were considered at four points in time (2030, 2050, 2080 and 2100). Using these revised bathymetries we calculated the wave parameters using SWAN, and predicted the likelihood of seagrass occurring using the SDM.

For both the spatial and non-spatial models, the area of habitat on the transect suitable for seagrass depended on whether reef growth occurred in response to SLR, and was less affected by sediment accretion in seagrass (Fig. 4). When both habitats 'kept pace' with SLR, the area of seagrass in 2100 did not change compared to present. When neither sediment accretion nor reef growth, or only sediment accretion in seagrass, occurred, all seagrass suitable habitat was lost, because  $T_p$ ,  $H_s$  and  $U_{RMS}$  increased in the lagoon. When only reef growth occurred, seagrass habitat remained suitable,



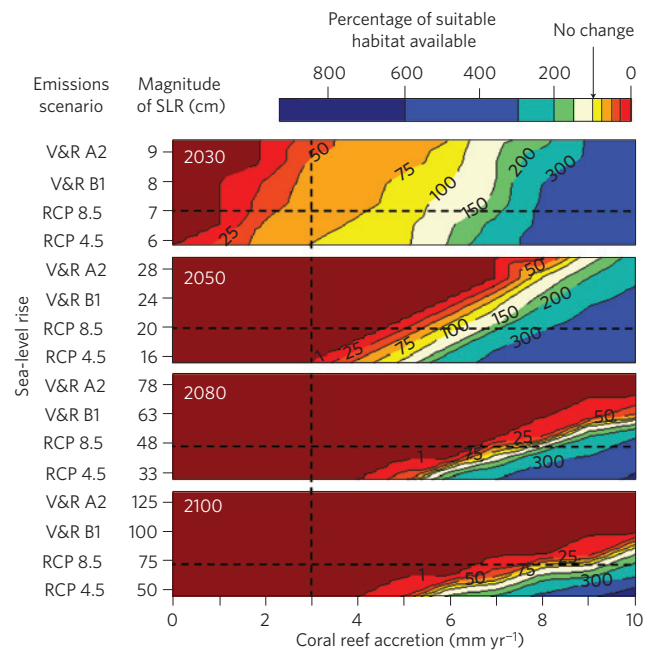


**Figure 4 | The relative (%) area of seagrass-suitable habitat available along a transect spanning coral reef and seagrass ecosystems at Lizard Island, Great Barrier Reef, Australia.** Results are for scenarios of wave conditions resulting from a 1 m sea-level rise by 2100 and various combinations of ecosystem-specific accretion of 1 m magnitude. Habitats become unsuitable for seagrass in scenarios where accretion does not occur on the coral reef. Symbols indicate coral reef and lagoon seagrass, respectively. Images reproduced with permission from Tracey Saxby and Catherine Collier, Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/imagelibrary](http://ian.umces.edu/imagelibrary)).

but declined to ~20% relative to present. Together, this suggests that seagrass will be strongly affected by altered wave conditions resulting from changing water depth.

The likelihood of seagrass suitable habitat occurring along the transect at particular points in time decreased with increasing magnitudes of SLR, and increased with increasing magnitudes of reef growth (Fig. 5). For concision we show only spatial model results, as trends did not vary between different representations of the 1D model (for example, Fig. 4). For a given scenario of reef accretion and SLR the area of seagrass suitable habitat declined through time. Impacts on seagrass are evident as early as 2030, when rates of accretion <5 mm yr<sup>-1</sup> result in wave conditions less suitable for seagrass for all emissions trajectories. This surprising finding was driven by nonlinearities in seagrass response to increased wave height, period and orbital velocity, whereby threshold conditions in wave disturbance were surpassed. By 2050, rates of accretion ≥3 mm yr<sup>-1</sup> are required to maintain suitable conditions for seagrass for the most conservative SLR trajectory, and rates of accretion >4.5 mm yr<sup>-1</sup> are required to maintain the present-day extent of seagrass habitat. By 2080 and 2100 conditions for seagrass become unsuitable except for under the most conservative SLR trajectory and for rates of reef accretion >4 mm yr<sup>-1</sup>. By 2100, habitat is unsuitable for seagrass, for all rates of coral accretion examined, for SLR of ~1 m or greater.

Healthy coral reef flats accrete at a maximum rate of ~3 mm yr<sup>-1</sup>; higher rates tend only to be observed on productive reef slopes<sup>15,20</sup>. Our results suggest that reef growth of 3 mm yr<sup>-1</sup> will facilitate seagrass habitat suitability until 2050 under moderate greenhouse gas emissions scenarios (RCP 4.5), but will not support seagrass habitat for higher SLR trajectories or at later points in time. Degraded reef environments accrete more slowly or may even erode<sup>19,28</sup>, contributing additional relative SLR over reefs. The multiple stressors affecting reefs, including overfishing, coastal development, pollution, disease, warming temperatures and acidification<sup>12</sup> reduce carbonate budgets and therefore diminish capacity of reefs to accrete in response to rising seas<sup>19,28</sup>. Here we have identified that negative impacts on reefs may also be felt indirectly in adjacent seagrass habitats.



**Figure 5 | Relative (%) area of seagrass-suitable habitat in years 2030, 2050, 2080 and 2100, compared with present day, based on changes to the wave environment resulting from a range of sea-level rise and coral reef accretion scenarios (null accretion in seagrass).** Sea-level rise is indicated by the magnitude (cm) and by the corresponding emissions scenarios (IPCC AR5 (ref. 16): RCP 4.5, RCP 8.5; Vermeer and Rahmstorf 2009 (ref. 17): V&R A1, V&R A2). Horizontal and vertical dashed lines indicate the most likely SLR scenario given business-as-usual CO<sub>2</sub> emissions and the maximum likely rate of coral reef platform accretion for healthy coral reefs, respectively<sup>20</sup>.

Our study shows that seagrass distribution depends on wave conditions, which in reef-lagoonal systems are mediated by the depth of the surrounding reef<sup>1,2,29</sup>. Maintaining net accretion capacity of reefs through mitigation of regional stressors (for example, fishing regulations)<sup>28</sup> will therefore benefit adjacent seagrass meadows subject to SLR. This will be required for the continued provision of ecosystem services provided by seagrass, such as nursery areas, grazing grounds and carbon sequestration<sup>13</sup>. Conversely, loss of seagrass could also have further negative consequences for coral reefs, due to decreased availability of nursery habitats, increased turbidity, reduced pH (refs 7–9), or further modifications to the wave environment, although these processes were not examined in the present study.

There are several caveats to this research. Only seagrass occurring in 0–5 m depth was modelled, which may result in a conservative estimate of loss, because deep seagrass will be negatively affected by reduced light from increasing water depth<sup>14</sup>. Although the effects of warming and acidification on reefs were accounted for implicitly by considering scenarios with low accretion rates, effects on seagrass were not explicitly considered. This could be addressed through developing mechanistic models for seagrass dynamics, which could additionally consider shoreline erosion and sediment transport. To date, such models for seagrass have typically been limited to single locations (for example, ref. 30). This would overcome limitations of statistical models, which have a number of key assumptions<sup>23</sup>.

Predicting the redistribution of interacting ecosystems in response to climate change is significantly more complex than modelling the responses of individual ecosystems. However, failure to account for interdependencies in ecosystem response to stressors may produce inaccurate predictions of future habitat extent. Intricate dependencies among ecosystems may be disrupted by

rapid climate change, and both reductions in greenhouse gas emissions and effective local-scale management across multiple habitats will probably be required to maintain ecological functions and the delivery of ecosystem services.

## Methods

**Study site.** Lizard Island (14.7° S, 145.5° E) is a granitic island located 30 km off the coastline of Northern Queensland, Australia (Fig. 2). A barrier reef encloses a 10 m deep lagoon, inshore of which patch reefs and seagrass meadows comprised primarily of *Thalassia hemprichii*, *Halodule uninervis* and *Halophila ovalis* occur. The climate is tropical with winds predominantly from the southeast. Long-period swells are dissipated by the outer Great Barrier Reef. Tides are semi-diurnal, with a maximum range of 3 m.

**Modelling overview.** A habitat distribution model for presence versus absence of seagrass in 0–5 m depth was developed based on  $U_{RMS}$ ,  $T_p$  and  $H_s$ . A graphical overview of the approach is available in Supplementary Fig. 4.

The model was first developed and implemented using 2D spatial data at 5×5 m resolution for the entire study area. Wave conditions in 2100 based on 1 m SLR without any reef growth or sediment accretion were then simulated and used to predict occurrence of seagrass in the future in the absence of geomorphic response to SLR.

For computational efficiency, subsequent analyses used data along a 1D transect sampled at 1 m resolution traversing the reef crest and through the seagrass meadows towards shore (Fig. 2a). The effect of varying magnitudes of seagrass sediment and reef accretion on hydrodynamic conditions were calculated using SWAN. Resultant wave parameters were used to calculate the probability of seagrass habitat occurring in the future under various scenarios.

The total area examined was 39.6 km<sup>2</sup> (1,585,142 cells of 5×5 m); of this, 6.1 km<sup>2</sup> (244,000 cells) were between 0 and 5 m depth and used to model the 2D scenario. The 1D transect was 2,173 m long and sampled every 1 m; 1,812 cells were between 0 and 5 m depth. Data layers were collated using ESRI ArcMap 10.0 and exported to RStudio v.0.98.501 for analysis. Further information is available in the Supplementary Methods.

**Input data.** Spatial data were based on a Worldview 2 satellite image (2×2 m pixel size) captured in October 2011, and field data collected in December 2011 and October 2012. A digital elevation model (DEM) was derived using multiple data sources<sup>21</sup>. Habitat data were collected using geo-referenced photo transects at 1–5 m depth by snorkel and scuba. Photos were analysed for benthic habitat and substrate composition. A map of benthic habitats was generated using object-based image analysis with the field data for calibration and validation.

**Wave modelling.** Synoptic maps of wave parameters were created using the Simulating WAVes Nearshore (SWAN) model across Lizard Island<sup>29</sup>. The model was generated using half-hourly wind speed and direction from the Australian Government Bureau of Meteorology Station at Cape Flattery from 1999 to 2009. For each location six wave parameters were derived: mean and 90th percentile over 10 yr of significant wave height ( $H_s$ ), peak period ( $T_p$ ) and benthic wave orbital velocity ( $U_{RMS}$ ), respectively.

**Species distribution model (SDM).** SDMs for seagrass presence versus absence were developed using wave parameters as predictor variables. Separate models were built for 2D and 1D scenarios. For each, presence versus absence of seagrass was predicted by fitting a generalized linear model assuming a binomially distributed response and using a logit link function. Spatial autocorrelation identified using global Moran's  $I$  was accounted for using the residuals autocovariate (RAC) method<sup>25</sup>. Two scenarios are presented: the full RAC model including the autocovariate term used for model prediction; and parameters estimated using the model, but predictions made with the autocovariate term set to zero.

A cross-validation procedure<sup>14,23</sup> was used to assess model performance by splitting the data set randomly into 75% for model fitting and 25% for model validation, repeated for 100 iterations for various threshold probability values, above which seagrass was classified as present. The threshold cut-off value was selected as the value where Kappa and Percent Correctly Classified were maximized.

**Modification of bathymetry by SLR and accretion.** SLR was modelled based on nonlinearly increasing rates of SLR in decadal increments starting with 3 mm yr<sup>-1</sup> in 2010. For each model run, the rate of increase of SLR varied between 0.5 and 3 mm decade<sup>-1</sup>, to reach SLR of 45–135 cm by 2100. In each time step, depth increased according to SLR, and the reef platform accreted vertically at a temporally uniform maximum rate of 0–10 mm yr<sup>-1</sup> (ref. 20), depending on scenario. If a location reached -1.2 m relative to mean sea level, equivalent to the shallowest presently observed depth of coral, it was prevented from accreting in

that time step. For illustrative purposes data are presented against four SLR trajectories representative of emissions scenarios<sup>16,17</sup>.

**Prediction of seagrass distribution under future conditions.** To predict habitat suitability for seagrass under future conditions, wave parameters for the modified bathymetries were re-calculated using SWAN, and the coefficients of the SDM used to predict seagrass presence in the future.

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### Author contributions

M.I.S., P.J.M., S.R.P., J.X.L., O.H.-G. and C.E.L. designed the study. M.I.S., C.M.R., J.X.L., C.J.B., S.H., D.P.C., T.B. and C.D.W. conducted the field work. M.I.S., J.X.L., C.M.R. and S.H. provided input data. M.I.S., D.P.C., A.G., T.B. and C.J.B. developed and ran the models. M.I.S. wrote the manuscript with input from all co-authors.

### Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at [www.nature.com/reprints](http://www.nature.com/reprints). Correspondence and requests for materials should be addressed to M.I.S.

### Competing financial interests

The authors declare no competing financial interests.