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Author for correspondence:

J. Rocha
e-mail: juan.rocha@stockholmresilience.su.se

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Marine regime shifts: drivers and impacts on ecosystems services

J. Rocha¹, J. Yletyinen^{1,2}, R. Biggs^{1,3}, T. Blenckner^{1,2} and G. Peterson¹

¹Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, 114 19 Stockholm, Sweden

²Nordic Centre for Research on Marine Ecosystems and Resources under Climate Change (NorMER), Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden

³Centre for Studies in Complexity, Stellenbosch University, Stellenbosch, South Africa

Marine ecosystems can experience regime shifts, in which they shift from being organized around one set of mutually reinforcing structures and processes to another. Anthropogenic global change has broadly increased a wide variety of processes that can drive regime shifts. To assess the vulnerability of marine ecosystems to such shifts and their potential consequences, we reviewed the scientific literature for 13 types of marine regime shifts and used networks to conduct an analysis of co-occurrence of drivers and ecosystem service impacts. We found that regime shifts are caused by multiple drivers and have multiple consequences that co-occur in a non-random pattern. Drivers related to food production, climate change and coastal development are the most common co-occurring causes of regime shifts, while cultural services, biodiversity and primary production are the most common cluster of ecosystem services affected. These clusters prioritize sets of drivers for management and highlight the need for coordinated actions across multiple drivers and scales to reduce the risk of marine regime shifts. Managerial strategies are likely to fail if they only address well-understood or data-rich variables, and international cooperation and poly-centric institutions will be critical to implement and coordinate action across the scales at which different drivers operate. By better understanding these underlying patterns, we hope to inform the development of managerial strategies to reduce the risk of high-impact marine regime shifts, especially for areas of the world where data are not available or monitoring programmes are not in place.

1. Introduction

Human action is transforming the biota, chemistry and temperature of the world's oceans at unprecedented rates. While these changes are often gradual, in some cases they can lead to regime shifts: persistent, substantial reorganizations of the structure and function of marine ecosystems [1,2]. A regime is a persistent organization of mutually reinforcing structures and processes. A regime shift occurs when a combination of stronger destabilizing feedbacks, weaker stabilizing feedback processes and external shocks cause the system to reorganize around a different set of mutually reinforcing structures and processes. Regime shifts have been identified and analysed across a broad range of terrestrial and aquatic ecosystems, including lakes, coral reefs, kelp forests and drylands [3–5].

Better understanding of regime shifts is needed as they pose major challenges for ecosystem management and governance. Regime shifts often have substantial impacts on ecosystem services and human well-being [6,7], but are typically difficult to predict and costly to reverse [8,9]. For instance, the collapse of fisheries or reconfiguration of marine food webs can have major impacts on fish yields, the fishing industry and fishers [10,11]; coral reef degradation can harm local tourism, fishers' livelihoods and decrease protection from coastal shoreline erosion [12]; while the melting of icecaps is expected to cause major sea-level rise with massive costs for coastal people and settlements [13–15].

This paper aims to assess the patterns of co-occurrence of drivers and ecosystem service consequences of marine regime shifts, in order to inform better managerial strategies. Regime shifts have been extensively studied in marine ecosystems, but

most of these studies have focused on particular places, such as Florida Bay and the Baltic Sea, or particular types of regime shifts, such as coastal hypoxia [16]. There have been no systematic and general comparisons of the forces driving different types of marine regime shifts or their consequences on ecosystem services. Based on scientific literature review, we identified 13 general types of marine regime shifts (e.g. marine eutrophication, fisheries collapse) and synthesized information on the reported causes and consequences of each. We also identified the scale at which ecosystem management can alter regime shift drivers, to facilitate understanding of management actions at the local, national or international scales across different types of regime shifts. By synthesizing across case studies and focusing on general types of marine regime shifts, our approach enables us to identify general patterns across different types of marine regime shifts, providing a novel global picture of patterns of marine regime shift drivers and their impacts.

2. Material and methods

The types of regime shifts used in our analysis are based on a systematic review and synthesis of published academic literature, available online in the regime shifts database (www.regimeshifts.org). This database contains information at two different levels: documentation of individual cases of regime shifts in particular places, and a synthesis of general types of regime shifts based on multiple cases (see the electronic supplementary material). The database only includes regime shifts where the literature: (i) suggests the existence of feedback mechanisms, and therefore potential for hysteresis; (ii) reports potential impacts on ecosystem services and (iii) where the shift occurs on a time scale relevant for management. For each regime shift, the certainty about the existence of the regime shift and the underlying mechanism are assessed based on the literature (see the electronic supplementary material and figure S1). Each entry in the database is reviewed by a senior scientist or an expert in the field, to ensure quality and completeness of the assessment.

Here, we analyse the drivers and ecosystem service consequences for general types of regime shifts in marine biomes (table 1 and electronic supplementary material, figure S1). We define a driver as any natural or human-induced factor that directly or indirectly causes change in marine systems. While direct drivers influence ecosystem processes (feedbacks), indirect drivers operate diffusely affecting one or more direct drivers [7,29]. The dataset we extracted for this analysis consists of 13 types of marine regime shifts, 54 drivers and 26 ecosystem services. Eight of these regime shifts we judged as well established, two as contested and three as speculative; while the underlying mechanisms are well established for eight regime shifts, and speculative for five regime shifts (see the electronic supplementary material).

Using network theory, we analysed the co-occurrence patterns among drivers, similarity among regime shifts and clusters of potential impacts on ecosystem services. This approach is based upon methods that have been successfully used to analyse similar types of relations in complex systems [30,31], such as the relationships between genes and human diseases [32,33]. To analyse the co-occurrence of drivers and ecosystems services across regime shifts, we constructed a tripartite network with three types of nodes: drivers, regime shifts and ecosystem services. A link appears in our network if there is a reference in the scientific literature indicating that a driver is likely to cause a regime shift (individually or in combination with other drivers), or if the occurrence of a regime shift has an impact on a particular ecosystem service. As emphasized above, this analysis of drivers and ecosystem services is aggregated at a generic regime shift level. Each generic regime shift

includes all drivers found in the literature across case studies, since a future instance of the regime shift could arise from any previously reported drivers. By including all drivers, we could assess their importance only based on network structure, not their particular assessment within a historical snapshot given data availability. Therefore, we do not distinguish between necessary and sufficient causes. Furthermore, our analysis focuses on how regime shifts can influence ecosystem services, not how drivers of global environmental change impact ecosystem services through mechanisms other than regime shifts.

To enable analysis of the different types of connections in the tripartite network, we decompose or project this network into four simpler types of one-mode network [34]. A projection is a one-mode network where nodes of the same type are connected if they share links to the same nodes of the second node type. In our network, the four projections we analysed were: (i) a network of drivers connected by sharing causal links to regime shifts, (ii) a network of regime shifts connected by sharing drivers, (iii) a network of regime shifts connected by sharing impacts on ecosystem services and (iv) a network of ecosystem services connected by sharing regime shifts. Note that the projection's links are weighted by the number of nodes shared in the tripartite data.

To determine whether the relationships among drivers, regime shifts and ecosystem services are due to chance or represent a real pattern, we compared our data against simulated random networks as suggested by Newman *et al.* [30]. To do this, we converted our tripartite network into two bipartite networks (drivers–regime shifts and regime shifts–ecosystem services). We compared each of these networks against 10 000 random bipartite networks, in which the number of connections per node (degree) was maintained but the connections randomized. This approach preserves the relative importance of each variable in the original dataset but varies the connections among variables. We compared the actual and one-mode projections of the random networks by the average degree and co-occurrence index [35,36], and the clustering coefficient for the bipartite networks [30]. If the co-occurrence index is higher and the average degree lower than expected by chance, it implies that the patterns between regime shifts and drivers or between regime shifts and ecosystem services are non-random, and that observed patterns are not due to chance.

We analysed whether regime shift drivers impact similar ecosystem services by multiplying the matrices representing each of the two bipartite networks together to construct a matrix linking regime shift drivers to changes in ecosystem services [37]. We applied hierarchical clustering on the Euclidean distance between the rows and columns of this matrix to cluster similar drivers and ecosystem services. We conducted this analysis in R, using the *statnet* package [36,38].

To compare our analysis against previous regime shift and global change assessments [3,29], we grouped our drivers into seven major categories of global change drivers: climate, water cycle, land cover change, biodiversity loss, biogeochemical cycles, biophysical and indirect human activities. Finally, we identified the scales at which each driver could be managed and calculated the proportion of drivers whose management requires local action, regional interventions or international cooperation (see the electronic supplementary material).

3. Results

All regime shifts in our dataset have multiple drivers, with an average of 12 (out of a total of 54) drivers. The regime shift *mangrove collapse* had the largest number of identified drivers (20), followed by marine eutrophication (19) and coral transitions (17). The regime shifts with the fewest number of identified drivers are collapse of the thermohaline circulation

Table 1. Summary of regime shifts analysed. Regime shifts names in the table correspond to those in the Regime Shifts Database, but for readability they have been shortened in the figures. Names usually describe the two regimes, but if the shift has more than two regimes reported in the literature we called them 'transitions', and if the shift is characterized by the absence of function we called them 'collapse'. We reported a key reference that captures how the regime shift type works (feedbacks), generally a review paper; further information and detailed references for the dynamics underlying the regime shifts and individual case studies are available at www.regimeshifts.org and electronic supplementary material, table S2. Information about certainty, evidence and reversibility of each regime shift is given in electronic supplementary material, figure S1. ENSO, El Niño Southern Oscillation.

regime shift name	key drivers	ecosystem services impacted	key reference
Arctic salt marshes	fishing global warming invasive species nutrient inputs sea-level rise sediments	soil formation primary production nutrient cycling biodiversity fisheries feed, fuel and fibre crops climate regulation water purification regulation of soil erosion natural hazard regulation recreation aesthetic values	[17]
Arctic sea ice	atmospheric CO ₂ global warming greenhouse gases temperature	water cycling biodiversity fisheries wild animal and plant foods climate regulation water purification water regulation aesthetic values knowledge and educational values spiritual and religious	[18]
bivalves collapse	agriculture deforestation demand disease erosion fertilizer use fishing fishing technology floods food supply human population nutrients input precipitation sewage turbidity urbanization	nutrient cycling biodiversity freshwater fisheries water purification aesthetic values	[19]
coral transitions	agriculture atmospheric CO ₂ deforestation	soil formation biodiversity fisheries	[20]

(Continued.)

Table 1. (Continued.)

regime shift name	key drivers	ecosystem services impacted	key reference
	demand	wild animal and plant foods	
	disease	water purification	
	fishing	regulation of soil erosion	
	global warming	pest and disease regulation	
	human population	natural hazard regulation	
	hurricanes	recreation	
	low tides	aesthetic values	
	nutrient input	knowledge and educational values	
	ocean acidification	spiritual and religious	
	pollutants		
	sediments		
	thermal anomalies in summer		
	turbidity		
	urbanization		
fisheries collapse	access to markets	primary production	[21]
	demand	nutrient cycling	
	ENSO-like events	biodiversity	
	fishing	fisheries	
	fishing technology	pest and disease regulation	
	global warming	recreation	
	nutrient inputs	aesthetic values	
	subsidies	knowledge and educational values	
	tragedy of the commons		
	upwellings		
	urbanization		
hypoxia	agriculture	primary production	[16]
	deforestation	nutrient cycling	
	demand	biodiversity	
	erosion	fisheries	
	fertilizers use	wild animal and plant foods	
	floods	water purification	
	flushing	recreation	
	human population		
	landscape fragmentation		
	nutrient input		
	rainfall variability		
	sewage		
	upwellings		
	urban storm water runoff		
	urbanization		
	water stratification		
kelps transitions	agriculture	primary production	[22]
	deforestation	biodiversity	
	demand	fisheries	
	ENSO-like events	feed, fuel and fibre crops	

(Continued.)

Table 1. (Continued.)

regime shift name	key drivers	ecosystem services impacted	key reference
	fertilizer use fishing floods global warming human population nutrient inputs precipitation sewage upwellings urbanization	recreation aesthetic values	[22]
mangroves transitions	agriculture aquaculture atmospheric CO ₂ deforestation droughts erosion floods global warming hurricanes infrastructure development irrigation infrastructure landscape fragmentation ocean acidification rainfall variability sea-level rise sea surface temperature sediments sewage temperature urbanization	soil formation water cycling biodiversity fisheries wild animal and plant foods timber wood fuel climate regulation water purification regulation of soil erosion natural hazard regulation aesthetic values	[23]
marine eutrophication	agriculture deforestation demand droughts erosion fertilizers use fishing floods flushing global warming human population impoundments irrigation landscape fragmentation	primary production nutrient cycling biodiversity fisheries water purification recreation aesthetic values	[24]

(Continued.)

Table 1. (Continued.)

regime shift name	key drivers	ecosystem services impacted	key reference
marine food webs	nutrient input		
	rainfall variability		
	sewage		
	urban storm water runoff		
	urbanization		
	demand	primary production	[25]
	ENSO-like events	biodiversity	
sea grass collapse	fishing	fisheries	
	global warming	pest and disease regulation	
	nutrient inputs	recreation	
	upwellings	aesthetic values	
	atmospheric CO ₂	primary production	[26]
	deforestation	nutrient cycling	
	disease	biodiversity	
thermohaline circulation	fishing	fisheries	
	infrastructure development	wild animal and plant foods	
	nutrient input	climate regulation	
	rainfall variability	water purification	
	sea-level rise	regulation of soil erosion	
	sediments	natural hazard regulation	
	sewage	recreation	
	temperature	aesthetic values	
	urbanization		
	atmospheric CO ₂	primary production	[27]
	global warming	water cycling	
West Antarctica Ice Sheet collapse	greenhouse gases	biodiversity	
	temperature	food crops	
		livestock	
		fisheries	
		climate regulation	
	climate variability (SAM)	water cycling	[28]
	global warming	biodiversity	
	glacier growth	fisheries	
	ice surface melting	wild animal and plant foods	
	ocean temperature (deep water)	climate regulation	
	sea-level rise	water regulation	
	sea surface temperature	aesthetic values	
	stratospheric ozone	knowledge and educational values	
	surface melt water	spiritual and religious	
	surface melting ponds		
	temperature		
	tides		
	upwellings		

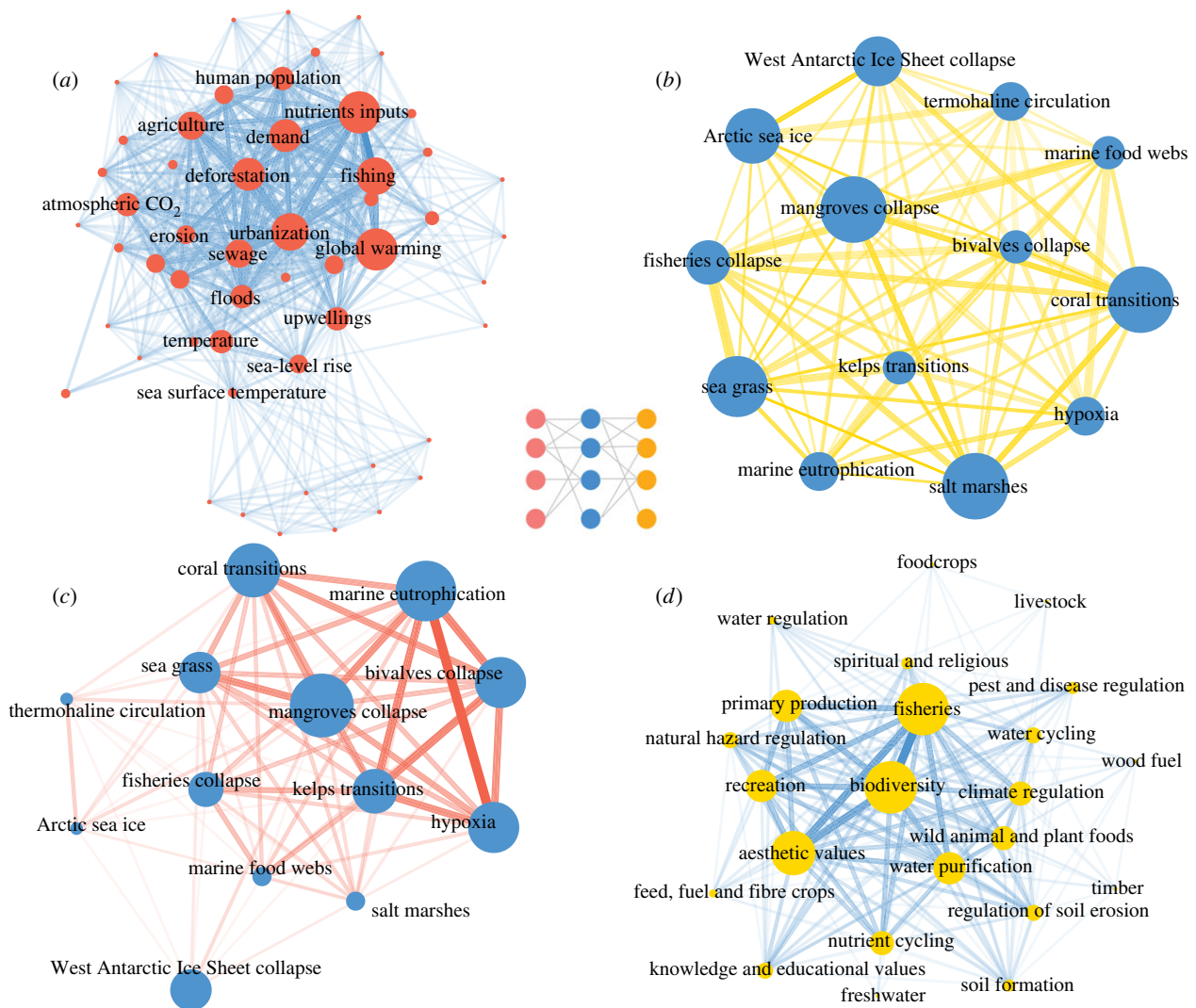


Figure 1. Tripartite network scheme (centre) where red nodes represent drivers, blue nodes are regime shifts and yellow ones ecosystem services. The tripartite network has four one-mode relevant projections: (a) drivers network projection ($N = 54$), (b) ecosystem services projection ($N = 26$), (c) regime shifts projection given drivers shared and (d) regime shifts projection given ecosystem services shared (both $N = 13$). The node size is scaled to represent the node degree on the relevant bipartite network where the projection was calculated. For example, in (c) nodes are regime shifts and their size correspond to the number of drivers they are linked to while in (d) is the number of ecosystem services affected. The number of nodes shared in each bipartite network weights links on the one-mode projections. For instance, in (a) nodes are drivers and links are weighted by the number of the regime shifts shared. All nodes have labels except in (a) where for readability only drivers with higher degree and betweenness were labelled.

and Arctic sea ice which each has four drivers (figure 1a,b). The pair of regime shifts that share the most drivers is marine eutrophication and hypoxia, which share 14 drivers, while the trio of regime shifts marine eutrophication, bivalves collapse and kelps transitions share 11 drivers.

A handful of drivers affect more than half of the analysed regime shift types (figure 1a). The drivers global warming, nutrient inputs, urbanization, fishing, demand for food and fibre, and deforestation contribute to the most (seven to nine) regime shifts. The same group of drivers plus agriculture, floods and sewage have the highest co-occurrence with other drivers.

The most frequently co-occurring drivers are nutrient inputs and fishing, which co-occur as drivers for eight regime shifts. Also frequently co-occurring are four pairs of drivers (nutrient inputs and demand for food and fibre; nutrient inputs and urbanization; deforestation and agriculture; deforestation and urbanization), which all co-occur as drivers for seven regime shifts (figure 1a). All regime shifts share drivers with between nine and 12 other regime shifts (figure 1c).

Climate-related drivers and biophysical processes are the dominant driver categories in our analysis (figure 2a). Biodiversity loss and land cover change are categories of drivers that often co-occur together in our sample. Despite being terrestrial drivers, they are common across many regime shifts in the ocean. Climate-related drivers appear in many regime shifts but their co-occurrence is not particularly strong with any of the other categories of drivers. Human indirect activities are the category of drivers which is least represented in our dataset, as they are not reported for five regime shifts (figure 2a).

Regime shift types affect on average four (out of 26 possible) ecosystem services (figure 1d). All regime shift types affect biodiversity (supporting) and fisheries (provisioning) services. Another commonly affected supporting service is primary production (eight of 13 regime shifts). The most commonly affected ecosystem services were for provisioning services, wild animal and plant foods (six of 13 regime shifts), for regulating services, water purification (eight of 13 regime shifts) and for cultural services, aesthetic values (11 of 13 regime shifts).

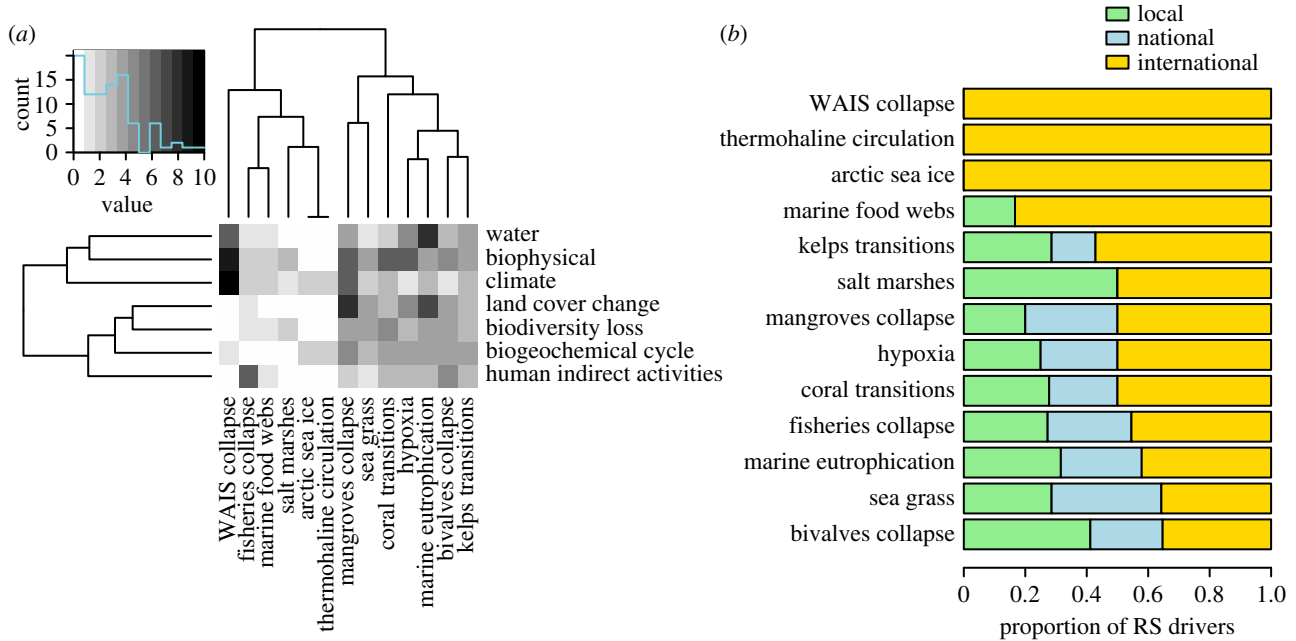


Figure 2. Scale of management and drivers categories. Each driver was classified according to (a) major categories of global change and (b) the scale at which management actions are required. The matrix shows the number of drivers per regime shifts per categories, thus it shows the matrix multiplication of the bipartite data by the drivers categorization. Note that drivers can belong to more than one category. Dendrograms were calculated using the Euclidean distance on the bipartite data for columns and on drivers categories for rows. WAIS, West Antarctica Ice Sheet.

Many ecosystem services are similarly impacted by different regime shift types. The one-mode network projection for ecosystem services by regime shift types (figure 1d) reveals that both fisheries and biodiversity are impacted by all regime shift types, whereas both fisheries and aesthetic values as well as biodiversity and aesthetic values are impacted by most types of regime shifts (11 of 13). Another cluster of ecosystem services that are frequently impacted together are fisheries and biodiversity, aesthetic values and recreation, primary production and water purification (six to eight regime shift types each). Different types of regime shifts have similar impacts on ecosystem services (figure 1b). The most similar impact on ecosystem services is found between salt marshes and sea grass collapse, and Arctic and West Antarctic sea ice collapse (figure 1b). Each of these pairs of regime shift types impacts 10 of the same ecosystem services.

The driver–regime shift and regime shift–ecosystem service networks are significantly different from random. Our simulations show that for all randomized bipartite networks of drivers and regime shifts, the projections from our dataset present a much higher co-occurrence index and a lower average degree than expected by chance (electronic supplementary material, figure S1; t -test for both statistics and both projections $p < 10^{-15}$). Similar results were found when simulating the network of regime shifts and ecosystem services (see the electronic supplementary material). Strong significant couplings between drivers and between ecosystem services are further supported by a higher clustering coefficient than expected by chance ($p < 10^{-15}$).

Using the matrix linking drivers to ecosystem service impacts, we can group drivers that impact similar sets of ecosystem services (figure 3). The cluster of ecosystem services most commonly impacted by marine regime shifts (fisheries, biodiversity, aesthetic values, water purification, nutrient cycling, primary production and recreation) is affected primarily by

two clearly defined groups of drivers. The first corresponds to the highly connected drivers: nutrient inputs, fishing, global warming, urbanization, deforestation, sewage, agriculture and demand for food and fibre. The second group of drivers includes: (i) climate-related drivers such as El Niño Southern Oscillation (ENSO)-like events, floods, rainfall variability, sea-level rise, temperature, upwellings and atmospheric CO_2 ; and (ii) biophysical processes closely related to agriculture, including fertilizer use, erosion and sedimentation (figures 2a and 3). To a lesser extent (through fewer regime shifts), both groups of drivers also impact the following sets of ecosystem services: (i) natural hazard regulation, regulation of soil erosion and soil formation; (ii) water cycling and climate regulation; as well as (iii) spiritual and religious values, knowledge and educational values, and pest and disease regulation.

Most regime shifts arise from a set of drivers that require management at different scales. Regime shifts that often occur at a local scale have more reported drivers while large-scale shifts typically have fewer reported drivers (figure 2a). We found that for most (nine out of 13) of the regime shifts we analysed, at least half of their drivers require international cooperation to be managed (figure 2b). This is particularly true for regime shifts in polar or sub-polar areas, where all of the drivers need to be addressed across international boundaries.

4. Discussion

This analysis presents a novel cross-scale and cross-type comparison of 13 generic types of marine regime shifts. We find that these different types of regime shifts impact a similar but variable set of ecosystem services and are driven by forces operating across a range of scales. Our results point to significant management opportunities based on similarities and connections among drivers of different regime shifts.

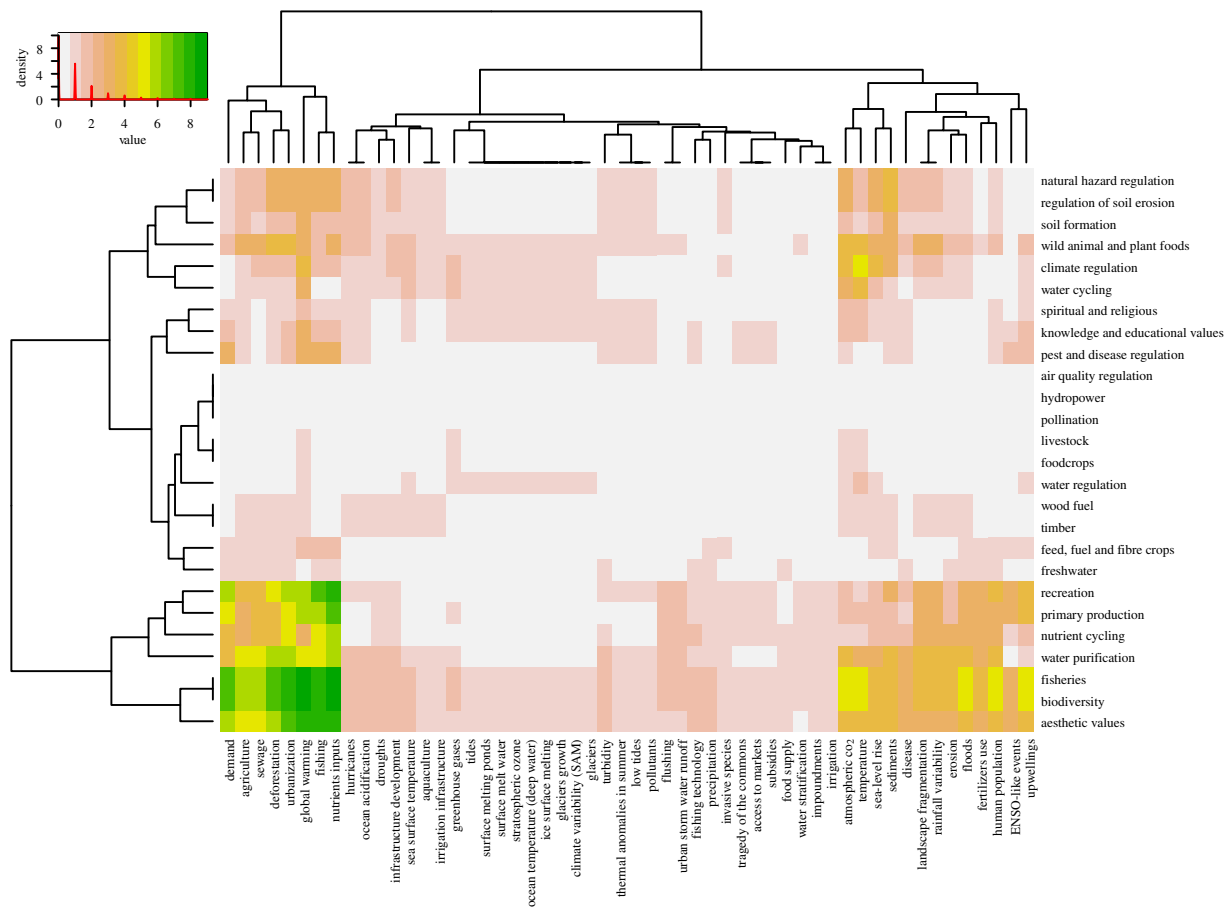


Figure 3. Pathways between drivers and impacts on ecosystem services: colour scheme shows the number of pathways where a given driver can have an effect on ecosystem services by causing regime shifts. Dendrograms show the similarity of drivers or regime shifts based on the Euclidian distance on the respective matrix.

We identified three types of drivers that are primarily responsible for all types of marine regime shifts. The first includes drivers related to food production, such as fishing, agriculture and use of fertilizers. Fishing is a direct driver with strong effects on food webs and collapse of fish stocks [39–41], while agriculture and use of fertilizers have a strong influence in coastal areas by affecting water runoff, sedimentation, turbidity and nutrient load in coastal systems [4,42]. The second cluster includes drivers related to coastal development, namely urbanization, sewage, deforestation and sedimentation. These drivers are indirectly influenced by human population growth and increasing demand for food and fibre. The third cluster of drivers is related to climate change and includes global warming, atmospheric CO₂, temperature, ocean acidification, rainfall variability, sea-level rise and ENSO variability. Overall, nutrient input is a key direct driver of several regime shifts and is affected by all three categories: agricultural activities, urban development in coastal areas or climate-driven upwelling systems. These results suggest significant increased vulnerability to marine regime shifts in future, as these drivers are likely to intensify over the coming decades, particularly in developing regions [7].

While our clustering of drivers across regime shifts is novel, the results are consistent with previously reported drivers of marine ecosystem change. Marine areas are threatened by over-fishing, climate change, demand and fish prices, subsidies, technological change, shifting food preferences and illegal fishing [7]. Coastal ecosystems are among the most highly threatened and productive systems in the world, with the biggest threats being loss of habitat due to urbanization, human

population growth, infrastructure development, increasing sewage and pollution, declining water quality and increasing disease risk [7]. Not all drivers reported in the Millennium Ecosystem Assessment [7] appear in our marine regime shift dataset. We believe that many indirect drivers, such as shifting food preferences or trade, are important drivers but have not been analysed in the current literature on marine regime shifts, because these drivers can be difficult to identify and are not usually analysed by the scientific disciplines that have historically researched marine regime shifts.

The analysis of categories of drivers reveals that climate drivers are common to all regime shifts types but do not co-occur strongly among themselves, while strong co-occurrence is found in biophysical, land cover change and biogeochemical drivers (figure 2a). Human indirect activities co-occur especially in coastal systems; drivers in this category seem to be less reported in polar areas where regime shifts are usually driven by climate. This result does not suggest that polar regime shifts are not caused by human activities; we rather interpret this result as missing drivers coupling climate warming to specific human indirect activities. The deviation from randomness in the network analysis suggests that there must be processes that make drivers co-occur strongly. We speculate that strong driver couplings suggest synergistic effects, or that marine regime shifts have similar underlying feedbacks. Most of the strongly connected drivers are indirect, meaning that there are often intermediate or more direct drivers between them and the feedback loops they impact. It also means that there might be different causal pathways between indirect drivers and the processes affected.

The ecosystem services most commonly impacted by marine regime shifts fall into several clusters, with fisheries, biodiversity, aesthetic values, water purification, nutrient cycling, primary production and recreation co-occurring most frequently (figure 3). These services are most at risk of experiencing surprising and persistent changes in their supply as global changes intensify. This clustering further supports the notion that sets of ecosystem services tend change in tandem [43]. While climate regulation is mainly affected by drivers whose management options require international efforts, primary production, fisheries and biodiversity are affected by localized drivers manageable at local to regional scales. The number of primarily coastal regime shifts that can impact aesthetic values was surprising and suggests the potential for abrupt persistent declines in aesthetic values in coastal areas should be considered more seriously in regional analyses of coastal ecosystem services.

The results of this analysis emphasize that avoiding regime shifts requires addressing multiple drivers, and that shared drivers offer strategies for prioritization and synergistic action. More than half of the marine regime shifts we analysed (seven to nine) share the drivers global warming, nutrient inputs, urbanization, fishing, agriculture, demand for food and fibre, and deforestation, which suggests that better managing these widely shared drivers could decrease the risk of most types of marine regime shifts. Our findings further show that the scale of management of regime shift drivers varies from local to international and suggests that avoiding marine regime shifts requires coordinated management actions across multiple scales. However, this scale diversity means that even when international management fails to occur, such as for climate change, reducing drivers locally has the potential to at least partially compensate for global drivers of regime shifts. For example, local management of fisheries and watersheds has been found to delay coral reef collapse by up to a decade in the Caribbean [44]. The occurrence of marine regime shifts appears to be highly determined by local ecosystem conditions such as trait diversity [20], the latitudinal location of the sea, how enclosed it is [45], structure of food web [46], as well as the heterogeneity of drivers changing from place to place [47–49]. The significant impact of global drivers indicated by our analysis emphasizes the importance of regional transboundary management and international efforts, because most drivers, for instance global warming [50], urbanization [51], population growth [52,53] and demand for food [52,54], are expected to continue to increase.

This analysis is based upon a review of the scientific literature. Therefore, it is a synthesis of what is known about regime shifts, and it is biased towards well-established scientific knowledge. In order to compare regime shifts in different ecosystems across different spatial and temporal scales, we focused on generic types of regime shifts. While the underlying mechanisms driving changes in many regime shift types are well understood, whether these changes are actually regime shifts are less well established, in the sense that we do not know whether the feedbacks are strong enough to produce hysteresis. Similarly, because there has been uneven research effort on different regime shifts, there are likely to be many unidentified drivers of regime shifts. As we gain better knowledge about regime shifts dynamics, our analysis could be repeated to discover how the relative importance of different drivers, regime shift types or

ecosystem services change. However, because it is more likely that drivers have been missed than incorrectly identified, these gaps in scientific research are unlikely to alter our findings on the importance of multiple drivers for regime shifts or the richness of ecosystem services impacted.

In order to compare similar phenomena in different ecosystems across different spatial and temporal scales, we needed to reduce the system abstraction to generic types of regime shifts where they only share causes and impacts. This simplification limits the analysis losing all the information richness of case studies but has the advantage of enabling comparison. The analysis presented here evidences some level of circularity between drivers and impacts on ecosystem services. This is not an artefact of our method, as even without simplifying case studies to a generic regime shift type, the literature points out such circularity. For example, regime shifts in circumpolar areas are caused by climate change and in turn affect climate regulation [55]. Rather than circularity, this shows that many regime shifts can produce feedbacks that in turn increase the likelihood of further regime shifts, a phenomenon known as cascading effects [56,57] or domino effect [58–60]. Further research is needed to assess potential domino effects and their likelihood. Given the high co-occurrence of drivers and potential similarities in terms of feedbacks, marine regime shifts seems highly susceptible to such cascading effects.

Network analysis was a useful, moderately complex method for comparing regime shifts. It allowed us to identify co-occurrence patterns, which would not have been possible if we had relied only on literature review. Network analysis allowed us to detect emergent patterns that have not been previously reported. For example, fishing and nutrient inputs are common drivers but they are not often reported together despite the fact that they co-occur strongly. Similarly impacts on cultural services appear to be common across a wide range of regime shifts. Many published analyses of regime shifts rely strongly on statistical methods whose assumptions avoid colinearity. This might constrain managerial advice to factors with strong statistical signals and leave aside other potential pathways that can also cause the regime shift. Using network analysis allowed us to include less-studied variables, potentially colinear, that give us a more holistic perspective regarding drivers, impacts and potential management opportunities.

5. Conclusion

The diverse ways in which human activities are reshaping marine ecosystems can produce a variety of regime shifts that have substantial impacts on a broad set of ecosystem services. These regime shifts are all produced by many different drivers. Most of these drivers require international management, indicating that avoiding marine regime shifts requires a substantial increase in international environmental cooperation and management. However, the diversity of drivers also means that there is substantial potential to manage local drivers to increase the resilience of marine ecosystem to global drivers, despite global inaction. Local and international cooperation to manage marine regime shift drivers could probably be improved by awareness that there are many shared drivers and ecosystem services among marine regime shifts. These shared drivers and impacts provides incentives for collaboration among fishers, agriculturalists, scientists and diverse sets of policy-makers to collaborate to build the resilience

of multiple marine regimes and the ecosystem services they produce.

The results presented here may be particularly useful for managers and practitioners in under-studied areas, where data to guide decisions are poor or unavailable. By identifying potential drivers of marine regime shifts (table 1), we provide a guide to which drivers could be expected to influence each type of regime shift, even though the drivers of particular cases will probably be subsets of this list. Knowing that multiple drivers produce regime shifts suggests alternative combinations of strategies to simultaneously manage multiple drivers, or to focus on controllable drivers. Our results suggest that managing single dominant drivers is unlikely to be sufficient to

avoid regime shifts if similar drivers, which may be colinear or correlated in time-series data, are not accounted for in the management strategies.

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