Homogenization and miniaturization of habitat structure in temperate marine forests

Albert Pessarrodona[1,*], Karen Filbee-Dexter[1,2], Teresa Alcoverro[3,4,≠], Jordi Boada[3, 5,≠], Colette J. Feehan[6,≠], Stein Fredriksen[2,7,≠], Sean P. Grace[8,≠], Yohei Nakamura[9,≠], Carla A. Narvaez[10,≠], Kjell Magnus Norderhaug[2,≠], Thomas Wernberg[1,2,11]

[1] UWA Oceans Institute and School of Biological Sciences, University of Western Australia, Crawley, Western Australia 6009, Australia
[2] Institute of Marine Research, His, Norway
[3] Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Carrer d'Accés a la cala Sant Francesc 14, Blanes 17300 Spain
[4] Nature Conservation Foundation, Amritha, 1311, 12th Cross, Vijayanagara 1st stage, Mysore 570017 India
[5] Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain
[6] Department of Biology, Montclair State University, Montclair, NJ, 07043, USA.
[7] Department of Biosciences, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway
[8] Department of Biology and Werth Center for Coastal and Marine Studies, Southern Connecticut State University, New Haven, CT, 06515, USA.
[9] Faculty of Agriculture and Marine Science, Kochi University, Nankoku, Kochi 783-8502, Japan
[10] Department of Biology, Villanova University, Villanova, PA, 19085, USA.
[11] Roskilde University, Box 260, Roskilde 4000, Denmark

≠ Authors listed in alphabetical order
*Correspondence: Email: pessa3@gmail.com

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Abstract

Humans are rapidly transforming the configuration of the planet's ecosystems. Understanding the ecological and socioeconomical repercussions of these changes is however challenged by the diversity of drivers and species characterizing such shifts at local and regional scales. Here we show that the loss of forest-forming seaweeds and the rise of ground-covering 'turfs' across four continents consistently resulted in the simplification of underwater habitat structure, with seascapes converging towards flattened habitats that were structurally more homogenous and less complex than forests. Surprisingly, convergence occurred despite these seascapes consisting of vastly different species richness and seaweed groups providing architecture, as well as disparate drivers of forest loss. We also found that turf-driven habitat structural changes across 100s of km resulted in extensive reductions (1300%) in ecosystem carbon storage and massive increases (2300%) in the accumulation and retention of sediments on reefs. Indeed, high amounts of sediments where found in all the regions studied, probably as a result of the high sediment trapping efficiency of turfs. Together, this work demonstrates that the replacement of marine forests by turfs is a generalizable phenomenon that has profound consequences for the ecology of temperate reefs.

Trees is documented on land, much less is known in underwater forests. Spatially variable trajectories reflects differences in the driver of change at the regional and nature

Multi-layered and structurally complex coastal forests transition to marshes with very little complexity following saltwater intrusion. Losses in structural complexity have important implications for carbon storage.
While the implications of losses in forest structural complexity

Introduction

Humans are increasingly modifying natural systems at a global scale, reconfiguring their species composition and transforming their three-dimensional structure which ultimately leads to changes in ecosystem processes and the services they provide to humanity (*1*, *2*). Declines in foundation species such as trees, corals or large seaweeds are major drivers of ecosystem-level shifts, as their architectural traits define the habitat structure that is directly responsible for supporting enhanced biodiversity (*3*), modifying local environmental conditions and regulating numerous physical and biological processes (*4*). In contrast, the novel conditions imposed by global change appear to favour species able to capitalize on rapidly shifting environmental conditions (*5*), allowing them to competitively displace foundation species and become habitat dominants (*6*). As Earth's habitats continue to change at an accelerating rate, a pressing challenge is to understand how such transformations affect biodiversity and ecosystem functions (*7*). Yet, achieving a unified understanding is challenged by the mismatch between the global manifestation of changes and local-scale differences in the species compositions and environmental settings characterizing shifts to new habitats.

The architectural traits of foundation species such as trees, corals or large seaweeds define the habitat structure that is directly responsible for supporting enhanced biodiversity (*3*), modifying local environmental conditions and regulating numerous physical and biological processes (*4*). Yet, humans are increasingly modifying natural systems at a global scale, reconfiguring their species composition and transforming their three-dimensional structure which ultimately leads to changes in ecosystem processes and the services they provide to humanity (*1*, *2*). are major drivers of ecosystem-level shifts, as their architectural traits In contrast, the novel conditions imposed by global change appear to favour species able to capitalize on rapidly shifting environmental conditions (*5*), allowing them to competitively displace foundation species and become habitat dominants (*6*). As Earth's habitats continue to change at an accelerating rate, a pressing challenge is to understand how such transformations affect biodiversity and ecosystem functions (*7*). Although local evidence suggests that these are changing, the patterns of marine forest change are regionally variable,

Yet, regionally variable trajectories of change, achieving a unified understanding is challenged by the mismatch between the global manifestation of changes and local-scale differences in the species compositions and environmental settings characterizing shifts to new habitats.

given their disproportionate
importance to forest structure, function, and carbon storage

In the marine realm, marine forests provide a great framework to assess how foundational changes in species composition affect habitat complexity and refuge provision. Marine forests are created by seaweeds that form canopies that modify the surrounding environment, are typically competitively dominant and support distinct associated biodiversity and sustain coastal economies worldwide (*8*).

Forests across the globe are rapidly reconfiguring into novel states dominated by new forest-forming species (e.g. warm-affinity species) and non-forest-forming organisms such as corals, sea urchins or seaweed turfs (*9*). Systems dominated by turfs – aggregations of single or multiple species of low-lying seaweed characteristic of opportunistic or early successional states – are emerging as one of the most extensive configurations arising from forest decline (*10*–*12*). The expansion of turf seascapes is a relatively new phenomenon which has intensified in many regions of the world over the last two decades (*13*), presumably in response to accelerating impacts of humans to the marine environment. Turfs generally have rapid rates of growth and invasion (*14*), and anthropogenic pressures such as warming, eutrophication, sedimentation or ocean acidification promote their growth and allow them to become competitively superior, often expanding over vast areas of the seafloor (*14*, *15*).

Although shifts towards turf-dominance have been reported along multiple coasts globally (e.g. (*13*, *16*)), we only have scarce empirical evidence of their geographic variation. While it is clear than turf seascapes represent architecturally new configurations compared to forests (*13*), whether these novel habitats share any general characteristics remains unresolved (*12*). 'Turfs' encompass aggregations of species that are extremely phylogenetically diverse and exhibit a wide range of morphologies, densities and vastly different heights (*12*) and may thus provide equally diverse habitat structures to those erected by forests. Measuring species architectural traits is a promising way to examine how composition shifts affect overall habitat complexity and ecosystem functioning across biogeography, as not only are these traits directly related to physical structure of a habitat, but also to several aspects of a species' life-history strategy (*17*).

Here, we characterize the transformation of habitat structural complexity experienced when seascapes transition from forest to turf dominance at six distinct temperate marine ecoregions spanning four continents. To understand the structure of these emerging habitats across disparate ecological and biogeographical contexts, we focused on locations described to have undergone shifts towards turf dominance, using our sampling sites as case studies that can help quantitatively project ongoing transformations in other regions. All sampling sites had experienced forest loss during the last half-century, albeit as a result of a wide range of abiotic (e.g. warming, eutrophication) and biotic (e.g. biological invasions) anthropogenic pressures (Table S1). We first quantified the so-called 'turf' assemblages at multiple sites at each study region. To document changes in habitat structure and track the architectural configuration evolution of individual reefs through their transition from forests to turfs, we then used comparisons with historical datasets as well as a trait-based approach.

Materials and Methods

Vegetation structure of turf seascapes

Within each ecoregion, three (most regions) to eight (Scotian Shelf) study sites were selected based on the following criteria: i) sites had to be presently dominated by seaweed turfs, but historically dominated (i.e. had the greatest cover) by forest-forming seaweeds; and ii) sites should be not influenced by atypical, localized landscape features (e.g. large rivers, sewage outfalls). Seaweed turfs were defined following the nomenclature used by previous studies at each of the sampling regions (Table S1), which criteria was mostly based on space use in the water column, i.e. a low-lying layer of single or multiple species of seaweeds. Forest-forming species on the other hand referred to seaweeds that are able to establish canopies (e.g. kelps, *Desmarestia spp.*, *Cystoseira spp., Sargassum spp.*). In each ecoregion, we targeted our sampling depth (0.5-8 m below Chart Datum) to where marine forests were documented to have been most abundant (Table S1; Supplementary Text). Sampling sites within ecoregions were at least 2 km apart.

To characterize the turf assemblage at each site, SCUBA divers haphazardly placed 0.04 m^2 (most regions), 0.1 m^2 (Scotian Shelf), or 0.25 m^2 (Narragansett Bay) quadrats over a flat area covered by seaweed turfs and took a picture of the quadrat to later estimate the cover of its seaweed species (n=2-10; Table S1). Different sampling areas were used so that the quadrat was visually greater than the structural pattern of the turf assemblage, quadrat sizes being comparable to other studies (e.g. ref. 28). The number of quadrats collected varied depending on weather and diving conditions. The height of the turf vegetation was estimated at 5 fixed points within the quadrat with a teeth-graded wire-mesh comb. All the non-encrusting algae was then scraped off the rock using a putty knife and collected in 125 µm mesh bags attached at the end of a Venturi suction sampler. Suitable sampling surfaces were flat (<45° from horizontal) areas on bedrock or large boulders (>10 m wide) without any large sediment-retaining pits or sessile organisms. Quadrats were at least 5 m apart. Samples were frozen within six hours of collection and transported to the laboratory. Upon processing, samples were carefully washed through a 2 mm sieve to separate the sediment and algal components. All algal fragments gathered in the sieve were then identified to the lowest taxonomical resolution possible. After identification, algae were weighed separately and grouped into the following morphofunctional classifications following ref. 17: Filamentous (e.g. *Ceramium*, *Polysiphonia*), Foliose (e.g. *Porphyra*), Corticated (e.g. *Dictyota*, *Chondrus*, *Phyllophora*), Leathery (e.g. *Ecklonia*, *Cystoseira*)and Articulated calcareous (e.g. *Amphiroa*, *Corallina*, *Marginosporum*).

Habitat structure change

We drew upon two independent sources of insight to establish how habitat structure changed through the transition from forests to turf dominance: (i) we compared the contemporary vegetation structure with data from historical studies and quantified the architectural traits between currently- (turf-forming) and historically-dominant (forest-forming) species, and (ii) quantitatively measured how the multidimensional architectural configuration of reefs changed through time using landscape-level surveys of species/group abundance and trait information.

Historical comparisons. We compared two key vegetation structure metrics (plant height and vegetation biomass) of contemporary turf seascapes with their historical forested states as they are important drivers of overall habitat structure. We used the measurements derived from our sampling programme and values reported in the literature also targeting vegetation at the seacaspe level (Table S5). Biomass data for the forested state was usually collected in larger (0.1 – 1 m^2) quadrats than the ones used for turfs and so extrapolating turf values to larger areas (i.e. assuming a linear relationship between biomass and area) likely overestimated turf biomass and underestimated differences observed between forests and turf seascapes in field settings. Plant height was generally measured in adult, fully-grown specimens in the field and used as a proxy for canopy height.

Species architectural traits. We collected species-level data on five architectural traits that are important determinants of the abundance, species richness and body-size distribution of organisms inhabiting macroalgal habitats (*11*, *39–41*). Plant height was selected as proxy for canopy height, an important indicator of forest structure and species ecological strategy that relates to competitive dominance, resource acquisition and also correlates with plant cellular complexity and plant biomass (*18*, *42*). Plant surface area was selected as an indication of the total surface available for colonization by epiphytes (*43*). The perimeter area ratio (P/A) —an index relating to 3D complexity and overall plant shape— was selected to compare the shape of thalli between species. We used the corrected version ($P/A = 0.282 * \text{Perimeter} / \sqrt{\text{Area}}$), as the ratio is otherwise dependent on size (*43*). The final two traits related to the interstitial spaces created by a species branching pattern, which are important habitats for meso- and micro-fauna (*44*). Interstitial space surface area was defined as the area between branches that have the same point of bifurcation (*39*) (Fig. S5). Interstitial space did not extend beyond the two branches, but was measured by drawing a straight line between the ends of the branch tips. For filamentous algae, interstitial spaces were delineated where filaments crossed (*32*). The trait interstitial space density (defined as the number of interstitial spaces divided by the total interstitial area) provides a measurement of the relative abundance of interstitial spaces that can be potentially colonized by fauna, whereas mean interstitial space surface area relates to the size of those potential habitats, which is an important factor determining the body-size structure of colonizing fauna (*39*). We tested for correlation between traits using a Pearson correlation coefficient and no traits were correlated above 0.70.

To obtain all architectural trait values, we measured images of pressed and dried thalli of the principal (>2 % cover or biomass) turf and dominant forest-forming species of each ecoregion (n=5-14). Digitized images were downloaded from the Macroalgal Herbaria Portal (www.macroalgae.org), which contains scaled images from macroalgal specimens from all over the world. While we recognize that pressed scans might not capture equally well the structural intricacies of each species of seaweed, we used this approach as it could be consistently applied to different seaweed groups and was transferrable across biogeography, which could help future efforts to quantify habitat transformations in other regions. To better capture trait variation in species with complex morphologies (e.g. *Polysiphonia*), a greater number of replicates was digitized. All architectural traits were measured using the line, selection and particle analyser tools in ImageJ (*45*).

Reef habitat structure. To quantify the reef architectural configuration at any given point in time, we used habitat surveys and a community weighted mean (CWM) analysis of the 5 architectural traits measured above. Surveys were conducted at the seascape level (i.e. 10s-100s m) to estimate the percent cover of different seaweed taxa and the following habitat components: sponges, hard and soft corals, other habitat-forming organisms (e.g. mussels, oysters), bare rock and sand. Surveys in each region used a variety of methods (e.g. photoquadrats, visual estimates, drop camera surveys) depending on weather conditions, diving regulations and study purposes (See Table S3 for details).

Our analysis focused on seaweed taxa, bare rock and sand as other habitat structuring organisms (e.g. sponges, corals, gorgonians) were absent from Skagerrak, Narragansett Bay and the Scotian Shelf (Fig. S1) or presented minimal cover (i.e. a maximum of <6% at the seascape level at any given point) in the other regions. The historical survey from the NW Mediterranean was an exception, were a 15-30% cover of mussels was reported in the quadrats (total n=4). The relative abundance of seaweed taxa, sand and rock was subsequently recomputed based on the total of these categories. Seaweed taxa included species-level covers for the largest habitat-forming species (i.e. *Ecklonia radiata*, *Ecklonia cava*, *Cystoseira* spp. *Saccharina latissima*, *Desmarestia viridis*, *Sargassum spp*., *Codium fragile*) as well as multi-species assemblage covers in the case of turfs and encrusting algae (see below). Seaweeds that could not be identified at any of these levels contributed minimally to the mean seascape percentage cover (i.e. a maximum of <2.5%), and were classed as 'other'. Seaweed species contributing <1% to the mean cover at a given site were not included in the analysis, as they would have contributed relatively minimally to the CWM.

The historical cover of non-forest forming taxa and habitat components could not be determined at four of our sites (Mill Cove, S6/7, S15 and Fort Wetherhill; Table S3). For these subset of observations (11/104 total) we assumed than the rest of the habitat was covered by turfs. This assumption was based on the fact that turfs were the next most abundant cover category in the historical states of other sites and regions, and other habitat components contributed relatively minorly to the total cover (Fig. S1). Non-forest forming cover for historical data from SW Japan was categorized as 'rock or turf', and the same assumption was made.

The architectural configuration of a reef was therefore defined by the CWM of the 5 architectural traits measured above, with the CWM value being the mean trait value of a given seaweed taxa or habitat component, weighted by its relative abundance (i.e. relative percent cover). Encrusting algae, rock and sand were considered to provide no structure and therefore had a value of zero for any trait. Species of *Sargassum* and *Cystoseira* could not reliably be identified during the seascape level surveys and were grouped into a genus-level category. In that case, the traits of the most common species of that group at our sites were used to compute the trait values (i.e. *Sargassum okamurae* and *Sargassum fallax* for Sargassum *spp*. in SW Japan and the W Australian Shelf respectively, *Cystoseira mediterranea* for *Cystoseira spp.* in the NW Mediterranean).

To obtain architectural trait values for the 'turf' assemblage, which contains several species, we computed an additional CWM for each trait based on the relative percent cover or relative biomass (i.e. % fresh weight) of each species within the turf assemblage obtained during our assemblage surveys above (Fig. S6). This assumed that the species composition recorded in our surveys was representative of the 'turf' assemblage observed through time. Percent cover was measured in Adobe Photoshop CC (Adobe Systems Inc.) with the aid of a reticulum of 25 cells (5×5) superimposed over the photographed quadrats; the cover within each cell in which a species appeared was recorded. Turf-forming species contributing <2% to the mean cover or biomass at a given site were not included in the analysis. Biomass data was used for the Scotian Shelf and Narragansett Bay regions. Turf CWM trait values were site-specific when the assemblage-sampling sites matched the seascape-survey sites; when that was not the case (i.e. 4/14 sites: PGS1, PGN1, S6/7, Illa de Tossa), a regional mean value of each trait was used.

Consequences of habitat change

To explore the ecosystem consequences of the habitat structural changes documented above, we quantified carbon storage and sediment accumulation in reefs across the Western Australia study region (Fig. SXA). We chose mid-Western Australia as a case study as it suffered one of the most extensive and well-documented marine forest losses on the planet (*20*), and focused on these two ecosystem properties as they are key drivers of carbon cycling and the trophic transfer of energy (*22*, *23*).

We measured the standing biomass (stock) and sediment loads associated with the benthic habitat-forming categories as per our surveys above. The biomass and sediment load of turfs was derived from the turf vegetation structure surveys described above, while the biomass and sediment associated with the rest of benthic taxa was derived from additional sampling. In these, quadrats (n=X) were placed above an area 100% covered by the habitat-forming taxa (e.g. Sargassum,); Corals, sponges and XX were assumed to have accumulate. The area of derive before (2006) and after (2017).

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with and quantified the area covered by kelp was derived from (*20*), which used species distribution models employing bathymetry derived terrain variables and georeferenced towed video data to predict the distribution of kelp. The number of pixels containing kelp was summed for each latitudinal interval to yield the area estimates. The sediment loads accumulated on reefs were measured. While, the discharge of nearby rivers has experienced no discernable increase in the last few years (Fig. SXB), and so we assumed that the input of riverine sediments had not changed between the years where reefs where forest- or turf-dominated.

Architectural traits of global marine forests and turf seascapes

To put the documented patterns in habitat architecture into context of the broader configurations of marine forests globally, we compiled architectural trait data on other forest-forming species and compared it to the trait measurements of forest- and turf-forming species used in our analysis. Additional data on other turf-forming species was not collected as the species examined in the present study already represented the entire trait range of turfs (*12*, *32*). We focused on ‘plant height’ and ‘plant surface area’ as they both were important traits in our analysis of habitat structure shifts, and are commonly reported. Data was compiled from unpublished studies and the literature (Dataset S1), where it was reported in the text of the manuscript or obtained using the WebPlotDigitizer tool (*46*). For each study we recorded the mean and standard deviation of each trait when available, as well as the date, location, depth, number of individuals measured and duration of the study (e.g. monthly measurements). Values from as many sites as possible within a given species range were compiled.

Statistical analyses

All our statistical analyses were performed in the R environment (*47*) using linear mixed-effects models (LMM) using the nmle, vegan and multcomp packages.

To test whether the vegetation height and species richness of turf seascapes differed across the sampled ecoregions, we used a LMM using ecoregion as a fixed effect (n=6 and n=5, respectively) and sampling site (n=3) as a random factor nested within each ecoregion. Tukey HSD multiple comparisons of means were used post-hoc to compare results between ecoregions. Data required square root transformation to achieve homoscedasticity and normality, which was assessed by plotting residuals vs. fitted values and via quantile-quantile plots.

To compare changes in present with historical vegetation structure at our sites, we computed the global means and standard deviations of each state (i.e. forested versus turfed) from the means, standard deviations and number of observations of each ecoregion. We pooled data from all our ecoregions in this analysis because we were interested in the global comparison of turf versus forested seascapes. To test whether there were differences between vegetation height and biomass of the forested and turf states, we performed Welch’s *t*-tests, as states had differing variances. We assumed that our response variables were normally distributed, as lack of the raw data on habitat structure precluded any investigation of its frequency distribution.

To examine whether the five architectural traits related to habitat provision differed between turf- and forest-forming species, we run LMMs for each trait using each trait as a response variable and group (forest-forming or turf-forming) as a fixed effect and species as a random effect nested within group. Turf seascapes consisted of multiple species in varying degrees of abundance (n=21 species in total) while forests in each ecoregion were dominated by one forest-forming species (n=4 species in total). Species with low abundance (<1% cover at a site) were not included. Given that data were strongly skewed (Fig. 3C-F), we log-transformed our response variables to achieve homoscedasticity and normality of the residuals. Fitting non-normal distributions did not improve overall model fit, so we used gaussian distributions. For the strongly skewed variables “mean IS surface area” and “IS density” (Fig. 3E, F), we used a logarithm base 100 transformation to achieve homoscedasticity and normality of the residuals.

To tests for shifts in the multidimensional architectural configuration of the sampled sites, we performed a permutational multivariate analysis of variances (PERMANOVA; Anderson, 2001), with the CWM of each of our five architectural traits as a response variable. Only reefs that had historical cover data available were considered for this analysis (14 reefs in total; see Table S3). Variables had different units and were normalized prior to analysis to give them equal weights. We performed the analysis with the software PRIMER using a similarity matrix based on Euclidian distances (*48*). The effect of Region (fixed factor; 6 levels), Site (random factor nested within region; 14 levels) and seascape configuration (fixed factor; 2 levels) on the architectural structure was tested with 9999 unrestricted permutations. The configuration of a reef was determined by the most abundant (in terms of percent cover) habitat category used in our surveys and therefore could theoretically adopt 6 distinct levels (rock, sand, forest, turf, encrusting algae and other algal taxa), although only forested or turfed configurations ended up dominating our sites at any given point of time. We chose to use configuration as a factor rather than analysing individual reef trajectories through time as reefs were sampled at disparate times and frequencies both within and between ecoregions, leading to a severely unbalanced design with not enough degrees of freedom to conduct our analysis. We conducted tests of heterogeneity of dispersions for significant effects, which revealed that reef configurations exhibited significantly different dispersions (PERMDISP test; $F_{1,88}$ = 24.289, p < 0.0001), while sites did not ($F_{1,13}$ = 1.78, p = 0.36). This could have arisen due to the unbalanced nature of the design (i.e. we reefs were sampled more times near the present when they had already shifted to turf dominance), but the heterogeneity persisted even after balancing the dataset using a random selection of turf configurations ($F_{1,45}$ =15.084, p < 0.001), suggesting that dispersion asymmetries between configurations reflect natural differences.

To visualize the shift in architectural configuration of the sampling sites we performed a principal component analysis (PCA) on the CWM of the five architectural traits, using normalized values.

Results

Vegetation structure of turf seascapes

Seaweed turfs were presently the most abundant habitat component at all sites and regions, but all the studied reefs were once dominated by forests (Fig. 1). To characterize turf seascapes we identified the relative abundance of different seaweed morphological forms and functional types (as per ref. 17) and mean vegetation height at a range of sites in each ecoregion (n=3-8). Turf seascapes were markedly heterogenous between ecoregions and sampling sites, featuring a range of vegetation heights (0.3 cm – 16.0 cm; Fig. 2A), varying species richness (1 – 35 species · 100 cm^{-2}; Fig. 2B) and being composed of different anatomical complexity and growth morphology forms (Fig. 2C). Seaweed turfs in the Western Australian Shelf were dominated by filamentous morphotypes (58.8 ± 24.5 %; mean percentage of dry weight biomass ± standard deviation), while articulated coralline algae were the predominant forms in the NW Mediterranean and SW Japan (71.6 ± 31.2 and 56.3 ± 44.4 %, respectively), and corticated algae dominated in the Skagerrak (Norway), Scotian Shelf (Canada), and Narragansett Bay (USA) (68.7 ± 29.0, 85.4 ± 10.5 and 65.3 ± 22.4 %, respectively). Southwestern Japan featured the least speciose seaweed turf assemblages (3.6 ± 2.3 species · 100 cm^{-2}; mean ± SD), while turfs in the Western Australian Shelf were the most diverse (24.1 ± 5.8 species · 100 cm^{-2}). Seaweed turfs also formed aggregations with highly different heights, from the short, carpet-forming turfs of the Western Australian Shelf and Southern Japan (1.94 ± 1.23 cm and 2.20 ± 1.14, respectively; mean ± SD), to the taller, bush-like seascapes of Narragansett Bay (9.21 ± 2.7 cm).

Habitat structure change

Historical comparisons. Our analyses revealed substantial changes in vegetation structure following the loss of forest canopies, with significant overall reductions in plant height (Welch'ts t-test, df=1463, t= 87.7, p < 0.0001) and vegetation biomass (df= 164, t= 12.2, p < 0.0001) across all ecoregions. On average, the height and biomass of vegetation diminished 23 and >3-fold respectively (Fig. 3A, B), with the greatest height reductions occurring in the Western Australian Shelf (30-fold reduction), and greatest biomass losses in Southern Japan (5.6-fold reduction).

Species architectural traits. We selected a suite of architectural traits (plant height; plant surface area; interstitial space density and mean area; perimeter-to-area ratio) with well-documented relationships with habitat provision (see Methods), and compared them between turf- and forest-forming species using measurements from pressed specimens digitally stored at the Macroalgal Herbarium Portal (macroalgae.org; following ref. 10).

Specimens of forest-forming species typically attain large sizes, and so specimens preserved in herbaria tend to be smaller than individuals measured in the field (Fig. S2), likely underestimating differences observed between forests and turf seascapes in field settings. Even so, comparison with turf-forming taxa revealed substantial differences in architectural traits: globally, forest-forming species had significantly greater heights and plant surface areas, and featured fewer but larger habitable interstitial spaces between branches and holdfasts (Fig. 3C–D, Table S2; LMM, $p < 0.0001$). The perimeter-to-area ratio, a measure relating to overall shape, was not significantly different between forest and turf-forming species (Fig. S3; LMM, $p = 0.63$). Forest-forming species had broader trait distributions for plant height, surface area and mean interstitial space surface area, while turf-forming species had a broader trait range for the interstitial space density (Fig. 3C–D).

Reef habitat structure. We quantified how the multidimensional architectural configuration of reefs, determined by the 5 architectural traits measured above, was transformed following the loss of forests. To do so, we measured changes in the abundance (% cover) of habitat-providing seaweed taxa and other habitat components (e.g. bare rock, sand) at the reef level through time, and related them to the traits using a community-weighted-mean (CWM) approach. That is, each of the traits was weighted by the relative cover of vegetation, rock or sand for any given reef at any given point in time. In this way, the architectural configuration of reefs changed through time dictated by shifts in the relative abundance of seaweed taxa inhabiting it and the cover of rock or sand, which was deemed to provide no structure (i.e. CWM of the traits equalling zero). This analysis was performed on a subset of reefs as historical cover data was not available for all of them (Fig. S1; Table S3).

The configuration of reefs varied significantly between sites, as different species and their relative abundance created architecturally distinct configurations (Fig 4A-F; Table S4). For instance, forests in the Mediterranean are characterized by short, bushy forests, while those in the Atlantic have prostrate canopies that lay over the seafloor. Reefs within each region followed unique trajectories in their transition towards turf dominance, as their architectural configuration through time varied depending on the relative abundance of seaweeds providing structure (e.g. kelps, *Codium*, encrusting algae, turfs) and the cover of rock and sand. In some regions, the loss of dominant forest-forming species resulted in the rise of other subordinate forest-forming seaweeds (*Sargassum* spp., *Desmarestia* spp.), although those reefs eventually turned to turf as these subordinate species are non-perennial (Fig. 4A, D). Regardless of their initial structure or trajectory however, all reefs ultimately converged towards a significantly distinct multidimensional architectural configuration (PERMANOVA, Pseudo-$F_{1,8} = 10.266$, $p = 0.002$; Table S4), characterized by an overall miniaturization of the habitat (i.e. smaller vegetation height, plant surface area and habitable spaces).

On a global scale, turfs formed habitats that were architecturally more homogenous between themselves than forests, as shown by significantly smaller mean deviations from their centroid (PERMDISP test; $F_{1,88} = 24.289$, $p < 0.0001$). This resulted in a reduced architectural trait space (pink shaded area in Fig. 5), with variation in habitat structure between turf reefs restricted to a gradient of plant interstitial space density and overall shape (perimeter-to-area ratio). The distance between forested and turf states, and therefore the magnitude of architectural transformation after the loss of forests, was not equal between regions or reefs, as indicated by a significant interaction between site and configuration (PERMANOVA, Pseudo-$F_{1,8} = 4.027$, $p < 0.0001$). The greatest overall architectural reconfigurations were experienced by some of the reefs in the Western Australian Shelf, where forests formed by medium-sized kelps transitioned to short turfs with densely packed interstitial spaces (Fig. 4A). On the other hand, the NW Mediterranean, where low-lying forest canopies with high interstitial space densities where replaced by short coralline algal turfs with also high interstitial space densities, experienced the least change (Fig. 4E).

Discussion

Accelerating human pressures on Earth's ecosystems are driving unprecedented and rapid ecological change, with declines in dominant foundation species resulting in drastic habitat transformations and alterations of a wide range of ecosystem processes (*4*). In the marine environment, an increase of the severity and frequency of anthropogenic disturbances have resulted in the decline of numerous foundation species and their replacement by competitively subordinate and opportunistic taxa (*13*, *15*). We show that the replacement of forested seascapes by low-profile ground-covering turfs at six temperate marine ecoregions led to apparently contrasting structural outcomes, featuring dominance of a range of seaweed species and forms varying from densely-packed filamentous turf matrices to looser low-lying bushy seascapes. Yet, comparison of the vegetation structure of these new habitats with their historical forested configurations revealed a consistent transformation of habitat structure, with all seascapes experiencing a substantial a flattening of the habitat.

Increases in turf cover have been shown to lead to changes in habitat patchiness and complexity (*11*), but the different biogeographical contexts across which turf shifts occur have so far limited the extent to which local-scale studies can be used to understand and project habitat transformations in other regions. By using a trait-based approach across disparate biogeographic locations, we show that seascapes consistently converge towards a similar seascape structure, which is architecturally more homogenous than that of their historical configurations. Remarkably, this contraction to a simpler trait space occurred across a wide range of taxa and morphological growth forms, over different timescales, and drivers of forest decline (e.g. eutrophication, warming, biological invasions). For instance, forests in the Scotian Shelf gradually declined from the 1990s due a complex interaction of biotic and abiotic factors, with increases of seaweed turfs and invasive species (*19*). In contrast, forests in the Western Australian Shelf disappeared after a pulse perturbation (a marine heatwave) that resulted in large-scale kelp mortality and was associated to an increase in tropical species and filamentous turfs (*20*).

The turfed configurations of reefs sampled here were not only more homogenous than those from historical forests, but also differed from other habitat configurations arising from forest loss such as 'barrens' created by sea urchin overgrazing. This suggests that turf seascapes represent a novel and distinct structural state in these regions, as shown by turf seascapes being equally or more distant to the forested state than if they had transitioned to a barren (Fig. 5A), a more well-studied state (*13*). Yet, the forests that once dominated the reefs studied here only represent a small subset of the wide diversity of possible forested configurations encountered globally (Fig. 5B). A compilation of architectural trait data revealed that traits related to habitat provision of other forest-forming species spanned several orders of magnitude across the globe, and that marine forests in our analysis generally were on the lower spectrum of habitat size (Fig. S4A). In contrast, trait values amongst turf-forming species were equal or less variable than across those forming forests (Fig. S4B). Consequently, despite their apparent idiosyncrasies, it is equally useful to refer to structurally flat seascapes as 'turfs' as it is to refer to 'forests' to the seascapes dominated by seaweeds forming canopies.

The turf-driven contraction of habitat across 100s km of coastline in Western Australia resulted in drastic changes in the structure of reefs, which are likely to have a range of ecological repercussions. The retention of sediment in reefs increased by ca. 23 fold, with an estimated X Gg being trapped throughout the study area (ca. 200 km^2). For perspective, the suspended sediment inputs delivered to the coast by all the rivers in the nearby region is estimated at 31 Mg · year^{-1} (*21*). These turf-dominated reefs emerge now as key players in the system's sediment dynamics, essentially acting as sediment traps. Sediments are also likely to deeply affect the ecology of these reefs, as increased sediment loads modify a range of processes such as coral and seaweed settlement or fish herbivory (*22*, *23*). The vegetation carbon standing stock was reduced ca. 1300%, transitioning from a forest with multiple layers of vegetation to a flatter, structurally simpler seascape with low standing crop. Declines in vegetation structural complexity are linked to species losses (*24*), changes in competition, herbivory and predation (*25*), and modifications of other physical processes such as wave attenuation or sediment retention. Evidence to date shows that turf shifts can lead to up to a 44-fold reduction in community biomass and 40% decrease in species richness (*26*), as well as an inversion of community metabolism, with turf seascapes functioning as net heterotrophic carbon sources as opposed to marine forest net autotrophic carbon sinks (*27*). The rise of turf seascapes may also reshape predator-prey interactions, as vulnerability to predation is strongly mediated by habitat complexity and structure (*28*).

The paucity of long-term cover data across large spatial scales in other regions restricts our findings in Western Australia to a case study. The ecological changes observed in this system are however likely to manifest in some degree in other biogeographical contexts. For instance, elevated sediment loads where encountered in turfs of other regions, all of which exhibited values higher than those reported for marine forests (Fig. SX). That may be partly because the matrix formed by algal turfs reduces flow speeds at the microscale level facilitating sediment deposition (*29*), whilst their mucilaginous nature promotes sediment retention (*30*). Contrastingly, scouring of the substrate by taller canopy-forming algae inhibits sediment deposition (e.g. (*31*). Similarly, reductions in , although further studies examining the spatial extensiveness of turf dominance in the other regions are needed.

Temperate reefs across the globe are moving away from their historically forested states and rapidly transitioning into novel configurations, some dominated by novel forest-forming species (e.g. warm-affinity *Sargassum* or kelps) and others by non-forest-forming organisms such as corals, sea urchins or turfs (*9*). Mounting evidence suggests that turf-dominated seascapes will be a prominent feature of the temperate reefs of the Anthropocene. Turfs are generally composed of species with physiological and life history traits that allow them to thrive in anthropogenically modified environments (*32*), and numerous anthropogenic pressures like eutrophication, warming and acidification promote turf dominance while driving forest loss (*13*–*15*). Further, human stressors can interact with natural disturbance regimes ‘trapping' landscapes into a given structural and functional state (*33*). For example, along urban coastlines, increases in nutrients and sediment loads interacting with natural storm removal of marine forests can interact to promote turf expansion (*34*). Several of the seascapes examined here do appear to have become ‘trapped', as cover of forest-forming species has remained minimal to non-existent and minimal to no recovery has been observed within the studied ecoregions (Fig. S1).

In the face of turf expansion and escalating anthropogenic threats, marine forests are at a crossroads. Active interventions such as restoration can recover some of the key functions forests support in coastal ecosystems, although attempts so far have not been able to match the scale of ecosystem deterioration, achieving success only at very small spatial scales (10s m^2; ref. 23). Restoration efforts at ecologically-relevant scales will need decision support systems to evaluate whether restoration is achievable, feasible and meaningful to stakeholders in each scenario and biogeographical context (*35*). In cases where contemporary reefs have transitioned too far away from their historical forested states, restoring them may not always be an option (*36*). That calls for a better understanding of how turf seascapes function, as well as the examination of other functional differences beyond habitat structure between sites and regions (*32*).

It is also possibility that turf seascapes foster certain ecosystem services that directly benefit humans. For instance, the meso-invertebrates living amongst turfs are an important trophic resource for certain groups of invertivorous fish (*37*) and the higher digestibility of the turf themselves compared to forest-forming macroalgae is also posited to benefit fish herbivory, which may lead to overall increases in fish biomass (*9*). Recalibrating conservation goals by identifying which ecosystem functions are to be maintained and which services are likely to change is a global challenge for ecologists in the Anthropocene (*7*). Evaluating the stability, function and opportunities of increasingly prevalent turf seascapes is therefore a key area for future research.

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Figures and Tables

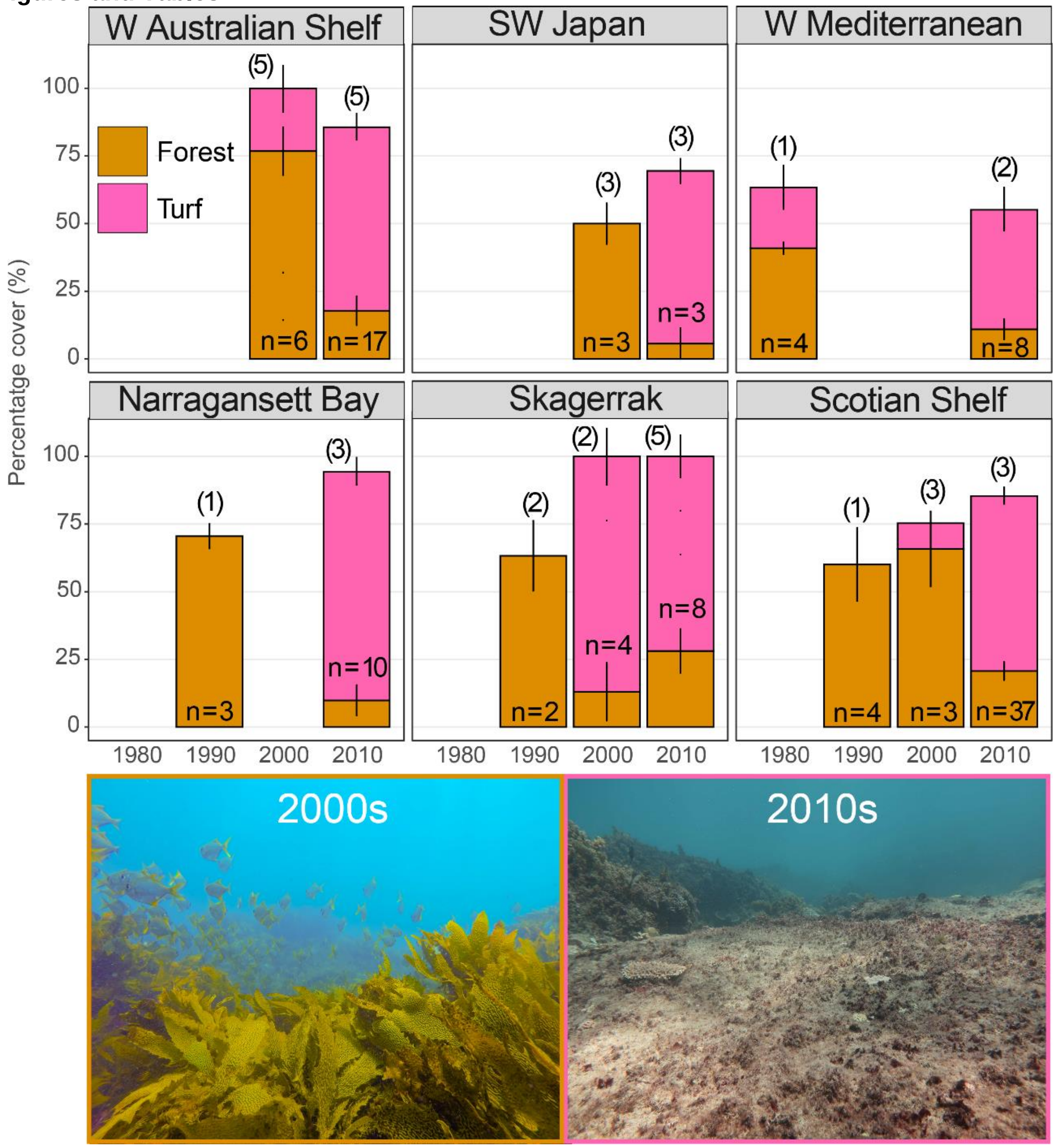

Fig. 1. Forest and turf habitat cover (mean site percent cover ± standard error, SE) across time in the study sites, derived from seascape level surveys. 1-5 sites were sampled in each of the following ecoregions: Western Australian Shelf; Southwestern Japan; Northwest Mediterranean, Narragansett Bay (USA), Skagerrak (Norway) and Scotian Shelf (Canada). The number of individual reefs surveyed each decade is indicated in parenthesis, while the total number of surveys conducted across a decade is shown at the bottom of the bars. Note that historical surveys did not always record the percentage cover of turf. An example of the seascape transformation from forest to turf dominance is shown below, featuring a reef surveyed in the Western Australian Shelf.

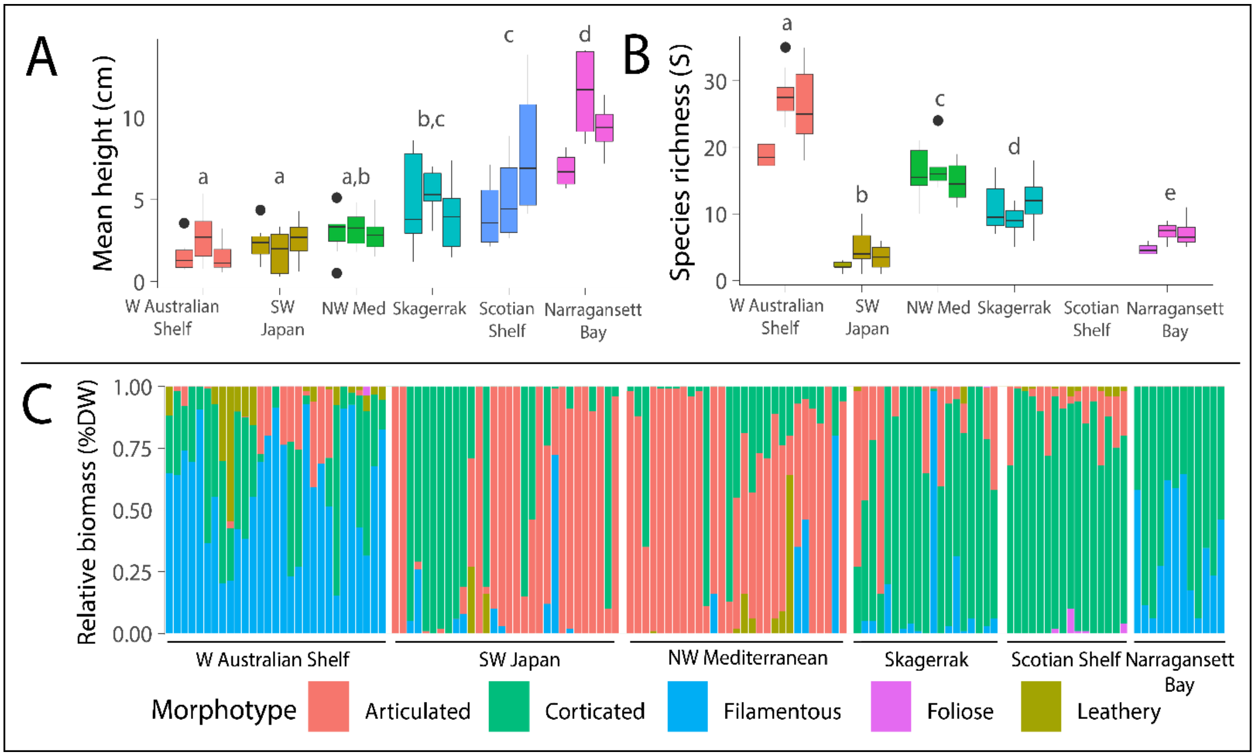

Fig. 2. Characteristics of turf seascapes across ecoregions. (A) Boxplot of mean vegetation height; (B) boxplot of species richness; and (C) biomass (percent of total dry weight) of different algal groups within the turf assemblage. Each bar in C represents a sample. Note that species richness data for the Scotian Shelf could not be obtained. Values are standardized by sample area (100 cm^2). Letters denote significant differences between ecoregions as indicated by Tukey's post-hoc tests ($p < 0.05$).

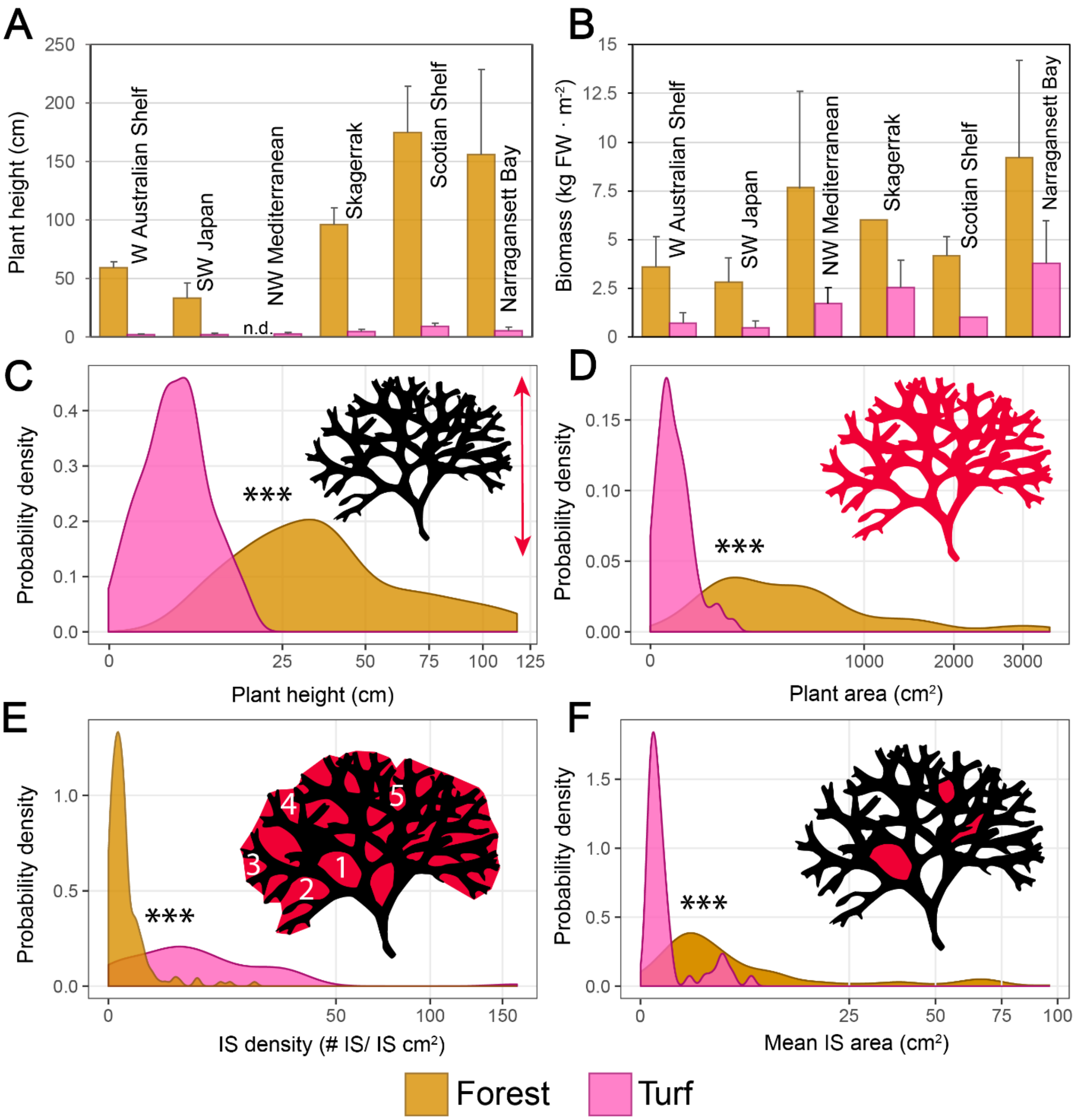

Fig. 3. (A-B) Historical (forest) and contemporary (turf) vegetation structure as indicated by two key vegetation structure metrics (A; plant height and, B; vegetation biomass). Bars indicate means + standard deviation (SD). Note that historical height data for the NW Mediterranean sites was not available in A (n.d.). (C-D) Distribution of key architectural traits among forest- and turf-forming species present at the sampled sites. Plots show the smoothed probability distribution of species-level traits within each group. The variable measured in each plot is indicated in red on the diagram. (C) Plant height, an architectural trait that relates to forest structure, plant competitive dominance and resource acquisition; (D) Plant surface area, an indication of the total surface available for colonization by epibiota; (E) Interstitial Space (IS) density, a measurement of the relative abundance of interstitial spaces within the canopy that can be potentially colonized by epibiota; and (F) Mean IS surface area, a measurement of the size of those potential habitats. The *x* axis is shown in a square-root scale to aid with data visualization.

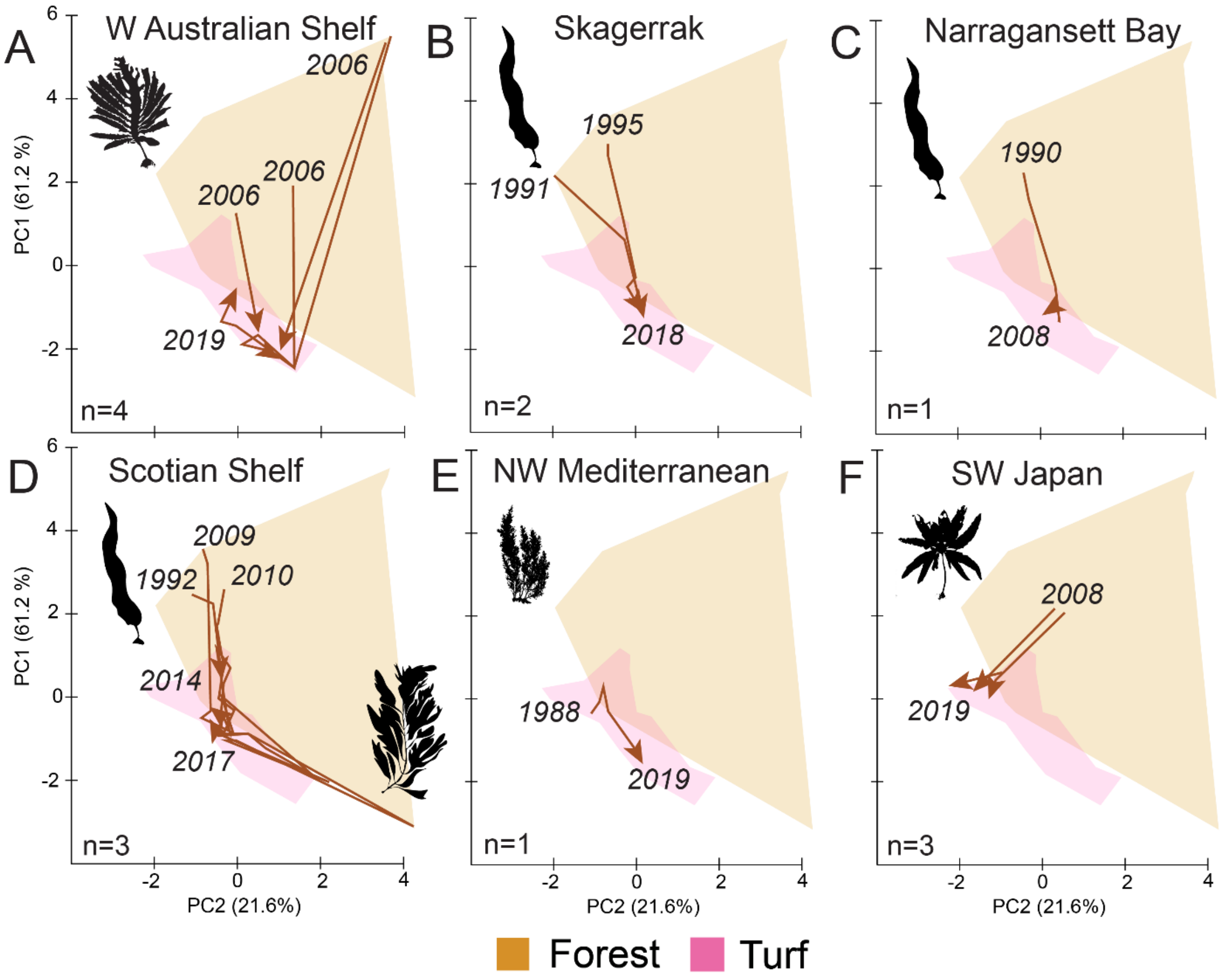

Fig. 4. Reef-level changes in the multidimensional architectural trait space following a shift to turf seascapes. Arrows indicate the trajectory of individual reefs within six ecoregions: Western Australian Shelf (A), Skagerrak (B), Narragansett Bay (C), Scotian Shelf (D), NW Mediterranean (E) and SW Japan (F). The position of each reef through time is determined by the relative abundance (% cover) of the different habitat-providing species. The brown polygon bounds the ordination space occupied by reefs dominated by marine forests globally, while the purple and pink polygon bounds those occupied by reefs dominated by non-perennial forest-forming species and seaweed turfs respectively (cf. Fig. 5). The number of reefs where historical cover data was available is indicated in the bottom of the panels.

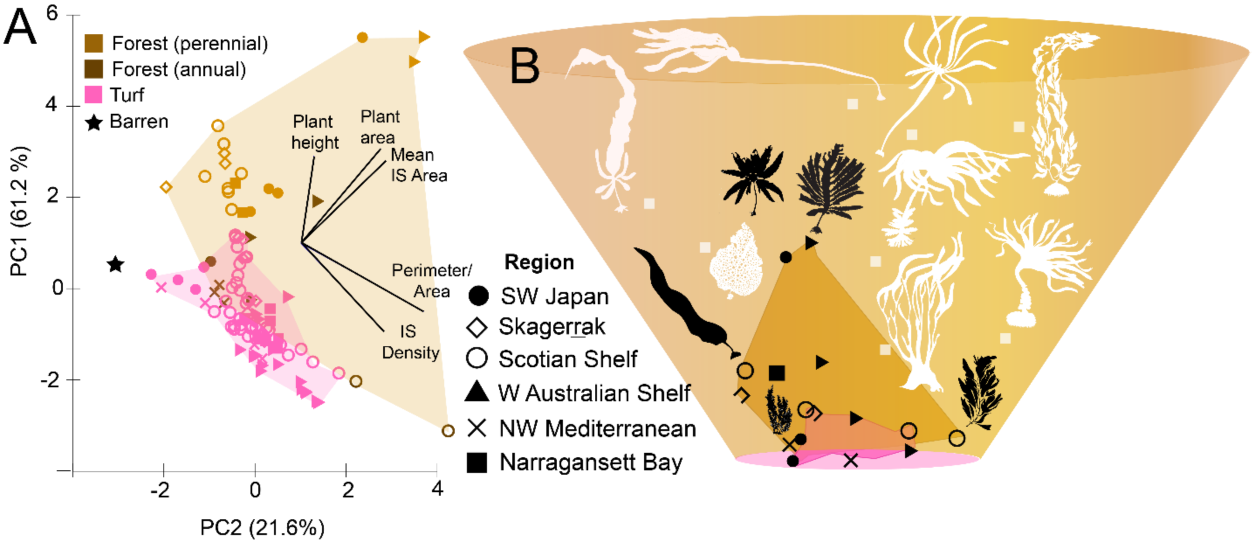

Fig. 5. Changes in the multidimensional architectural trait space of temperate seascapes following a shift to turf seascapes. (A) Principal Component Analysis (PCA) showing the habitat architecture of, where each reef is positioned depending on the community-weighted mean values of 5 architectural traits at a given time point. Symbols depict the ecoregion each reef belongs to, with colours denoting the dominant (i.e. highest % cover) seaweed category at that reef and timepoint. The structural configuration of an urchin barren, whereby architectural traits have a value of 0, is indicated by a star. The shaded pink and brown areas indicate the trait space (i.e. all the possible architectural configurations) of forested and turfed seascapes. (B) Conceptual diagram showing a convergence from architecturally diverse and highly variable multidimensional forest configurations to a much less variable, and structurally similar habitat structure upon dominance by seaweed turfs. Sampled forest-forming species are shown in black, while a few iconic forest-forming species from other ecoregions— and their hypothetical position in the trait space — are shown in white.