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Title: Forecasting marine invasions under climate change: biotic interactions and demographic processes matter

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Abstract: Biological invasions are one of the most significant threats to marine biodiversity, and can be facilitated and amplified by climate change. Among all aspects of invasion biology, biotic interactions between invaders and native species are of particular importance. They strongly influence the invasion velocity as well as species responses to climate-induced stressors. Yet the effects of biotic interactions and other important demographic processes remain overlooked among most studies of climate-mediated invasions. We critically assessed current modelling techniques for forecasting marine invasions under climate change, with a particular focus on their ability to account for important biotic interactions and demographic processes. We show that coupled range dynamics models currently represent the most comprehensive and promising approach for modelling and managing marine invasions under climate change. We show, using the crown-of-thorns seastar (Acanthaster planci), why model architectures that account for biotic interactions and demographic and spatial processes (and their interaction) are required to provide ecologically realistic predictions of the distribution and abundance of invader species, both under present-day conditions and into the future. We suggest potential solutions to inform data-poor situations, such as Bayesian parameter estimation and meta-analysis, and identify strategic and targeted gaps in marine invasion research.

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Forecasting marine invasions under climate change: biotic interactions and demographic processes matter

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Abstract

Biological invasions are one of the most significant threats to marine biodiversity, and can be facilitated and amplified by climate change. Among all aspects of invasion biology, biotic interactions between invaders and native species are of particular importance. They strongly influence the invasion velocity as well as species responses to climate-induced stressors. Yet the effects of biotic interactions and other important demographic processes remain overlooked among most studies of climate-mediated invasions. We critically assessed current modelling techniques for forecasting marine invasions under climate change, with a particular focus on their ability to account for important biotic interactions and demographic processes. We show that coupled range dynamics models currently represent the most comprehensive and promising approach for modelling and managing marine invasions under climate change. We show, using the crown-of-thorns seastar (*Acanthaster planci*), why model architectures that account for biotic interactions and demographic and spatial processes (and their interaction) are required to provide ecologically realistic predictions of the distribution and abundance of invader species, both under present-day conditions and into the future. We suggest potential solutions to inform data-poor situations, such as Bayesian parameter estimation and meta-analysis, and identify strategic and targeted gaps in marine invasion research.

1. Introduction

Marine invasive species are a major threat to biodiversity worldwide and can have profound ecological and economic impacts on marine ecosystems (Bax *et al.*, 2003). Although the criteria that categorise a species as invasive remain somewhat controversial, invaders are commonly characterised as species that undergo rapid increases in abundance and/or spatial occupancy with adverse effects on recipient ecosystems (Valery *et al.*, 2008). This definition includes the case of ‘native invaders’ that can spread within their historical range by exploiting niche opportunities resulting from human activities and/or loss of other species: by attaining extreme abundances and exerting severe per-capita effects on local communities, native invaders can indeed cause ecological impacts that rival those of non-native invaders (Valery *et al.*, 2009; Carey *et al.*, 2012). Whether native or not, invaders can impact recipient communities directly through competition, predation, and hybridization, and indirectly by modifying habitats and potentially disrupting their suitability. Over 1500 species have invaded locations throughout the world's oceans, and more are discovered every year (European Environment Agency, 2012). The potential economic costs incurred by even a single marine invasive species can reach US$250 million yr^{-1} (Williams & Grosholz, 2008) and eradication seems possible only in highly constrained situations (Bax *et al.*, 2002). Future climate change is predicted to increase the introduction and spread of invasive species, accelerating marine invasions and resulting in widespread biodiversity loss (Garcia Molinos *et al.*, 2016).

The ecological traits that commonly characterize marine invasive species are disproportionately favoured under climate change, potentially exacerbating future impacts of marine invasions (Poloczanska *et al.*, 2013). This is because marine invaders often tend to be generalist and/or opportunists with relatively plastic life histories (Clavel *et al.*, 2011), making them able to better adapt to rapidly changing environmental conditions and fare better in warming waters than native species (Sorte *et al.*, 2013; Bates *et al.*, 2013). By relaxing some of the physiological constraints on temperature-dependent growth and survival while also altering connectivity, human-induced climate change has already enabled some non-native invasive species to expand into regions where they previously could not survive and reproduce, as exemplified by the green ‘killer’ algae *Caulerpa taxifolia* in the Mediterranean (Walther *et al.*, 2009). Additional climate-related factors that might enhance a species’ invasive ability include: extensions of spawning periods and increases in *per capita* reproductive output (Walther *et al.*, 2009); altered timing of recruitment and faster growth in warmer years (Stachowicz *et al.*, 2002); faster developmental rates (Walther *et al.*, 2009); and modified local dispersal patterns due to altered hydrodynamic conditions (Diez *et al.*, 2012). In the case of native invaders, climate-driven environmental changes at local scales (e.g. eutrophication, altered connectivity due to changes in ocean currents) can favour the dominance of invaders in parts of their historical range where they previously could not survive or reproduce (Carey *et al.*, 2012).

Despite these established physiological and demographic responses to climate change, there have been few attempts to forecast the potential impact of invasive species under climate change and test the efficacy of alternative management actions (Sorte, 2014). Most existing knowledge is based on local field observations or mesocosm experiments (e.g., Cockrell & Sorte, 2013) that are often conducted at small scales and/or do not necessarily represent realistic environmental conditions. More integrated approaches that combine empirical data on local and regional ecological processes with simulation models are urgently needed in marine invasion biology to improve our knowledge of impending invasions and to manage existing and future invasive species (Fordham, 2015).

A commonly overlooked consequence of climate change affecting marine invasions is the way climate change alters ecological interactions in native communities (Sorte *et al.*, 2010). Climate-driven changes in invasive ability affect the way native communities are organised, facilitating the formation of novel ecological communities characterised by new arrangements and ecological interactions (Lurgi *et al.*, 2012). Such new configurations can create ecological vacuums that facilitate future invasions, especially if top predators are depleted (as frequently reported in response to global change; Cheung *et al.*, 2015). Other anthropogenic stressors such as fisheries exploitation, terrestrial runoff, and eutrophication can act in synergy with climate change to facilitate not only invasions by alien species but also state-shifts of species dominance, as for example, in the case of invasive jellyfish (gelatinous plankton; Fig. 1) (Licandro *et al.*, 2010; Lynam *et al.*, 2011). These interactions can be complex, with climate change and other anthropogenic stressors having both direct and indirect effects on the strength of biotic interactions (*e.g.* competition, predation). Consequently, not only is the dominance of invasive species likely to change owing to synergies between anthropogenic stressors, but also the number and strength of their biotic interactions between invasive and other species, with potentially multiplying effects brought about by trophic cascades (Lynam *et al.*, 2011).

Anticipating and managing future threats from invasive species to marine biodiversity thus requires accurate forecasts of marine invasions that account for biotic interactions between native and invasive species, and how they are likely to change in response to multiple anthropogenic stressors. Here we appraise the quantitative methods that have been applied to forecast marine invasions, focusing on their strengths and shortcomings, and on whether they can explicitly account for biotic interactions. We then implement a spatially explicit simulation model as a proof-of-concept of how biotic interactions, demographic processes and their climate-induced variation can and should be integrated into forecasts of marine invasions under climate change. Our model organism is *Acanthaster planci,* the crown-of-thorns seastar, which is a major threat to the Great Barrier Reef, and the only threatening process of contemporary global change that is amenable to direct management actions (De'Ath *et al.*, 2012). Rapid outbreaks of *A. planci* currently pose one of the most serious management problems for the Great Barrier Reef, leading to conservation implications (e.g., extirpation of foundation species and destruction of essential fish habitats) that are similar to those of any non-native invasive species.

2. Recent developments for forecasting marine invasions under climate change

2.1 Species distribution models

Correlative species distribution models (SDMs; i.e. ecological niche, bioclimatic envelope, or habitat suitability models) describe or predict the probability of presence or spatial abundance of a species across environmental gradients or in a specific geographical area based on habitat suitability (Pearman *et al.*, 2008). SDMs have very simple data requirements, needing only point location data and associated environmental variables (Table 1). However, predictions are often constrained by important limiting assumptions (Elith *et al.*, 2010; Robinson *et al.*, 2011). Indeed, SDMs typically assume that species occurrences represent the range of environmental conditions in which an organism can persist (Schurr *et al.*, 2012) and rarely account for demographic processes such as dispersal in an ecologically realistic way (Travis *et al.*, 2013). These assumptions are particularly concerning in the case of recently introduced invasive species because their ranges are by definition expanding (e.g., Kearney *et al.*, 2008), thus representing a non-equilibrium distribution (Thuiller *et al.*, 2005). As a result, models calibrated in the native range often underperform in the exotic range (and vice versa) (Fitzpatrick *et al.*, 2007), an issue that can be partially addressed by considering the species' global range (Mainali *et al.*, 2015).

The failure of SDMs to account explicitly for biotic interactions (as well as demographic processes) has been identified as a major limitation of these models, affecting predictions of distributional shifts under changing climatic conditions (Araujo & Luoto, 2007). While biotic interactions can keep a species in check in climatically suitable conditions, they can also fail to restrict invasions in new territories where a predator or competitor is absent or in low abundance (Fig. 1) (Mainali *et al.*, 2015). In such a situation, SDMs unrealistically consider the invaded range as climactically broader than the native range (e.g., Fitzpatrick *et al.*, 2007). Recognition of these limitations has prompted the development of new methods for incorporating biotic interactions into SDMs (Kissling *et al.*, 2012). These methods include: (*i*) adding the occurrence of an interacting species as an additional covariate in the SDMs (Araujo & Luoto, 2007); (*ii*) developing a separate SDM for the interacting species and using it to constrain the distribution of the focal species, minimizing the issues of false absences and collinearity where both species are related to the same environmental predictors (Schweiger *et al.*, 2008); or (*iii*) calibrating an interaction matrix among species to define the error matrix for multivariate logistic regression models (Kissling *et al.*, 2012).

Existing methods for incorporating biotic interactions into SDMs remain problematic for at least two reasons: biotic interactions can change over time (even more so in the context of an invasive species under climate change; Fig. 1) and it is difficult to include more than one interaction at a time. Therefore, biotic interactions remain absent from most SDMs under the assumption that, at least at biogeographic scales (as opposed to local; Wisz *et al.*, 2013), biotic interactions are not a determinant of invasive species distributions (Mainali *et al.*, 2015), which seems unrealistic in most situations (Araujo & Luoto, 2007). Recent studies using SDMs to forecast marine invasions have focused primarily on the susceptibility of environments to invasions for management purposes (de Rivera *et al.*, 2011; Jones *et al.*, 2013). Biotic interactions have, however, been consistently ignored in these marine SDMs (Robinson *et al.*, 2011).

2.2 Biophysical models

Biophysical models (i.e. process-based models) rely on species physiological tolerance limits and, in doing so, enable species distributions to be modelled across environmental gradients without using occurrence data (Kearney *et al.*, 2008) (Table 1). Biophysical models should, in theory, yield more robust forecasts of climate-driven distributional shifts because they explicitly account for relationships between climate conditions and organismal performance. In doing so, biophysical models overcome problems associated with non-equilibrium situations, since they do not rely on occurrence data that could misrepresent the species' potential range due to biotic interactions (see above) or human-driven impacts such as depletion from harvesting (Buckley *et al.*, 2010). Biophysical models are increasingly used to model range dynamics in response to climate change (Kearney *et al.*, 2008; Cheung *et al.*, 2011) or environmental gradients (Monahan, 2009), and can be coupled with SDMs to constrain their predictions (Elith *et al.*, 2010; Buckley *et al.*, 2011; Fordham *et al.*, 2013b). For example, biophysical models have been used to show that invasion of the Indo Pacific lionfish (*Pterois volitans*) into the Mediterranean is unlikely to occur due to low connectivity between suitable sites (Johnston & Purkis, 2014). Biophysical models subsequently allowed to recreate the success/failure of invasions of introduced fish in the Hawaiian Islands, providing insight into the demographic properties that predispose fish species to successful invasion (Johnston & Purkis, 2016). Biotic interactions cannot currently be implemented in biophysical models in their original form but would represent an important and desirable extension to this class of models (Buckley *et al.*, 2010; but see Tingley *et al.*, 2014).

2.3 Spatially explicit demographic models

Spatially explicit demographic models, which directly account for species vital rates in model predictions, are used with increasing frequency to model the effects of climate change on the range dynamics and persistence of species, including those in the marine realm (e.g., Fordham *et al.*, 2013b). While incorporating important information on habitat suitability (e.g., Mellin *et al.*, 2012), such models relax some of the limiting assumptions constraining SDMs since they explicitly account for dispersal and source-sink dynamics, enabling demographic rates (such as growth or fertility) to vary in space and time (Dunstan & Bax, 2007). Models can be either population-based (i.e. they account for population-level parameters such as survival and fertility rates, dispersal kernels) or individual-based (e.g. incorporating individual heterogeneity in parameters such as body size, movement and feeding behaviour, phenotype). For both population- and individual-based demographic models, user-friendly and fully customisable modelling platforms are now broadly available (Lurgi *et al.*, 2015) (Table 1). Most recently, some of these frameworks have been adapted to explicitly account for simple (one-way) biotic interactions in predictions of how climate change is likely to affect species range dynamics (e.g., Fordham et al., 2013a).

In spite of readily available modelling platforms, and available demographic data for some species, marine applications of spatially explicit demographic models for invasive species remain scarce. Demographic (stage-structured) models have for example been used to predict the future population growth of invasive species using laboratory mesocosms to estimate survival, growth, and fecundity rates within epibenthic communities under present-day conditions and with ocean warming (Cockrell & Sorte, 2013). This approach is informative in situations where the population dynamics of local communities are explained mainly by intrinsic demographic properties of the constituent species. Demographic models have also been used to understand how range dynamics can be affected by environmental changes and to forecast potential effects on abundance and geographic distributions. For example, commercial fisheries researchers now use hybrid demographic models (named Dynamic Bioclimate Envelope Model), which explicitly account for demographic and range dynamics (Cheung *et al.*, 2009; Cheung *et al.*, 2011), to incorporate competition for resources into predictions of species distributional shifts (Fernandes *et al.*, 2013). Forecast latitudinal shifts decreased by 20% when species interactions were considered, further highlighting the importance of biotic interactions in forecasting distributional shifts and marine invasions.

In aggregate, if we are to better forecast marine biological invasions and understand their effects on recipient communities, there needs to be a much stronger focus on developing quantitative approaches that account for key ecological processes (demography and biotic interactions) in simulation models of marine invasions. Coupled range dynamics models, accounting for metapopulation processes and simulating the mutually reinforcing effects of climate change and biotic interactions (Fig. 1), provide appropriate modelling frameworks that have not yet been used to simulate marine invasions. This is despite the necessary tools being widely accessible, and similar methodologies having been developed for modelling species range dynamics under climate change in terrestrial ecosystems (both aspects reviewed by Lurgi *et al.*, 2015) including invasive terrestrial species (Fordham *et al.*, 2012) and harvested marine species (Fordham *et al.*, 2013b). The demonstrated utility of this approach indicates the immediate need for an assessment of its transferability to the case of marine invasions.

3. Incorporating biotic interactions into forecasts of marine invasions

To demonstrate the feasibility of coupling demographic models with SDMs (i.e. coupled range dynamics models) in order to forecast spatially explicit changes in the range and abundance of marine invasive species, we developed a population-based cellular automaton (Durrett & Levin, 1994). We use this coupled range dynamics model to show (*i*) how biotic interactions can be incorporated into forecasts of invasion dynamics under climate change and (*ii*) the extent to which doing so influences model outcomes and potential management applications (Box 1; see Supplementary Material SM1 for a full description of the framework). We chose the coral-eating crown-of-thorns seastar (*A. planci*) as a model organism. Outbreaks of *A. planci* have been a major contributor to the loss of half of the coral cover on Australia’s Great Barrier Reef since 1985 (De'Ath *et al.*, 2012). It was suggested that the frequency of such outbreaks has increased over the last century, partly as a result of increasing terrestrial runoff and primary productivity that promotes larval survival (Fabricius *et al.*, 2010). Since *A. planci* can become sporadically hyperabundant in its native range, threatening the regional persistence of many corals and causing as much ecological damage as any non-native invasive species, it makes an interesting ‘proof-of-concept’ case study for modelling (and managing) marine invasions under climate change.

We considered two different model-based scenarios: a trophic interaction between *A. planci* and its coral prey (*Scenario I*) *vs*. no biotic interactions (*Scenario II*). We then developed three artificial seascapes reflecting increasing levels of habitat clustering (from evenly distributed to highly aggregated suitable habitat) to gauge the potential effect of patch structure (and corresponding connectivity) on the population dynamics and distribution of *A. planci*. Climate change was simulated based on a latitudinal change in potential climate suitability, with the southernmost habitats becoming more suitable and northernmost habitats becoming less so over the 100-year time period considered (Lamare *et al.*, 2014). Finally, we accounted for demographic traits and processes including fertility, dispersal, population growth, and density-dependent survival (e.g., accounting for the fact that individuals die and populations are reduced to non-outbreaking sizes once they reach a critical density threshold; Pratchett, 2005) (Box 1 and Supplementary Material).

Ecologically realistic fluctuations in total population size mirrored the outbreaking dynamics observed on the Great Barrier Reef (Fabricius *et al.*, 2010) only when biotic interactions were explicitly modelled (*Scenario I*; Fig. 2A). Occupancy patterns were characterised by temporal fluctuations that reflected lagged changes in the spatial distribution of prey abundance (Fig. 2A bottom panel). In contrast, in the scenario without biotic interactions (*Scenario II*), we show a steady decline in the total occupied range area and total population abundance of the invasive species over time (Fig. 2B). The effects of habitat clustering were more pronounced when no biotic interactions were considered (differences among rows in Fig. 2B). More clustered aggregations of suitable habitat generated smoother changes in population dynamics as habitat suitability shifted in response to climate change. The mechanism behind this is a greater connectivity among local populations within highly clustered habitats, which facilitates synchronisation among populations, homogenising the response to climate change. In Scenario I, this greater level of connectivity in highly clustered habitats also caused higher outbreak population sizes of *A. planci*. Moreover, climate change only affected occupancy patterns in Scenario I, with the average spatial extent an outbreak (i.e. number of occupied cells at each peak) decreasing over the 100 year period (Fig. 2A bottom panel). Conversely, there was no evidence of decrease in the size of the outbreaking population over time (Fig. 2A top panel).

4. Forecasting and managing marine invasions under climate change

Previous research has started to unravel the importance of accounting for population dynamics when trying to forecast range shifts and changes in abundance (Keith *et al.*, 2008; Fordham *et al.*, 2013b). A more recent, critical consideration is how to incorporate intra- and inter-specific biotic interactions into forecasts of future trends in abundance and geographical range limits under climate change (Figure 1). Such biotic interactions can strongly influence the effect of climate change on marine invasions, sometimes even reversing the direction of species-specific responses to a particular stressor (when a species is affected by a stressor only in the presence or absence of another species) (e.g., Teng & Apperson, 2000). If we are to fully understand and better forecast marine invasions, we need coupled range dynamics models that are able to incorporate the most relevant aspects of species-level biology and ecology, along with their major interactions. Our coupled range dynamics model for *A. planci* builds upon recent and flexible platforms for modelling single-species invasions (e.g., Savage & Renton, 2014), providing a proof-of-concept that, for this simple system, direct biotic interactions can be integrated into forecasts of marine invasions under climate change with relative ease. Notably, our “proof-of-concept” modelling exercise demonstrates that accounting for simple prey-predator interactions strongly influences forecasts of range movement and population abundance; and that real-world population trends (i.e., those observed on the Great Barrier Reef) can only be reproduced using simulations that account explicitly for biotic interactions. Our findings highlight the importance of identifying the most important sources of environmental and biotic interactions and then integrating them with an appropriately scaled spatially explicit demographic model to forecast invasions under climate change.

Our modelling framework provides a generic tool that can readily be applied to any other marine pest (see Python code in Supplementary Material) where data is available for model parameterisation. Its flexibility allows to incorporate variable biotic interactions under climate change, as well as the impact of thermal or other stress on demographic rates (e.g., decreased fertility; Fordham *et al.*, 2013b). Nonetheless, we suggest that only the most pertinent biotic interactions should be included, based on expert knowledge, published literature, meta-analysis or experimentation. This is because not all aspects of ecosystems can or should be accounted for in model projections since doing so will result in over-parametrized models that are computationally unwieldy and difficult to validate or duplicate (Grimm *et al.*, 2005; Fulton *et al.*, 2015). Finally, it is worth noting that the specificities and constraints particular to the model we developed for *A. planci* can be easily relaxed to capture different processes and mechanisms affecting corals, such as bleaching and cyclones. Including recent data-driven observations of coral impact and recovery following disturbance (Mellin *et al.*, 2016) in the model is a key next step forward.

Arguably, tight integration of the ecological processes considered above into a comprehensive modelling framework for marine invasions can be dauntingly complex and prohibitively challenging, partly because of the difficulties in collecting the data needed to parameterise such models. However, there are solutions. Plausible parameter estimation can be achieved using approximate Bayesian computation (Beaumont, 2010) or the elicitation of expert knowledge (Martin *et al.*, 2005). Model parameters can then be calibrated by comparing model predictions with independent observations (Wells *et al.*, 2015). Indeed, not all model parameters will have a significant effect on model outcomes, and sensitivity analysis (McCarthy *et al.*, 1995) can help determine where future research efforts should be focused to improve model parameters and subsequent predictions. In the case of *A. planci* for example, our sensitivity analysis showed that natural mortality rate was the most important determinant of population size and occupancy (Suppplementary Material). Since natural mortality is typically difficult to quantify (Pratchett *et al.*, 2014), estimates are somewhat uncertain and future research efforts should therefore focus on improving such estimates of mortality. Second, while it is crucial to consider stressors other than temperature and the potential interactions among them, there remain significant gaps in our understanding of responses to such stressors, as well as how species-specific responses will propagate at the community level (Sorte, 2014). This is where meta-analyses can provide invaluable sources of information on how an organism might respond to a given stressor based on the taxon, life stage, habitat, and potential interactions with other stressors (e.g., Przeslawski *et al.*, 2015). Meta-analyses can also help define the strength and direction of interactions among stressors in an integrative model, irrespective of divergences in defining the type of interactions considered (i.e. synergistic, antagonistic, and additive effects) (Piggott *et al.*, 2015).

Two critical post-hoc steps will determine the successful uptake of model outcomes by stakeholders, namely (*i*) model validation and (*ii*) quantification of uncertainty through each step of the model. Demographic models are typically validated by hindcasting abundance over the period for which independent observations are available, and comparing model predictions with observations (Wells *et al.*, 2015). Ideally, in the most data-rich situations, validation can also be done using genetic estimates of population relatedness and source-sink dynamics (Fordham *et al.*, 2014). Uncertainty on the other hand, is a neglected issue that can be complex to address. Attempts have been made to quantify data-related (observational or aleatory) vs. model-based (epistemic) uncertainty (Fordham et al., 2013c), and software developed to allow uncertainty in model parameters (and their interactions) to propagate through to model outputs and influence decision-making (Fordham *et al.*, 2016).

The framework described here can and should be used to examine and rank the efficacy of alternative control strategies (in space and time) including: actively removing the invader; altering habitat suitability (e.g., through predator protection in no-take areas); and managing key dispersal corridors for the invasive species or its predators. The approach can also be used address whether management effort should focus on controlling the centre (source) of a population or the spreading periphery (Williams & Grosholz, 2008) under climate change. Due to epistemic uncertainty, forecasts of any invasion should be considered with caution, and it will often be more desirable to focus on differences among scenarios rather than on specific forecasts *per se*. In this way, the benefit of a particular management action should be measured against its counterfactual, i.e. what would happen if resources were spent on an alternative control option (Wilson *et al.*, 2006), to provide a more sound basis for decision making than individual forecasting.

5. Conclusion

During recent decades, invaluable knowledge has been gained about the mechanisms and consequences of biological invasions in warming oceans, and there is now a need to shift attention from the properties of invading organisms to forecasting invasions in a changing world. Our methodology begins this task by building on previous modelling efforts to incorporate range dynamics, demography, and biotic interactions. Importantly, methodologies exist to tackle data limitation issues (e.g. Bayesian parameter estimation, meta-analysis, expert elicitation), making demographic model development tractable as part of an adaptive learning process. We suggest that strategic pathways should be developed to inform model inputs, interactions among stressors and their inherent uncertainty- the successful integration of which will determine model uptake and benefits in terms of conservation. Finally we emphasize the importance of validating model predictions and interpreting model results in a way that reduces the effects of epistemic uncertainty.

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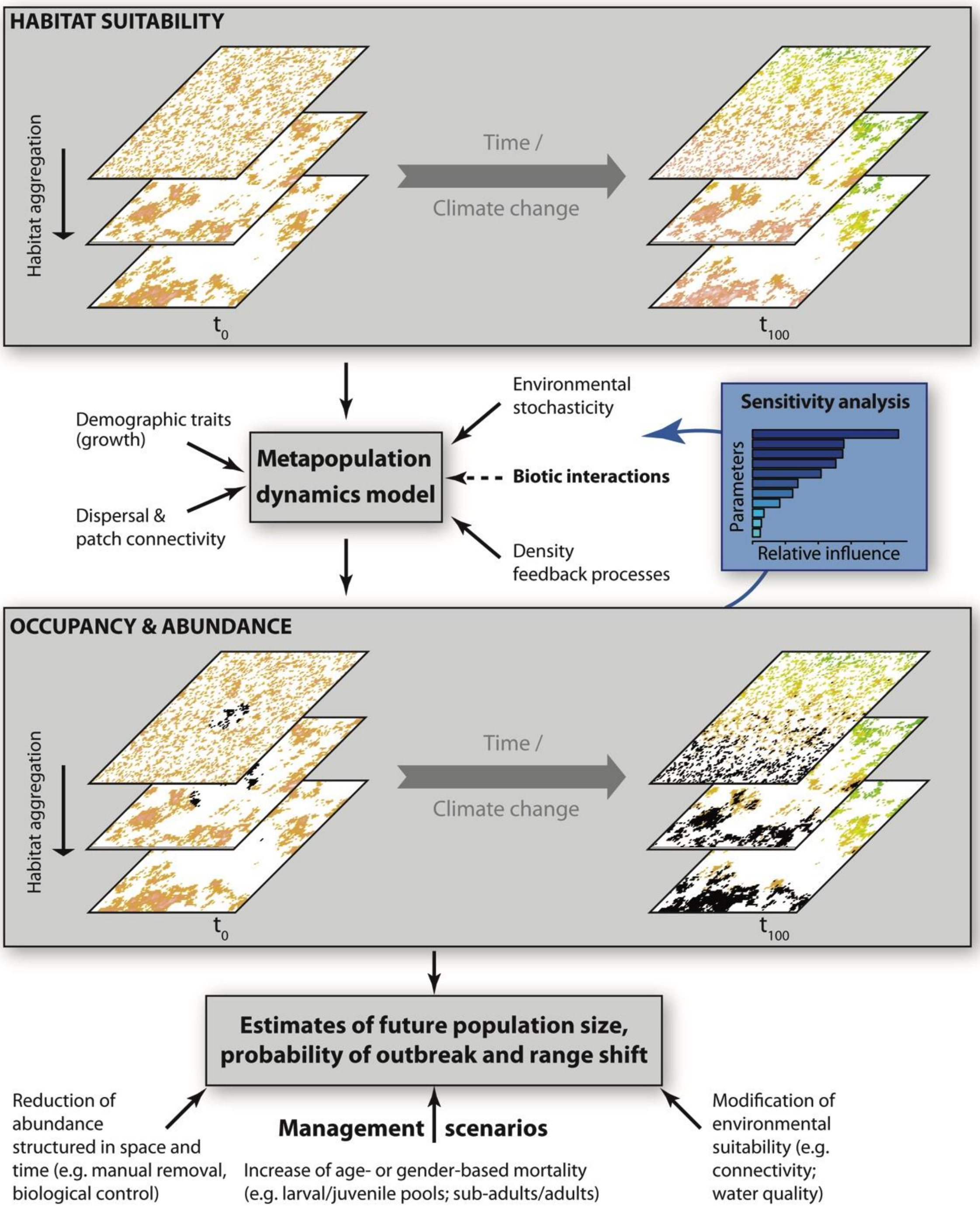
Table 1: Modelling techniques currently available for forecasting marine invasions under climate change: data requirements, ecological processes captured, and examples of previous applications.

Model designation	Data requirements									Processes accounted for	Marine examples
	Occurrence	Abundance/density	Environmental data	Physiological data	Demographic data	Dispersal	Individual behaviour	Predator Prey	Larval Connectivity		
SDM	▯	▯	▯							Species-environment relationships	(de Rivera *et al.*, 2011) (Tyberghein *et al.*, 2012) (Jones *et al.*, 2013)
Biophysical models			▯	▯						Physiological tolerance	(Fordham *et al.*, 2013b) (Cheung *et al.*, 2015)
Population-based demographic models	▯	▯	▯	▯	▯	▯				Growth, survival, dispersal	(Dunstan & Bax, 2007) (Cheung *et al.*, 2011) (Cockrell & Sorte, 2013) (Fordham *et al.*, 2013b)
Individually-based demographic models	▯		▯	▯	▯	▯	▯	▯		Reproduction, aggregation, Behaviour	(Rijnsdorp *et al.*, 2009) (Anderson *et al.*, 2013)

Box 1: Simulation model



Box 1 Figure 1: conceptual representation of the population model. Habitat suitability across the seascape (layers) ranges from low (green) to high (pink). White cells are unsuitable and occupied cells are shown in black.

We constructed a population-based cellular automaton (Durrett & Levin, 1994) model for the crown-of-thorns seastar (*Acantaster* planci) that simulated population and range dynamics under climate change according to two scenarios: dispersal + population growth + biotic interactions (*Scenario I*) and dispersal + population growth (*Scenario II*). Essential aspects of the model can be summarised as follows (see Supplementary Material for full model description and implementation details):

- ***Habitat suitability***: defined based on 2D simulated seascapes characterized by variable levels of clustering (i.e. aggregation) from numerous small patches (cluster 1) to a few large patches (cluster 3). The distribution of habitat suitability values across grid cells was kept constant among clustering levels. The resulting maps carry information on habitat suitability, which in turn determines the carrying capacity.
- ***Simulating the effects of climate change***: This was achieved by altering dynamically the potential climate suitability of each local unit of the meta-population (grid cell) at each iteration of the model, and combining it with the original habitat suitability layer. The temporal change in habitat suitability across the seascape reflected a southerly range shift commonly observed in conjunction with latitudinal range dynamics (Parmesan, 2006), with northernmost habitats becoming progressively unsuitable and southernmost habitats becoming more so.
- ***Demographic traits***: We modelled fertility, survival, dispersal and population growth. Survival and fecundity varied spatiotemporally in response to environmental variability (see below).
- ***Local populations connectivity via dispersal processes***: We allowed propagules (i.e. pelagic larvae) of the invasive species and its interacting prey species (*Scenario I* only) to disperse across the seascape. We defined dispersal from local populations based on a dispersal kernel and individual-level probabilities of dispersal. Adults were considered sessile.
- ***Environmental stochasticity*** accounted for stochastic variation in population growth rates.
- ***Biotic interactions***: Predator-prey interactions between *A. plancii* and a generic coral prey species were simulated using Lotka-Volterra (predator-prey) equations (*Scenario I* only).
- ***Density dependent processes*** were modelled by allowing population density to increase up to the carrying capacity, after which individuals die and density returns to non-outbreaking levels.

We ran 100 simulations of 120 time steps each, discarding the first 20, which were used as the burn-in period. We summarised the outputs across simulations in terms of abundance and occupancy of the invasive species and its coral prey (*Scenario I* only).We ran a sensitivity analysis with the main model parameters varying between ± 20 % over a total of 200 models as determined by Latin hypercube sampling, and then used boosted regression trees to determine the most important parameters (Supplementary Material).

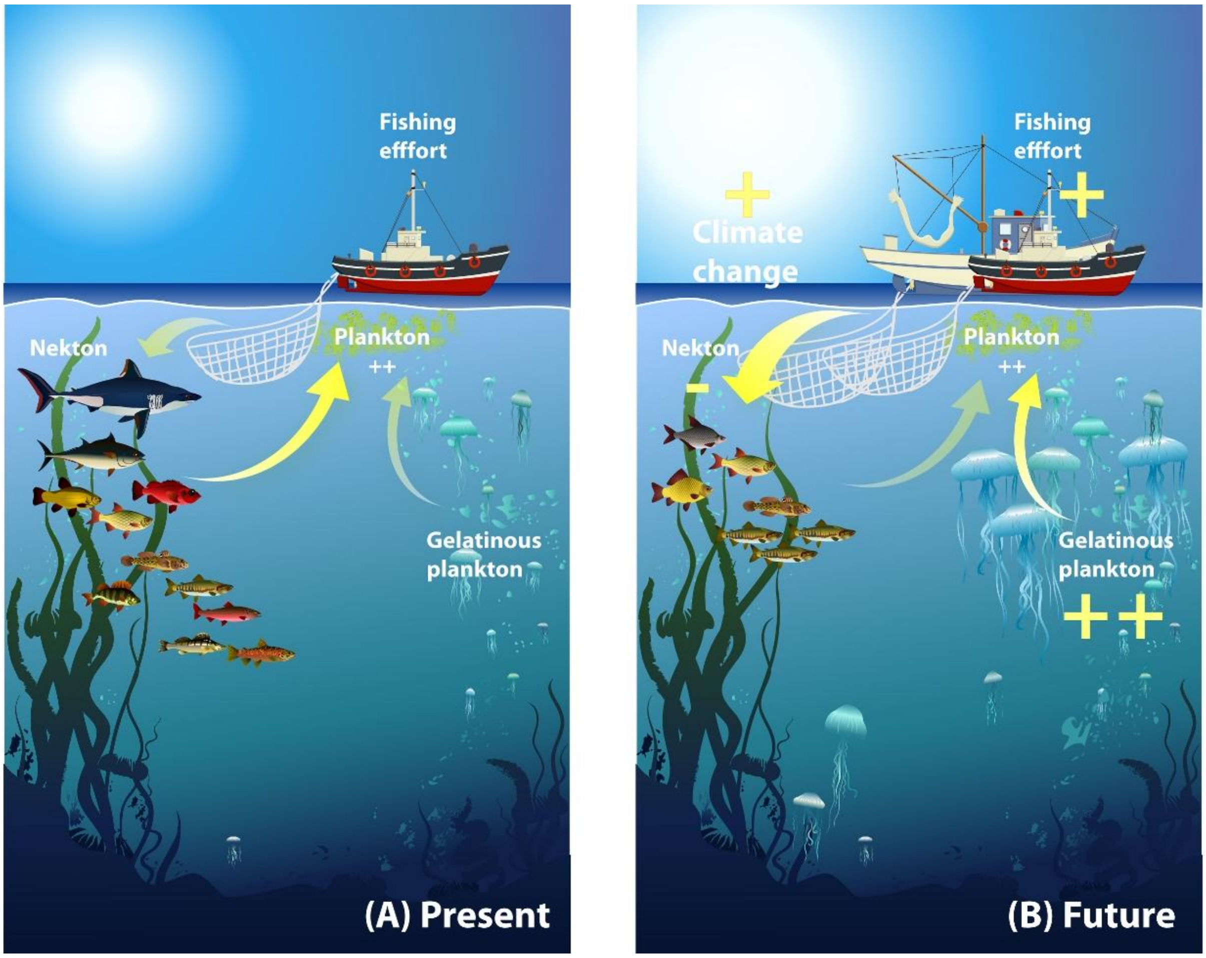


Figure 1. One conceptual model of mutually reinforcing effects of climate change and other anthropogenic stressors on native invasive jellyfish (*gelatinous plankton*), with biotic interactions (i.e., predator-prey relationships) represented by the arrows. **(A)** Increasing terrestrial runoff and nutrients loads contribute to eutrophication, leading to unusually high phytoplankton (*plankton*) concentrations associated with low oxygen concentrations (Miller & Graham, 2012). These conditions promote the growth of jellyfish populations, sustained by plankton resources usually consumed by fish stocks and fish larvae (*nekton*). Fish stocks are subsequently impacted by this reduced availability of plankton resources, as well as by continuously increasing *fishing effort* (e.g. Pauly *et al.*, 2002). The reduced size of fish stocks results in a reduced uptake of planktonic resources, thus made available to sustain further jellyfish blooms (Licandro *et al.*, 2010; Lynam *et al.*, 2011). **(B)** *Climate change* favours gelatinous plankton species that are able to adapt to new environmental conditions and increase in abundance rapidly (Lynam *et al.*, 2011). The composition of nekton communities and fish stocks is altered not only as increasing fishing efforts remove fish predators (Pauly *et al.*, 2002) but also as surface temperature increases leading to the dominance of (sub)tropical species (Cheung *et al.*, 2013). Because these subtropical species are unlikely to prey on the same plankton species as their temperate peers, planktonic resources not consumed by fish are more readily available to sustain increasingly frequent and extensive jellyfish blooms.

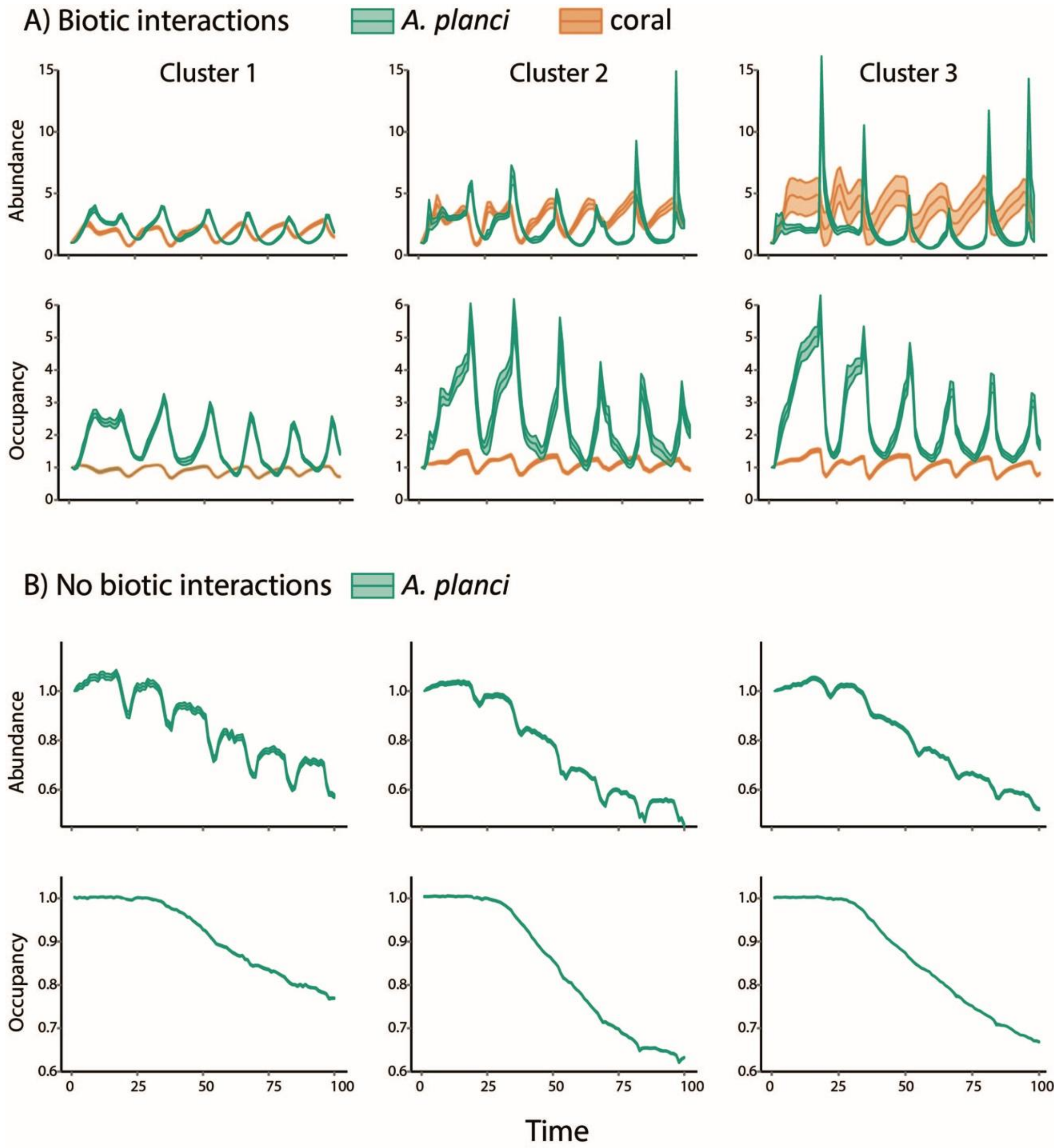


Figure 2. Forecasts of a marine invasion process under climate change using a spatially explicit demographic modelling framework. Model parametrisation is based on a synthetic example for the coral-eating crown-of-thorns seastar (*Acanthaster planci*) and its coral prey (see text). (A) *Scenario I* includes a trophic interaction between the marine invasive species and its coral prey, while (B) *Scenario II* considers only dispersal and population growth. In both panels (A, B), top and bottom rows show population size and spatial occupancy over time, respectively; columns represent levels of clustering (i.e. aggregation) in suitable habitat from cluster 1 (numerous small patches) to cluster 3 (few large patches). Climate change was modelled using variable habitat suitability layer from time step 1 to 100 (the length of simulations). See Supplementary Material for a detailed description of the model implementation.