Modelling marine community responses to climate-driven species redistribution to guide monitoring and adaptive ecosystem-based management

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Abstract

As a consequence of global climate-driven changes, marine ecosystems are experiencing polewards redistributions of species – or range shifts – across taxa and throughout latitudes worldwide. Research on these range shifts largely focuses on understanding and predicting changes in the distribution of individual species. The ecological effects of marine range shifts on ecosystem structure and functioning, as well as human coastal communities, can be large, yet remain difficult to anticipate and manage. Here, we use qualitative modelling of system feedback to understand the cumulative impacts of multiple species shifts in south-eastern Australia, a global hotspot for ocean warming. We identify range-shifting species that can induce trophic cascades and affect ecosystem dynamics and productivity, and evaluate the potential effectiveness of alternative management interventions to mitigate these impacts. Our results suggest that the negative ecological impacts of multiple simultaneous range shifts generally add up. Thus, implementing whole-of-ecosystem management strategies and regular monitoring of range-shifting species of ecological concern are necessary to effectively intervene against undesirable consequences of marine range shifts at the regional scale. Our study illustrates how modelling system feedback with only limited qualitative information about ecosystem structure and range-shifting species can predict ecological consequences of multiple co-occurring range shifts, guide ecosystem-based adaptation to climate change and help prioritise future research and monitoring.

Keywords: climate change, management support tool, qualitative modelling of system feedback, qualitative network models, range shifts, temperate reef, trophic cascade, tropicalisation

Introduction

Persistent climate-driven changes in the latitude, or depth distribution of species, known as range shifts, have been documented over recent decades for a wide variety of taxa in both terrestrial (Loarie *et al.*, 2009) and aquatic (Perry *et al.*, 2005) ecosystems across all latitudes (e.g. tropical, temperate and polar). These sustained contractions and extensions in species distributions occur as a consequence of climate-driven changes in environmental conditions (Sunday *et al.*, 2012). Despite growing evidence of marine range shifts, identifying drivers and quantifying the extent and velocity of range shifts in the ocean are challenging (Loarie *et al.*, 2009; García Molinos *et al.*, 2015; Sunday *et al.*, 2015).

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The general effects of climate-driven changes on marine ecosystems have been documented and predicted at the global scale (Cheung *et al.*, 2013; Beaugrand *et al.*, 2015; Boyd *et al.*, 2015; García Molinos *et al.*, 2015). However, at a regional scale, changes in ecosystem structure and functioning in response to local ocean changes can be highly complex (Johnson *et al.*, 2011; Marzloff *et al.*, 2015). Moreover, ecological, economic and social consequences of range shifts can be large (Van Der Putten *et al.*, 2010) and difficult to reverse (Johnson *et al.*, 2011; Marzloff *et al.*, 2015). While a significant proportion (18–80%) of species within marine ecosystems simultaneously shift their distribution polewards (Sunday *et al.*, 2012), current research largely focuses on individual species (Bates *et al.*, 2014) and often overlooks the broader impacts of co-occurring species shifts on ecosystem structure and functioning (Van Der Putten *et al.*, 2010). Hence, the direct and

indirect effects of these species redistributions on marine ecosystem dynamics and coastal industries are poorly characterised (Van Der Putten et al., 2010; Marzloff et al., 2015), which limits the effectiveness of ecosystem-based management approaches (Hall & Mainprize, 2004).

Here, we predict ecological impacts of range-shifting species to help inform ecosystem-based management in south-east Australia, where rapid ongoing ocean warming is occurring (Hobday & Pecl, 2013; Oliver & Holbrook, 2014; Sunday et al., 2015) (Fig. 1). Our predictive framework, based on modelling ecosystem feedback (Dambacher et al., 2002), only requires qualitative knowledge about community structure and climate-driven species redistribution. Temperate reef communities off eastern Tasmania, an island state of Australia, have been affected by rapid changes in ocean conditions (Johnson et al., 2011) largely due to the strengthening of the southern extension of the East Australian Current (Oliver & Holbrook, 2014) (Fig. 1). Several reef species have been identified as extending their range from Australia's mainland to eastern Tasmania (Ling et al., 2009b; Robinson et al., 2015), including the common Sydney octopus (Octopus tetricus), several species of reef fish and macro-invertebrates, such as the eastern rock lobster (Sagmariasus verreauxi) and the long-spined sea urchin (Centrostephanus rodgersii). The latter has

demonstrated the ability to act as an ecosystem engineer and form extensive 'barren' by destructively grazing on macroalgal beds (Ling et al., 2009a). This new alternative ecosystem state is synonymous with dramatic loss of habitat, species diversity and reef productivity (Ling, 2008) and has direct negative effects on the high-value abalone and rock lobster fisheries (Marzloff et al., 2013). Only large rock lobster individuals can naturally control sea urchin density through predation (Ling et al., 2009a), and where widespread urchin-induced underwater deserts establish, restoration of productive seaweed beds is virtually impossible (Marzloff et al., 2015). While preventing extensive barren formation currently receives full attention from regional management authorities (Marzloff et al., 2015), a wide range of other species are simultaneously shifting their distribution in eastern Tasmania (Johnson et al., 2011; Robinson et al., 2015). Yet the potential ecological impacts of these other shifting species remain poorly understood.

We developed qualitative models of system feedback that holistically capture the general dynamics of reef communities in eastern Tasmania across six key functional groups (Fig. 2). Using three alternative models to account for uncertainties in community structure, we generated qualitative predictions under alternative scenarios about species poleward redistributions and/or management interventions. Qualitative predictions were derived both symbolically (Marzloff et al., 2011) and with a simulation-based approach (Melbourne-Thomas et al., 2012), where we reported ecological consequences as probabilities of model groups responding negatively, that is declining in abundance. With these qualitative models, we address several important questions for the regional management of range shifts, in particular: (i) we identify range-shifting species that can affect regional ecosystem structure and functioning; and (ii) show how qualitative model results might inform future monitoring and management of species redistribution.

Material and methods

Modelling approach

Based upon available information about key functional groups and ecological interactions (Grubert et al., 1999; Guest et al., 2008, 2009; Ling, 2008; Pederson et al., 2008; Ling et al., 2009a; Strain & Johnson, 2009; Vergés et al., 2014; Briceño et al., 2015), qualitative modelling of system feedback can predict the effects of simultaneous range shifts. We based our models on qualitative information regarding temperate reef community structure (Table 1) and climate-driven changes in the abundance of range-shifting species (Table 2). We represented the long-term regional effects of range shifts as sustained
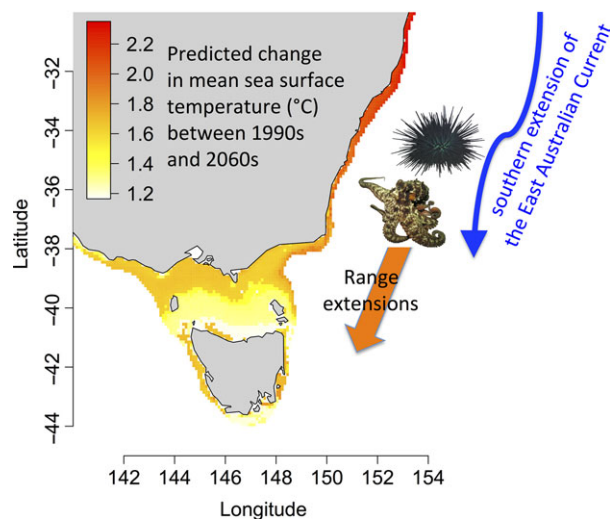

Fig. 1 Predicted increase in annual mean coastal sea surface temperature in south-east Australia, between 1990s and 2060s (Oliver & Holbrook, 2013). All near-shore waters in the region are projected to warm by >1 °C, with current rates of increase almost four times the global average (Hobday & Pecl, 2013). Sustained rapid and ongoing ocean changes have led to southwards range extensions of reef species (including the long-spined sea urchin or the common octopus; pictured) from Australia's mainland to eastern Tasmania (Robinson et al., 2015).
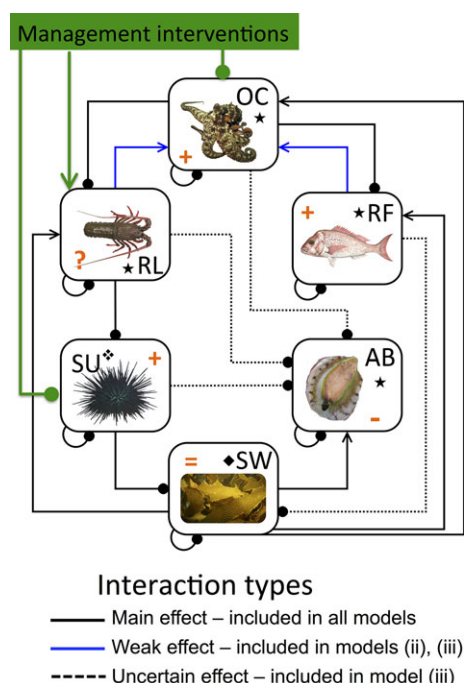
Fig. 2 Sign-directed graph of the Tasmanian reef ecosystem, representing interactions between: SU for long-spined sea urchin (*Centrostephanus rodgersii*), SW for seaweed bed (*Ecklonia radiata, Phyllospora comosa*, etc...), AB for abalone (both blacklip and greenlip species), RL for rock lobster (southern rock lobster and northern counterpart eastern rock lobster), OC for octopus (different species, including *Octopus maorum* and *Octopus tetricus*), RF for reef fish (different species, including several range-shifting species); →positive interactions; --● negative interactions; each variable is self-regulated; blue and dashed lines correspond to weaker and uncertain interactions, respectively (see Table 1 for details on modelled interactions and alternative model structures). Orange symbols (+,−, ?, =) within each node represent expected changes in the regional abundance of model groups (increase, decline, uncertain or neutral, respectively). Green arrows reflect the effects of the management scenarios simulated in our study (see Fig. 5). ★ denotes commercial species, ❖ destructive grazer and ◆ habitat former.

population abundance changes (increase or decline due to range extension or contraction, respectively).

Building on limited qualitative species-specific information available about range shifts, the qualitative model of Tasmanian rocky reef community dynamics (Fig. 2) has a broad-scale management focus and only considers six key species or functional groups: the seaweed bed (SW); abalone (AB) including both blacklip (*Haliotis rubra*) and greenlip abalone (*Haliotis laevigata*); rock lobster (RL) including both southern rock lobster (*Jasus edwardsii*) and eastern rock lobster (*S. verreauxi*); long-spined sea urchin (SU, *C. rodgersii*); reef fish (RF); and octopus (OC) including a local species *Octopus maorum* and the range-extending *O. tetricus* (Ramos *et al.*, 2015) (pictured in Fig. 2). The seaweed bed comprises canopy-forming algae (e.g. *Ecklonia radiata* pictured in Fig. 2), numerous

understorey seaweeds and assemblages of invertebrates. Reef fishes include several species such as snapper (*Pagrus auratus*), blue-throated wrasse (*Notolabrus tetricus*) and banded morwong (*Cheilodactylus spectabilis*).

These holistic general models of Tasmanian rocky reef communities include key ecological interactions (Table 1) and core feedbacks, while omitting specific details of temperate reef dynamics. Community structure can be represented as a sign-directed graph (Fig. 2), where functional groups (the nodes) interact with each other (conventionally represented by an arrow for a positive effect and a line terminating in a filled circle for a negative effect). Density-dependent processes regulate changes in each model group and are represented as negative self-effects on each node. The graphical representation of reef community structure given in Fig. 2 includes three alternative model structures (i, ii and iii) of increasing complexity: blue and dashed lines correspond to weaker and uncertain interactions, respectively; 'weaker' refers to positive effects in pairwise prey–predator interactions as the rate of prey depletion exceeds the rate of predator population growth due to prey consumption (Hosack *et al.*, 2008); 'uncertain' links represent ecological processes that may play a role in temperate reef community dynamics but are not clearly demonstrated in the study region. Weak and uncertain interactions not considered in model i are included in models ii and iii (see Table 1).

Analyses and predictions

The adjoint matrix associated with the sign-directed graph depicted in Fig. 2 presents the qualitative predictions of reef community responses to long-term perturbations (Dambacher *et al.*, 2002; Marzloff *et al.*, 2011), where the effects of both climate-driven range shifts and management actions are additive and represented as sustained changes in the population growth or death rates of the model group(s) (see Table 3 for assumptions associated with each simulated scenario). Elements of the symbolic adjoint matrix (Fig. 3) represent the signs of each variable's responses to a positive input in the abundance of other model groups: for instance, the minus sign in the bottom row of the fourth column indicates that 'SW' (the seaweed bed) responds negatively to an increase in the abundance of 'SU' (sea urchin). Ambiguous prediction, that is when both negative and positive effects contribute to a variable response (e.g. effects of seaweed increase on rock lobster), can often be elucidated with simple assumptions about the relative strength of the different feedback contributing to an individual response. In this case, the response sign is given assuming the condition referenced by a superscript number is met. Symbolic qualitative predictions are given as positive (+), negative (−) or unaffected (0) within the matrix (Fig. 3), and the algebraic conditions supporting the predicted signs are given beside the adjoint matrix (Fig. 3). Symbolic analyses were performed using the Maple script provided as supplementary information in Dambacher *et al.* (2002). Full details regarding adjoint matrices and symbolic formalism are available in Data S1 and detailed in Marzloff *et al.* (2011).

Table 1 Major trophic and indirect (e.g. habitat provision) interactions between temperate reef species or functional groups explicitly represented in our qualitative models of seaweed-based communities in eastern Tasmania. 'Weak' refers to positive effects in pairwise prey–predator interactions as the rate of prey depletion exceeds the rate of predator population growth due to prey consumption; 'uncertain' links represent ecological processes that may play a role in temperate reef community dynamics but are not clearly demonstrated in the study region. Weak and uncertain interactions, not considered in model i, are included in models ii and iii. Model nodes are abbreviated as follow: SW: seaweed bed; RL: rock lobster; AB: abalone; RF: reef fish; OC: Octopus; SU: long-spined sea urchin. → and —• symbolise positive and negative interactions, respectively

Interaction	Description	Strength	Models	References
SW → RL	Source of habitat and food	Strong	(i), (ii), (iii)	Guest *et al.* (2009)
SW → AB	Source of habitat and food	Strong	(i), (iii), (iii)	Guest *et al.* (2008)
SW → RF	Source of habitat and food	Strong	(i), (iii), (iii)	Ling (2008)
SW → OC	Source of habitat and food	Strong	(i), (iii), (iii)	Ling (2008)
RL —• SU	Predation by large rock lobster	Strong	(i), (iii), (iii)	Ling *et al.* (2009a)
SU —• SW	Destructive grazing	Strong	(i), (iii), (iii)	Ling (2008)
OC —• RL	Predation	Strong	(i), (iii), (iii)	Briceño *et al.* (2015)
OC —• RF	Predation	Strong	(i), (iii), (iii)	Grubert *et al.* (1999)
RL → OC	Consumption	Weak	(ii), (iii)	Briceño *et al.* (2015)
RF → OC	Consumption	Weak	(ii), (iii)	Grubert *et al.* (1999)
RL —• AB	Predation on juveniles	Uncert. /weak	(iii)	Pederson *et al.* (2008)
SU —• AB	Competition for space and resources	Uncert. /weak	(iii)	Strain & Johnson (2009)
OC —• AB	Predation	Uncert. /weak	(iii)	Grubert *et al.* (1999)
RF —• SW	Destructive grazing	Uncert. /weak	(iii)	Vergés *et al.* (2014)

Table 2 Summary of the mean observed and expected changes in abundance of major range-shifting species in eastern Tasmania. Locally, abundance changes due to range-shifting species and hence their ecological impacts are more heterogeneous and more diverse than the regional-scale long-term predictions presented in this paper

Species (model group)	Change in distribution	Long-term abundance change	References
Southern rock lobster (*Jasus edwardsii*)	Contraction	Decline	Pecl *et al.* (2009, 2014)
Blacklip abalone (*H. rubra*)	Contraction	Decline	Pecl *et al.* (2014)
Greenlip abalone (*H. laevigata*)	Contraction	Decline	Pecl *et al.* (2014)
Sea urchin (*C. rodgersii*)	Extension	Increase	Ling *et al.* (2009b)
Eastern rock lobster (*Sagmariasus verreauxi*)	Extension	Increase	Robinson *et al.* (2015)
Sydney octopus (*Octopus tetricus*)	Extension	Increase	Ramos *et al.* (2014, 2015)
Snapper (*Pagrus auratus*)	Extension	Increase	Last *et al.* (2011), Robinson *et al.* (2015)
Other reef fish species	Contraction for native species. Extension for newcomers	Increase	Last *et al.* (2011), Robinson *et al.* (2015)
Seaweed bed (Assemblage of many taxa)	- Overall change in species composition - Species likely to move polewards and/or deeper	Decline (e.g. *M. pyrifera*) Stable (e.g. *E. radiata*, most common kelp in temperate Australia)	Johnson *et al.* (2011), Wernberg *et al.* (2010), Mohring *et al.* (2014)

As a complement to these symbolic qualitative predictions that require a degree of manual postanalyses to gain a mechanistic causal understanding of key drivers (i.e. interactions and/or feedback) of system dynamics, Figs 4 and 5 present the results of simulation-based qualitative modelling of range shifts (Melbourne-Thomas *et al.*, 2012). This simulation-based approach provides an easy-and-fast-to-implement means to evaluate ambiguity and incorporate uncertainty in qualitative network analysis (Melbourne-Thomas *et al.*, 2012, 2013). Note that the method of prediction weights (Dambacher *et al.*, 2002, 2003), and its probabilistic interpretation (Hosack *et al.*, 2008), provides a fully equivalent alternative to the simulation-based approach presented here. Figures 4 and 5 report the predicted signs of response of each model group under a given scenario.

Table 3 Scenarios summary. Each simulated scenario directly relates to changes in model group abundances due to climate-driven range shifts and management actions: the first two sets of scenarios capture the effects of range-shifting species in south-eastern Australia, considered in isolation or simultaneously and presented as the left-hand and right-hand columns of graphs in Fig. 4, respectively. The final set of scenarios presented in Fig. 5 considers all range shifting simultaneously under different adaptive management scenarios, where (a) harvesting of the range-extending octopus, (b) stock rebuilding of the depleted and range-contracting rock lobster and/or (c) culling or harvesting of the range-extending long-spined sea urchin are implemented together or in isolation

Scenario	SW	RL	AB	SU	OC	RF	Comment(s)
Individual range shifts							
SW −	−						Decline in seaweed bed
RL −		−					Decline in southern rock lobster
RL +		+					Increase in eastern rock lobster
AB −			−				Decline in abalone
SU +				+			Increase in the long-spined sea urchin
OC +					+		Increase in octopus
RF +						+	Increase in reef fishes
Multiple simultaneous range shifts							
Contractions		−	−				Range contractions (Tasmanian species)
Extensions		+		+	+	+	Range extensions from Australia's mainland
All shifts (RL−)		−	−	+	+	+	All (eastern rock lobster increase < southern rock lobster decline)
All shifts (RL+)	0	−		+	+	+	All (rock lobster species replacement implies no change in abundance)
All range shifts under alternative management scenarios							
(a)		−	−	+	0	+	No effective sea urchin control No effective rock lobster stock rebuilding Octopus control (harvesting)
(b)	0	−		+	+	+	No effective sea urchin control Lobster stock rebuilding compensates decline No effective octopus control
(c)		−	−	0	+	+	Sea urchin control (harvesting / culling) No effective rock lobster stock rebuilding No effective octopus control
(b) + (c)	0	−		0	+	+	Sea urchin control (harvesting / culling) Lobster stock rebuilding compensates decline No effective octopus control
(a) + (b)	0	−		+	0	+	No effective sea urchin control Lobster stock rebuilding compensates decline Octopus control (harvesting)
(a) + (c)		−	−	0	0	+	Sea urchin control (harvesting / culling) No effective rock lobster stock rebuilding Octopus control (harvesting)
All interventions (RL−)	0	−		0	0	+	Sea urchin control (harvesting / culling) Lobster stock rebuilding compensates decline Octopus control (harvesting)
All interventions (RL+)	+	−		0	0	+	Sea urchin control (harvesting / culling) Rock lobster stock rebuilding Octopus control (harvesting)

To visualise the full range of consequences of range shifters, we adopted a white/blue-grey-red colour scale that categorises simulation-based qualitative predictions into four main types: (i) Neutral responses, shown in white, when there is no effect of a perturbation to a response variable; (ii) Positive responses, shown in red, when more than 2/3 of the predicted responses across Monte Carlo simulations are positive; (iii) Negative responses, shown in blue, when more than 2/3 of the predicted responses across Monte Carlo simulations are negative; (iv) Highly ambiguous responses, shown in grey (see the vertical double-arrow corresponding to 'ambiguous' along the colour bar of Figs 4 and 5), when <2/3 of the predicted responses across Monte Carlo simulations are of the same sign. In this case, a mix of positive feedback and negative feedback contributes to variable response and, to a large extent, both cancel each other out; hence, the overall sign of the response is dependent on the relative strength of these counteracting feedbacks. Consequently, numerical predictions
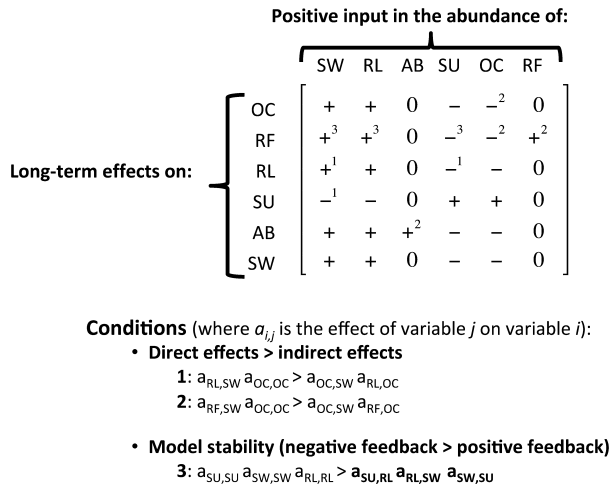
Positive input in the abundance of:

	SW	RL	AB	SU	OC	RF
OC	$+$	$+$	0	$-$	$-^2$	0
RF	$+^3$	$+^3$	0	$-^3$	$-^2$	$+^2$
RL	$+^1$	$+$	0	$-^1$	$-$	0
SU	$-^1$	$-$	0	$+$	$+$	0
AB	$+$	$+$	$+^2$	$-$	$-$	0
SW	$+$	$+$	0	$-$	$-$	0

Long-term effects on:

Conditions (where $a_{i,j}$ is the effect of variable j on variable i):
- Direct effects > indirect effects
  1: $a_{RL,SW}\, a_{OC,OC} > a_{OC,SW}\, a_{RL,OC}$
  2: $a_{RF,SW}\, a_{OC,OC} > a_{OC,SW}\, a_{RF,OC}$

- Model stability (negative feedback > positive feedback)
  3: $a_{SU,SU}\, a_{SW,SW}\, a_{RL,RL} > a_{SU,RL}\, a_{RL,SW}\, a_{SW,SU}$

Fig. 3 Adjoint matrix for *model i* predicting community effects of long-term increase in model groups: SU for long-spined sea urchin, SW for seaweed bed, AB for abalone, RL for rock lobster, OC for octopus and RF for reef fish. Each matrix element symbolically represents the sign of a variable's response to a positive input in the abundance of another model group. Ambiguous predictions are given superscripts and will be of the given sign if the conditions shown below the matrix are met. Note the influence of the positive feedback $a_{SU,RL}\, a_{RL,SW}\, a_{SW,SU}$ (highlighted in bold; See also Data S1) in structuring the signs of community responses.

switch from positive to negative across Monte Carlo simulations depending on each numerical specification of the community matrix.

Note that for negative and positive responses, the level of shading reflects the degree of sign determinacy across Monte Carlo simulations, where deep colours are associated with a fully determined response, while paler colours denote less sign consistency. Note that, on the basis of comparison with symbolic predictions, we consider negative or positive responses associated with <80% of sign consistency across Monte Carlo simulations to be ambiguous. The simulation algorithms are implemented in the R package 'QPress' (http://rforge.net/QPress/).

The simulation-based framework (Melbourne-Thomas et al., 2012) allows for rapid assessment of multiple scenarios across model structures of increasing complexity. We considered three sets of scenarios for each model (see Table 3 for details) related to: (i) range shifts of individual species; (ii) multiple range shifts occurring simultaneously (*All contractions* assumes declining abundance of range-contracting abalone and rock lobster; *All extensions* corresponds to increasing abundance of range-extending rock lobster, sea urchin, octopus and reef fishes; and *All shifts* combines all these changes) and (iii) simultaneous range shifts under alternative management interventions (i.e. rock lobster stock rebuilding via reduction in fishing pressure or translocation; sea urchin and octopus control through culling/harvesting). For this last set of scenarios (Fig. 5), we assume that management interventions can effectively mitigate projected cli-

mate-driven changes in the regional abundance of these three groups: for instance, under a sea urchin culling or harvesting that aims at controlling climate-driven population increase, we simulate that sea urchin regional abundance does not increase significantly (see Table 3 for details). When all range shifts are considered simultaneously, alternative scenarios reflect uncertainty about whether or not the net regional change in rock lobster biomass is positive ('RL+') or negative ('RL−'): as both eastern and southern rock lobsters play a similar functional role (Fig. 2) (Ling et al., 2009a), the net change in rock lobster abundance will depend on whether the range-extending eastern rock lobster replaces its range-contracting southern counterpart. In these scenarios that consider combined range shifts, the seaweed bed is assumed to stay constant as *Ecklonia radiata*, the main habitat former in temperate Australia, can overall adapt to projected warming (Mohring et al., 2014).

For each scenario, 5000 quantitative community matrices were randomly selected following the sign-directed interactions presented in Fig. 2. Each matrix was checked for stability and against two criteria characterizing known reef community responses to sea urchin biomass building (Ling, 2008), and lobster biomass rebuilding in the Maria Island marine reserve (Barrett et al., 2009); this latter criterion only applied to models ii and iii with detailed interactions. Both the sign-directed graph and R code are provided as online Supplementary Information (Data S2).

Results

Ecological effects of individual range shifts

Qualitative model predictions for scenarios of individual range shifts discriminate between those range shifters that have marginal detrimental effects on reef structure and functioning and those that can induce large community-wide impacts (Figs 3 and 4, left-hand panels). Examples of range shifts with negligible negative ecosystem-level effects in our model system include the range extensions of eastern rock lobster or reef fishes, or the contraction of abalone. While these range shifters are predicted to induce significant community responses, our interpretation relies on the idea that as long as key ecological groups do not decline in abundance, the effects of range shifts are unlikely to affect ecosystem structure and functioning dramatically. Note, importantly, a negative response in the barren-forming sea urchin *C. rodgersii* corresponds to a positive ecosystem outcome (Figs 3, 4 and 5). Conversely, climate-driven declines in native habitat-forming macroalgae (e.g. the emblematic giant kelp *M. pyrifera*) or the abundance of southern rock lobster, or increases in the abundance of the range-extending octopus or long-spined sea urchin can all have community-wide negative impacts (2–5 model groups negatively impacted; Figs 3 and 4).
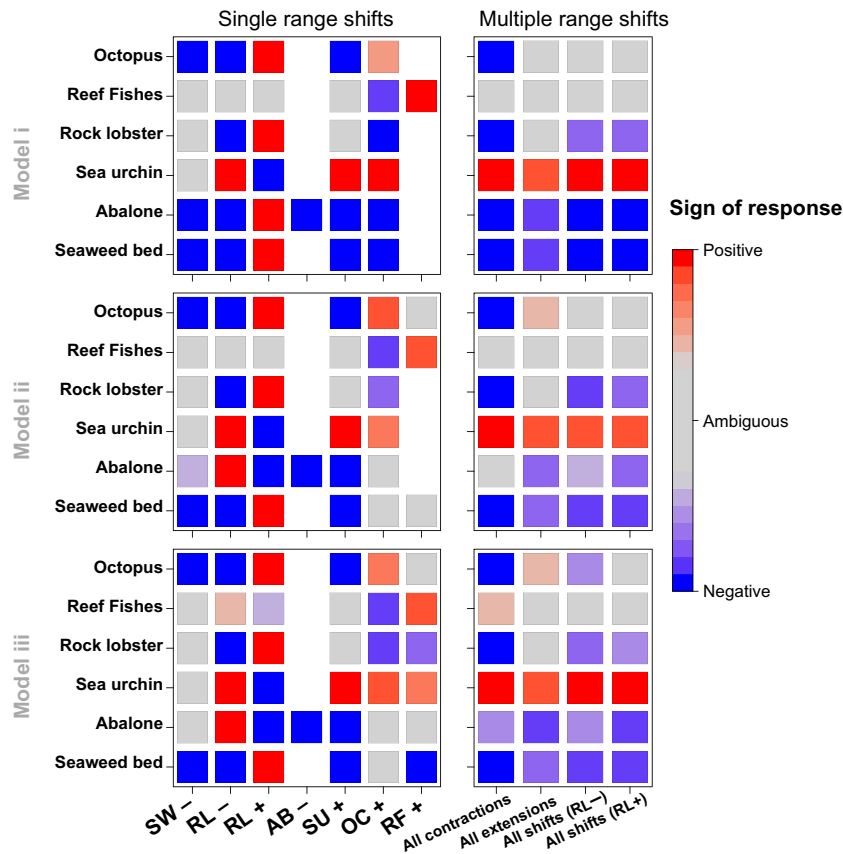
Fig. 4 Ecological effects of range-shifting species on temperate reef dynamics in eastern Tasmania. Coloured squares represent the sign of response of each model group (x-axis) to a given scenario (y-axis): white for neutral; grey for ambiguous; red for positive; blue for negative. When responses are positive or negative, the degree of shading increases with prediction uncertainty. 'RL+' and 'RL−' correspond to a net increase or decline in rock lobster abundance, respectively. The left-hand column considers the community effects of individual range shifts in isolation, while the right-hand column presents consequences of future scenarios where range shifts occur simultaneously (see Table 3 for details). To account for model structure uncertainty, we simulated each scenario using three alternative model structures (specified as row labels).

Symbolic and simulation-based qualitative modelling predictions with model *i* for scenarios related to single range shifts (Fig. 3, and top-left panel of Fig. 4, respectively) are perfectly consistent for unambiguous (neutral, positive or negative) responses. However, when both positive and negative feedback loops contribute to a variable response, the two approaches sometimes predict opposite directions of responses. For instance, under a long-term decline in seaweed bed, rock lobster abundance is predicted to increase with the simulation-based approach (faded red colour; Fig. 4) but to decline with the symbolic approach (assuming that condition 1 is met; Fig. 3). In this case, condition 1 is almost certain given that the direct provision by the seaweed bed of habitat and food to rock lobster is highly likely to overwhelm its indirect effect via provision of habitat and food to predatory octopus (Fig. 3).

Ecological effects of multiple co-occurring range shifts

When considered in combination, the negative community impacts of individual range shifts generally add up and become more likely (i.e. sign consistency for negative predictions increases): indeed, for all scenarios considering all range-contracting and range-extending species simultaneously (Fig. 4; right-hand panels labelled *All shifts*), the abundance of the barren-forming sea urchin in eastern Tasmania is highly likely to increase (deep red colours), while key ecological and commercial groups (e.g. rock lobster, abalone, seaweed bed) are likely to decline (deep blue colours). Overall, the negative ecological effects of individual range shifters (Fig. 4, left-hand panels) add up when they occur simultaneously (Fig. 4, right-hand panels). However, in certain cases, some range shifters might buffer each other's ecological
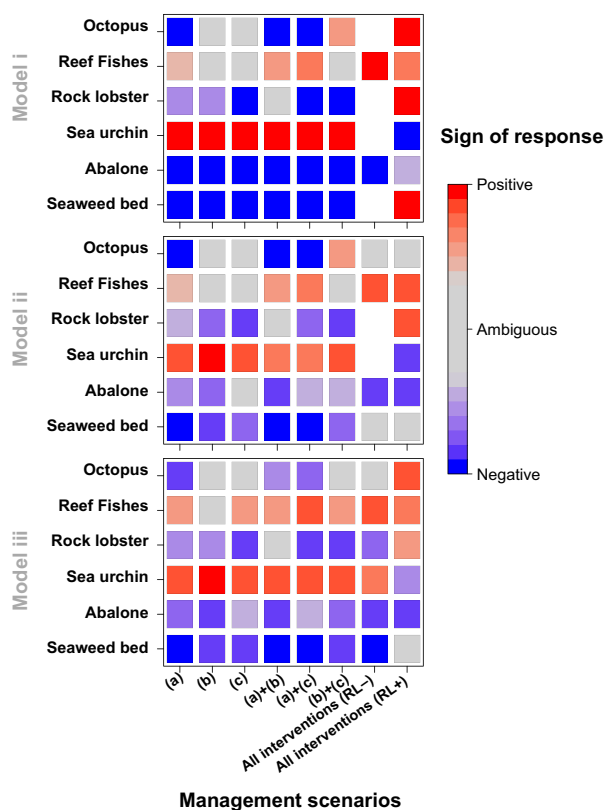
Fig. 5 Effectiveness of management strategies for mitigating ecological effects of range-shifting species on temperate reef dynamics in eastern Tasmania. Coloured squares represent the sign of response of each model group to a given scenario: white for neutral; grey for ambiguous; red for positive; blue for negative. When responses are positive or negative, the degree of shading increases with prediction uncertainty. All scenarios include range contractions and extensions of Tasmanian and Australian mainland species (occurring simultaneously) as well as the effects of alternative management interventions implemented either individually or combined: (a) harvesting of the range-extending octopus; (b) rebuilding the depleted stock of the range-contracting southern rock lobster; (c) culling or harvesting of the range-extending long-spined sea urchin (see Table 3 for details). 'RL+' and 'RL−' correspond to a net increase or decline in rock lobster abundance, respectively. Scenarios were simulated using three alternative model structures (specified as row labels).

impacts: for instance, only 2 groups (i.e. abalone and the seaweed bed) are highly likely to be impacted negatively under the all range extensions scenario (Fig. 4, column labelled *All extensions*), as opposed to 3–4 groups declining when simulating the individual range extension of octopus or sea urchin in isolation (Fig. 4, column labelled *CR+* or *OC+*, respectively); this can be explained because, for this scenario, two interacting predator/prey couples (i.e. octopus/rock lobster and rock lobster/sea urchin) extend their range simultaneously and trophic interactions buffer community responses to long-term abundance changes. The predicted responses of two model groups (i.e. octopus and reef fishes) to multiple range shifts are ambiguous, as indicated by paler colours (associated with <2/3rd of sign consistency across Monte Carlo simulations). Note that the actual sign of their responses can even switch depending on model structure (i.e. model i, ii or iii). Overall, the sea urchin is the only likely ecosystem winner, as its regional abundance is consistently predicted to increase under future climate scenarios. Increase in the barren-forming sea urchin population is a negative outcome for reef community structure and functioning.

Effectiveness of regional management strategies

Qualitative predictions suggest that, individually or in pairs, possible management interventions of adjusting lobster harvest rules or implementing targeted culling of urchins are virtually ineffective at altering the sign direction of the predicted ecological impacts of range shifts (Fig. 5): for instance, in all scenarios associated with single or pairs of management interventions (first 6 columns of Fig. 5), 3–4 key commercial or ecological groups are likely to decline, while the regional abundance of the barren-forming sea urchin is consistently predicted to increase as indicated by deep red colours. Models only predict a high likelihood of mitigating these community-wide negative effects of range-shifting species when a suite of management interventions that includes octopus population control strategies (currently overlooked in eastern Tasmania) are implemented concurrently: indeed, it is only when all three management interventions are combined that rock lobster, reef fishes, octopus and the seaweed bed, which are overall negatively impacted by range shifts, are then likely to thrive, while the abundance of the barren-forming sea urchin remains under control. Note that, regardless of the management strategy in place, abalone appears as the consistent ecosystem loser, highly likely to regionally decline in the long term.

Identifying important ecological processes

However, the degree to which these groups are likely to respond as expected (i.e. positively for commercially important groups, or negatively for the destructive sea urchin) to a comprehensive ecosystem-based management strategy will to some extent depend on uncertain community interactions and the rate of species range shifts. For instance, the scenarios assuming a net increase, or no change, in rock lobster biomass (*RL+*)

show limited negative community impacts relative to the scenario assuming a net decline in rock lobster biomass (RL−) (Figs 4 and 5). Thus, the timing of the replacement of southern rock lobster by its northern counterpart will have important implications for the maintenance of ecosystem structure and functioning, as both species are key top predators of the barren-forming long-spined sea urchin.

By capturing the range of possible community structures, our approach identifies uncertain ecological interactions that can have crucial effects on community responses to ongoing range shifts, and so can help to prioritise the focus of future research and monitoring. Qualitative model predictions about community-wide responses are overall consistent across alternative model structures (Figs 4 and 5; Data S1). Importantly, the transparent symbolic approach (Fig. 3) provides an important complement to the simulation-based approach (Fig. 4) when it comes to ambiguous predictions. Indeed, the symbolic conditions that determine the sign of ambiguous responses allow for a direct mechanistic interpretation of the counteracting feedback loop that contribute to variables responses (Fig. 3), while simulation-based predictions may suggest an ambiguous response which sign is somehow arbitrary and unlikely to be correct (e.g. ambiguous response of rock lobster to a decline in the seaweed bed; Fig. 4). Moreover, the predicted sign of response of certain model groups switches as a function of model complexity. One case where predicted community impacts are sensitive to model structure is the isolated increase in range-extending reef fishes abundance (Fig. 3; 'RF+' scenario): this scenario has neutral (model i), uncertain (model ii) or even negative (model iii) ecological effects, when assuming that tropical coral reef fishes can destructively graze on kelp beds; under a 'model iii' specification, range-extending tropical reef fishes can dramatically impact Tasmanian temperate reefs by depleting habitat-forming macroalgae. Thus, potential destructive grazing of Tasmanian kelp beds by range-extending tropical reef fishes constitutes a priority for monitoring and research. Highly ambiguous responses shown in grey (i.e. predictions where <2/3rd of responses across Monte Carlo simulations are sign-consistent) can only be elucidated based on knowledge of the magnitude of counter-acting ecological feedback (Figs 4 and 5).

Symbolic predictions highlight the key role of positive feedbacks in structuring community responses and creating the potential for alternative persistent states and dramatic shifts in system dynamics. For instance, the positive feedback loop 'seaweed bed–rock lobster–sea urchin–seaweed bed' exerts a strong influence on the qualitative sign of predictions of our model community (see sign structure in adjoint matrices of Fig. 3

and Data S1). Contingent on strong positive feedback and model stability (specified conditions in Fig. 3 and Data S1), qualitative model predictions highlight that long-term perturbations will force the model community towards one of these two community states: (i) a sea urchin barren state, characterised by an increase in sea urchin abundance and a decline in other model groups; or, (ii) a productive seaweed bed community, where sea urchin numbers remain low, while other reef model groups generally thrive.

Discussion

As large proportions of species within marine ecosystems undergo climate-driven redistribution (Sunday *et al.*, 2012), providing cost-effective and relatively rapid integrated assessments of the ecological effects of multiple range-shifting species is an imperative (Van Der Putten *et al.*, 2010). Here, we demonstrate that qualitative modelling of system feedback is an effective means of evaluating and predicting community impacts of single and multiple species redistribution and help identify those range-shifting species that constitute priorities for monitoring, future research and effective ecosystem-based management.

Ecological consequences of multiple co-occurring range shifts

Our qualitative model predictions provide a general assessment of the ecological impacts of range shifts on regional ecosystem dynamics. For instance, model predictions identify the range extensions of the long-spined sea urchin and the common octopus, or range contractions of rock lobster and certain macroalgal species, as climate-driven range shifts that can have broad negative impacts on Tasmanian reef community structure and functioning (Figs 3 and 4). Although they certainly provide useful insights, most global studies on the community-wide consequences of marine range shifts predict regional changes in ocean productivity (Cheung *et al.*, 2010), or biodiversity (Beaugrand *et al.*, 2015; García Molinos *et al.*, 2015) from modelling the co-occurring redistributions of individual species or groups using macro-ecological theories that cannot accommodate (Cheung *et al.*, 2009), or can only coarsely capture (Fernandes *et al.*, 2013) interactions between species. As range shifts are characteristic of up to 80–85% of species within regional marine assemblages (Wernberg *et al.*, 2011; Sunday *et al.*, 2012), considering their combined impact on local ecological dynamics is essential (Van Der Putten *et al.*, 2010) as community responses to climate-driven changes can be

complex (Suttle *et al.*, 2007). Thus, qualitative modelling of community feedback offers a practical and easy-to-implement framework to assess the potential consequences of multiple range shifts on regional ecosystem structure and functioning.

Qualitative modelling predicts that the negative community impacts of multiple co-occurring range shifts are likely to add up. For instance, in our temperate reef community example, a climate-driven decline in rock lobster abundance along with an increase in octopus abundance conjointly facilitates, via predation and cascading trophic effects, population building of the range-extending sea urchin. This in turn facilitates a shift towards a sea urchin barren state characterised by a species-poor, low-productive community where rocky reefs are denuded of macroalgal beds due to sea urchin destructive grazing (Ling, 2008; Marzloff *et al.*, 2015). We are not aware of other studies on the combined ecological impacts of multiple range shifts, but drawing a parallel between species introduction and climate-driven invasions (Sorte *et al.*, 2010), terrestrial examples of multiple invasions are consistent with our qualitative model predictions. For instance, introductions of multiple pest species have weakened the resilience of native ecological communities and facilitated secondary invasions in Christmas Island (Green *et al.*, 2011). Importantly, both probabilistic and symbolic predictions detect the potential for range shifts to trigger a shift in ecosystem structure and functioning to an alternative state by capturing the influence of positive feedback to community responses (Dambacher & Ramos-Jiliberto, 2007; Marzloff *et al.*, 2011).

Priorities for monitoring & future research

Qualitative predictions can help prioritise future monitoring and research by identifying range shifters of ecological concern and key interactions and feedback loops driving community responses to climate-driven perturbations. In particular, qualitative modelling detects climate-driven redistributions that can impact on community structure and functioning and thus require dedicated monitoring and research. The list of species, groups or interactions that should rank highly in terms of resource allocation for future research and monitoring, based on our results, includes the following:

1 Range contractions of pivotal ecological groups, such as key predators (e.g. rock lobster), or habitat formers. In Tasmania, dedicated modelling efforts building on extensive field experiments and observations have helped redefine ecologically sustainable harvest objectives so as to rebuild densities of large predatory lobsters, which provide key ecosystem services and minimise the risk of sea urchin barren

forming in eastern Tasmania (Johnson *et al.*, 2014; Marzloff *et al.*, 2015);

2 Range extensions of trophically significant species or groups: in our Tasmanian example, these include (a) the barren-forming long-spined sea urchin (Ling, 2008), and (b) the gloomy octopus (Ramos *et al.*, 2015) that can facilitate barren formation via predation on rock lobster (Briceño *et al.*, 2015);

3 Species replacement, where a range-extending species replaces a range-contracting species within a functional group that contributes to maintaining community dynamics. For instance, compensation of the decline in the range-contracting southern rock lobster by the range extension of its northern counterpart, the eastern rock lobster that fills the same functional role (Ling *et al.*, 2009a), will be key to maintaining reef community structure and functioning in the long term.

4 Species and interactions involved in positive feedback loops: model predictions, in particular symbolic conditions (Fig. 3; Data S1), highlight the key role of positive feedbacks in structuring community responses and creating the potential for alternative persistent states and dramatic shifts in system dynamics (Marzloff *et al.*, 2011). While the demonstration of positive feedback is necessary but not sufficient as evidence for alternative persistent states (Scheffer & Carpenter, 2003), qualitative model predictions highlight the need for cautionary management and for future research to validate and confirm the existence of alternative states in the real world. In Tasmanian reef communities, experiments (Johnson *et al.*, 2014) and further quantitative modelling (Marzloff *et al.*, 2013, 2015) have confirmed that sea urchin barrens constitute a persistent alternative state to productive seaweed beds.

5 Uncertain interactions that can create novel positive feedbacks and/or affect key variables or interactions driving community responses to perturbations require specific attention. In the Tasmanian example, the potential for herbivorous fishes to cofacilitate the depletion of kelp beds into barren habitat requires close monitoring (model iii; Fig. 4). Indeed, if tropical grazing fishes extend their distribution to south-eastern Australia, their destructive grazing of macroalgal beds will facilitate the persistent shift to a barren state, as observed at the most northern subtropical range boundary of temperate *Ecklonia radiata* beds on both western and eastern seaboards of Australia (Vergés *et al.*, 2014; Bennett *et al.*, 2015).

Conversely, abalone, which represents a valuable commercial resource in Tasmania, appears as a passive ecological player that contributes little to overall reef community functioning. It also the most likely ecosys-

tem loser under a warmer climate, regardless of the management strategies in place. Thus, our results highlight that, while abalone research can usefully focus on local stock enhancement and potential for fish farms to compensate for the decline in wild production, ecosystem monitoring and/or management interventions to mitigate community-wide effects of range shifts should rather be invested into other groups.

The need for adaptive ecosystem-based management

Our qualitative predictions emphasise that the negative ecological impacts of simultaneous range-shifting species are most likely to add up, which requires that management holistically consider ongoing ecosystem changes to effectively mitigate the undesirable consequences of climate-driven range shifts (Creighton *et al.*, 2015). Indeed, our models suggest that regional management can miss critical components of the climate change adaptation puzzle if it fails to consider range shifters as interacting ecological players (Van Der Putten *et al.*, 2010). For instance, single-species-based management that solely focuses on controlling the abundance of known pests (e.g. the barren-forming sea urchin in Tasmania) or valuable target species (e.g. rock lobster or abalone in our regional example) will likely fail at mitigating negative community impacts of multiple range shifts. Again, in our Tasmanian case study, only ecosystem-based management strategies that aim at a combined controlling of range-extending sea urchin and octopus while rebuilding densities of predatory lobsters are likely to mitigate community-wide negative consequences of range-shifting species. Moreover, as multiple climate-driven changes and other human activities that impact natural resources can induce hard-to-reverse and undesirable shifts in regional ecosystem dynamics and structure (Marzloff *et al.*, 2015), ecosystem-based management (Hall & Mainprize, 2004) becomes a necessity rather than a precautionary approach.

In this study, we demonstrate how qualitative modelling can point management effort towards ecologically important range-shifting species. In our Tasmanian case study, these include (i) declining seaweed species, (ii) the range-extending sea urchin, (iii) the range-contracting rock lobster and (iv) the range-extending octopus; Costly geo-engineering solutions (e.g. cooling of coastal waters; cultivating macroalgal beds on reefs) aside, management interventions that can directly prevent the decline in seaweed and kelp species are limited. However, regional management authorities could mitigate climate-driven changes in the abundance of lobster, sea urchin and octopus populations by, for example, adjusting harvest rules (Marzloff *et al.*, 2015), or by implementing targeted culling

of sea urchin (Sanderson *et al.*, 2015; Tracey *et al.*, 2015). To date, management and research investment to preserve kelp beds in eastern Tasmania have solely focused on preventing the formation of extensive sea urchin barren via population control of sea urchin (Sanderson *et al.*, 2015; Tracey *et al.*, 2015) and southern rock lobster (Johnson *et al.*, 2014; Marzloff *et al.*, 2015), which predate on sea urchins (Ling *et al.*, 2009b). However, our work highlights that, in the long term, effective strategies also need to account for biomass building of the range-extending octopus (Ramos *et al.*, 2015). Increasing predation on lobster by existing and range-extending octopus species (Briceño *et al.*, 2015; Ramos *et al.*, 2015) will require careful monitoring, and regional management will need to ensure that harvesting of the range-extending octopus achieve moderate predation mortalities on lobster; if octopus predation on lobster increases significantly, current effort to minimise the risk of sea urchin barren formation via reduced fishing pressure on predatory lobster (Marzloff *et al.*, 2015) will be void.

Monitoring of long-term climate-driven community changes is key to informing adaptive management and effectively responding to the broad community-wide effects of species redistributions at a regional scale (Hobbs *et al.*, 2009; Plaganyi *et al.*, 2011). Regular assessment and adjustment of the management strategy in place given ongoing changes in community composition will be crucial to prevent catastrophic shifts in ecosystem structure and functioning, especially in global hotspots for ocean warming (Hobday & Pecl, 2013) where climate-driven changes are extensive and rapid.

Generality and limitations of the approach

Based on available observations and qualitative predictions, the range shift scenarios considered here attempt to integrate the effects of a range of climate-driven environmental changes (e.g. primary productivity, recruitment, temperature, ocean acidification) on the regional population abundance of model groups. However, future climate-driven changes can impact Tasmanian reef communities in a number of ways that our general approach does not explicitly capture, for instance via modified interactions (Dambacher & Ramos-Jiliberto, 2007; Reum *et al.*, 2015), or stage-specific effects (e.g. decline in larval development with ocean acidification; Reum *et al.*, 2015). Moreover, while our general models predict broad reef community responses to climate-driven changes in the abundance of key functional groups, they do not resolve the detailed responses of individual reef species to climate change and the potential for more complex ecological surprises (Doak *et al.*, 2008).

Qualitative models in essence provide a general, holistic understanding of system dynamics, and their usefulness becomes limited for large complex systems (c.a. >15 nodes) as predictions become ambiguous. Note the complementarity of the two approaches presented here (Fig. 3 vs. Figs 4 and 5): in particular, when it comes to ambiguous predictions, the symbolic approach allows for a mechanistic interpretation and understanding of the counteracting feedback loops that contribute to variables responses (see also Marzloff *et al.*, 2011), while the simulation-based approach provides automated qualitative predictions which signs need to be interpreted cautiously. Indeed, simulation-based ambiguous predictions might be of the wrong sign; nonetheless, these are useful indication of overall system dynamics (Dambacher *et al.*, 2003), specifically in cases where the symbolic approach becomes limited due to the large size of the model system (i.e. with a large number of highly connected variables), the high number of simulated scenarios or alternative models or when qualitative reasoning cannot elucidate the sign of ambiguous responses based on inference about the relative strengths of counteracting effects.

Further exploration of the sensitivity of predictions to increasing model complexity, by, for instance, separating the seaweed bed functional group into guilds, or using a suite of models to capture spatial variability in reef community structure, would be sensible next steps for this work as more data become available. While we illustrate the general usefulness of qualitative modelling to guide broad adaptation strategies to climate-driven species redistribution, further monitoring, empirical research and quantitative modelling will be key complements to inform specific management decisions under future climates (Plaganyi *et al.*, 2011).

Conclusions

With this example from temperate reef communities in south-eastern Australia, we illustrate the value of qualitative modelling to provide an integrated assessment of the ecological effects of multiple range-shifting species, and a means to prioritise regional ecosystem management, monitoring and future research. The approach relies only on qualitative knowledge about community interactions and climate-driven changes in species abundance and hence is transposable to other aquatic or terrestrial ecosystems. Probabilistic qualitative predictions enable decision-makers to implement precautionary principles in natural resource management (Anthony *et al.*, 2013), which will be crucial in ecosystems with potential for hysteresis where dramatic hard-to-reverse shifts in ecological dynamics can occur (Doak *et al.*, 2008; Marzloff *et al.*, 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1 Technical details on the derivation of symbolic adjoint matrices for each of models i, ii, and iii, as presented in a succinct form in Fig. 3.

Data S2 The sign-directed graph (DIA file equivalent to Fig. 2) and the R code used to generate all the simulation-based results and the graphs presented in Figs 4 and 5.