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Grazing halos reveal differential ecosystem vulnerabilities in vegetated habitats

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Abstract

The dynamic balance between primary production and herbivory is key to the resilience of plant-dominated ecosystems across the world. However, many vegetated ecosystems are becoming increasingly susceptible to herbivore-triggered collapses, as this balance is disrupted due to predator declines, increasing nutrients, and other interacting impacts of global change. Yet without accessible, cost-effective tools to evaluate the production-consumption relationship, it is difficult to know how close an ecosystem is to imminent overgrazing collapse. Here, we explore the effectiveness of individually formed

sea urchin grazing halos as robust indicators of marine habitat vulnerability to overgrazing. Halos are grazed patches of bare rock on macrophyte-dominated substrates that represent the balance between macrophyte production and per capita herbivore consumption. We measured 1211 halos in 31 locations across the Mediterranean Sea to characterize how plant-herbivore interactions are mediated by endogenous (i.e., species identity, habitat type, and sea urchin size) and exogenous factors (i.e., environmental factors influencing biotic and abiotic contexts: depth, nutrients, temperature, or protection level). Our results show that halo size was effective in detecting differences in the effect of endogenous and exogenous factors on these interactions. Across locations, halo size was sensitive to differences in (i) species identity, with some species being more impactful than others; (ii) the type of habitat, with some habitats being more vulnerable than others; (iii) protection level, with halo size consistently lower inside marine protected areas; (iv) urchin size, with halo size increasing consistently with herbivore size; (v) nutrient conditions, with halo size increasing as nutrient availability decreased; as well as (vi) depth, with halo size increasing consistently with depth. These results indicate that overgrazing vulnerability is highly contingent on local ecological contexts, which strongly mediate plant-herbivore interactions. While drivers of ecosystem collapse may be global, the ability of ecosystems to cope is often inherently local. We need locally responsive measures and contextually meaningful solutions to manage ecological integrity in the face of global change. In this context, individually measured grazing halos can be a powerful tool in assessing and managing the resilience of macrophyte ecosystems.

KEYWORDS

ecosystem vulnerability, macroalgal forests, overgrazing, plant-herbivore interactions, sea urchins

INTRODUCTION

Plant-herbivore interactions shape the structure and functioning of the world's ecosystems (Pringle et al., 2023; Wood et al., 2017). The role of herbivory in regulating the abundance of primary producers is typically much more pronounced in aquatic vegetated ecosystems, where herbivores can remove up to 10 times more plant biomass than their terrestrial counterparts (Bakker et al., 2016; Worm et al., 2002). However, terrestrial herbivores can also strongly regulate plant communities, and meta-analyses of exclusion studies have shown a pervasive effect of herbivores on plant abundance, biomass, survival, and reproduction (Jia et al., 2018; Trepel et al., 2024). In both terrestrial and marine systems, trophic interactions controlling primary producers' abundance are intensifying with anthropogenic global change, as higher trophic groups are overharvested, temperatures rise, and nutrient inputs increase (Burkepile & Hay, 2006; Tylianakis et al., 2008;

Wood et al., 2017). At the same time, the cumulative impacts of global change erode the resilience of vegetated habitats, making them notably prone to higher rates of herbivory (Filbee-Dexter & Wernberg, 2018; Strain et al., 2014; Zarnetske et al., 2012). For instance, the growing records of trophic cascades in terrestrial and marine ecosystems have been linked to the simplification of food webs and herbivore population explosions caused by reduced predator populations worldwide, through anthropogenic impacts like defaunation, hunting, and overfishing (Estes et al., 2011; Myers & Worm, 2003; Sala et al., 1998; Shurin et al., 2002). In addition, global environmental change, by affecting other biotic (e.g., competitors) and abiotic factors (e.g., eutrophication or warming) within ecosystems, may disrupt plant-herbivore interactions with detrimental effects for macrophytes communities (Burkepile & Hay, 2006; Filbee-Dexter & Wernberg, 2018; Gilman et al., 2010).

Apart from coral reefs, where high herbivory rates maintain reefs in coral-dominated states by controlling

space-occupying algae (Fung et al., 2011; Mumby et al., 2007; Steneck et al., 2017), in most benthic ecosystems dominated by plants, herbivory pressures can lead to significant declines in ecosystem condition. Here, herbivore activity can result in an average reduction of 68% in producer abundance, with greater herbivore impacts on intertidal and subtidal rocky reefs (Poore et al., 2012). Unchecked by predators, marine herbivore populations can soar, severely depleting highly productive macrophyte ecosystems (Barrientos et al., 2022; Christianen et al., 2023; Steneck et al., 2002). Once critical herbivory thresholds are breached, ecosystems may shift rapidly towards impoverished and highly stable alternative states devoid of vegetation (Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014). The inherent hysteresis of these depauperate states makes recovery pathways highly protracted; a simple reduction in herbivore numbers (i.e., stressor) does not guarantee a return to the original vegetated state (Ling et al., 2015; Scheffer et al., 2001). While herbivore numbers are clearly important in determining these trajectories, a host of other factors influences the nonlinear dynamics shaping the resistance and recovery (i.e., resilience) of macrophyte ecosystems (Conversi et al., 2015; Wood et al., 2017). There is now mounting evidence showing that marine regime shifts can be mediated by: (i) endogenous factors associated with specific herbivore and macrophyte traits (Barrientos et al., 2022; Vergés et al., 2014), (ii) exogenous abiotic factors related to climatic-driven seawater temperature or site-specific nutrient conditions (Boada et al., 2017; Wernberg et al., 2016), (iii) exogenous biotic factors influencing predator control over herbivores (Pessarrodona et al., 2019; Steneck et al., 2002), or (iv) interactions between these factors (Conversi et al., 2015; Ling et al., 2009; Sala et al., 2012). Given this complexity of response, preventing marine vegetated habitats from tipping over in the first place is likely the most robust strategy for their management (Scheffer et al., 2001).

The fundamental relationship between habitat productivity and herbivore consumption is central to assessing the vulnerability of plant-dominated systems to overgrazing-mediated collapses (Suskiewicz & Johnson, 2017), since the production-consumption ratio describes how close a system is to overconsumption. While several studies have explored how the production-consumption relationship is modified by endogenous (e.g., species identity, body size) or exogenous factors (e.g., predator presence, temperature, nutrients), most have tested these factors individually or in laboratory conditions (Kriegisch et al., 2019; Pessarrodona et al., 2019; Suskiewicz & Johnson, 2017). The challenge is to have a clear, field-based integrative measure that signals changes in ecosystem structure and function that can serve as a reliable and comparable index of changing plant-herbivore

interactions. This would help compare the production–consumption relationship across large spatial scales and could be applied to a range of local ecological contexts to determine their relative vulnerability (Burkepile & Hay, 2006; Wood et al., 2017; Worm et al., 2002).

Herbivorous sea urchins are among the most notorious barren-forming organisms worldwide (Ling et al., 2015; Shurin et al., 2002). Their numbers have often been seen as robust predictors of imminent macrophyte collapse, with numerous studies focusing on determining the abundances at which sea urchins could trigger catastrophic regime shifts (Filbee-Dexter & Scheibling, 2014; Ling et al., 2015). However, while quantitative approaches have been successful at identifying thresholds of herbivory stress for each local context, the ability to generalize such estimates across macrophyte ecosystems is hindered by the considerable natural variation in biotic and abiotic factors and their effect on site-specific productivities and herbivory (Dayton, 1985; Mann, 1973). Most of this variance is related to specific endogenous traits of both macrophytes and herbivores, and with exogenous factors that together determine the productivity of each habitat and set the context for such plant–herbivore interactions (Burkepile & Hay, 2006; Poore et al., 2012). Macroalgal-dominated ecosystems range from thin turfs to highly structured macroalgal forests with a diverse set of morpho-functional types, varying considerably in their structural and functional resistance to herbivory (Filbee-Dexter & Wernberg, 2018; Hereu et al., 2008). In addition, primary production can vary considerably between habitats (Dayton, 1985, Mann, 1973), with the productivity of a healthy kelp forest being up to 10 times higher than that of an intertidal macroalgae assemblage, and both being considerably more productive than turf-dominated ecosystems in temperate regions (Filbee-Dexter & Wernberg, 2018; Smale et al., 2013). Similarly, herbivorous sea urchin species differ in their biological or ecological traits such as individual morphometry, diet preferences, and/or behavior, which can mediate their foraging and feeding preferences and, therefore, herbivory pressures on macroalgal forests (Agnetta et al., 2013, 2015; Wangensteen et al., 2011).

Besides endogenous traits, exogenous abiotic factors such as nutrients, temperature, and light can shape both macrophyte primary production (Dayton, 1985; Sant & Ballesteros, 2021) and herbivore consumption rates between regions or across depths (Boada et al., 2017; Nikolaou et al., 2023). Under oligotrophic or light-limiting conditions, decreased primary production and compensatory grazing by sea urchins (among other behavioral changes) both alter the production–consumption relationship, making macroalgal systems much more prone to catastrophic collapses than regions with higher nutrient availability

(Boada et al., 2017; Dayton, 1985; Nikolaou et al., 2023). Nonlethal temperature increases can enhance primary production, but may also modify herbivore metabolic requirements, which affect the balance of these interactions (O'Connor, 2009; Pagès et al., 2018). Among the exogenous biotic factors that influence this relationship, the presence of predators can shape herbivore behavior by inducing fear that indirectly influences herbivory rates and reduces their impacts on macroalgal forests (Hereu, 2005; Pagès et al., 2021). These nonconsumptive effects linked to the abundance of predators have been well established by comparing populations inside and outside marine protected areas (MPAs) across different seas (Babcock et al., 2010; Pessarrodona et al., 2019).

Here, we evaluate the effectiveness of sea urchin grazing halos as indicators of the relative vulnerability of temperate macroalgal communities to overgrazing across the Mediterranean Sea. Halos are grazed patches of bare rock on macroalgal-dominated substrates that are commonly found associated with physical refuges. We assumed that, when maintained by a single urchin, a halo represents the per capita relationship between the production of the habitat and the rate of herbivore consumption. The size of the halo therefore is a simple measure of the balance between productivity and herbivory, and integrates the influence of context-specific, endogenous, and exogenous factors on both production and consumption rates (see Figure 1a). Using grazing halos produced by single urchins of the two most abundant sea urchins in the Mediterranean Sea (Figure 1b,c), we explore how the vulnerability of temperate macroalgal communities is mediated by endogenous (species/habitat identity and sea urchin size) and exogenous factors (predator-induced fear, nutrient, temperature, and light conditions). For this, we measured the size of grazing halos over a wide range of sites in the Mediterranean Sea spanning gradients of nutrient conditions, temperatures, depths, and protection levels (Figure 1a). This last factor was employed as a proxy to assess the influence of predator-induced fear on sea urchin grazing (Pessarrodona et al., 2019) in MPAs characterized by high predator abundance (see *Discussion*).

MATERIALS AND METHODS

Study area and species

The Mediterranean is a confined and highly human-modified sea. It is an excellent model to test the impacts of global change as many of its drivers are more strongly felt than in the rest of the oceans (Cramer et al., 2018). For instance, the rate of warming is more than threefold faster in the Mediterranean than in the

global ocean (Pisano et al., 2020). In addition, the Mediterranean Sea is characterized by pronounced spatial gradients for crucial environmental variables such as nutrients, temperature, and salinity (Nikolaou et al., 2023; Santana-Garcon et al., 2023). At the same time, this sea has experienced a high level of local anthropogenic pressure, and overfishing has been (and still is) a major stressor, exhibiting some of the lowest values of fish biomass for shallow reefs (Cramer et al., 2018; Sala et al., 2012). These reasons make the Mediterranean Sea an ideal scenario to test the main drivers modifying the oceans today.

Our study focuses on shallow rocky reefs dominated by macroalgal communities where drastic sea urchin overgrazing events can occur (Boada et al., 2017; Sala et al., 1998). When undisturbed, these vegetated habitats are dominated by macroalgae of the order Fucales (mainly *Cystoseira* sensu lato) and other shrub-forming macroalgal communities (Ballesteros, 1989). These macroalgal communities are critical ecosystem engineers in benthic sublittoral Mediterranean assemblages, which are of paramount ecological importance, accounting for most of the biomass and production of these shallow ecosystems (Ballesteros, 1989). These macroalgal-dominated communities are also in decline due to a host of local and global forces, being often replaced by simplified habitats dominated by algal turfs or urchin barrens (see e.g., Pessarrodona et al., 2021; Sala et al., 1998). *Paracentrotus lividus* and *Arbacia lixula* are ubiquitous sea urchin species in Mediterranean rocky reefs, able to form barrens where healthy macroalgal forests used to thrive (Bulleri et al., 1999; Kempf, 1962). Despite the similarity between these two sea urchin species, they differ in fundamental features. *P. lividus* is a large sea urchin species, reaching diameters of up to 8 cm (Boudouresque & Verlaque, 2020). It inhabits rocky reefs, as well as *Posidonia oceanica* and *Cymodocea nodosa* meadows, which provide shelter opportunities and allow juvenile individuals to recruit and grow to large sizes and thus "escape in size" from predators (Boudouresque & Verlaque, 2020; Sala et al., 1998). Only large sparid fish (*Diplodus sargus*, *D. vulgaris*, and *Sparus aurata*) can routinely prey on adult *P. lividus*, while juveniles are mainly targeted by labrids such as *Coris julis* and *Thalassoma pavo* (Boudouresque & Verlaque, 2020; Sala et al., 1998). In contrast, although *A. lixula* reaches slightly smaller sizes than *P. lividus* and shares its main predators with *P. lividus* (Guidetti, 2006), adult individuals of this species experience significantly lower predation rates in the hard, exposed substrates they inhabit (Gianguzza, 2020). This is attributed to specific traits such as its attachment tenacity, test robustness, and spine length (Guidetti, 2006; Guidetti & Mori, 2005). Moreover, as foragers, they also have distinct
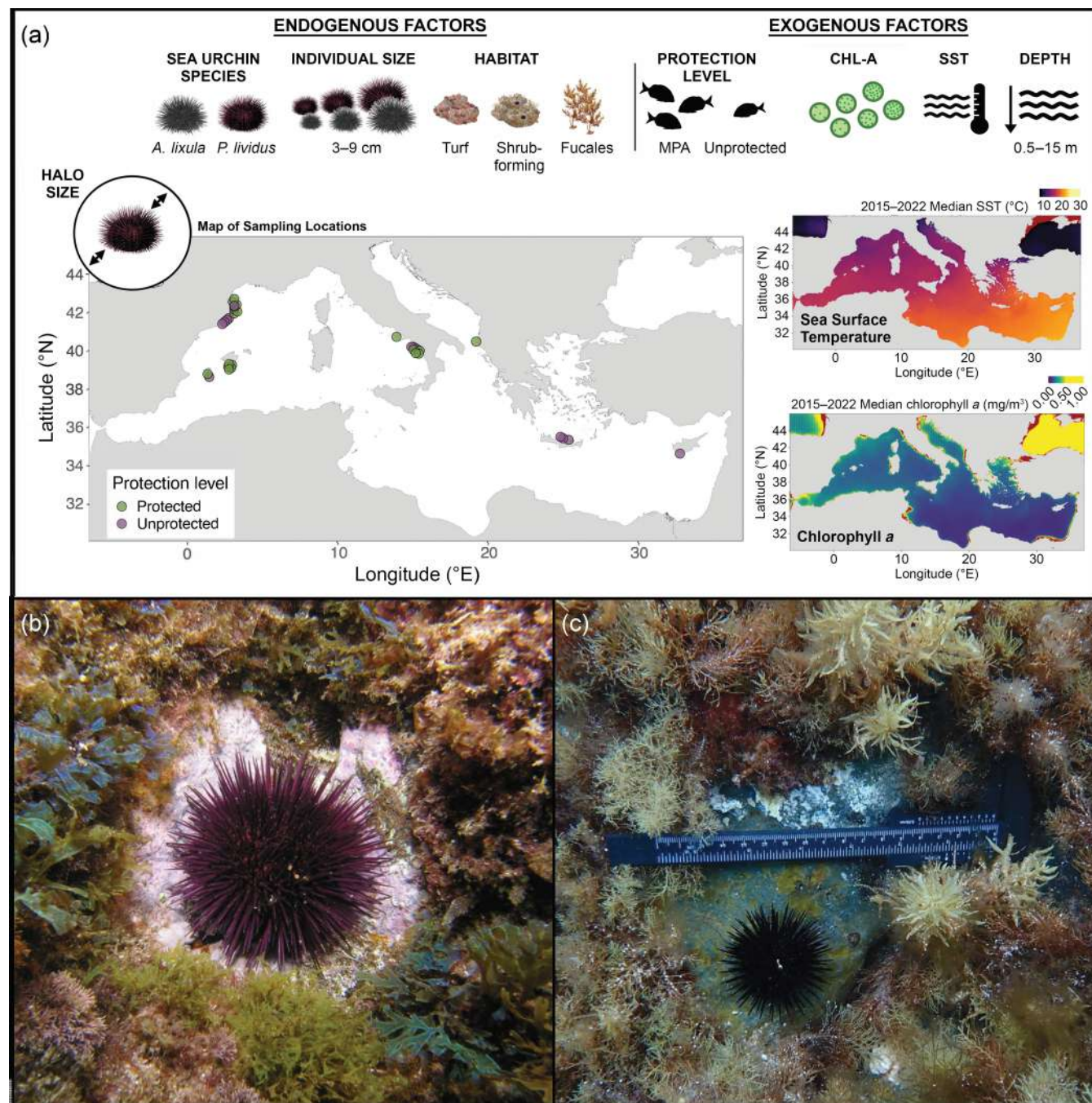
FIGURE 1 (a) Schematic representation of the endogenous and exogenous factors influencing the relationship between primary production and herbivore consumption (i.e., grazing halos) and shaping the vulnerability of macroalgal forests to herbivory. Halos were measured in 31 locations inside and outside marine protected areas (green and purple points, respectively) across the Mediterranean Sea. Maps on the right panel show the median sea surface temperature (top) and median chlorophyll *a* (bottom) for the study period between 2015 and 2022, as an example of the spatial gradient of nutrients and seawater temperature in the Mediterranean Sea (data extracted from NOAA's ERDDAP service). Chlorophyll *a* values higher than 1 mg m^{-3} are depicted in red. Photos in (b) and (c) have been gently provided by Manuel Maldonado and Teresa Alcoverro, respectively, showing grazing halos produced by *Paracentrotus lividus* and *Arbacia lixula*, respectively. Sea urchins and habitat type illustrations in (a) are courtesy of Toni Llobet.

dietary preferences: *P. lividus* is a strict herbivore, grazing on species of erect macroalgae and turf, whereas *A. lixula* is a more functional omnivore (with a clear carnivorous tendency) that acts as a "bulldozer" when moving across rocky reefs, rooting out all macroalgae as it forages for benthic organisms (Agnetta et al., 2013, 2015; Wangensteen et al., 2011).

Study design and measures of sea urchin halos

Individually formed sea urchin halos are patches of bare rock on macroalgal-dominated bottoms maintained by sustained sea urchin grazing (see Figure 1b,c), typically associated with small refugia (Pessarrodona et al., 2019). In this study, we explored the effectiveness of grazing halos produced by the two focal species (*P. lividus* and *A. lixula*) as indicators of the net balance between macroalgae production and sea urchin consumption along a gradient of environmental conditions at multiple locations across the Mediterranean Sea. We measured halos along gradients of nutrients, temperature, light, and contrasting management protection levels. The size of these halos (i.e., using halo diameter as a proxy) can help evaluate how different sets of endogenous and exogenous factors of biotic and abiotic nature alter the strength of these producer–consumer interactions (see Figure 1a). While the halo size does not represent absolute herbivory pressure, the urchin does not wander far from its refuge (Hereu, 2005), focusing the bulk of its grazing on the area around it (Bulleri, 2013), which allows us to use halo size as a comparative measure between locations.

We measured the diameter of 1211 individually produced sea urchin halos formed by *P. lividus* ($n = 912$) and *A. lixula* ($n = 299$) in 31 locations across the Mediterranean Sea (Figure 1a). The data were collected from 2015 to 2022. Field measurements were collected once per location, with the exception of some opportunistic measurements taken at three locations (less than 6% of our observations). To minimize seasonal effects, the sampling period was concentrated during the warm season (i.e., late May to mid-October). At each sampled location, we surveyed the site actively searching for grazing halos by snorkeling or scuba diving, at depths ranging from 0.3 to 15 m. We looked for (i) solitary sea urchins so we could attribute their grazing activity to a single individual and (ii) individuals larger than 3 cm, since smaller sea urchins rarely generate distinctive halos (Pessarrodona et al., 2019; Verlaque, 1984). We measured the halo diameter either in situ with a ruler or ex situ by taking a picture and using a caliper as a scale to analyze the images with the software ImageJ. Sea urchin barrens were excluded since they preclude the identification of halos.

Endogenous and exogenous factors shaping halo size

For each halo observation, we noted the sea urchin species (*P. lividus* or *A. lixula*), its test diameter without spines (measured between the spines with a vernier caliper), the depth, and the type of habitat in which each halo was measured. Most sampled locations consisted of patchy habitats, dominated by distinct foundation species. We classified these habitats based on criteria defined by Sala et al. (2012) and Monserrat et al. (2022): (i) ephemeral, fast-growing algae forming a horizontal mat that facilitates sediment retention or turfs, (ii) arborescent shrub-forming photophilic macroalgae with complex three-dimensional structure, and (iii) canopy- or forest-forming macroalgae of high complexity and productivity dominated by species of the order Fucales. In addition, we used information on the level of protection (two categories, areas with some protection level or completely unprotected coastal areas) (Hereu, 2005), and data on chlorophyll *a* and sea surface temperature (SST) were collected for each study site, using the NOAA's ERDDAP service through the *rerddap* R package (Chamberlain, 2022). From each dataset, we selected the annual maximum chlorophyll *a* and maximum SST at each study location in the year in which the data were collected, to best characterize the differences between locations and assess how temperatures and nutrients across these gradients in the Mediterranean Sea influenced the size of halos. During data extraction, we excluded any chlorophyll *a* outlier from the datasets used for modeling. Outliers were identified as inconsistent peaks within the time series.

Data analysis

We evaluated the relationship between "Halo size" (i.e., halo diameter measured in cm) and different endogenous and exogenous factors using linear mixed-effects models (LMMs). To assess the distribution of the response variable, we used the *fitdistrplus* R package (Delignette-Muller & Dutang, 2015). We applied a maximum likelihood estimate method to fit the data to three likely distributions (gamma, log-normal, and Weibull), whose model fittings were evaluated visually and statistically (Appendix S1: Table S1).

To test the effect of predictors on "Halo size," we fitted a set of candidates LMMs with a log-normal distribution of errors (Appendix S1: Table S1), using the *lmerTest* R package (Kuznetsova et al., 2017). These models integrated, therefore, the effect of both endogenous factors—"Species" (two levels: *A. lixula* and *P. lividus*), "Size," "Habitat type" (three levels: turf, shrub-forming, and Fucales); and exogenous factors—"Protection level" (two levels: protected and unprotected locations); "Annual maximum chlorophyll *a*," "Annual maximum SST," and "Depth". We included "Location" (31 levels) and "Sampling date" as random factors, including random slopes for each "Species" within each "Location." The most informative model was chosen

based on the second-order corrected Akaike information criterion (AIC$_c$) and likelihood ratio tests (LRTs), and using the variance inflation factor (VIF) to assess collinearity among explanatory variables (Burnham & Anderson, 2004; Zuur et al., 2009). Models exhibiting VIF values greater than five in any of their predictors or interactions were discarded. The general model selected (i.e., including both species together) was tested using AIC$_c$ and LRTs against other candidate models obtained through multi-model inference and an iterative stepwise procedure derived from the *dredge()* function in the *MuMIn* R package (Bartoń, 2022) (Appendix S1: Table S2). Our preliminary results showed differences among species, so we applied the same criteria to fit LMMs for each species separately, thus testing the relationship between species-specific halos and all predictor variables.

In all cases, model assumptions were visually and statistically explored using the functions in the *performance* R package (Lüdecke et al., 2021). In the general model, despite logarithmic transformation, model residuals did not meet the assumption of normality. However, fixed effects in LMMs have been found to be sufficiently robust to violations of residual normality (Schielzeth et al., 2020). We tested spatial autocorrelation by (i) including the geographical coordinates of each location as predictor variables (i.e., they were dropped from models using model selection criteria described above) (Zuur et al., 2017) and (ii) by running a Moran's I test for distance-based autocorrelation with the *DHARMa* R package (Hartig, 2022). Statistical significance of fixed predictor variables in all LMMs was assessed by running the Type III Wald chi-squared tests using the *Anova()* function from the *car* R package (Fox et al., 2012). To examine the level effect of the different categorical predictors analyzed, we ran Tukey's post hoc analyses for pair-wise comparisons using the *emmeans* R package (Lenth, 2024), which estimated least-square means using the Kenward-Roger approximation for denominator degrees of freedom.

RESULTS

This study demonstrates that halo size varied reliably with varying ecological contexts across the Mediterranean basin. The results of the two types of models included in this study (i.e., a general model including both species together; Table 1 and species-specific models; Table 2), to explore the relationship between habitat productivity and sea urchin consumption, showed that both exogenous and endogenous factors influenced the size of grazing halos. However, the importance of different predictors varied among sea urchin species as explained by our species-specific models

(Table 2). In our general model, species identity strongly affected halo diameter (Table 1); in fact, *A. lixula* grazing halos were more than twice as large as *P. lividus* grazing halos (overall mean $\pm$ SE = 28.0 $\pm$ 0.97 vs. 12.4 $\pm$ 0.26 cm, respectively; Figure 2), despite the similarity of mean test diameter of the sea urchins measured (overall mean $\pm$ SE = 5.13 $\pm$ 0.06 vs. 5.22 $\pm$ 0.04 cm, respectively). In this model, the predictor "Species" also showed interaction effects with the annual maximum chlorophyll *a* (Table 1) and habitat type (Table 1). Halos were larger in areas with lower nutrients, but only for sea urchins larger than 4 cm test diameter (Table 1). The significance of this size-dependent nutrient effect was also confirmed for each species separately (Table 2; Figure 3). *A. lixula* halos showed a marginal statistical relationship with the type of macroalgal habitat, but not those of *P. lividus* (Table 2; Figure 3). The average halo size was larger in communities dominated by Fucales (*A. lixula*, mean $\pm$ SE = 35.4 $\pm$ 5.25; *P. lividus*, mean $\pm$ SE = 14.5 $\pm$ 0.62) than in habitats dominated by shrub-forming macroalgae (*A. lixula*, mean $\pm$ SE = 28.2 $\pm$ 1.17; *P. lividus*, mean $\pm$ SE = 12.1 $\pm$ 0.30) or turfs (*A. lixula*, mean $\pm$ SE = 25.8 $\pm$ 1.69; *P. lividus*, mean $\pm$ SE = 9.4 $\pm$ 0.31). However, our species-specific model outputs (Figure 3), which integrate the natural variability associated with other predictors of halo size, detected marginally significant smaller halos in habitats dominated by Fucales than in habitats dominated by shrub- or turf-forming algae for *A. lixula* (Appendix S1: Table S3). Thus, *A. lixula* halos in habitats dominated by turfs and shrub-forming algae were 72% and 65% larger than those found in forests of Fucales. In contrast, halos of *P. lividus* in forests of Fucales or turf grounds were 8% greater compared to halos found in habitats dominated by shrub-forming algae.

Our general model results indicate that the protection level had a strong negative effect on halo sizes (Table 1). Halos were larger outside MPA than inside them for both *A. lixula* (MPA: mean $\pm$ SE = 23.6 $\pm$ 1.34; outside: mean $\pm$ SE = 31.4 $\pm$ 1.31) and *P. lividus* (MPA: mean $\pm$ SE = 10.6 $\pm$ 0.23; outside: mean $\pm$ SE = 15.2 $\pm$ 0.53). In the species-specific model, only *P. lividus* showed this effect (Table 2; Figure 3), whereas *A. lixula* did not (Table 2; Figure 3). We found very strong evidence for a positive effect of depth on halo size (Table 1), which was consistent across species (Table 2; Figure 3). Conversely, our data revealed no evidence of a potential effect of annual maximum SST on halo size in any of the models proposed (Table 1; Table 2).

Our selected general LMM model (Appendix S1: Table S2) accounted for a high proportion of the variance in our data as shown by the proportion of the variance explained by both fixed and random effects (conditional $R^2 = 0.75$) and that explained only by fixed effects (marginal $R^2 = 0.53$). In contrast, the

TABLE 1 Type III Wald chi-squared tests of fixed effects from the general linear mixed-effects model (LMM) (i.e., including halos of *Arbacia lixula* and *Paracentrotus lividus*) explaining halo size (halo diameter in centimeters) as a function of all predictor variables.

Predictors	LR χ^2	df	*p*-value
Intercept	0.118	1	0.732
Species	80.501	1	<0.001
Sea urchin size	239.423	1	<0.001
Protection level	15.565	1	<0.001
Habitat type	8.812	2	0.012
Annual maximum chlorophyll *a*	0.421	1	0.516
Annual maximum SST	0.098	1	0.755
Depth	31.150	1	<0.001
Species × Annual maximum chlorophyll *a*	4.659	1	0.031
Sea urchin size × Annual maximum chlorophyll *a*	16.328	1	<0.001
Species × Habitat type	6.508	2	0.039

Abbreviations: LR, likelihood ratio; SST, sea surface temperature.

TABLE 2 Type III Wald chi-squared tests of fixed effects from species-specific linear mixed-effects models (LMMs) explaining the size of the halos produced by *Arbacia lixula* and *Paracentrotus lividus* as a function of all predictor variables.

Predictors	LR Chisq	df	*p*-value
Arbacia lixula			
Intercept	0.005	1	0.945
Sea urchin size	15.914	1	<0.001
Protection level	0.938	1	0.333
Habitat type	6.003	2	0.050
Annual maximum chlorophyll *a*	0.866	1	0.352
Annual maximum SST	0.168	1	0.682
Depth	9.490	1	0.002
Sea urchin size × Annual maximum chlorophyll *a*	4.181	1	0.041
Paracentrotus lividus			
Intercept	0.496	1	0.481
Sea urchin size	258.266	1	<0.001
Protection level	4.293	1	0.038
Habitat type	2.768	2	0.251
Annual maximum chlorophyll *a*	2.576	1	0.109
Annual maximum SST	0.069	1	0.793
Depth	29.696	1	<0.001
Sea urchin size × Annual maximum chlorophyll *a*	12.495	1	<0.001

Abbreviation: SST, sea surface temperature.

species-specific models showed marked differences in their marginal effects, as the LMM of *A. lixula* obtained a marginal $R^2 = 0.18$, whereas the LMM for *P. lividus* approximately doubled this value ($R^2 = 0.39$). In both models, the inclusion of random effects contributed to explaining a substantial additional part of the variance (conditional $R^2 = 0.61$ and $R^2 = 0.60$, for *A. lixula* and *P. lividus* models, respectively).

DISCUSSION

Here, we introduce a new field-based, cost-effective, integrative tool—individually formed sea urchin halos—as an indicator of marine habitat vulnerability to overgrazing. Our field study across the Mediterranean Sea shows that the relationship between macroalgal productivity and sea urchin consumption can be easily measured using the sizes of grazing halos and that these sizes are mediated by several endogenous and exogenous factors of biotic and abiotic nature that can shape ecosystem vulnerability to overgrazing collapses (Figure 4). Sea urchin species differed in their foraging impact on macroalgal communities, reflecting differences in their life history traits. Although sea urchin sizes strongly determined these plant-herbivore interactions, this broad pattern was mediated by significant effects of the type of habitat, exogenous factors such as depth, nutrients, or the protection level of each locality.

Individually formed grazing halos are a simple, integrative, and elegant measure of the balance between production and consumption in macrophyte-dominated habitats. This study demonstrates that halo size varied reliably with varying ecological contexts across the Mediterranean basin. A broad range of field and laboratory experimental studies have demonstrated that grazing rates can be modified by nutrients, temperature, fear, depth, and plant anti-herbivory responses, among others (Boada et al., 2017; Kriegisch et al., 2019; Ling et al., 2009; Nikolaou et al., 2023; Pagès et al., 2018; Pessarrodona et al., 2019; Santana-Garcon et al., 2023). Across larger spatial scales, studies using standardized protocols have also successfully evaluated the main factors influencing plant-herbivore interactions in both marine and terrestrial systems (Bakker et al., 2016; Gruner et al., 2008; Poore et al., 2012). However, the challenge remains to find an adequate indicator that integrates the multiple factors influencing plant-herbivore interactions in natural conditions, since they often vary
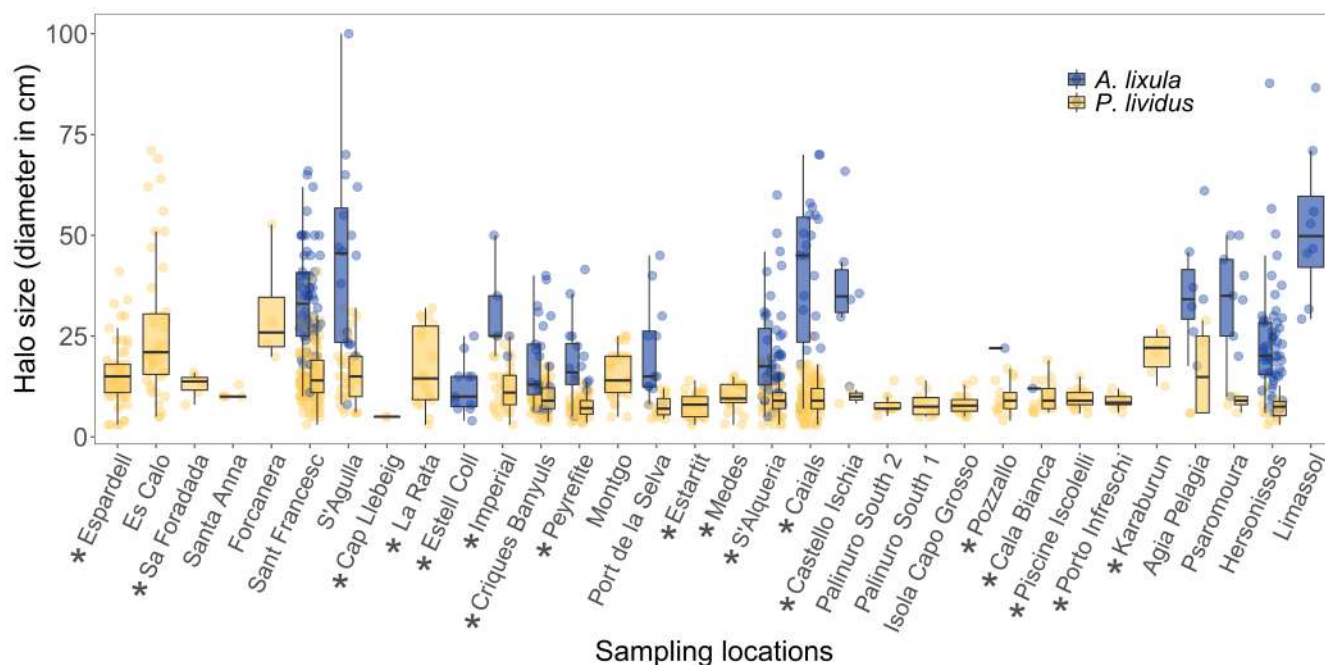
FIGURE 2 Halos measured across sampling locations in the Mediterranean Sea grouped by sea urchin species: *Arbacia lixula* and *Paracentrotus lividus*. Locations are ordered by longitude, and asterisks indicate that they are within an area with some level of protection.

together in complex ways (Hereu et al., 2008; Kriegisch et al., 2019; Wood et al., 2017). Our results show that the grazing halos are an innovative method that adequately meets this challenge. The value of using individually produced grazing halos is that they provide an ideal, cost-effective in situ index by which herbivore consumption (here by sea urchins) can be compared with inherent primary production values in real-world systems. With the assumption that halos have reached a relatively unchanging size, they provide a simple yet powerful integration of all the factors influencing the interaction between primary production and herbivore consumption. While, as a general rule of thumb, herbivore numbers are a powerful indicator of overgrazing episodes in vegetated ecosystems, this study demonstrates that alone it does not always represent an accurate predictor, since a host of context-dependent factors influence shifts to impoverished states devoid of vegetation (Conversi et al., 2015; Eklöf et al., 2008; Hereu et al., 2008; Ling et al., 2015). Using this basic measure, our study shows that the strength of the interaction between macrophyte communities and herbivores is much more complex than population numbers alone can capture (Wood et al., 2017). The wide variation in halo size indicates that ecosystem vulnerability to overgrazing could be influenced by a suite of endogenous and exogenous factors that shape plant-herbivore interactions, highlighting its value as a tool to evaluate relative resilience at managerially meaningful scales.

Across the Mediterranean basin, the factor that most affected consumption rates was the size of individual sea urchins, regardless of species. Although sea urchins smaller than 3 cm were unable to produce a halo, since their rates of consumption were always lower than macroalgal production (Pessarrodona et al., 2019; Verlaque, 1984), beyond this threshold, halo diameters increased in length considerably with individual urchin size, as generally expected for herbivores (Bakker et al., 2016). The implication here is that sea urchin numbers, important as they are, may not be as critical as their demographic structure (Ling et al., 2019; Pessarrodona et al., 2019). While ecological indicators such as sea urchin biomass or abundance can partly account for the overall effect of herbivory impact, it is only beyond a certain size that sea urchin consumption begins to generate overgrazing, and not in a simple linear way (Pessarrodona et al., 2019). The identity and traits of sea urchin species also matter, helping explain a large component of the variation in halo sizes. *P. lividus* is a selective feeder, grazing only on preferred types of vegetation (Agnetta et al., 2013, 2015). In contrast, the feeding strategy of *A. lixula* results in a "bulldozer" effect, clearing the forest around it while feeding on a diverse set of benthic organisms (Bulleri, 2013; Wangensteen et al., 2011). The upshot of these foraging differences is that *A. lixula* halos tended to be twice the size of *P. lividus* halos and were not significantly influenced by most factors examined here, probably given their omnivorous nature. Thus,
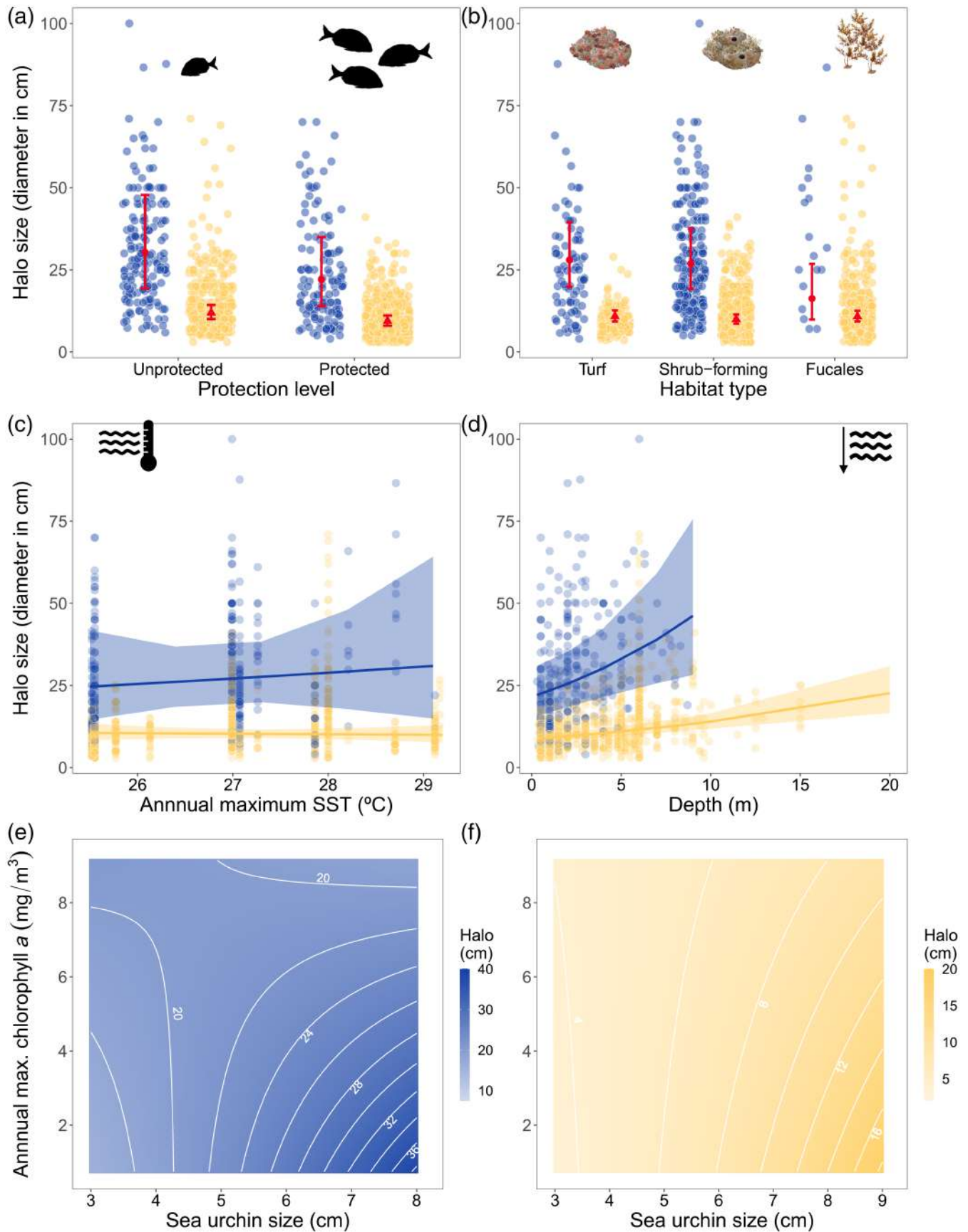
FIGURE 3   Legend on next page.
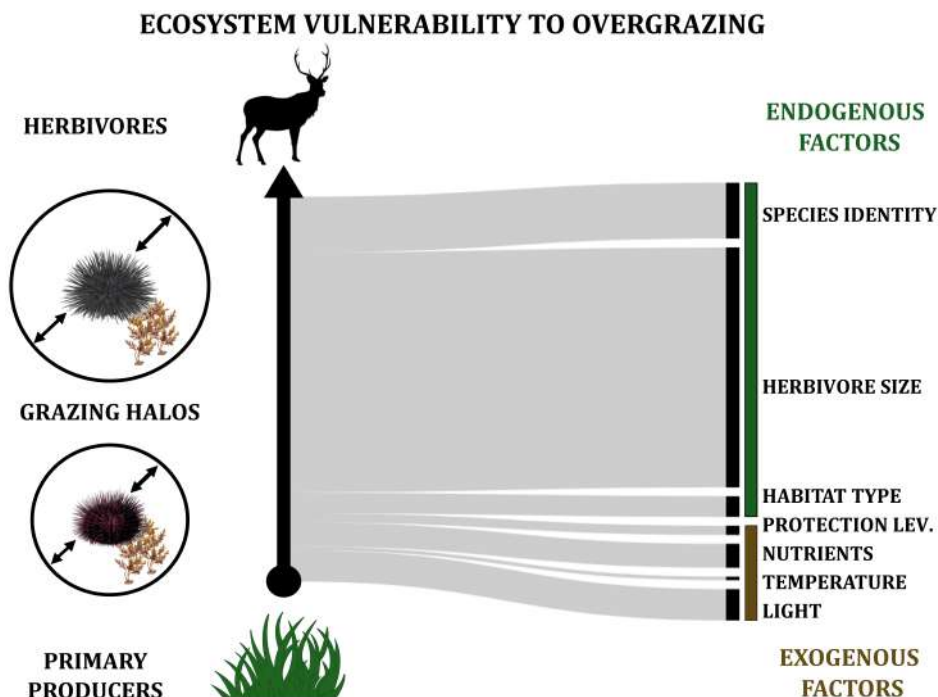
FIGURE 4 Conceptual model illustrating the relationship between primary production and herbivore consumption (i.e., grazing halos) and the influence of endogenous and exogenous factors on plant-herbivore interactions. The Sankey diagram, adapted from general model outcomes, serves as a conceptual representation of the relative strength of each predictor's contribution to halo size. "Protection lev." refers to the level of protection of the location of study. Sea urchins and algae illustrations are courtesy of Toni Llobet. Deer symbol by Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library) under a Creative Commons Attribution-ShareAlike 4.0 International license (https://creativecommons.org/licenses/by-sa/4.0/). Grass symbol by Sketchify Education on Canva.

community composition may also strongly influence the grazing and extirpation rates of macroalgal forests in shallow coastal communities where sea urchins thrive (Agnetta et al., 2013, 2015).

While the species- and size-specific differences we found in production-consumption ratios are expected, this relationship also varied with other, subtler, context-specific factors across the Mediterranean Sea. Within MPAs with different levels of fisheries management, halo sizes were generally smaller, indicating that exogenous biotic factors like fear can significantly reduce grazing impact. More broadly, this adds to the now large body of evidence of the importance of securing higher trophic functions, since their contribution to ecosystem resilience goes beyond their purely trophic effects (Babcock et al., 2010; Sala et al., 1998; Steneck

et al., 2002). Within the Mediterranean Sea, our model outcomes largely conformed with the earlier studies that show that predator abundance can induce distinct fear responses in both sea urchin species (Boudouresque & Verlaque, 2020; Pessarrodona et al., 2019). Our approach adequately registered these effects even though not all the MPAs in this study have strong fishing restrictions in place. However, we need to be careful about how universally we assume the fear of predators operates since its effects were only significant for *P. lividus* (Pagès et al., 2021). In contrast, *A. lixula* may perceive and respond much less to predation risk. *A. lixula* has a range of species-specific traits related to its morphology; its greater attachment tenacity, test robustness, and spine length protect it from high predation risk (Guidetti, 2006; Guidetti & Mori, 2005). Therefore, species-specific traits

FIGURE 3 Data points represent *Arbacia lixula* (blue) and *Paracentrotus lividus* (yellow) halos measured in the field. Halos are explained by each predictor variable: protection level (a), habitat type (b), annual maximum sea surface temperature (SST) (c), depth (d), and the interaction between annual maximum chlorophyll *a* and sea urchin size (e, f). Data points are shown with fitted linear mixed-effects model (LMM) (log-normal distribution) estimates (red points) or smooths, and 95% CIs for each species-specific model. Heatmaps show the result of each species-specific model for the interaction between individual size and the annual maximum of chlorophyll *a*. Illustrations in (b) are courtesy of Toni Llobet.

determine the differential resistance to predation and elicit different responses to predator presence, which may moderate the positive effect of MPAs on macroalgal communities (Guidetti & Mori, 2005; Hereu, 2005).

Nutrient-rich areas of the Mediterranean also had smaller halos, given the higher algal production and lower sea urchin consumption rates in these waters, as has been demonstrated in other field and laboratory studies (Boada et al., 2017). Our analysis shows that other factors, such as the type of habitat and depth, can also influence grazing consumption ratios to differing degrees. While of less overall relevance, it is essential to consider them in any vulnerability assessment, since they may interact with other factors in ways that are not straightforward (Conversi et al., 2015; Kriegisch et al., 2019; Ling et al., 2009). For instance, while deeper reefs are in general more prone to overgrazing as a result of reduced light penetration limiting algal production at depth, these deeper reefs may be protected from the more harmful *A. lixula* that is typically found in shallower reefs (Bulleri et al., 1999; Nikolaou et al., 2023). Similarly, although the largest halos were observed in habitats dominated by Fucales, turf- or erect-forming algae had a greater effect on the size of halos produced by *A. lixula* (see Appendix S1: Table S3). This variation between raw field data and model estimates can be attributed to the virtual absence of larger sized individuals at miniaturized habitats devoid of canopy-forming algae. Sea urchins in these habitats may be subject to higher levels of predator exposure or potential sedimentation impacts (Babcock et al., 2010; Kriegisch et al., 2019). Despite unbalanced data for some of our predictors (e.g., *A. lixula* halos on Fucales forests), these subtle but complex patterns highlight the value of using LMM models to integrate ecological responses mediated by a range of multiple interacting factors. Although they may be more difficult to interpret, they are much more representative of real-world systems and call for caution when applying reductionistic assumptions of the relevance of single drivers (Bolker, 2008). Finally, the absence of evidence for an effect of temperature on halo size seems to align with previous findings in the literature on these and other species. For instance, Pagès et al. (2018) reported sustained feeding rates of *P. lividus* on *Cystoseira mediterranea* across a range of temperatures, and Suskiewicz and Johnson (2017) found little evidence in their review of the extrinsic and intrinsic controls of consumption rates in *Strongylocentrotus droebachiensis*.

Nonetheless, the use of grazing halos has a few key assumptions and caveats. As mentioned before, we assume that grazing halos have reached a relatively unchanging size, so these halos can be considered "fully formed." Additionally, we assume that the sea urchin within each halo was solely responsible for its creation and that it does the bulk of its feeding within these halos. Given what we know of sea urchin behavior, these are simplifying but reasonable assumptions (Hereu, 2005; Ling and Johnson 2012; Pessarrodona et al., 2019). The method cannot be used to quantitatively assess individual sea urchin effects in locations where they clump together to form combined halos or grazing fronts, since it is difficult in these circumstances to attribute grazing impacts to individual sea urchins. However, grazing halos are relatively common in most Mediterranean rocky reefs (Bulleri, 2013; Pessarrodona et al., 2019), providing a useful way to tease apart the relative importance of endogenous and exogenous factors that influence the relationship between production and grazing and helping identify the relative vulnerability of macroalgal communities.

CONCLUSION

What do all these interactions mean for the vulnerability of vegetated ecosystems to overgrazing? The emphasis has long been on understanding herbivore population dynamics and their key drivers, intending to identify abundance thresholds beyond which vegetated habitats exhibit catastrophic shifts to depauperate states devoid of vegetation (Eklöf et al., 2008; Filbee-Dexter & Scheibling, 2014; Ling et al., 2015; Steneck et al., 2002). However, there are inherent difficulties in predicting and generalizing these ecosystem thresholds (e.g., see Conversi et al., 2015). Our study suggests that we need to shift our focus towards understanding the many context-specific interacting factors that influence plant-herbivore interactions, since these may provide better insights of the multiple underlying mechanisms of collapse. As our study shows, these interactions are often strongly influenced by the identity of the biotic agents involved and local environmental conditions like nutrients, depth, and/or predators' presence, making predictions all the more complex (Boada et al., 2017; Pagès et al., 2018; Pessarrodona et al., 2019). To improve the robustness of our predictions at managerially meaningful scales, we need to move from measuring states to understanding interactions. The vulnerability of macrophyte ecosystems to collapse pivots on the abundance of herbivores and the strength of the production-consumption relationship. Understanding this interaction requires a deeper knowledge of the many specific factors that influence it, and the local conditions that mediate it (Boada et al., 2017; Hereu et al., 2008; Pagès et al., 2018). When attempting to protect vegetated habitats from overgrazing, ecosystem managers need a bespoke, integrative approach suited to each region, community composition, and degree of protection. Ecosystems with

similar biomasses of herbivores and macrophytes could exhibit markedly different vulnerabilities to catastrophic collapses, depending on local conditions (Ling et al., 2015). In general, nutrient-enriched areas, with greater light availability, dominated by smaller herbivores of less impactful species and with a full complement of their predators, will be far more resilient to overgrazing events. Hence, in the current context of cumulative impacts resulting from global change, it becomes imperative to understand these context-specific differences to implement adequate management measures, whether they rely on securing trophic relationships, reducing anthropogenic pressures, controlling herbivore populations, or other forms of habitat management. Integrating general trends with context specificity is critical, since real-world ecosystems dominated by vegetation are rarely, if ever, driven by a single controlling variable (Conversi et al., 2015; Hereu et al., 2008). Managing ecosystems requires us to engage meaningfully with this inherent local complexity.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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REFERENCES

Agnetta, D., F. Badalamenti, G. Ceccherelli, F. Di Trapani, C. Bonaviri, and P. Gianguzza. 2015. "Role of Two co-Occurring Mediterranean Sea Urchins in the Formation of Barren from *Cystoseira* Canopy." *Estuarine, Coastal and Shelf Science* 152: 73–77.

Agnetta, D., C. Bonaviri, F. Badalamenti, C. Scianna, S. Vizzini, and P. Gianguzza. 2013. "Functional Traits of Two Co-Occurring Sea Urchins across a Barren/Forest Patch System." *Journal of Sea Research* 76: 170–77.

Babcock, R. C., N. T. Shears, A. C. Alcala, N. S. Barrett, G. J. Edgar, K. D. Lafferty, T. R. McClanahan, and G. R. Russ. 2010. "Decadal Trends in Marine Reserves Reveal Differential Rates of Change in Direct and Indirect Effects." *Proceedings of the National Academy of Sciences* 107: 18256–61.

Bakker, E. S., K. A. Wood, J. F. Pagès, G. C. Veen, M. J. A. Christianen, L. Santamaría, B. A. Nolet, and S. Hilt. 2016. "Herbivory on Freshwater and Marine Macrophytes: A Review and Perspective." *Aquatic Botany* 135: 18–36.

Ballesteros, E. 1989. "Production of Seaweeds in Northwestern Mediterranean Marine Communities: its Relation with Environmental Factors." *Scientia Marina* 53: 357–364.

Barrientos, S., C. Piñeiro-Corbeira, and R. Barreiro. 2022. "Temperate Kelp Forest Collapse by Fish Herbivory: A Detailed Demographic Study." *Frontiers in Marine Science* 9: 817021.

Bartoń, K. 2022. "MuMIn: Multi-Model Inference." R Package Version 1.47.1. https://CRAN.R-project.org/package=MuMIn

Boada, J., R. Arthur, D. Alonso, J. F. Pagès, A. Pessarrodona, S. Oliva, G. Ceccherelli, L. Piazzi, J. Romero, and T. Alcoverro. 2017. "Immanent Conditions Determine Imminent Collapses: Nutrient Regimes Define the Resilience of Macroalgal Communities." *Proceedings of the Royal Society B: Biological Sciences* 284: 20162814.

Bolker, B. M. 2008. *Ecological Models and Data in R*. Princeton, NJ: Princeton University Press.

Boudouresque, C. F., and M. Verlaque. 2020. "*Paracentrotus lividus*." In *Sea Urchins: Biology and Ecology*, edited by J. M. Lawrence, 4th ed. 447–485. Amsterdam, The Netherlands: Elsevier.

Bulleri, F. 2013. "Grazing by Sea Urchins at the Margins of Barren Patches on Mediterranean Rocky Reefs." *Marine Biology* 160: 2493–2501.

Bulleri, F., L. Benedetti-Cecchi, and F. Cinelli. 1999. "Grazing by the Sea Urchins *Arbacia lixula* L. and *Paracentrotus lividus* Lam. in the Northwest Mediterranean." *Journal of Experimental Marine Biology and Ecology* 241: 81–95.

Burkepile, D. E., and M. E. Hay. 2006. "Herbivore vs. Nutrient Control of Marine Primary Producers: Context-Dependent Effects." *Ecology* 87: 3128–39.

Burnham, K. P., and D. R. Anderson. 2004. *Model Selection and Multimodel Inference*. New York, NY: Springer New York.

Chamberlain, S. 2022. "Rerddap: General Purpose Client for 'ERDDAP' Servers." R Package Version 1.0.0. https://CRAN.R-project.org/package=rerddap

Christianen, M. J. A., F. O. H. Smulders, J. A. Vonk, L. E. Becking, T. J. Bouma, S. M. Engel, R. K. James, et al. 2023. "Seagrass Ecosystem Multifunctionality under the Rise of a Flagship Marine Megaherbivore." *Global Change Biology* 29: 215–230.

Conversi, A., V. Dakos, A. Gårdmark, S. Ling, C. Folke, P. J. Mumby, C. Greene, et al. 2015. "A Holistic View of Marine Regime Shifts." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20130279.

Cramer, W., J. Guiot, M. Fader, J. Garrabou, J.-P. Gattuso, A. Iglesias, M. A. Lange, et al. 2018. "Climate Change and Interconnected Risks to Sustainable Development in the Mediterranean." *Nature Climate Change* 8: 972–980.

Dayton, P. K. 1985. "Ecology of Kelp Communities." *Annual Review of Ecology and Systematics* 16: 215–245.

Delignette-Muller, M. L., and C. Dutang. 2015. "fitdistrplus: An R Package for Fitting Distributions." *Journal of Statistical Software* 64: 1–34.

Eklöf, J. S., M. De La Torre-Castro, M. Gullström, J. Uku, N. Muthiga, T. Lyimo, and S. O. Bandeira. 2008. "Sea Urchin Overgrazing of Seagrasses: A Review of Current Knowledge on Causes, Consequences, and Management." *Estuarine, Coastal and Shelf Science* 79: 569–580.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, et al. 2011. "Trophic Downgrading of Planet Earth." *Science* 333: 301–6.

Filbee-Dexter, K., and R. Scheibling. 2014. "Sea Urchin Barrens as Alternative Stable States of Collapsed Kelp Ecosystems." *Marine Ecology Progress Series* 495: 1–25.

Filbee-Dexter, K., and T. Wernberg. 2018. "Rise of Turfs: A New Battlefront for Globally Declining Kelp Forests." *Bioscience* 68: 64–76.

Fox, J., S. Weisberg, D. Adler, D. Bates, G. Baud-Bovy, S. Ellison, D. Firth, M. Friendly, G. Gorjanc, and S. Graves. 2012. *Package 'Car'*. Vienna: R Foundation for Statistical Computing.

Fung, T., R. M. Seymour, and C. R. Johnson. 2011. "Alternative Stable States and Phase Shifts in Coral Reefs under Anthropogenic Stress." *Ecology* 92: 967–982.

Gianguzza, P. 2020. "Arbacia." In *Developments in Aquaculture and Fisheries Science*, 419–429. Amsterdam, The Netherlands: Elsevier.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. "A Framework for Community Interactions under Climate Change." *Trends in Ecology & Evolution* 25: 325–331.

Gruner, D. S., J. E. Smith, E. W. Seabloom, S. A. Sandin, J. T. Ngai, H. Hillebrand, W. S. Harpole, et al. 2008. "A Cross-System Synthesis of Consumer and Nutrient Resource Control on Producer Biomass." *Ecology Letters* 11: 740–755.

Guidetti, P. 2006. "Marine Reserves Reestablish Lost Predatory Interactions and Cause Community Changes in Rocky Reefs." *Ecological Applications* 16: 963–976.

Guidetti, P., and M. Mori. 2005. "Morpho-Functional Defences of Mediterranean Sea Urchins, *Paracentrotus lividus* and *Arbacia lixula*, against Fish Predators." *Marine Biology* 147: 797–802.

Hartig, F. 2022. "Dharma: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models."

Hereu, B. 2005. "Movement Patterns of the Sea Urchin *Paracentrotus lividus* in a Marine Reserve and an Unprotected Area in the NW Mediterranean." *Marine Ecology* 26: 54–62.

Hereu, B., M. Zabala, and E. Sala. 2008. "Multiple Controls of Community Structure and Dynamics in a Sublittoral Marine Environment." *Ecology* 89: 3423–35.

Jia, S., X. Wang, Z. Yuan, F. Lin, J. Ye, Z. Hao, and M. S. Luskin. 2018. "Global Signal of Top-Down Control of Terrestrial Plant Communities by Herbivores." *Proceedings of the National Academy of Sciences* 115: 6237–42.

Kempf, M. 1962. "Recherches d'écologie comparée sur *Paracentrotus lividus* (Lmk.) et *Arbacia lixula* (L.)." *Recueil des Travaux de la Station Marine d'Endoume* 25: 47–115.

Kriegisch, N., S. E. Reeves, C. R. Johnson, and S. D. Ling. 2019. "Top-Down Sea Urchin Overgrazing Overwhelms Bottom-Up Stimulation of Kelp Beds despite Sediment Enhancement." *Journal of Experimental Marine Biology and Ecology* 514–515: 48–58.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.

Lenth, R. 2024. "emmeans: Estimated Marginal Means, aka Least-Squares Means." R Package Version 1.10.1.

Ling, S. D., and C. R. Johnson. 2012. "Marine Reserves Reduce Risk of Climate-Driven Phase Shift by Reinstating Size-and Habitat-Specific Trophic Interactions." *Ecological Applications* 22: 1232–45.

Ling, S. D., C. R. Johnson, S. D. Frusher, and K. R. Ridgway. 2009. "Overfishing Reduces Resilience of Kelp Beds to Climate-Driven Catastrophic Phase Shift." *Proceedings of the National Academy of Sciences* 106: 22341–45.

Ling, S. D., N. Kriegisch, B. Woolley, and S. E. Reeves. 2019. "Density-Dependent Feedbacks, Hysteresis, and Demography of Overgrazing Sea Urchins." *Ecology* 100: e02577.

Ling, S. D., R. E. Scheibling, A. Rassweiler, C. R. Johnson, N. Shears, S. D. Connell, A. K. Salomon, et al. 2015. "Global Regime Shift Dynamics of Catastrophic Sea Urchin Overgrazing." *Philosophical Transactions of the Royal Society B: Biological Sciences* 370: 20130269.

Lüdecke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. "performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6(60): 3139.

Mann, K. H. 1973. "Seaweeds: Their Productivity and Strategy for Growth: The Role of Large Marine Algae in Coastal Productivity Is Far more Important than Has Been Suspected." *Science* 182: 975–981.

Minguito-Frutos, M., and T. Alcoverro. 2025. "Grazing Halos Reveal Differential Ecosystem Vulnerabilities in Vegetated Habitats." Zenodo. https://doi.org/10.5281/zenodo.17012364

Monserrat, M., D. Catania, V. Asnaghi, M. Chiantore, R. Lemée, and L. Mangialajo. 2022. "The Role of Habitat in the Facilitation of *Ostreopsis* spp. Blooms." *Harmful Algae* 113: 102199.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. "Thresholds and the Resilience of Caribbean Coral Reefs." *Nature* 450: 98–101.

Myers, R. A., and B. Worm. 2003. "Rapid Worldwide Depletion of Predatory Fish Communities." *Nature* 423: 280–83.

Nikolaou, A., K. Tsirintanis, G. Rilov, and S. Katsanevakis. 2023. "Invasive Fish and Sea Urchins Drive the Status of Canopy Forming Macroalgae in the Eastern Mediterranean." *Biology* 12: 763.

O'Connor, M. I. 2009. "Warming Strengthens an Herbivore–Plant Interaction." *Ecology* 90: 388–398.

Pagès, J. F., F. Bartumeus, J. Romero, and T. Alcoverro. 2021. "The Scent of Fear Makes Sea Urchins Go Ballistic." *Movement Ecology* 9: 50.

Pagès, J. F., T. M. Smith, F. Tomas, N. Sanmartí, J. Boada, H. De Bari, M. Pérez, J. Romero, R. Arthur, and T. Alcoverro. 2018. "Contrasting Effects of Ocean Warming on Different Components of Plant-Herbivore Interactions." *Marine Pollution Bulletin* 134: 55–65.

Pessarrodona, A., J. Boada, J. F. Pagès, R. Arthur, and T. Alcoverro. 2019. "Consumptive and Non-consumptive Effects of Predators Vary with the Ontogeny of their Prey." *Ecology* 100: e02649.

Pessarrodona, A., K. Filbee-Dexter, T. Alcoverro, J. Boada, C. J. Feehan, S. Fredriksen, S. P. Grace, et al. 2021. "Homogenization and Miniaturization of Habitat Structure in Temperate Marine Forests." *Global Change Biology* 27: 5262–75.

Pisano, A., S. Marullo, V. Artale, F. Falcini, C. Yang, F. E. Leonelli, R. Santoleri, and B. Buongiorno Nardelli. 2020. "New Evidence of Mediterranean Climate Change and Variability from Sea Surface Temperature Observations." *Remote Sensing* 12: 132.

Poore, A. G. B., A. H. Campbell, R. A. Coleman, G. J. Edgar, V. Jormalainen, P. L. Reynolds, E. E. Sotka, et al. 2012. "Global Patterns in the Impact of Marine Herbivores on Benthic Primary Producers." *Ecology Letters* 15: 912–922.

Pringle, R. M., J. O. Abraham, T. M. Anderson, T. C. Coverdale, A. B. Davies, C. L. Dutton, A. Gaylard, et al. 2023. "Impacts of Large Herbivores on Terrestrial Ecosystems." *Current Biology* 33: R584–R610.

Sala, E., E. Ballesteros, P. Dendrinos, A. Di Franco, F. Ferretti, D. Foley, S. Fraschetti, et al. 2012. "The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications." *PLoS One* 7: e32742.

Sala, E., C. F. Boudouresque, and M. Harmelin-Vivien. 1998. "Fishing, Trophic Cascades, and the Structure of Algal Assemblages: Evaluation of an Old but Untested Paradigm." *Oikos* 82: 425.

Sant, N., and E. Ballesteros. 2021. "Depth Distribution of Canopy-Forming Algae of the Order Fucales Is Related to Their Photosynthetic Features." *Marine Ecology* 42: e12651.

Santana-Garcon, J., S. Bennett, N. Marbà, A. Vergés, R. Arthur, and T. Alcoverro. 2023. "Tropicalization Shifts Herbivore Pressure from Seagrass to Rocky Reef Communities." *Proceedings of the Royal Society B: Biological Sciences* 290: 20221744.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. "Catastrophic Shifts in Ecosystems." *Nature* 413: 591–96.

Schielzeth, H., N. J. Dingemanse, S. Nakagawa, D. F. Westneat, H. Allegue, C. Teplitsky, D. Réale, N. A. Dochtermann, L. Z. Garamszegi, and Y. G. Araya-Ajoy. 2020. "Robustness of Linear Mixed-Effects Models to Violations of Distributional Assumptions." *Methods in Ecology and Evolution* 11: 1141–52.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. "A Cross-Ecosystem Comparison of the Strength of Trophic Cascades." *Ecology Letters* 5: 785–791.

Smale, D. A., M. T. Burrows, P. Moore, N. O'Connor, and S. J. Hawkins. 2013. "Threats and Knowledge Gaps for Ecosystem Services Provided by Kelp Forests: A Northeast Atlantic Perspective." *Ecology and Evolution* 3: 4016–38.

Steneck, R. S., D. R. Bellwood, and M. E. Hay. 2017. "Herbivory in the Marine Realm." *Current Biology* 27: R484–R489.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner. 2002. "Kelp Forest Ecosystems: Biodiversity, Stability, Resilience and Future." *Environmental Conservation* 29: 436–459.

Strain, E. M. A., R. J. Thomson, F. Micheli, F. P. Mancuso, and L. Airoldi. 2014. "Identifying the Interacting Roles of Stressors in Driving the Global Loss of Canopy-Forming to Mat-Forming Algae in Marine Ecosystems." *Global Change Biology* 20: 3300–3312.

Suskiewicz, T. S., and L. E. Johnson. 2017. "Consumption Rates of a Key Marine Herbivore: A Review of the Extrinsic and Intrinsic Control of Feeding in the Green Sea Urchin." *Marine Biology* 164: 131.

Trepel, J., E. Le Roux, A. J. Abraham, R. Buitenwerf, J. Kamp, J. A. Kristensen, M. Tietje, E. J. Lundgren, and J.-C. Svenning. 2024. "Meta-Analysis Shows that Wild Large Herbivores Shape Ecosystem Properties and Promote Spatial Heterogeneity." *Nature Ecology & Evolution* 8: 705–716.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. "Global Change and Species Interactions in Terrestrial Ecosystems." *Ecology Letters* 11: 1351–63.

Vergés, A., F. Tomas, E. Cebrian, E. Ballesteros, Z. Kizilkaya, P. Dendrinos, A. A. Karamanlidis, D. Spiegel, and E. Sala. 2014. "Tropical Rabbitfish and the Deforestation of a Warming Temperate Sea." *Journal of Ecology* 102: 1518–27.

Verlaque, M. 1984. "Biologie des juvéniles de l'oursin herbivore *Paracentrotus lividus* (Lamarck): séléctivité du broutage et impact de l'espéce sur les communautés algales de substrat rocheux en Corse (Méditerranée, France)." *botm* 27: 401–424.

Wangensteen, O., X. Turon, A. García-Cisneros, M. Recasens, J. Romero, and C. Palacín. 2011. "A Wolf in Sheep's Clothing: Carnivory in Dominant Sea Urchins in the Mediterranean." *Marine Ecology Progress Series* 441: 117–128.

Wernberg, T., S. Bennett, R. C. Babcock, T. De Bettignies, K. Cure, M. Depczynski, F. Dufois, et al. 2016. "Climate-Driven Regime Shift of a Temperate Marine Ecosystem." *Science* 353: 169–172.

Wood, K. A., M. T. O'Hare, C. McDonald, K. R. Searle, F. Daunt, and R. A. Stillman. 2017. "Herbivore Regulation of Plant Abundance in Aquatic Ecosystems." *Biological Reviews* 92: 1128–41.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. "Consumer Versus Resource Control of Species Diversity and Ecosystem Functioning." *Nature* 417: 848–851.

Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. "Biotic Multipliers of Climate Change." *Science* 336: 1516–18.

Zuur, A. F., E. N. Ieno, and A. A. Saveliev. 2017. *Beginner's Guide to Spatial, Temporal and Spatial-Temporal Ecological Data Analysis with R-INLA. Volume I: Using GLM and GLMM.* Newburgh: Highland Statistics Ltd.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R.* New York, NY: Springer New York.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.