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Differential vulnerability to climate change yields novel deep-reef communities

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The effects of climate-driven ocean change on reef habitat-forming species are diverse[1,2] and can be deleterious to the structure and functioning of seafloor communities[3–5]. Although responses of shallow coral- or seaweed-based reef communities to environmental changes are a focus of ecological research in the coastal zone[1,4–6], the ecology of habitat-forming organisms on deeper mesophotic reefs remains poorly known. These reefs are typically highly biodiverse[7,8] and productive as a result of massive nutrient recycling[9]. Based on seafloor imagery obtained from an autonomous underwater vehicle[8], we related change in community composition on deep reefs (30–90 m) across a latitudinal gradient (25–45° S) in southeastern Australia to high-resolution environmental and oceanographic data, and predicted future changes using downscaled climate change projections for the 2060s[10–12]. This region is recognized as a global hotspot for ocean warming[13]. The models show an overall tropicalization trend in these deep temperate reef communities, but different functional groups associate differentially to environmental drivers and display a diversity of responses to projected ocean change. We predict the emergence of novel deep-reef assemblages by the 2060s that have no counterpart on reefs today, which is likely to underpin shifts in biodiversity and ecosystem functioning.

Climate-induced decay of coral colonies in the tropics[6] or regional decline[14,15] of kelp beds in temperate latitudes[3–5] can precipitate community-wide consequences for reef ecosystems and fisheries that are difficult to reverse[3,4,16]. However, while community-level responses to climate-driven ocean change on shallow (<30 m depth) habitat-forming reef species are well studied and are, to some extent, predictable[6,16], the biogeography and ecology of habitat-forming species on deep reefs are poorly understood. We refer here to 'deep reefs' as the benthic communities on hard substratum in the mesophotic zone (30–90 m depth), where low light limits photosynthetic activity. Similar to their shallow counterparts (for example, corals, kelps), habitat-forming organisms are also important to the structure[17] and functioning[18,19] of deep reef communities, which support high biodiversity[8] and valuable commercial species[20,21]. For example, large suspension feeders such as sponges provide habitat structure and can dominate benthic–pelagic coupling and benthic production via recycling of nutrients and organic matter[9,18,22]. However, despite the acknowledged importance of these deep reef communities, there is limited understanding of how they will respond to climate-driven ocean change.

Here we assess the vulnerability of sessile invertebrate communities to environmental change on mesophotic continental shelf reefs (30–90 m) from subtropical to temperate latitudes (25–45° S) in eastern Australia. This region is recognized as a global hotspot for ocean warming[13], and downscaled projections for the 2060s indicate substantial ongoing warming (Fig. 1). For instance, surface temperatures are projected to increase by >1.2° C above current annual means in the whole region, with higher rates of warming expected at lower latitudes (Fig. 1). We relate the present distribution of major benthic functional groups to ocean environmental variables, and predict the range contractions and extensions of each group in response to projected changes associated with the increased southwards incursion of the tropical, nutrient-poor East Australian Current for the 2060s. The projected range shifts in individual functional groups are combined to assess shifts in deep-reef community structure (and, by implication, ecosystem functioning) in the anticipated future climate.

We developed distribution models using Random Forests relating presence/absence of 13 major functional groups across the full latitudinal range of temperate eastern Australia[7] (derived from seafloor imagery at 44 independent reef locations) to environmental covariates of bathymetry, seafloor features and oceanographic and biogeochemical conditions for which regionally downscaled projections are available for the 2060s[10] (see Supplementary Fig. 2). The 13 functional groups (Fig. 2), each of which corresponds to a variety of similar species[7], are defined based on the morphological and phyletic features of the organisms recognizable from seafloor imagery[23]. They include large habitat-formers that are the typical dominant groups at these depths in the region (for example, sponges, ascidians, bryozoans, gorgonians and octocorals), but also rarer morphotypes such as black corals[7]. Hence, although our ecological dataset does not comprehensively capture community diversity at the species level, it is unique in providing a consistent quantitative survey of deep-reef community composition across a large latitudinal range spanning subtropical to temperate latitudes[7]. Seafloor features considered were reef complexity (hereafter relief), seafloor slope and aspect. The oceanographic and biogeochemical variables included were temperature (mean, variance, skewness, minimum and maximum), primary production, salinity and nitrate concentration. We used Random Forests (1) to model the probability of presence of each functional group across the latitudinal gradient based on these environmental features and (2) to predict climate-driven shifts in their distribution based on projected changes by the 2060s[12].

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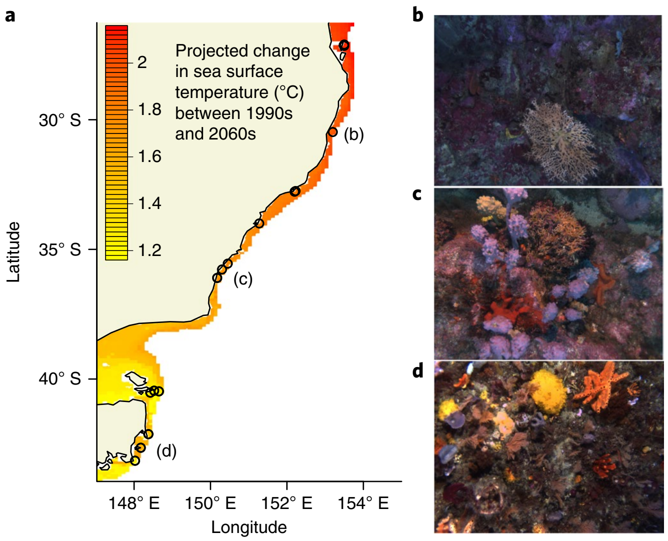

Fig. 1 | Study region. a, Predicted warming in mean sea surface temperature (SST) between the 1990s and 2060s of up to ~2 °C confirms the region as a global 'hotspot', and shows that the absolute magnitude of warming is expected to be greater in the subtropics than temperate regions. Survey sites where the autonomous underwater vehicle (AUV) collected seafloor imagery on multiple transects are shown as open circles. **b**–**d**, AUV images show examples of organisms that are largely restricted to particular regions: subtropical octocorals (**b**); warm temperate stalked solitary ascidians (**c**) and cold temperate yellow ball sponges (**d**), illustrating large-scale variability in sessile benthic communities. Each photo covers ~1.2 × 1.4 m^2 of the seafloor. Credits: AUV *Sirius*, Australian Centre for Field Robotics, University of Sydney.

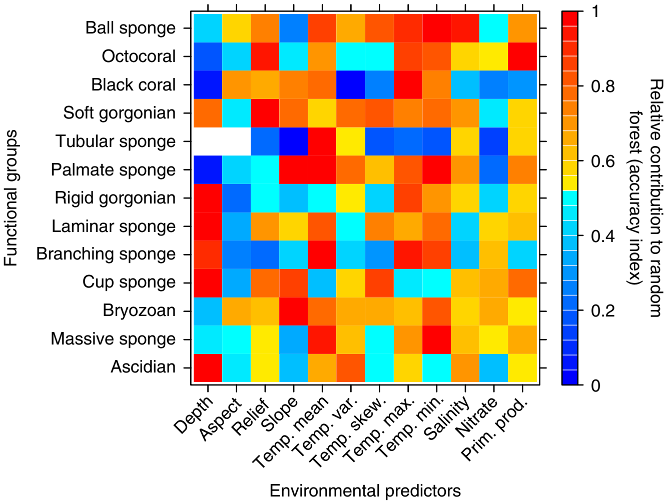

Fig. 2 | Contribution of environmental predictors to Random Forest predictions for each functional group. Relative importance of environmental predictors (*x* axis) to the accuracy of Random Forest predictions reflects diverse relationships between the occurrence of the 13 functional groups (*y* axis) and environmental conditions. White squares symbolize no influence of predictor. The regional occurrence of certain groups, such as soft gorgonians or bryozoans, associates with local seafloor features (that is, depth, slope, aspect and relief). Conversely, the overall distribution of other groups, such as cold-bound massive or ball sponges, relates tightly to regional-scale gradients in oceanographic conditions, for example SST characteristics. Temp., temperature; var., variance; skew., skewness; max., maximum; min., minimum; prim. prod., primary production.

Model predictions of present-day distributions proved reliable to characterize the large-scale latitudinal range of each of the 13 functional groups and indicates four broad types of biogeographic distribution across the latitudinal gradient (Figs. 1 and 3; Supplementary Fig. 17). Figure 3 illustrates that the models identify functional groups that manifest truncated distributions limited to (1) subtropical (for example, octocorals; Fig. 3a; rigid gorgonians, black corals; Supplementary Fig. 17), (2) warm temperate (for example, ascidians; Fig. 3b), or (3) cold temperate (for example, ball sponges; Fig. 3c; massive form sponges, soft gorgonians; Supplementary Fig. 17) latitudes, and (4) those that occur, either sparsely or abundantly, across the entire latitudinal gradient of the study (for example, branching sponges; Fig. 3d; bryozoans and cup, tubular, laminar and palmate sponges; Supplementary Fig. 17). These four groups depicted in Fig. 3, in particular the first three, which are characteristic of the three dominant community types in the region[7], display strong biogeographical responses to projected ocean changes. Local-scale predictions for a few broadly distributed and locally sparse groups, such as tubular sponges, should be interpreted with caution, but overall predicted present-day latitudinal ranges show good agreement with available observational data (Fig. 3; Supplementary Fig. 17). More importantly, when combined together, predictions capture the observed gradient in community structure across the survey sites (Fig. 4). The modelled presence/absence of each functional group also relates to a unique combination of environmental covariates (Fig. 2), which suggests diverse ecologies and biogeographies across all groups and raises the possibility of diverse responses to environmental change. For example, the Tasmanian-bound distribution of cold temperate groups (for example, massive and ball-shaped sponges) is constrained by large-scale oceanographic variables such as ocean temperature and salinity (Fig. 3). Conversely, the modelled occurrence of widely distributed cup sponges relates to local-scale reef features of depth, seafloor relief and slope, as well as larger scale oceanographic variables (for example, temperature skewness) (Fig. 2). Overall, the distribution of most of the 13 functional groups is primarily related to ocean temperature (mean, variance, minimum and/or maximum) (Fig. 2), which suggests a certain sensitivity of present-day biogeographic patterns to ongoing[24] and future[25] regional warming of coastal waters.

Given that the distribution of different functional groups relates differentially to environmental variables (Fig. 2), it is not surprising that biogeographic responses to projected climate-driven ocean warming are diverse (Fig. 3). Nonetheless, broad patterns emerge in the predicted redistribution of invertebrate functional groups on these deep reefs by the 2060s (Fig. 3). Subtropical groups, such as octocorals, currently restricted to the northern edge of the study area (~25–30° S), are likely to extend their range poleward in response to ocean warming (Fig. 3a). Most functional groups restricted to warm temperate regions are predicted to contract their northern range boundary, while the southward extension of their distribution to higher temperate latitudes (>40° S) is limited (for example, ascidians; Fig. 3b). For most of the cold-bound habitat-forming functional groups (Fig. 3c), a large southwards range contraction is predicted by the 2060s and the south coast of Tasmania provides the last refuge against ocean warming, in other words there is no further continental shelf habitat to the south to which these groups and species can move. For those populations currently distributed across the whole study area (Fig. 3d), present-day regional environmental suitability is expected to decline by the 2060s by 3% to 26% (for cup sponges and bryozoans, respectively). These widely distributed groups (for example, branching, laminar and hollow cup sponges) appear more resilient than temperate groups to projected ocean changes (Fig. A17) as regional warming may only induce slight poleward contractions

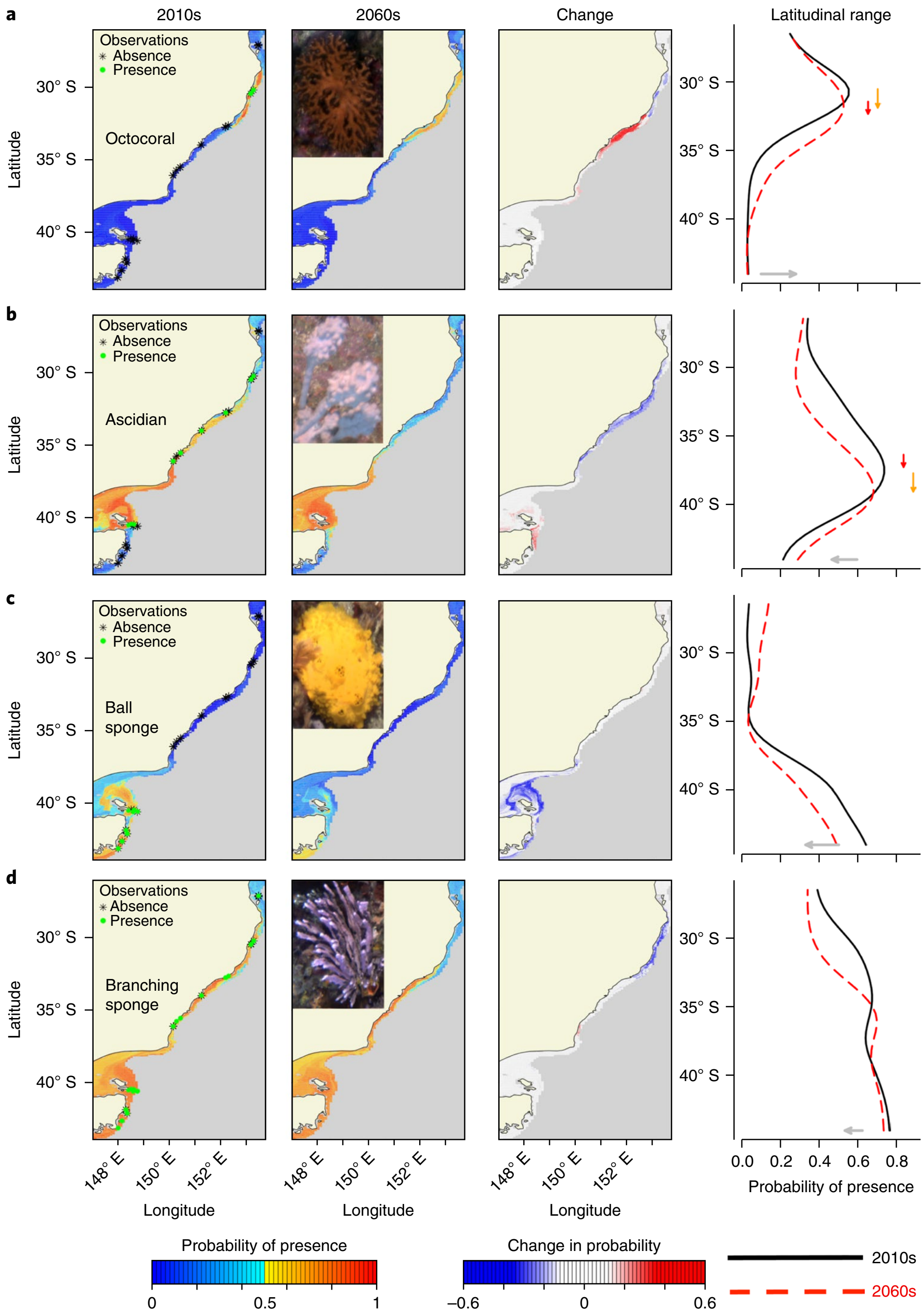

Fig. 3 | Random Forest predictions of functional groups' distributions. Predictions of present-day distributions (first column), distributions in the 2060s (second column) and the relative change in the probability of presence (third column) indicate four broad types of range shift response across the 13 functional groups. **a**, Southwards range extension of subtropical groups (for example, octocorals, rigid gorgonians, black corals). **b**, Retraction of northern range of warm temperate groups (for example, stalked solitary ascidians). **c**, Retraction of northern range of cold temperate groups (for example, ball sponges and massive sponges). **d**, Marginal regional decline of broadly distributed groups (for example, branching sponges, bryozoans, soft gorgonians, hollow cup sponges, tubular sponges, palmate sponges and laminar sponges). The longitudinally integrated latitudinal distributions (that is, predicted probability of presence) are shown in the fourth column for the present-day (black solid line) and the 2060s (red dashed line). The grey arrow reflects relative change in the probability of presence across the entire study region; red and orange arrows symbolize latitudinal shifts in the median and the maximum of the predicted distribution, respectively.

of their subtropical boundaries. This is consistent with existing studies on mobile fish species and other marine fauna[26–28].

The combination of the projected range shifts across all functional groups under future climate-driven ocean change suggests the emergence of novel deep-reef assemblages (Fig. 4). AUV surveys characterize north–south transitions between three main community types (that is, subtropical, warm and cold temperate)[7], which are captured accurately in the model predictions across this latitudinal

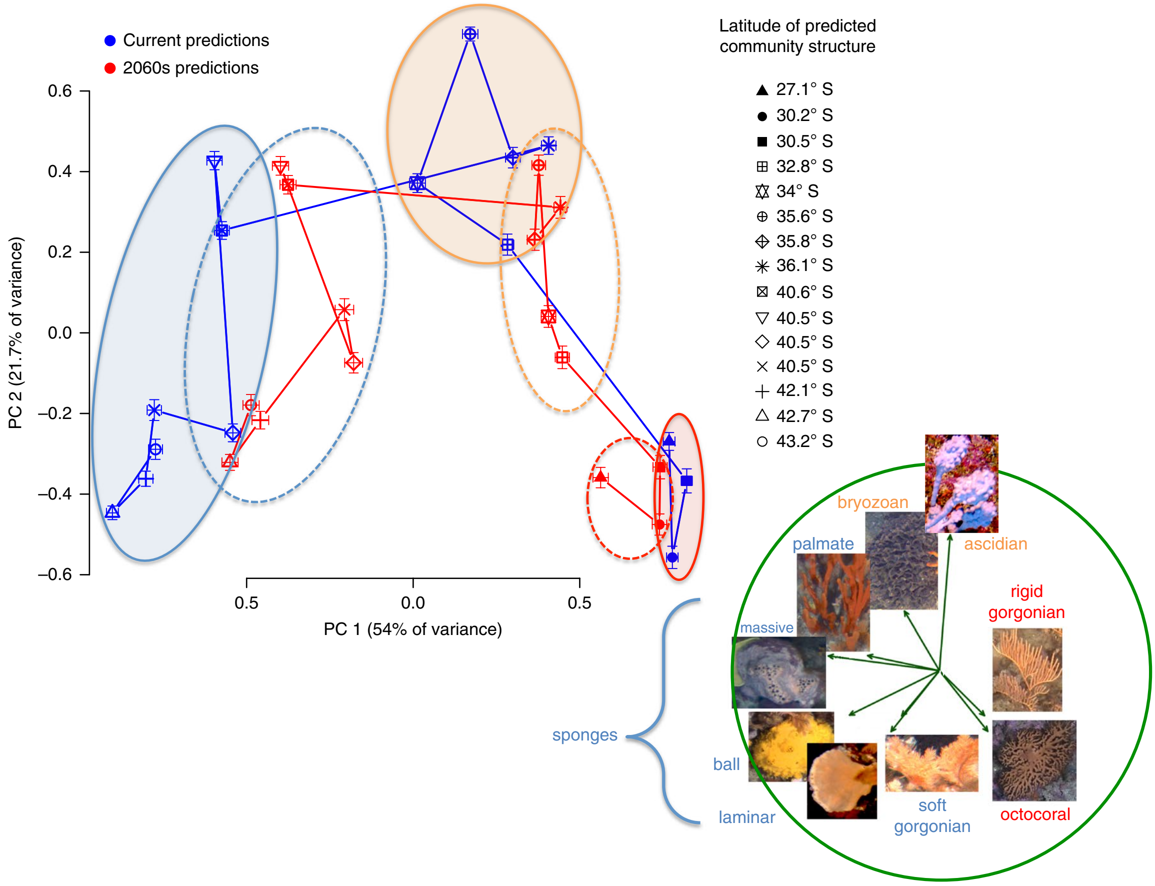

Fig. 4 | Predicted community structures at each monitoring site. Community structures predicted for the present-day (blue) and 2060s (red) for deep temperate reef communities in eastern Australia reveal the emergence of novel ecological assemblages under projected climate-driven ocean changes. Scores shown in principal components space correspond to rocky reef community structure along a large latitudinal gradient (25–45° S) as characterized by predicted probabilities of presence of 13 major functional groups at 15 regular AUV monitoring locations. Symbols and continuous lines represent the north–south gradient in AUV monitoring sites from southern Queensland (filled triangle) to southeastern Tasmania (open circle). Error bars represent 95% confidence intervals. Ellipses characterize shifts in community structure from present-day (filled and solid lines) to future (dashed lines) assemblages associated with cold temperate (blue), warm temperate (orange) and subtropical (red) sites. The green circle overlay represents projected scores (>0.3) of individual groups (with associated pictures) onto the first and second principal component axes, and identified as cold temperate, warm temperate or subtropical groups (colour coding as above).

gradient for the present time (blue symbols and shaded ellipses on Principal Component Analysis (PCA); Fig. 4). Consistent with ongoing and anticipated ecological changes on shallow reefs in the region[27–29], the predicted changes in deep-reef community structure by the 2060s suggest an overall 'tropicalization' (red symbols and transparent ellipses on PCA; Fig. 4). The subtropical groups are predicted to extend to intermediate latitudes (~32–35° S), the warm temperate groups are expected to dominate community structure south of 35° S, while the occurrence of cold-bound invertebrates decline at the higher latitudes (~40° S). It is particularly important that model predictions also highlight that climate-driven range shifts are likely to lead to novel assemblages as a result of differential responses by different functional groups. For example, by the 2060s, a mix of cold-water invertebrates (for example, massive sponges) and range-extending warm temperate organisms (for example, ascidians; Fig. 4) are predicted to dominate reef communities in northeastern Tasmania (~40° S). As multiple simultaneous range shifts can have complex, hard-to-reverse effects on regional ecosystem dynamics[16,28], it is difficult to anticipate the precise ecological consequences of these broad changes in the structure of deep-reef communities. However, given the central contribution of sessile organisms to deep-reef ecosystem dynamics[18,19] and benthic–pelagic coupling[9,18,22], the predicted emergence of novel invertebrate assemblages, which have no counterpart on the continental shelf today, can be expected to also significantly modify functioning of benthic communities[30]. Changes in the productivity of benthic communities, which support valuable commercial species, can be expected given that organic matter recycling relies on the diversity and identity of seafloor suspension-feeding communities[19,30]. Note that our results are based on combining statistical distribution models across individual groups additively and do not account for ecological interactions or species traits, which may further facilitate dramatic shifts in community dynamics[27].

Seafloor communities are often portrayed as threatened by the long-lasting impacts of physical disturbances, such as bottom trawling[31]. However, similarly to terrestrial[32], freshwater[33] or shallow marine[28] ecosystems where novel ecological assemblages emerge as a result of shifts in regional climates[34], deeper marine ecosystems are also likely to be significantly impacted by climate-driven environmental changes[35,36]. As the ecological and/or physiological knowledge required to develop a deterministic understanding of deep-reef community responses to climate-driven changes in ocean biogeochemistry (via altered regional ocean circulation) is currently limited, our results provide a valuable initial insight into anticipated shifts in deep-reef community structure due to changes in ocean climate, in particular warming. With the emergence of novel underwater sampling technologies over recent decades[37], there is potential to monitor trends and changes in deep-reef assemblages[38,39], although in most areas worldwide this kind of work is, at best, just beginning. Climate-driven changes in deep-reef ecosystems remain largely understudied relative to terrestrial and coastal ecosystems; however, new initiatives are attempting to overcome the challenges of managing climate change impacts on deeper communities in a data-poor context[36]. While coastal reef research investment and associated management effort is gradually expanding for some temperate seaweed-based communities[40], our study highlights the crucial need to better understand and monitor the deep-reef communities pivotal to benthic ecosystem diversity and productivity in temperate areas. Structural shifts in these communities in response to climate change will be mediated by ecological processes[3] and species traits[27], and may have dramatic consequences for benthic productivity and other aspects of ecosystem functioning. Developing understanding of the physiological and ecological mechanisms that underpin deep-reef communities dynamics will be critical to confirm our findings, assess their generality and to adequately manage these ecosystems that appear sensitive to climate-driven changes[36].

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at https://doi.org/10.1038/s41558-018-0278-7.

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Author contributions

All authors provided comments on the paper. M.P.M. led the research, performed the analyses and wrote the paper. E.C.J.O. performed the statistical downscaling of the climate projections for the 2060s. L.J. analysed the seafloor imagery and consolidated the ecological dataset. S.J.W. provided guidance about statistical modelling techniques. C.R.J., N.S.B. and N.J.H. conceived the project and provided guidance in the conduct of the research.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Study area. Southeast Australia is a global hotspot for climate-driven ocean warming (Fig. 1a)[13], where shallow temperate reef communities have been affected by rapid changes in ocean conditions[16] related to an increase southwards penetration of the East Australian Current[24].

Ecological data. Presence and absence of 13 key habitat-forming functional groups, including sponges, ascidians, bryozoans and cnidarians, were derived from ~1,800 seafloor images obtained from the Integrated Marine Observing System (IMOS) AUV *Sirius* between 2010 and 2013[7,37] (see Fig. 1 for example images). Each image was scored using the standardized CATAMI classification[23]. Sampling occurred at depths ranging from 30 to 90 m following a hierarchical design: seven out of the eight marine bioregions identified across the eastern seaboard of Australia were surveyed from subtropical southern Queensland (25° S) to temperate southern Tasmania (45° S) (Fig. 3, Supplementary Fig. 17). Individual sites may be difficult to distinguish on Fig. 3, but given that they are tens of kilometres apart they constitute independent replicates and provide an assessment of local-scale variability within any given bioregion[7]. Within each survey site, several transects, which are hundreds of metres apart, form the basis of our dataset. Note that hierarchical sampling efforts are comparable across survey sites so our dataset is overall homogeneous across regions: each bioregion includes 3–5 sites; each site 3–6 transects, for which there are at least 10 images each covering ~2 m^2. We based our analysis on presence/absence data of the 13 groups derived from aggregating scored images (Fig. 1b–d) along 120 transects from a total of 44 independent reef sites[7] (see Supplementary Note 5 and/or Supplementary Fig. 19, Supplementary Data). Reef habitat was surveyed at the scale of 100 × 100 m^2 at each of these sites and images were sampled along the AUV transect using a geostratified sampling design. We recognize some limitations of the image-based dataset, specifically: (1) IMOS regular AUV monitoring sites are not evenly distributed across the region (Fig. 1a); due to time-consuming image scoring (2) a set list of targeted easy-to-recognize benthic functional groups (rather than total community diversity) was identified (3) on a subset of available imagery at each site (rather than all available images). Nonetheless, our ecological dataset is unique because it provides a systematic quantitative survey of deep-reef community composition across a large latitudinal range spanning subtropical to temperate latitudes[7]. The description of seafloor communities based on broad functional groups (that is, using the CATAMI seafloor imagery annotation scheme[7]) reliably characterizes current latitudinal changes in deep-reef community structure[7].

Environmental data. To characterize the environmental niche of each group, we considered a range of environmental covariates related to seafloor features (depth, relief, slope, aspect), SST (mean, variance, skewness, minimum and maximum) and biogeochemical conditions (mean salinity, nitrate concentration and phytoplankton concentration as a proxy for primary production) for which high-resolution projections through the 2060s were available[10–12] (See Supplementary Fig. 2). Note that temperature–depth profiles through the water column suggest high mixing on the continental shelf, which legitimizes the use of SST as a proxy for bottom temperature[41] (see Supplementary Fig. 1). Ocean variables are derived from available 9-year time series for the 1990s and 2060s, and projections through the 2060s are based on dynamically downscaled ocean climate change projections from a coupled climate model taking account of CO_2 increases according to the IPCC AR4 'business as usual' A1B scenario[11,12]. Mean SST was further statistically downscaled to the coast[42] while the other variables were taken directly from the high-resolution ocean dynamical model[11,12]. We do not account for the long-term effects of ocean acidification, which might further alter community structure by impacting pH-sensitive groups (for example, calcifying octocorals, or sponges with limited acid-base regulation capacities)[43]. However, our predictions capture the effects of coastal ocean warming, which is expected to be a major signature of climate-driven changes in the following decades in the region[25].

Analyses. *Distribution modelling and prediction of climate-driven range shifts.* We compared the alternative statistical modelling techniques of bootstrapped–aggregated binomial generalized linear models, bootstrapped–aggregated binomial generalized additive models, and Random Forests, which all performed consistently and provided similar results. However, across all groups the Random Forest models were more accurate based on cross-validation, and hence we only present results based on Random Forests here (see Supplementary Information for details). Following sensitivity analyses on Random Forest parameters (that is, forest size, depth of the trees), all models presented here rely on aggregating 500 individual classification trees grown on bootstrapped samples of the ecological data using random selection of features to split each node, up to a maximum of four levels of branching. Thus, the number of nodes per tree varied from 2 to 16, with a mean of 7 (±2.5 standard deviation). Model performance was assessed based on cross-validation using bootstrapping (that is, subsampling of the data into two sets for model training and testing, respectively). Misclassification error rate, which accounts for both false positives and false negatives, was 16% (mean across all groups) and varied from ~2% for octocorals to ~33% for laminar sponges (see Supplementary Information Section 2). The accuracy of models varied from 'excellent' (see Supplementary Fig. 3 and Supplementary Table 1) to 'fair' for the few functional groups that occurred across the entire latitudinal range but were not detected at successive survey sites, either due to local environmental conditions (not captured in our predictors) or their low detectability (related to their sparse occurrence and/or the random sampling design). Despite some inaccuracy in local-scale prediction for these groups, Random Forests meaningfully characterized the broad latitudinal distribution of the 13 functional groups (Fig. 3; see also Supplementary Fig. 17). Models fits, predictions and permutation-based accuracy indices (Figs. 2–4) were implemented in R's Random Forest package[44]. Statistical modelling of the distribution of major deep-reef habitat-formers across space and time has limitations, including that model predictions do not explicitly account for ecologically or physiologically mediated responses to ocean changes[16,27]. However, in a data-poor context, in particular given the lack of mechanistic understanding of the ecological processes driving the ecological dynamics of these deep-reef communities, statistical distribution modelling with Random Forests provides unique initial insights on potential deep-reef community responses to climate-driven ocean warming across the broad latitudinal gradient considered in our study. Our models predict, in a consistent manner, both the current and 2060s biogeographical range of each functional group so we can interpret increase and/or decrease in predicted probabilities of presence at large scales as range extensions and/or contractions, respectively (Fig. 3; Supplementary Fig. 17). Only at the edge of our study domain (that is, in the northern-most subtropical areas) where limited data were used to train the models do predicted changes need to be interpreted with caution. In addition to commenting on predicted climate-driven changes in the leading and trailing edges of population ranges, we also characterize latitudinal shifts in the core distribution of each group by tracking the latitudinal change between the 2010s and 2060s in the median and the maximum probability of presence integrated across depth (Fig. 3; Supplementary Fig. 18).

PCA and prediction of changes in community structure. To describe large-scale changes in the community structure of deep-reef assemblages, we performed a PCA on the predicted current and future probability of presence of each of the 13 functional groups at 15 monitoring sites (Fig. 4). Error bars represent the 95% confidence intervals of the PC scores and were derived from Monte Carlo sampling (100 samples) of current and future community structure as characterized by predicted probabilities of presence across the 13 functional groups. Predicted climate-driven changes across the different groups translate into regional changes in functional diversity. The probability of occurrence of the different functional groups is predicted to change locally (and in certain region go from present to absent, or conversely), which implies significant shifts in community composition and emergence of assemblages that do not resemble any of the currently described community types (Fig. 4). These predicted changes in community structure are largely related to differential vulnerability of region-characteristic groups, which are likely to display responses similar to other sessile benthic taxa that share similar environmental niches but were not considered in our study. Although our current understanding of the different groups' ecology is limited, we can nevertheless expect changes in ecosystem functioning if there is a major change in functional diversity. A number of functional traits, which differ across the different groups, have direct implications for ecosystem functioning, such as nutrient recycling and provision of shelter via formation of complex three-dimensional habitat. Filter feeding rates are likely to vary across the different functional groups but, other than for sponges[9], there is limited quantitative information about organic matter and nutrient recycling functions filled by the different functional groups. Moreover, complex interactions between the different functional groups are likely to contribute to overall ecosystem functioning (for example, synergy between cold-water corals and sponges)[45]. Another important function associated with the different groups relates to their different abilities to form complex biogenic habitats, which has direct implications in terms of shelter from predation for the macro- and megafauna[46].

Supplementary Information This document provides technical details concerning the distribution models, specifically concerning environmental covariates; Random Forest model fits; projections of current and 2060s distributions for all groups; and projected change in latitudinal distributions.

Data availability

The ecological dataset derived from AUV imagery is extensively described[7]. All environmental datasets are available from public sources as referenced. Estimates of ecological and environmental variables associated with each transect, and which were used to fit the random forest models, are provided as online supplementary material. All the data that support the findings of this study, including R scripts, are available from the corresponding author upon request.

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