Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale

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Seagrass meadows are threatened by multiple pressures, jeopardizing the many benefits they provide to humanity and biodiversity, including climate regulation and food provision through fisheries production. Conservation of seagrass requires identification of the main pressures contributing to loss and the regions most at risk of ongoing loss. Here, we model trajectories of seagrass change at the global scale and show they are related to multiple anthropogenic pressures but that trajectories vary widely with seagrass life-history strategies. Rapidly declining trajectories of seagrass meadow extent (>25% loss from 2000 to 2010) were most strongly associated with high pressures from destructive demersal fishing and poor water quality. Conversely, seagrass meadow extent was more likely to be increasing when these two pressures were low. Meadows dominated by seagrasses with persistent life-history strategies tended to have slowly changing or stable trajectories, while those with opportunistic species were more variable, with a higher probability of either rapidly declining or rapidly increasing. Global predictions of regions most at risk for decline show high-risk areas in Europe, North America, Japan, and southeast Asia, including places where comprehensive long-term monitoring data are lacking. Our results highlight where seagrass loss may be occurring unnoticed and where urgent conservation interventions are required to reverse loss and sustain their essential services.

ecosystem decline | global status | cumulative pressures | modeling

Seagrass ecosystems provide valuable ecosystem services, including climate regulation and fisheries production (1, 2), but have undergone significant declines in extent (3, 4). Between 1990 and 2006, very high rates of decline were reported (3), and 19.1% of the area of monitored meadows has been lost since monitoring began (4). Although improved land management practices, restoration, and increased protection have led to a reversal of trends in some regions (5–7), seagrass meadows are continuing to decline elsewhere due to exposure to multiple pressures (4, 8). For large areas of the world's seagrass, there are insufficient monitoring data available to attribute the causes of loss (4) or even the trajectory of meadow area (3), so the relative contributions of the key pressures contributing to loss globally, and which regions are most at risk, are largely unknown. This lack of data is in contrast to other valuable coastal habitats, like coral reefs, which have extensive long-term monitoring programs (9), or mangrove forests, which can be observed in satellite imagery (10, 11). Large-scale assessments of drivers and of loss have raised the profile of coral reefs and mangroves, generating greater attention from decision makers and conservation funders (12). Similar efforts to map regions most at risk for loss and identify the key pressures

driving losses are needed for seagrass habitats to attract conservation attention commensurate to their value (12, 13).

At local scales, the main pressures affecting seagrasses are well documented (14, 15), and trends in meadows are relatively well known for some regions (4, 5). Declines in seagrass extent are primarily attributed to agricultural practices that lead to sediment and nutrient runoff, reducing light available for photosynthesis and other compounding issues (14, 16). Other important pressures include extreme temperature stress, sealevel rise, dredging, trawl fishing, anchoring, disease, and coastal development (15, 17–19). A recent meta-analysis found that ~15% of studies documenting seagrass trends made no attempt to assign a cause to changes in meadow extent, and of the studies that did, >40% were purely descriptive (4). Quantifying associations between change in seagrass extent and key pressures at a global scale could help predict the status of seagrass in unmonitored regions and identify pressures that are most important to manage.

Cumulative impact maps have been used to identify global hotspots where management is needed to reduce pressures

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Significance

Seagrasses are important for ecosystem services, including climate regulation and fisheries production. But they are threatened by multiple pressures including poor water quality and coastal development. Seagrass extent is not monitored in many places, so areas at most risk of decline and the management actions needed in these places are largely unknown. We examine associations between change in seagrass meadow area and key pressures globally, helping predict the trajectory of meadows in unmonitored regions. We find rapidly shrinking seagrass meadows in areas where water quality is poor and destructive fishing occurs. Trajectories of change also vary with seagrass life-history strategy. Finally, we identify several unmonitored locations at risk of decline, highlighting where urgent monitoring and management are required.

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(20, 21) or prevent rising pressures (22) under the assumption that such actions will avert ecosystem declines. However, human pressures do not affect all seagrass species equally because species with alternative life-history strategies differ in their response to disturbances, creating regional variation in vulnerability of seagrass meadows to human pressures (14, 23). Seagrass species with life-history traits characterized as colonizing (e.g., *Halophila* spp. with fast shoot turnover, short time to first sexual reproduction) are generally expected to have a greater ability to recover from disturbance, while species characterized as persistent (e.g., *Posidonia* spp.) are long-lived and have high physiological resistance to pressures but are slow to recover. Opportunistic species have a mix of colonizing and persistent life-history traits (e.g., *Zostera* spp.) (23, 24). Given this variation, identifying responses to pressures specific to life-history strategies should allow better predictions of the effects of pressures on seagrass ecosystem change. Additionally, the provision of ecosystem services varies with life-history strategy. Persistent seagrass species have restricted distributions globally, but where they occur, they are perceived to provide a wider range of services than colonizing species (25). Quantifying how species with different life-history strategies respond to pressures (both the magnitude and variation in responses) is critical to inform management actions and maximize service delivery (14).

Here, we modeled the response of seagrass meadow trajectories at 395 sites to global data on human pressures. We then predict the regions most at risk for seagrass meadow decline. The seagrass trends dataset is the most comprehensive time series of seagrass extent available, covering ~10% of the world's seagrass area across all seagrass bioregions [(4); *SI Appendix*, Fig. S1]. First, we reconstructed trajectories of seagrass extent between 2000 and 2010 using the same methods as ref. 4. This was the decade with the most complete data coverage and temporal overlap with pressure mapping data. Second, using comprehensive mapping of human pressures, we quantified how seagrass meadow trajectories related to eight seagrass-relevant pressures (14). There are uncertainties in the scale of pressure effects on ecosystems (26), so we also identified the spatial scale at which pressure data were most strongly associated with seagrass trajectories. Third, we tested how different seagrass life-history strategies affected the response of meadow extent to pressures. Finally, we predicted the locations that are at greatest risk of rapid declines in meadow extent across the globe.

Results

Trajectories of Seagrass Extent 2000 to 2010. At the global scale, variation in meadow trajectories ranged from total loss to doubling in area between 2000 and 2010. This variation reflects the rapid growth potential of some seagrass species. To aid interpretation and safeguard against the model prediction being influenced by outliers, we classified trajectories onto a five-point ordinal scale: rapidly declining, slowly declining, stable, slowly increasing, and rapidly increasing (Fig. 1).

During our focal decade (2000 to 2010), the Mediterranean (65%), Tropical Atlantic (81%), and Temperate North Atlantic East bioregions (60%) had a high percentage of sites with increasing trajectories of extent. At the same time, a high percentage of sites in the Temperate North Pacific (78%) and Temperate North Atlantic West (78%) were undergoing declines (Fig. 1 and *SI Appendix*, Fig. S1).

Quantifying How Global Seagrass Trajectories Are Related to Global Pressures. We modeled trajectories against eight pressures (Table 1; 2 collinear pressures were removed from the original list of 10). We first identified the spatial scale at which pressure data best predicted seagrass trajectories. We fit

multiple models of seagrass trajectories against the eight pressures. We averaged pressures at a range of buffer sizes around the location of each meadow (from 5 to 200 km radius) under the assumption that small buffers (e.g., 5 or 10 km) were representative of local pressures, while larger buffers (e.g., 100 or 200 km) were representative of the pressures facing seagrasses at the catchment scale. Comparison of models fit with the different buffers suggested the 100 km radius was optimal, so we used this model in the next stage (*SI Appendix*, Table S1).

Seagrass trajectories were associated with multiple pressures (Fig. 2A). Seagrass trajectories showed the strongest associations with pressures relating to water quality and fishing, with monthly variability in turbidity (representing acute stress) and destructive demersal fishing having high probabilities (>90%) of association. Higher intensities of these pressures resulted in a higher probability of a site having a "rapidly declining" trajectory (Fig. 3 A and B). Conversely, we found around a 20% chance of a site "rapidly increasing" when these pressures were low compared to a less than 10% chance when these pressures were high (Fig. 3 A and B). Higher pressures from organic chemical pollution, extreme sea surface temperature events, and shipping were associated with rapidly declining seagrass trajectories (Fig. 2A), but the evidence for these effects was weaker than for the aforementioned pressures (<85% probability). Finally, we found little evidence that seagrass trajectories were related to pressures from mean turbidity, nutrient pollution, and ocean acidification.

Seagrass Life-History Strategies. Seagrass meadows with mixed life-history traits or those that were dominated by persistent life histories were more likely to have stable or slowly changing trajectories than rapidly changing trajectories (Fig. 3C). Meadows with opportunistic seagrasses were most likely to be rapidly declining, though rapid increases were also common (Fig. 3C). Meadows with colonizing life histories were not strongly associated with any specific trajectory (Fig. 3C). Variation in trajectories was significantly different between life-history strategies. Meadows dominated by opportunistic strategies had the greatest variability in their trajectories, followed by those with colonizing species and finally those with persistent seagrasses, which had the lowest variability (SDs of 1.36, 1.00, and 0.75, respectively) (Fig. 2B)

Predicting Regions at High Risk of Seagrass Loss. The regions predicted to be at most risk of losing seagrass globally were in Europe, including the North and Baltic Seas and northern British Isles (Fig. 4). High-risk locations were also identified in the western North Atlantic, stretching along the United States–Canada border and into the Gulf of Saint Lawrence. Similarly, in the northeast Pacific Ocean, the southern United States–Canada border was identified as a high-risk region, as was Japan (Fig. 4). Southeast Asia had several hotspots near major cities and river discharges in the region. The locations most at risk for seagrass decline did not change depending on seagrass life-history strategies because the optimal model had no interaction between life-history strategy and the pressure effects.

Discussion

Trajectories of rapidly declining seagrass meadow extent at the global scale were associated with pressures from destructive demersal fishing, turbidity, shipping, extreme temperature events, and organic chemical pollution. These pressures are not unique to seagrass meadows, as other valuable coastal ecosystems, including coral reefs and kelp forests, are threatened by similar pressures (27, 28). The effect of pressures on seagrass meadows depended on seagrass life-history strategies: meadows dominated by species with persistent strategies were more likely to be associated with slowly changing or stable trajectories,
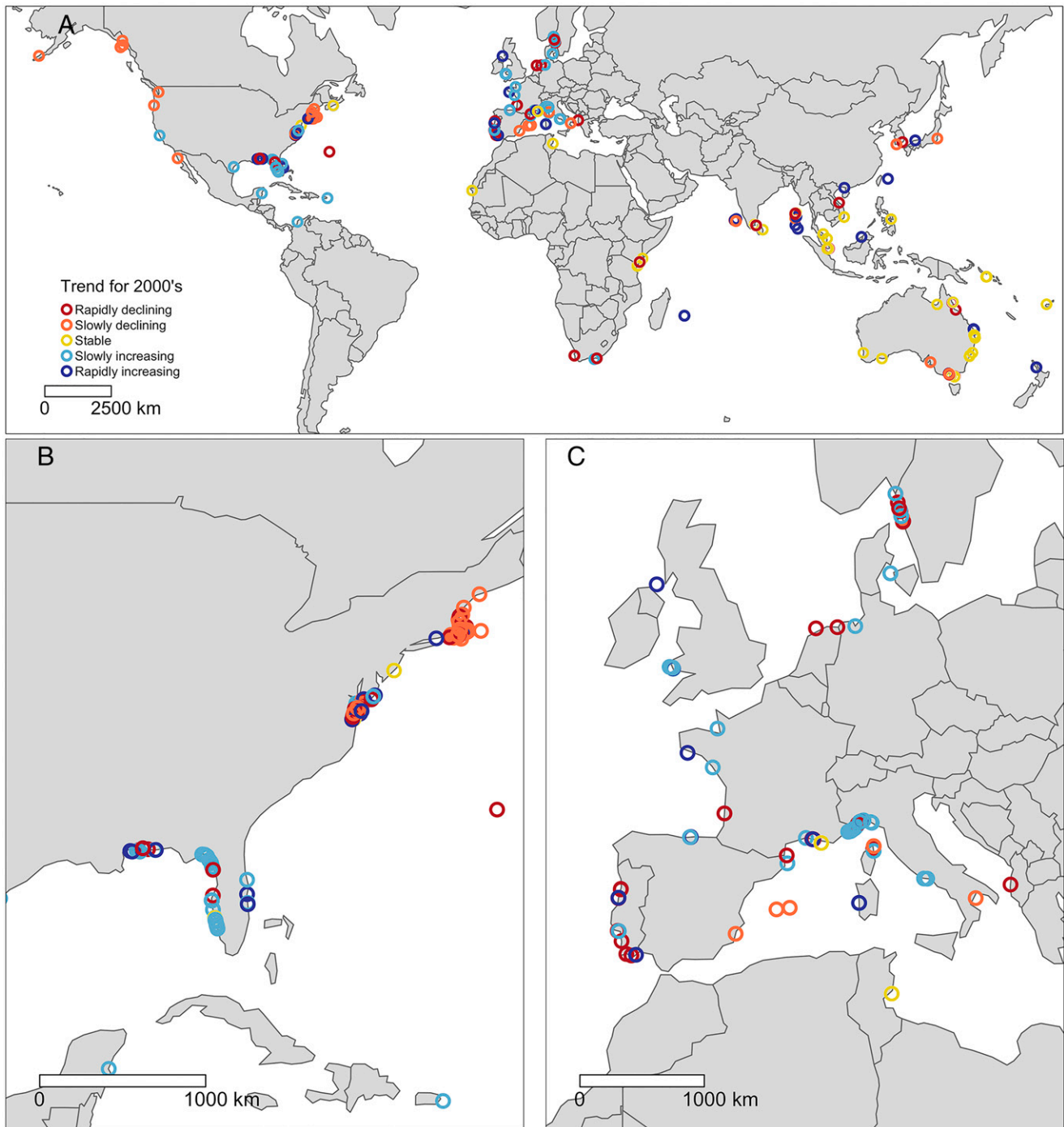
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Fig. 1. Maps of the global distribution of seagrass meadow trajectories for 2000 to 2010 as estimated from GAMs. (*A*) Within the the Temperate North Atlantic West, 75% of temperate seagrasses were on a declining trajectory. (*B*) The majority of sites in the Tropical Atlantic (West Africa not shown due to data paucity) were on an increasing trajectory. (*C*) European seagrass meadows had variable trajectories; more than 50% of sites were on an increasing trajectory in the Mediterranean, while most Temperate North Atlantic East sites were either rapidly declining or rapidly increasing. Note that some points are offset to aid visualization. We classified rapid decline as >25% loss per decade (*n* = 101 sites), slow decline as 5 to 25% loss per decade (*n* = 76), stable as ±5% change per decade (*n* = 70), slow increase as between 5 and 25% gain per decade (*n* = 84), and rapid increase as >25% gain per decade (*n* = 65).

while those with mainly opportunistic species had variable trajectories of change that were likely to be either rapidly declining or rapidly increasing. Our results agree with qualitative assessments that holistic management of multiple interrelated pressures is needed to mitigate the risk of future declines in seagrass extent (29). Moreover, our model predicted a high risk of seagrass decline in several regions where comprehensive

long-term monitoring data are lacking, particularly in parts of Europe, North America, Japan, and southeast Asia.

Quantifying How Global Seagrass Trajectories Are Related to Global Pressures. Intense pressure from destructive demersal fishing was most strongly associated with declining trajectories of seagrass extent. Destructive demersal fishing (which includes both

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Table 1. The 10 pressures relevant to seagrass

Indicator	Pressure description and source	Reasoning
Turbidity (mean)	Diffuse attenuation coefficient of light at 490 nm (Kd490) as a direct indicator of turbidity [sensu (30)] https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/Kd_490/	Turbidity is the closest available measure to the generalized pressure of development and land clearing in coastal catchments. Turbidity, and pulsed turbidity events, can cause seagrass mortality through reduced light availability (35, 65). We included an indicator of mean turbidity as a measure of chronic turbidity pressure and temporal variation (intermonthly) in turbidity as a measure of acute pressure from pulsed events. We hypothesize that higher turbidity and higher turbidity variability will be associated with declining trajectories of seagrass extent.
Turbidity (coefficient of variation)	Diffuse attenuation coefficient of light at 490 nm (Kd490) https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/Kd_490/	
Nutrient pollution (runoff)	Describes modeled nutrient pollution plumes from terrestrial fertilizer (nitrogen) use. Terrestrial data are based on fertilizer application at ~1 km resolution. https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Nutrient enrichment causes algal growth and reduces light available to seagrasses (48). We hypothesize that higher nutrient pollution will be associated with declining trajectories of seagrass extent.
Organic chemical pollution (runoff)	Describes modeled organic chemical pollution plumes based on the application of pesticides https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Chemical pollutants have been linked to seagrass decline. High levels of herbicides may leave seagrasses vulnerable to other simultaneous pressures (66). We hypothesize that higher organic chemical pollution will be associated with declining trajectories of seagrass extent.
Population density (not used in final model due to collinearity with organic chemical pollution)	Population density data https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Long-term declines in seagrass area due to land reclamation in highly urbanized environments (67). We hypothesize that higher direct human pressure will be associated with declining trajectories of seagrass extent.
Commercial fishing: destructive demersal	Based on annual wild-caught industrial fisheries catch for trawl and dredge fisheries https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Destructive fishing activities such as trawling cause mechanical damage to biogenic habitats (5, 31). We hypothesize that destructive demersal fishing will be associated with declining trajectories of seagrass extent.
Shipping	Describes the intensity of global shipping traffic, as measured by the maximum number of shipping tracks recorded in a grid cell https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Increased shipping traffic is associated with dredging activities to maintain shipping channels and ports (68), as well as greater risk of oil spills (69). We hypothesize that higher shipping will be associated with declining trajectories of seagrass extent.
Extreme sea surface temperature events	Describes the relative increase in the frequency of extreme temperature events (marine heatwaves) compared to a historical baseline period of 1985 to 1989 https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Extreme warming events are associated with seagrass mortality (19, 70). We hypothesize that higher pressure from extreme warming events will be associated with declining trajectories of seagrass extent.
Ocean acidification	Describes the degree of decline in aragonite saturation from human-induced increased atmospheric CO_2 levels https://knb.ecoinformatics.org/view/doi:10.5063/F12B8WBS	Ocean acidification may actually benefit seagrasses, as a number of studies have found up to fivefold increases in growth rates under acidifying conditions (71). We hypothesize that high pressure from ocean acidification will be associated with increasing trajectories of extent.
Sea-level rise (not used in final model due to collinearity with shipping)	Describes the magnitude of increasing sea level based on high-resolution altimetry data (0.25 degree) (https://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/gridded-sea-level-anomalies-mean-and-climatology.html)	Seagrass habitat predicted to have variable responses to sea-level rise, with projected increases in shallow waters but losses in deeper waters (72, 73). We hypothesize that there will be no association with increased sea-level rise and trajectories of extent.

All descriptions besides turbidity are derived from the original publication of ref. 62.

trawl and dredge fishing) impacts seagrass meadows directly through physical uprooting (31) and indirectly through sediment resuspension and subsequent light reduction (32). Destructive demersal fishing practices account for around one-quarter of global wild marine landings and have a large spatial footprint (33). In some European regions, large areas of the seabed are impacted by trawl fishing (33), likely contributing to large portions of Europe being classed as having a high risk of future declines in seagrass extent (Fig. 4). Fishing pressure is a primary cause of seagrass loss in Kenya, which is especially concerning as fishing pressures in the region are likely to intensify in the future (31). The strong response to demersal fishing pressure is consistent with previous work, which ranked both dredging and trawl fishing in the top 5 pressures (out of 18) on seagrass globally (14).

Pressures relating to water quality were also strongly associated with declining seagrass trajectories. In particular, seasonal
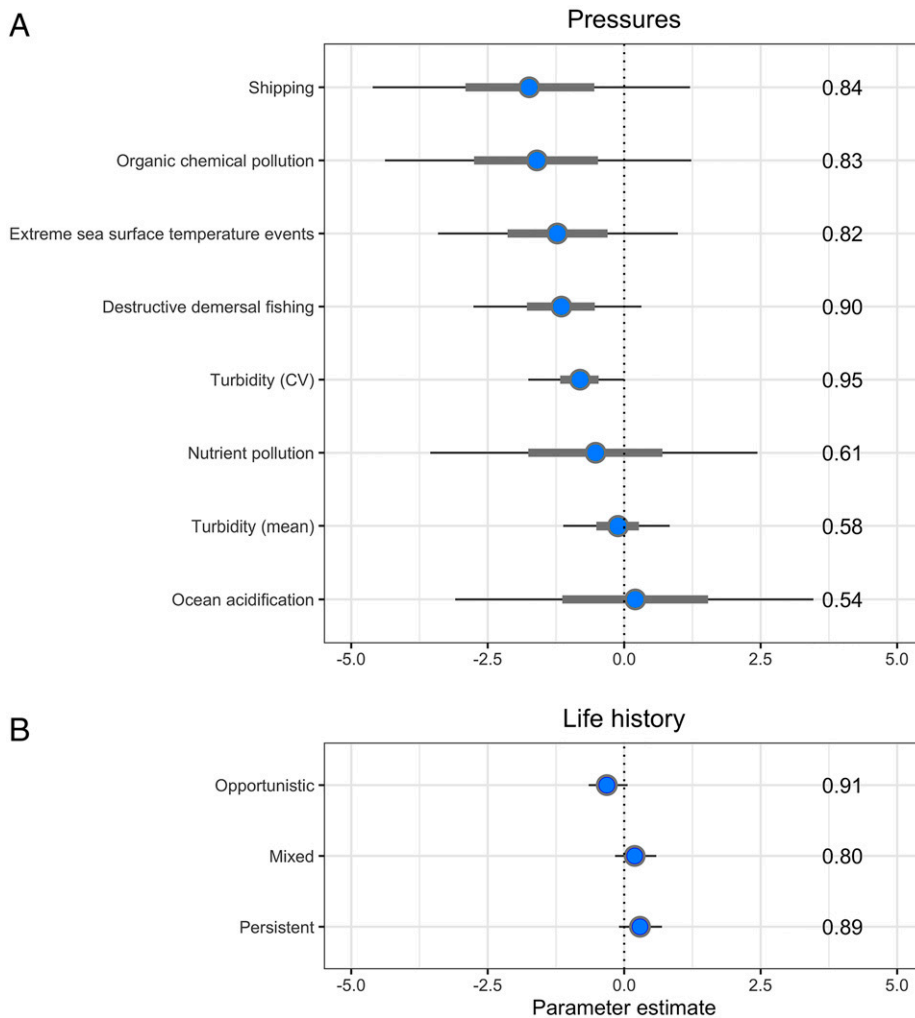
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Fig. 2. Fixed-effects parameter estimates from a Bayesian model (*A*) for eight globally available pressures hypothesized to impact trends in seagrass meadow extent globally (two confounded pressures were removed before model fitting; see *Materials and Methods*) and (*B*) for seagrass life-history strategies (where estimates represent the SD). Estimates (blue dots) are median, thick bars represent 50% credible intervals (weak inference), and thin bars represent 95% credible intervals (strong inference). Values adjacent to each effect are the one-sided probability that each parameter differs from zero. The colonizing life-history strategy was the reference category in the life-history model, meaning that its parameter was fixed at 0 and other strategies were measured relative to this baseline. Mixed represents sites reporting a mix of species with different life histories.

pulses of turbidity—reflected in our intermonthly turbidity variability pressure—may cause seagrass mortality by reducing light availability to meadows that are acclimated to higher-light environments (34, 35). In contrast, mean turbidity had no clear relationship with seagrass trajectories, possibly because seagrasses exhibit phenotypic plasticity in response to previous exposure to turbid conditions (36) [though some seagrasses have shown negative responses to chronic low light (37)]. Turbidity is influenced by several processes, including those in adjacent basins (e.g., rainfall, runoff, basin management), flocculation of organic matter, plume movement, resuspension by wind and tides, and local processes such as dredging and shipping (38). Our turbidity variability variable is likely to be influenced by large-scale processes, in particular, river runoff from seasonal storms, but is likely insensitive to local water quality conditions. Historical land clearing and subsequent turbidity are thought to contribute to seagrass absence in northern New Zealand (39), while climate extremes, large flood events, and associated sediment and nutrient runoff caused seagrass meadow extent to decline temporarily by 84 to 98% at locations throughout Queensland, Australia (40). Local management activities could reduce the risk of

seagrass loss due to high turbidity events by reducing compounding activities such as dredging (41), and reducing sediment loss from basins through basin management (42). Our results suggest that the variability of turbidity events is important, but the specific aspects and causes of variability that impede seagrass persistence need further investigation.

We also found moderate evidence that higher pressures from extreme sea surface temperature events are associated with rapidly declining trajectories of seagrass extent. The negative impacts of temperature stress on seagrasses are well documented (18, 19), and the correlation between extreme temperature events and declining seagrass trajectories is especially concerning given the projected increase in intensity and duration of marine heatwaves (43). The effects of temperature need to be considered in the context of its interaction with other co-occurring pressures, such as turbidity, since seagrasses stressed by low light are more susceptible to mortality from high temperature (44). We acknowledge that recent mortalities that were caused by heatwaves (e.g., ref. 45) are beyond the time period of our analysis (i.e., 2000 to 2010). Climate change will increase the importance of heatwaves as a driver of seagrass loss, so future studies should incorporate
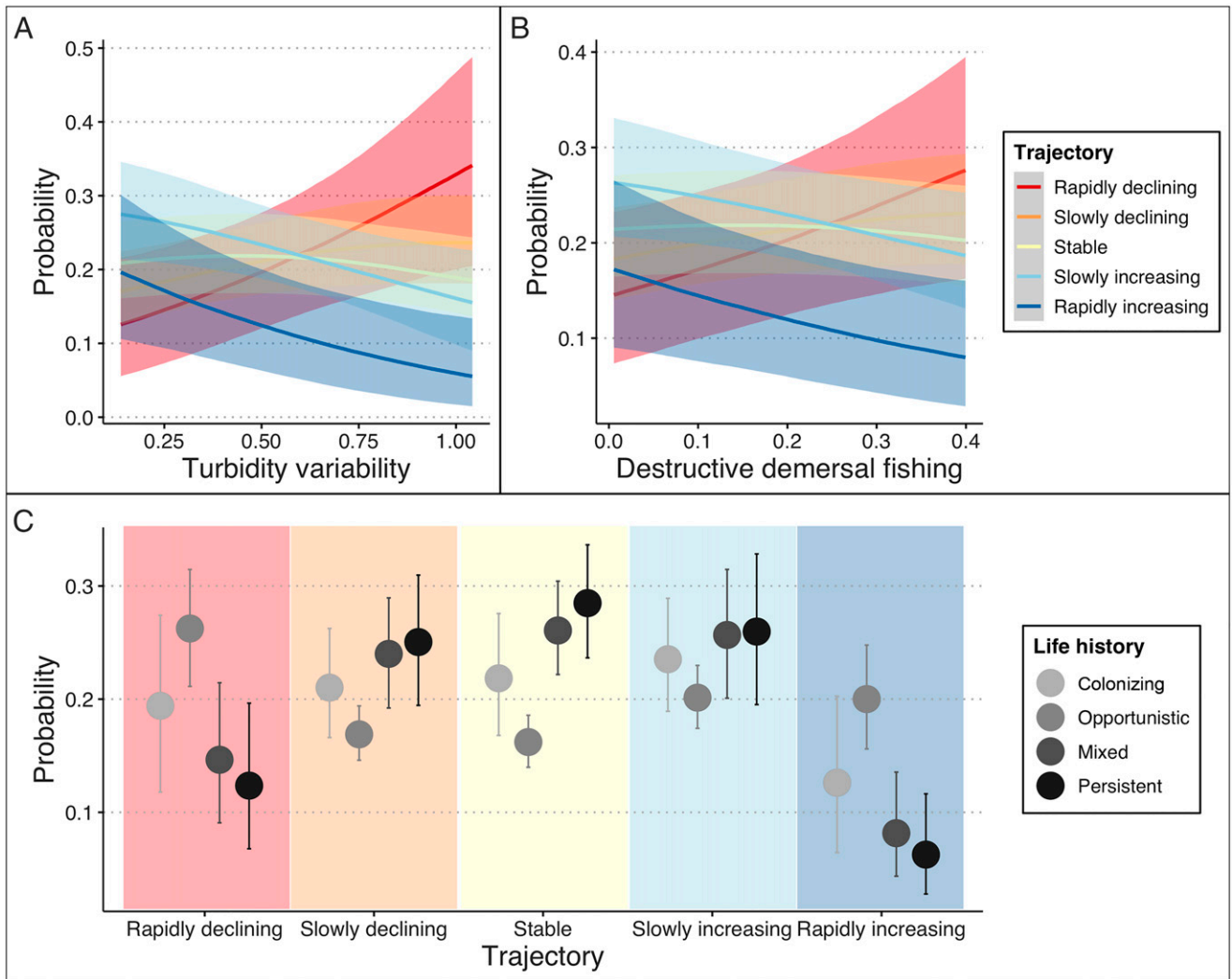
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Fig. 3. Conditional effects plots with 75% credible intervals (75% shown for visualization purposes). The probability of a site falling within a global seagrass trajectory category based on (A) variability in turbidity (CV = coefficient of variance), (B) the level of destructive demersal fishing, and (C) seagrass life-history strategy, while all other predictors in the models are held at mean values.

predictions of heatwaves and their interacting effects with water quality into risk maps.

Higher pressures from shipping traffic were also associated with declines in seagrass extent. There are a multitude of mechanisms associated with shipping that lead to seagrass loss. For example, higher shipping traffic increases the risk of oil spills, while dredging and associated sediment resuspension around ports and along shipping channels pose a high risk to seagrass meadows (14). Further, increased risk of bioinvasion through ballast water can drastically impact local assemblages, such as in the Northwest Mediterranean Sea, where alien macrophytes introduced through ballast discharge replaced native seagrass (46). Pressures from shipping are likely to accelerate in the future as developments such as the maritime Belt and Road Initiative lead to increased shipping traffic globally (47).

We found no clear directional response of seagrass trajectories to pressures from nutrients. This might be due to the context-dependent effect of nutrients (and particularly eutrophication) on seagrasses. For example, although eutrophic systems are generally associated with declines in seagrass extent (48, 49), elevated nutrient load in ground water was been associated with increasing extent of seagrass in nutrient-poor environments (50). The lack of relationship between trajectories and nutrients

observed in our study might also be due to a combination of the temporal lag between changes in nutrient loads and observed changes in seagrass extent (49) as well as the coarse scale of the available nutrient data (based on national-scale Food and Agriculture Organization reporting). Eutrophication is likely to continue to be an important influence on seagrass health around the world and is even predicted to increase (51).

Responses of Seagrasses with Different Life Histories. Across all life-history strategies, opportunistic seagrass species had the highest probability of rapidly declining and also the greatest variability in trajectories. Species with opportunistic life histories are generally more robust to disturbance than colonizing species and have an intermediate ability to recover (24), which means the decadal timescale of this analysis likely reflects true trajectories for these species. Colonizing species had lower variability in trajectories compared to opportunistic species; this was expected because they are more likely to fluctuate over seasonal or annual cycles, and the main threats are from interrupted recruitment or feedbacks that prevent re-establishment following loss (24). Meadows dominated by seagrasses with persistent strategies had the lowest variability in trajectories and were strongly related to stable and slowly changing trajectories.
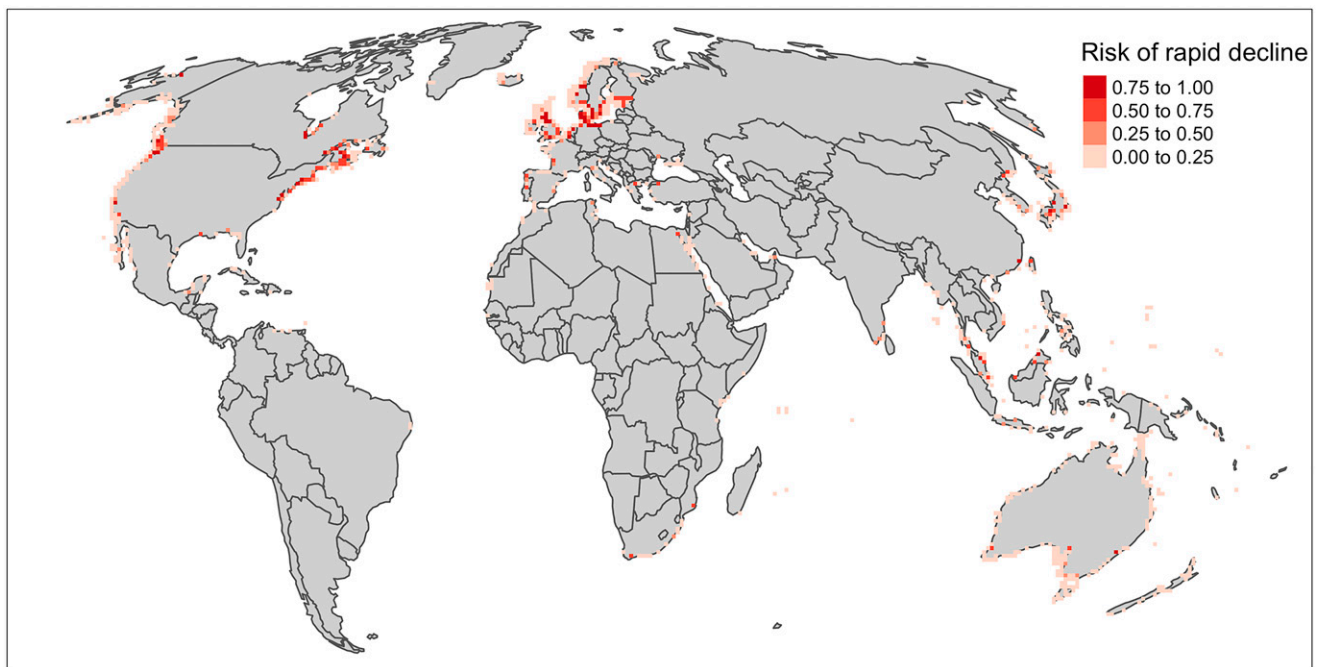
Fig. 4. Risk map predictions were from our best model predicted to 100 × 100 km grid cells. Risk of seagrass decline was predicted from pressure data across the global distribution of seagrass. Sites are colored by the probability of a site being ranked among the 10% of sites most likely to have a rapidly decreasing trajectory. Predictions were the same for all life-history strategies because the best model had no interaction between life-history strategy and the pressure effects. See *SI Appendix*, Fig. S2 for inset maps showing main pressures for Europe and northwestern United States.

This reflects their high physiological resistance to disturbance and long-lived nature (23). The timescale at which variability is assessed can greatly affect observations for persistent species, as patterns of variability assessed at monthly and annual timescales can be largely independent of each other.

Our findings are consistent with recent work showing more stable trends for persistent species and a higher proportion of declining trends for opportunistic species in European seagrass meadows (5). We acknowledge that the classification of sites into life-history strategies is based on regions where multiple species exist, especially in warmer waters, potentially limiting our ability to infer the trajectories of species in other regions. For example, all species within the genus *Zostera* were classified as opportunistic even though a single species in this genus can exhibit traits of multiple life-history strategies (52). Nevertheless, our results reinforce the notion that preventing the loss of persistent species is critical, as meadows dominated by these species are difficult to re-establish once lost (53). The variability in trajectories among life-history strategies supports suggestions that management actions be tailored to life-history strategies of seagrass in the region (23). For example, the management of colonizing or opportunistic species should focus on understanding and improving the drivers that constrain reproductive health, while managing environmental drivers that control growth and overall health is more important for persistent species (23)

Predicting Regions at High Risk. Identifying associations between pressures and measured changes in seagrass extent allowed us to gap-fill and predict risk of seagrass loss in regions where no long-term monitoring exists. Most risk hotspots we identified were consistent with site-specific decadal trajectories (e.g., northeastern United States, North Sea). Conversely, in some risk hotspots, observational data show increasing trends—for example, in southwest England. These apparent contradictions highlight the important role of management in preventing seagrass losses, where effective management can mitigate pressures at local scales and allow meadow extent to stabilize or increase. For

example, the establishment of anti-trawling reefs can stop trawling in meadows and can stem seagrass loss at local scales (54).

Large-scale strategic conservation and management is urgently needed for seagrasses (15). By identifying likely hotspots of change, we provide a stepping stone to guide future monitoring efforts to support the protection of seagrass meadows. For instance, while only a few time series were included from the region around Japan and bays in southeast Asia with intense human development, several grid cells were predicted to be at high risk of seagrass decline, and thus, these areas should be urgently considered for monitoring and pressure management. Similarly, parts of the Baltic Sea and along the coast of Norway were predicted to be at high risk, but no time series from these regions were available for the current analysis. Management and conservation can benefit from our predictions by prioritizing locations where future monitoring efforts could focus.

Although our findings suggest that seagrass ecosystems are impacted by multiple pressures, many of the associations between seagrass trajectories and different pressures were highly variable (indicated by wide credible intervals), and some associations were weak. The weak relationships may reflect the coarse resolution of the pressure data relative to the size of a typical meadow (while pressure data are available at high resolution, many layers are downscaled from low-resolution data). However, the data used represent the most comprehensive, standardized, and freely available data currently available and included eight pressures that seagrasses are most vulnerable to globally (14). The nature of global modeling efforts requires acknowledgment of some level of fine-scale inaccuracy, especially as several important coastal pressures that affect seagrass (e.g., tourism and coastal development) (15) are only represented indirectly in the pressure maps by human population density. Comprehensive consideration of threats requires developing new global layers that capture pressures from activities, such as coastal development, aquaculture, tourism, and recreational boating (15). Finally, interactions among pressures could also mask pressure-specific effects. It will be important to

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consider interactions among pressures in future higher-resolution studies because interacting pressures are a key cause of seagrass decline (19), and the efficacy of management can depend on how pressures interact (55).

Most seagrass time-series data in our study were collected from academic studies (4) that may be biased toward documenting strong trajectories of change rather than long-term monitoring of stable meadows (56). This also leads to spatial biases in the availability of time-series data. For example, well-researched regions such as Chesapeake Bay and Florida in the eastern United States have ample time-series data, while large regions of Africa, South America, and the Middle East are underrepresented. Similarly, subtidal meadows are monitored less often and with greater inaccuracies than intertidal meadows, raising another source of potential bias. In the United Kingdom, for instance, intertidal meadows are generally stable or increasing, but many subtidal meadows are in decline (57). A lack of comprehensive time-series data has been a longstanding issue for seagrass research (3), and around 40% of sites included in our analysis only had data from two time points, potentially limiting the inference of trends from these sites. Nevertheless, when we ran the model without sites with only two observations, both destructive demersal fishing and turbidity variability remained the most probable pressures related to trajectories (*SI Appendix*, Fig. S3).

Here, we assessed changes in seagrass extent in responses to pressures from 2000 to 2010. Seagrasses are at risk for future declines in extent due to several pressures, including destructive fishing practices and pulsed turbidity events. These pressures appear to impact seagrasses at broad spatial scales. Trajectories in extent varied depending on seagrass life history, highlighting that decision-making for conservation and management would benefit from considering species composition and their life-history strategies. For example, persistent species typically exhibit slow trajectories of extent change, so extended time series are required to identify meaningful losses or gains and the appropriate management and conservation responses. Finally, our model predicted risk of decline across the global distribution of seagrasses, identifying regions without long-term monitoring data as being at high risk of losses. Globally comprehensive mapping of seagrass extent (58) and risks to seagrass can help raise the profile of seagrass meadows—an overlooked coastal ecosystem—and ensure they get conservation attention commensurate with the benefits they provide (12). Our predictions can also guide future monitoring efforts to fill data gaps for the most at-risk regions. Long-term standardized seagrass monitoring and information on pressures that is appropriate to the spatial scale of the pressures will help to better manage human impacts on seagrass meadows into the future.

Materials and Methods

Seagrass Trends. Seagrass trends were reconstructed following ref. 4. Here, we analyze a subset of sites that included data for the decade 2000 to 2010 ($n = 395$ sites, with site defined as a location with at least two observations between 2000 and 2010). The Temperate North Atlantic West bioregion had the highest number of sites ($n = 121$ sites), while the Temperate North Pacific had the least ($n = 14$). All other bioregions had between 41 and 66 sites (*SI Appendix*, Fig. S1). For sites with time series containing at least three measurements spanning 2 or more years ($n = 344$), trends were estimated for each site and bioregion using hierarchical generalized additive models (GAMs), as described in ref. 4. Seagrass meadows can be highly dynamic in nature, so we used GAMs because of their ability to fit complex nonlinear relationships in data, allowing us to fit and estimate trends in seagrass extent. The complexity of the site-level smoothing term, k, varied depending on the length of the time series at each site, allowing more complex terms for sites with longer time series. Site was included as a random effect, allowing for site-specific intercepts (59). We reconstructed trends for the entire length of the available time series (from 1950) and only used predictions from the decade 2000 to 2010 for further analysis. We predicted seagrass extent at the start and end of

the decade (i.e., extent in the year 2000 and 2010) by simulating from the posterior distribution (GAMs are a type of empirical Bayesian analysis) of the parameters (1,000 samples). We estimated specific rate of change (yr^{-1}) over time interval, t (10 y in this instance), from the initial to final estimated areas (Ai and Af, respectively) as follows:

$$\ln\left(\frac{Af}{Ai}\right)/t.$$

For sites with only two observations (also spanning 2 or more years, $n = 51$), we calculated the specific rate of change using the same formula and assumed this rate was constant for the entire decade. Rates were extracted for each site and were used as the response variable in our predictive models. GAMs were fit in R using the package *mgcv* (60). Overall, our reconstructions accurately captured trends in seagrass extent for a decade (*SI Appendix*, Fig. S4).

We grouped sites on a five-point ordinal scale based on trajectories for the period 2000 to 2010: rapidly declining, slowly declining, stable, slowly increasing, and rapidly increasing (Fig. 5). This classification aligned with error rates in seagrass meadow estimates [~10% (61)], and the reasonably even distribution of sites by categories improved the statistical power of our tests. Sensitivity analyses indicated that parameter estimates from the best model were not sensitive to the rates used to classify trajectories (*SI Appendix*, Fig. S5). The direction of the parameter estimates did not change, and the estimates themselves were only slightly affected. In each case, turbidity variability was consistently selected as the pressure with the highest probability of an effect.

Pressure Data. For our global pressure layers, we compiled the most up-to-date marine pressure data available at annual intervals from 2003 to 2013 (62). We acknowledge that these data are a slight temporal mismatch to the seagrass trend (2000 to 2010); however, these data represent the finest resolution (~1 × 1 km grid) and globally comprehensive data on pressures to marine ecosystems. See ref. 62 for full details on how each of these pressures was calculated and derived. We used scaled intensity rasters (0–1) for 10 known seagrass pressures (only 8 were included in the final model due to collinearity) (14) (Table 1). We did not include light pollution, artisanal fishing, or four pressures related to pelagic fishing due to weak impacts of these pressures on seagrass extent at a global scale and collinearity with other pressures (63). We calculated the mean intensity value for each pressure within each raster cell across the time series (*SI Appendix*, Fig. S6). The frequency distributions of each pressure are shown in *SI Appendix*, Fig. S7.

Sea-level rise and human population density demonstrated collinearity (correlation coefficient > 0.7) with shipping and organic chemical pollution, respectively. Sea-level rise and population density were subsequently removed from the final model because shipping and organic chemical pollution are ranked higher on the vulnerability weighting for seagrass pressures (14). To further justify the removal of the two collinear predictors (population density and sea-level rise), we reran our model with these predictors, replacing organic chemical pollution and shipping, respectively. Population density and sea-level rise both had a lower probability of effect compared to the metrics they were collinear with and so were not considered further in the analysis (*SI Appendix*, Table S1).
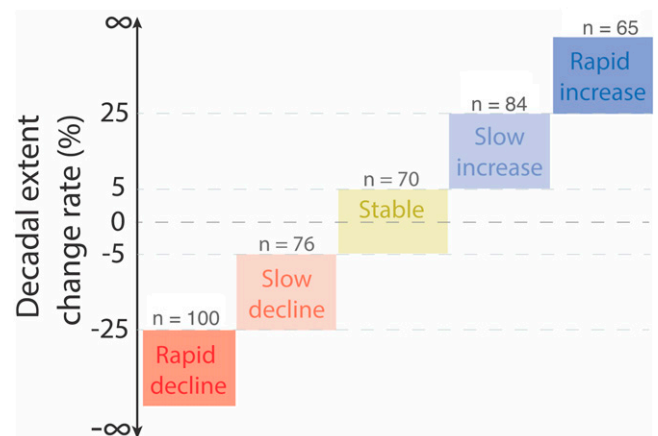

Fig. 5. Trajectory categories used in analyses. Each site was grouped into one of five trajectory categories based on the direction and magnitude of decadal extent change (trajectory).

We also included two indicators of turbidity pressure for the 2000s—mean turbidity and variability in turbidity—because seagrass decline is primarily attributed to poor water quality (15). We included two indicators relating to turbidity because they represent different threatening processes to seagrass relating to chronic stress versus pulsed acute stress [*sensu* (64)]. Mean turbidity represented a measure of overall chronic turbidity pressure, while temporal variation (intermonthly) in turbidity represented a measure of pressure from pulsed events. We used the diffuse attenuation coefficient of light at 490 nm (K_d490) as a direct indicator of turbidity [*sensu* (30)]. We obtained globally comprehensive, high-resolution (4×4 km) rasters of K_d490, which are available at monthly intervals from NASA's Earth Observing System Data and Information System Modis-Aqua satellite database (https://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/Kd_490/). Data were resampled to 1 km resolution, and we calculated the mean and coefficient of variation for each cell across the time series. Data were available from 2002 onward, so we calculated the indicators from 2002 to 2009 to match the decadal seagrass trajectories.

Seagrass Life-History Strategies. We included seagrass life-history strategy as a categorical predictor in our models as different seagrass life histories have previously been demonstrated for European meadows (5). The seagrass meadow at each study site was categorized as being dominated by either colonizing ($n = 15$ sites), opportunistic ($n = 246$), or persistent ($n = 47$) species based on the most abundant species present (23). Sites reporting a mix of species with different traits were classified as "mixed" ($n = 87$). Across a decade, we hypothesized that meadows with predominantly colonizing species would have the greatest variability in trends because of their boom/bust nature. We expected meadows with opportunistic species to have moderate variability in trends and to be associated with rapidly increasing and decreasing trajectories of extent because these species are more robust to disturbance than colonizing strategies and have an intermediate ability to recover, which is likely to be reflected at a decadal timescale. Finally, we hypothesized that meadows with persistent species would be the least variable and thus associated with more stable trajectories because they have high physiological resistance but are slow to recover from disturbances (23).

Spatial Data Processing. Seagrass study sites were converted to a spatial points object, and each site was buffered by 5, 10, 20, 30, 50, 100, and 200 km. For each pressure, the mean intensity value rasters were intersected with buffered seagrass sites, and the mean value of pressure scores was extracted from the buffer zone (*SI Appendix*, Fig. S6). This allowed us to test the scales at which global pressure maps correlate with seagrass extent change. All rasters and seagrass layers were projected to the WGS84 Mollweide projection prior to analysis. This projection preserves area so data toward the poles are not overrepresented. All spatial data processing was done in R using the *raster* (74), *sf* (75), and *rgdal* (76) packages.

Statistical Analysis. We used Bayesian continuous ordinal regression to relate seagrass trajectories to pressures and life histories. We used the trajectory in extent from 2000 to 2010 as the response variable to best match the time series of the individual pressures data (2003 to 2013). We modeled seagrass trends on an ordinal scale for three reasons. First, seagrass trends were highly variable, and during initial exploration, we found that model algorithms were not able to generate valid fits to such overdispersed data. Second, the ordinal scale down-weighted the influence of extreme values (78 sites had decadal trends that estimated complete meadow loss or meadow doubling). Third, seagrass meadow area estimates can be uncertain, but most studies did not report uncertainty intervals on area estimates. Hence, most previous studies of seagrass trends have also used categories for analysis (e.g., refs. 3 and 5). We also tested for interactions between life history and each individual pressure and found that the model with interactions performed similarly to the model with no interaction (*SI Appendix*, Table S2). The effect size of the interaction was weak, so we opted to use the no-interaction model to improve interpretation of results.

The ordinal score for seagrass trajectory, $\tilde{Y}_{ij}$, for the ith site in the jth bioregion was fit with a cumulative distribution and probit link:

$$\tilde{Y}_{ij} = n + \varepsilon = b_1 x_1 + b_k x_k + \varepsilon,$$

where n represents variation in $\tilde{Y}$ that can be explained by k predictors, $b_1 x_1 + b_2 x_2 + \dots b_k x_k$, while ε represents unexplained variation. We fit an unequal variance model, which allowed us to test whether residual variation in seagrass trajectories differed across categories of life history (77). Unequal variance was incorporated into the model with an additional regression formula for the variance component of the latent variable ε such that the variance became a function of life-history strategy (LH) with no intercept in the regression:

$$\varepsilon \sim 0 + \text{LH}.$$

The colonizing life-history strategy was the reference category in the model, meaning that its parameter was fixed at 0, and other strategies are discussed relative to this baseline. Seagrass bioregion was included in the models as a spatial random effect. We fit weakly informative Gaussian priors on fixed effects [*normal* (0, 2)] and exponential priors on the SD [*exp* 1]. We fit models with 3,000 iterations across 4 MCMC chains and discarded the first 1,000 iterations of each chain, leaving 8,000 iterations to calculate posterior samples. Model convergence was visually assessed and confirmed, with all $\hat{R}$ scores less than 1.01 (78). We fit models using the *brms* package (79) from R (80). Widely applicable information criterion (WAIC) (81) was used to compare models and assess the spatial extent at which pressures influence seagrass trajectories. The model with the lowest WAIC was used to make predictions.

Predicting Regions at High Risk. Using our best model and global pressure data, we predicted regions at risk for seagrass loss in all seagrass-bearing areas of the world. The resolution of predictions was 100×100 km grid cells, which matched the spatial scale that pressure data were most strongly associated with seagrass trajectories. First, the distribution of seagrass was defined at the 100×100 km grid scale by presence/absence of seagrass in a globally comprehensive dataset of seagrass presence (82). Second, we took the mean of each pressure layer within each 100 km grid cell to align the predictions of risk with the spatial scale of the best model. We then predicted the ordinal response, $\tilde{Y}_{ij}$, in every grid cell where seagrass is present and calculated the proportion of times each location fell in the bottom 10% of $\tilde{Y}_{ij}$ values from our 8,000 MCMC samples (i.e., the ordinal score for seagrass trajectories). The risk map thus represents locations that are most likely to be in the lowest (most negative) 10% of locations globally for their seagrass trend. Predictions are the same for all life-history strategies because the best model had no interaction between life-history strategy and the pressure effects. The model was verified by examining the distribution of site-level trajectories against the probability a site is ranked in 10% of sites most likely to have a rapidly decreasing trajectory (*SI Appendix*, Fig. S8).

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