Applying landscape metrics to species distribution model predictions to characterise internal range structure and associated changes

Running Title: "Better species range characterisation"

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Abstract

Distributional shifts in species ranges provide critical evidence of ecological responses to climate change. Assessments of climate-driven changes typically focus on broad-scale range shifts (e.g. poleward or upward), with ecological consequences at regional and local scales commonly overlooked. While these changes are informative for species presenting continuous geographic ranges, many species have discontinuous distributions - both natural (e.g. mountain or coastal species) or human-induced (e.g. species inhabiting fragmented landscapes) - where within-range changes can be significant. Here, we use an ecosystem engineer species (*Sabellaria alveolata*) with a naturally fragmented distribution as a case study to assess climate-driven changes in within-range occupancy across its entire global distribution. To this end, we applied landscape ecology metrics to outputs from species distribution modelling (SDM) in a novel unified framework. SDM predicted a 27.5% overall increase in the area of potentially suitable habitat under RCP 4.5 by 2050, which taken in isolation would have led to classify the species as a climate change winner. SDM further revealed that the latitudinal range is predicted to shrink because of decreased habitat suitability in the equatorward part of the range, not compensated by a poleward expansion. The use of landscape ecology metrics provided additional insights by identifying regions that are predicted to become increasingly fragmented in the future, potentially increasing extirpation risk by jeopardising metapopulation dynamics. This increased range fragmentation could have dramatic consequences for ecosystem structure and functioning. Importantly, the proposed framework - which brings together SDM and landscape metrics - can be widely used to study currently overlooked climate-driven changes in species internal range structure, without requiring detailed empirical knowledge of the modelled species. This approach represents an important advancement beyond predictive envelope approaches and could reveal itself as paramount for managers whose spatial scale of action usually ranges from local to regional.

Keywords (6-10 words or phrases)

Climate change | Range fragmentation | Engineer species | Species distribution modelling | Landscape metrics | Within-range structure | Patch dynamics

| INTRODUCTION

Geographic distributions of species are determined by complex interactions and feedbacks between climate, ecological and evolutionary processes (Parmesan and Yohe, 2003; Burrows et al., 2020; Paquette and Hargreaves, 2021). Several pioneering studies have shown the profound implications of climate-driven modification on assemblage composition, community structure and ecosystem functioning (Pecl et al., 2017; Walther, 2010). Under future climate conditions, the geographic ranges of many species are predicted to shift in size, latitude, depth and/or elevation (Poloczanska et al., 2016; Pinsky et al., 2020). Such changes have typically been documented for either the leading poleward or trailing equatorward range edges (i.e. the external range structure), thus overlooking changes taking place within ranges (i.e. the internal range structure; Csergő et al., 2020).

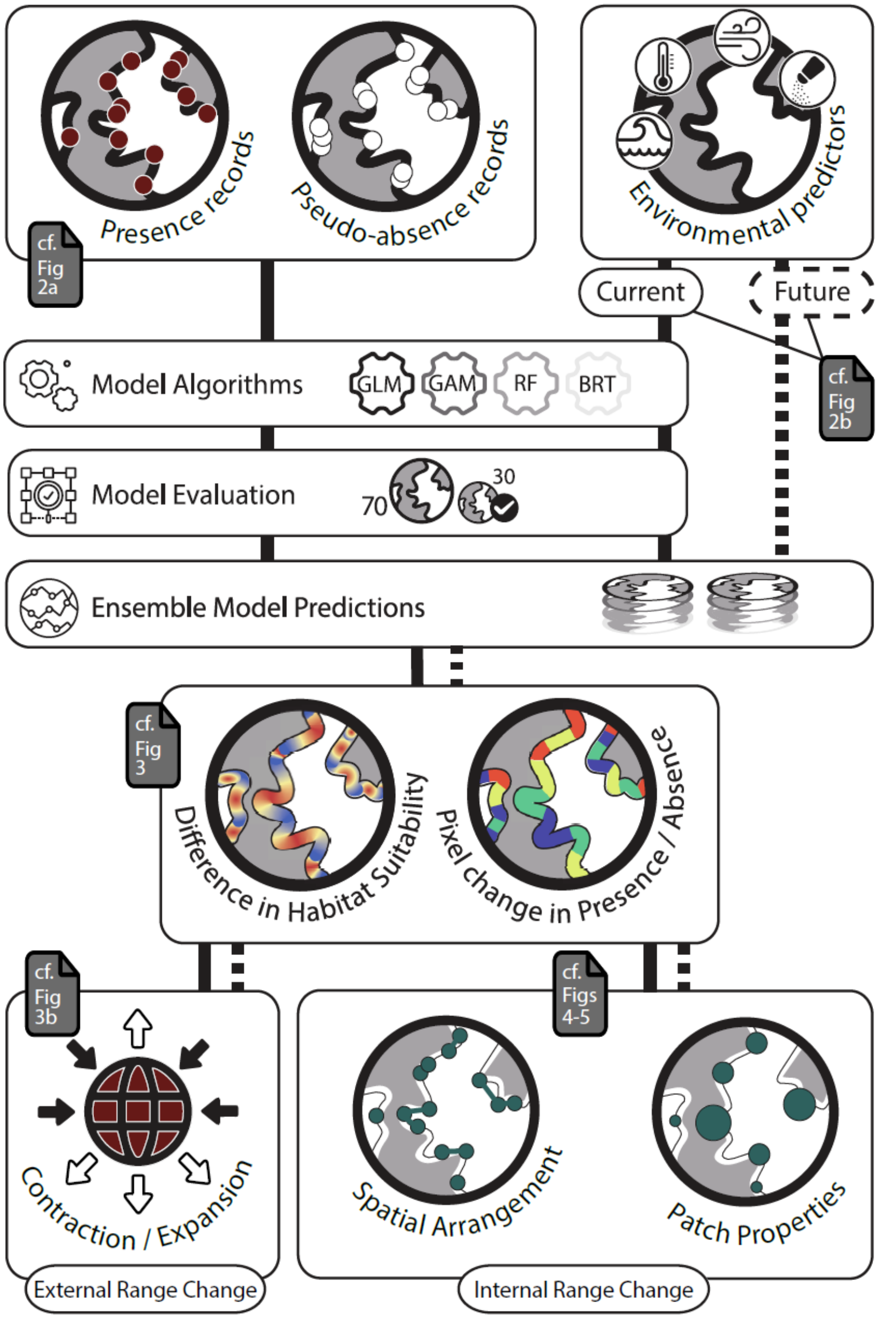

FIGURE 1. Modelling framework bringing together SDM outputs and landscape metrics. SDMs were fitted on spatially thinned presence records and randomly-generated pseudo-absences (see Figure 2a). Six environmental predictors: minimum air temperature, maximum sea surface temperature, fetch, salinity, wave height and tidal amplitude (see Figure 2b) were used to explain the species spatial distribution. Four algorithms were selected to build the models: GLM (generalized linear models), GAM (generalized additive models), RF (random forests) and BRT (boosted regression trees). We used an ensemble model approach

to predict and map the current and the future habitat suitability across the species latitudinal range. Habitat suitability is defined as the likelihood of occurrence of a species in association with environmental variables. Ensemble predictions were then binarised into presence/absence (P/A) maps. These P/A maps were then used to (1) evaluate changes in range size and distribution shifts (see Figure 3b) and (2) compute various landscape metrics using both current and future P/A predictions. The landscape metrics were then used to study the spatial arrangement of predicted patches of P/A within the species range over time (Figures 4-5). Note that we applied landscape metrics to outputs from the ensemble model, however this approach can be applied separately to each model output in order to obtain information regarding the influence of pseudo-absence datasets, model runs and algorithms on internal range change metrics.

Perhaps this omission betrays the implicit assumption that species distributions are spatially continuous (e.g. most IUCN polygons are continuous; Rocchini et al., 2011). Under this supposition, focusing on measuring changes in the external range structure such as changes in range size (Pither, 2003; Thomas, 2012), or quantifying the velocity at which the range centroid and/or margins (trailing and leading edges) may shift in the future may suffice (Sunday et al., 2012; Lenoir et al., 2020; Fredston-Hermann et al., 2020). However, by relying only on external metrics, these broad-scale studies overlook the changes that can take place within ranges and which ultimately determine the abundance, occurrence and connectivity of local populations (VanDerWal et al., 2013). For instance, regional persistence of rare species, or those living in fragmented landscapes such as mountainous, coastal or degraded areas, usually present discontinuous distributions that rely on complex networks of interconnected populations whose responses to climate-driven changes cannot be accurately assessed using metrics characterising broad-scale patterns in biogeographical distribution changes (Opdam & Wascher, 2004; Mestre et al., 2017). In such cases, quantifying changes in the internal structure of geographical ranges is critical for understanding species vulnerability to climate change. For instance, range fragmentation can increase local extinction risk by jeopardising metapopulation dynamics (Mestre et al., 2017). To illustrate this point, we focused on the naturally discontinuous distribution of an intertidal ecosystem engineer, the reef-building honeycomb worm *Sabellaria alveolata* (Linnaeus, 1767).

Intertidal ecosystems - and engineered intertidal habitats in particular - support high biodiversity and deliver important ecosystem services to society such as protection from erosion and flooding, water quality, food resources (shellfish, seaweeds), sites for aquaculture and fish nursery grounds (Barbier et al., 2011). These ecosystems are however facing strong pressures, being under the influence of multiple stressors acting at multiple scales (regional and local) whose effect on biodiversity can be reinforced by climate change (Bugnot et al., 2021). Moreover, intertidal species are exposed to both terrestrial and marine environmental conditions, which remain challenging to account for (Helmuth et al., 2006). Taking advantage of extensive occurrence records (Curd et al., 2020), coupled with fit-for-purpose resolution (0.083 decimal degrees,) current and future climatologies of marine and terrestrial conditions, we developed a species distribution model (SDM) to predict the current and future distribution of *S. alveolata* across its full global latitudinal range (32-61° N). We then assessed how the external and internal range structure of *S. alveolata* will be altered in response to climate change. The latter was assessed by making novel use of landscape metrics applied to SDM outputs.

Landscape ecology is a discipline all unto itself (Turner et al. 2005). A great variety of landscape composition (e.g., the number and amount of different habitat types) and configuration (the spatial arrangement of those classes) metrics have been developed for categorical data (Lausch et al., 2015). These metrics make it possible to improve our understanding of, for example, the effect of landscape complexity on biodiversity (Schindler et al., 2013) or habitat connectivity on metapopulation dynamics (Howell et al., 2018). The cornerstone of our approach is to have transformed species' predicted presence and absence into binary patches, where each patch is composed of one or several adjacent pixels of the same type (e.g. presences). This biotic-centred approach contrasts with the classical application of landscape metrics where patches are often derived from land-cover maps (Uuemaa et al., 2013). Once patches of predicted presences and absences are identified, various landscape metrics can be used to characterise patch properties and their spatial structure, ultimately providing a better characterization of the internal range structure and how it will evolve in response to external pressures (e.g. climate change).

2 | MATERIALS AND METHODS

Our workflow, which combines landscape ecology metrics with species distribution model outputs is illustrated in Figure 1.

2.1 | Study area and species

The honeycomb worm *Sabellaria alveolata* is an intertidal ecosystem engineer, capable of building tubes from sand and shell fragments on low- to mid-shore, in semi-exposed and exposed locations. As a colonial species, the multitude of fused tubes form biogenic structures ranging from veneers and hummocks to large reefs (Wilson, 1971; Curd et al., 2019). Reef-forming *S. alveolata* has the potential to provide important coastal protection (Naylor & Viles, 2000) and biogenic habitat for a diverse range of other species (Dubois et al., 2002; Jones et al., 2018). *Sabellaria alveolata* has a discontinuous distribution ranging from southern Morocco to southwest Scotland (Lourenço et al., 2020), with many distribution breaks (Firth et al., 2021a) (Figure 2a).

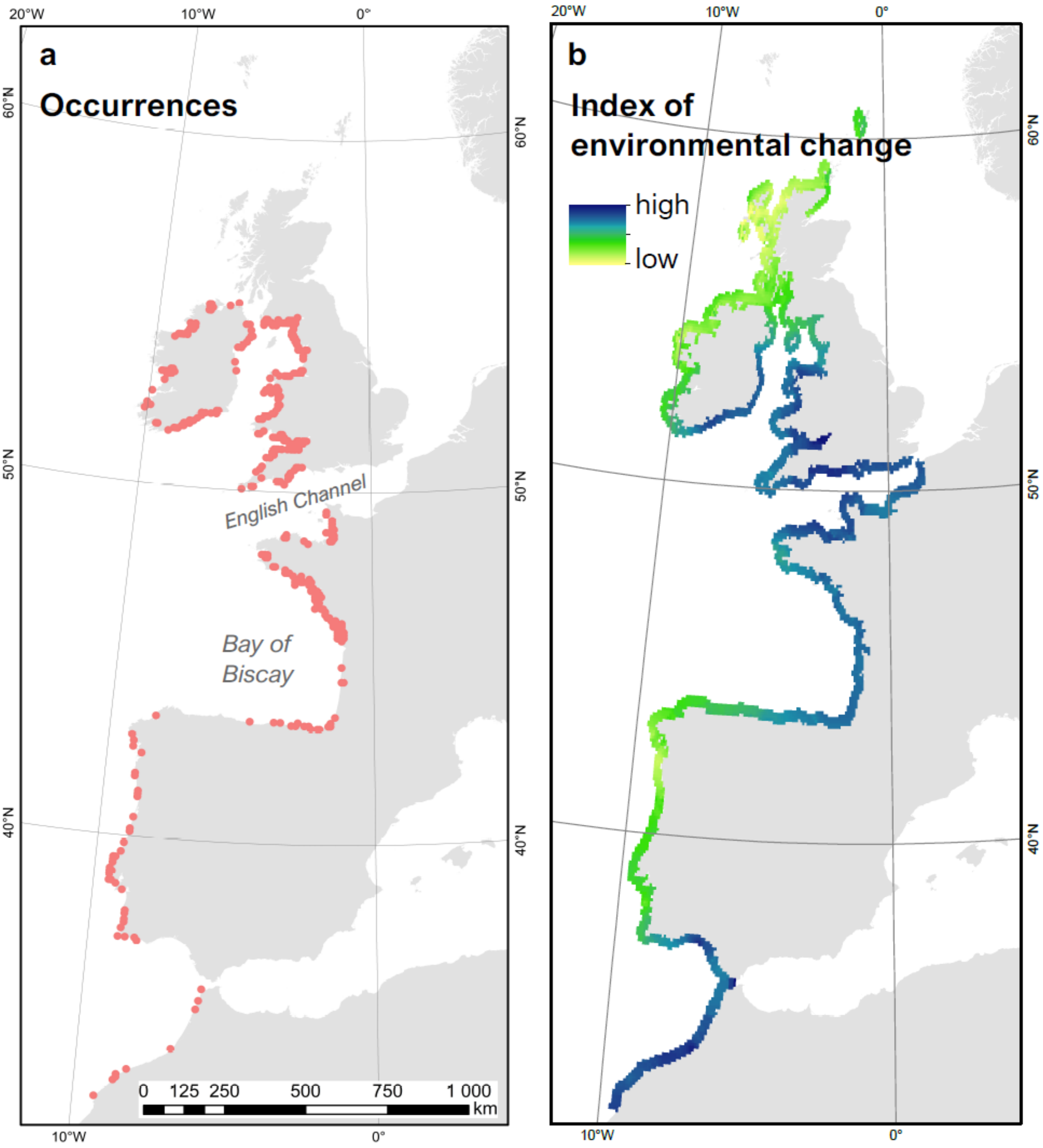

FIGURE 2. Species occurrence records and index of environmental change along the species distributional range. a, The 363 thinned occurrence records collated between 2000-2019 from multiple data sources highlight the broad but fragmented biogeographical range of *S. alveolata*. **b,** Index of change in local environmental conditions (Table S1) between current and future (RCP 4.5 in 2050) climatic layers. High values indicate the largest difference between current and future environmental conditions (for details regarding the index computation, see the Methods).

Our study was conducted across 29 degrees of latitude (from 32°N to 61°N) spanning a large gradient of climatic conditions (Figure S1). To the best of our knowledge *S. alveolata* is, and has always been, absent from the North Sea (Nunes et al., 2021). Although it has occasionally been cited as present in the North Sea (Richter, 1927), expert consensus is that these occurrences were *S. spinulosa* reefs (Reise, pers. comm.) (Figure S2). This distribution limit is thought to be due to the presence of a long-term hydrographic barrier to larval dispersal at the Cherbourg Peninsula in the English Channel (Salomon & Breton, 1993), and to competitive exclusion by *S. spinulosa* in the Greater North Sea. As both larval dispersal and biotic interactions cannot be accounted for by SDM, our study area does not extend to the North Sea. Since we only consider intertidal *S. alveolata* bioconstructions, our study area does not extend to the Mediterranean, where all *S. alveolata* records are subtidal owing to low amplitude tides.

2.1 | Occurrence records

An increasing number of SDM studies are based on presence data downloaded from the Global Biodiversity Information Facility (GBIF) (Alhajeri & Fourcade, 2019). Although these data have proved useful to model the distribution of some well-known species, records for *S. alveolata* are strongly affected by spatial sampling bias (Firth et al., 2021b) (Figure 2a). Here, we collated occurrence records from numerous sources, including field observations, research articles, citizen science observations, management reports and online databases (Curd et al., 2020). Presence records were considered between the years 2000-2019, a time span compatible with the temporal coverage of climatic layers classically used in SDM studies (e.g. Bio-ORACLE, Worldclim) (Assis et al., 2018; Hijmans et al., 2005; Tyberghein et al., 2012). Subtidal observations, and observations without geographic accuracy down to shore level, were excluded. Overall, 98 literature sources were included in the analysis, resulting in 14,960 occurrence records. Only 12.2% of these records were previously accessible via online databases (Curd et al., 2020). Occurrence records were spatially thinned so that only one record was retained per climatic-grid cell (Steen et al., 2021). This left us with 363 observations.

2.3 | Environmental variables

We retained only 'scenopoetic' variables (i.e. variables on which the species has no impact) as predictors (Hutchinson, 1978). We did not include available seabed substrate maps (although potentially relevant) because the best existing layer compilation (currently provided by EMODnet; https://emodnet.ec.europa.eu/en) was not deemed fit-for-purpose, due to low spatial accuracy in many areas and limited spatial coverage. All environmental predictors covered the full latitudinal distribution of *S. alveolata* and came at a spatial resolution of 0.083° decimal degrees. This corresponds to a distance of 9.3 km along the latitude axis and, along the longitude axis, while the distance along the longitude axis goes from 7.8km at the equatorward edge, to 4.5km at the poleward edge. Specifically, a set of 10 bioclimatic variables were chosen as climate-related candidate predictors (Table S1) including air temperature (min, max and mean) from WorldClim version 1.4 (Hijmans et al., 2005), sea-surface temperature (min, max and mean) and mean salinity from Bio-ORACLE (Assis et al., 2018; Tyberghein et al., 2012), wave height (Bricheno & Wolf, 2018), wave fetch (i.e. the distance over which wind-driven waves can build given the orientation of the coastline, Burrows, 2020) and tidal current and surface amplitudes from the TPXO8 ATLAS solution (www.tpxo.net) (Egbert & Erofeeva, 2002; Egbert et al., 2010). Present and future wave height was estimated by applying the WaveWatch III$^{\mathrm{TM}}$ spectral wave model at a regional scale (Atlantic Europe) (Tolman, 2009). Because wave fetch was estimated at a 100 m resolution, we re-projected and upscaled this raster (using average values) to match with the resolution of the other rasters (i.e. 0.083° degrees).

We checked for collinearity between variables using Pearson's correlation coefficients. For pairs with Pearson's | r | > 0.7, we retained the variable known to be the most ecologically relevant (Araújo et al., 2019). This process led us to select six predictors: maximum sea-surface temperature, average salinity, minimum air temperature, wave fetch, wave height and tidal amplitude (Figures S3-S7).

Future predictions for four of the six selected predictors were obtained for horizon 2050 under the Representative Concentration Pathway scenario RCP 4.5 (Meinshausen et al., 2011): salinity and sea surface temperature from Bio-ORACLE, air temperature from WorldClim and wave height from Bricheno & Wolf (2018). Tidal amplitude and wave fetch were assumed to stay constant in the future. To evaluate where, over the range, climate change might have the strongest effect on *S. alveolata* reefs, we calculated an index of environmental change. For this purpose, we first computed a climatic space using a principal component analysis (PCA) performed on the four standardised environmental variables that are predicted to change in the future (Figure S8). Then, we projected future environmental values within the two-dimensional space defined by the two first PCA axes (explaining 82% of the variance). Hence, a given pixel has two positions in this space. The index was calculated as the Euclidean distance between present and future conditions for each pixel (Figure 2b) with greater distances indicating larger changes.

2.4 | Model building

Model building was performed in R (R Core Team, 2019) using the package 'biomod2' (Thuiller et al., 2009). Four fundamentally different algorithms were selected to build the

SDMs: generalised linear models (McCullagh & Nelder, 1998), generalised additive models (Hastie & Tibshirani, 1986), random forests (Breiman, 2001), and boosted regression trees (Elith et al., 2008). The four algorithms have already proven useful in modelling benthic species distributions (Bučas et al., 2013) and were selected for their ability to model non-linear relationships while assuming different shapes for the response curves. These algorithms have their own set of strengths and weaknesses which can lead to contrasted predictions (de la Hoz et al., 2019). For instance, random forests generally display high predictive performance on the training dataset (Elith, 2006; Reiss et al., 2011) but are prone to overfitting which can yield inaccurate predictions when extrapolating to non-analog conditions (Wenger & Olden, 2012; Beaumont et al., 2016). Alternatively, GLMs often have a lower predictive accuracy on the training dataset but usually display higher transferability (Wenger & Olden, 2012; Heikkinen et al., 2012; Yates et al., 2018). Algorithms were fitted using the default settings of biomod2.

The four approaches require presence-absence data to be fitted. Since the absence records in our database had an uneven spatiotemporal spread (see Figure S1), we generated a random set of pseudo-absences over the study area. We generated the same number of pseudo-absences as available presences (i.e. 363) to give an equal weight to presences and absences in model predictions (Barbet-Massin et al., 2012). Models were then fitted on this presence/pseudo-absence dataset. To account for stochasticity regarding the selection of pseudo-absences, this procedure was repeated 10 times (i.e. ten pseudo-absence datasets were generated). Note that since we used pseudo-absences, the models predict a habitat suitability index ranging from 0 to 1 rather than a probability of presence (Guisan et al., 2017) (Figure S9).

2.5 | Model performance and ensemble predictions

Models were evaluated using a cross-validation approach based on repeated split-sampling (70% for calibration, 30% for evaluation) with 10 runs (Figure 1). For each run (and each pseudo-absence dataset), model performance was assessed using the true skill statistic (TSS) (Allouche et al., 2006) and the area under the ROC curve (AUC; Hanley and McNeil 1982). Both TSS (Sensitivity + Specificity - 1) and AUC are prevalence (i.e. the ratio of 'presence' to 'absence' in the dataset) independent. They provide information on the model's capacity to distinguish between presence and absence classes, with higher values pointing to better models (Lawson et al., 2014). Overall, a total of 400 models (4 algorithms times 10 cross-validations times 10 pseudo-absence samplings) were fitted. The importance of the different predictors across datasets and algorithms was evaluated using the "variables_importance" function of biomod2.

We used an ensemble modelling approach to perform current and future predictions over the distribution range (Hao et al., 2020). Only models whose predictions on the test data had a TSS ≥ 0.5 were retained for this procedure (99 GAM + 89 GLM + 100 RF + 99 BRT). Current and future predictions from the 387 contributing models were combined using a weighted average based on TSS scores (i.e. higher influence of models or datasets with higher TSS). Present and future predictive ensemble maps were reclassified into binary presence-absence surfaces using the threshold that maximises TSS evaluation scores (i.e. maxTSS; Guisan et al., 2017).

2.6 | Measuring broad-scale external range changes between periods

Binary predictions are classically used to estimate how species ranges will be affected in the future (Yalcin & Leroux, 2017). While the main object of inference focuses on range size

(Gaston, 1996), additional metrics can be found in the literature (e.g. the proportion of pixels lost or gained) (Thuiller, 2004). When considering a broad latitudinal gradient, a more accurate estimation of changes in range size can be obtained by giving an equal area to all pixels (Sillero & Barbosa, 2021). Here, we re-projected the predicted rasters (both for presence-absence and habitat suitability) with the ETRS89 Lambert Azimuthal Equal Area Coordinate Reference System (ETRS-LAEA), with the latitude and the longitude of origin adjusted to 44.3°N, -3.2°E, giving each pixel an area of 25 km² (5 km x 5 km). From the presence-absence rasters, we used the BIOMOD_RangeSize function to estimate the proportion and relative number of pixels lost, gained and stable. We also quantified range shifts, another measure frequently used to estimate the effect of climate change on species distribution (e.g. Lenoir et al., 2020). To measure this, we first characterised ranges in both periods considering the centre (median latitudinal value where the species was predicted to be present), the upper (97.5% percentile) and the lower (2.5% percentile) limits of the range. We then quantified range shifts for all three attributes as the difference between future and current values.

2.7 | Measuring fine-scale internal range changes between periods

In addition to broad-scale range metrics that describe external range changes, we used landscape metrics to better characterise the fine-scale internal structure of the species range (in both current and future climatic conditions) and provide additional insights regarding how this structure will be affected in the future. Landscape ecologists often conceptualise the landscape as a mosaic of discrete, ecologically homogeneous, patches embedded within a background matrix of inhabitable areas (Turner et al. 2005, Lausch et al. 2015). Patches are the basic statistical unit under this approach, and are defined as one isolated, or several adjacent, pixels of the same class (e.g. crops) that differ from their surroundings (e.g. forests).

Each patch has its own individual characteristics (e.g. shape, size, distance to nearest neighbour; Hesselbarth et al. 2019), while the landscape pattern emerges from the spatial composition and configuration of patches from different classes (Turner et al. 2005, Lausch et al. 2015). Pixels belonging to each patch can be monitored over time so that pixels transitioning from one class to another in response to external pressures (e.g. climate change) can be translated into patch dynamics. Thus, presence pixels switching to absence pixels within a presence patch lead to patch fragmentation. A suite of landscape metrics describing changes in patch properties (e.g. area, Euclidean distance to the nearest neighbour), and their spatial configuration (e.g. patch aggregation) can also be used to describe changes at various spatial scales. For instance, an increased distance to the nearest neighbour coupled with a decrease in patch aggregation for presence patches is indicative of population fragmentation.

Here, we propose to use landscape metrics on predicted binary (presence and absence) maps obtained from SDMs to simplify, often complex, spatial predictions into a mosaic of discrete patches of predicted presences and absences under both current and future environmental conditions. Landscape metrics can then be used to study presence and absence patch properties and how their spatial arrangement is predicted to change in the future, ultimately providing a better characterization of range changes.

Landscape metric analyses were performed using the R package ‘landscapemetrics’ (Hesselbarth et al., 2019). This package contains many functions to describe various patch properties (e.g. area, distance to nearest neighbour of the same class). These properties can be aggregated at different spatial scales (e.g. mean patch area at the range scale) and studied over time. Note that the package also provides functions to compute diversity metrics at the landscape scale (i.e. range scale in our case), however since our usage is constrained to binary outputs, most of these functions were not relevant for the purposes of this study. Here, we focused on the patch area for each class, the Euclidean distance to the nearest neighbouring patch of the same class, and the predicted habitat suitability of pixels within patches (a metric that uses an additional level of information derived from SDMs). The latter metric relies on the fact that each pixel contains additional quantitative information (i.e. the habitat suitability values that were used for thresholding which is a necessary step to identify patches) that can be used to better characterise patch properties and their spatial arrangement. Here, we used this information to run a patch-based linear regression to investigate whether average changes in patch suitability (i.e. the average difference between future and current suitability for all pixels within the patch) followed a latitudinal gradient, a classical biogeographical pattern where species are moving poleward to track suitable climatic conditions (Mieszkowska & Sugden, 2016).

3 | RESULTS

3.1 | Model performance and variable importance

Ensemble model predictions of present distribution performed well (AUC = 0.91±0.03; TSS = 0.67±0.05 - Table S2 and Figure S10) in characterising the large-scale, yet fragmented, latitudinal range of *S. alveolata* (specificity score 0.78±0.06; Figure 3a). Predicted areas of absence (e.g. southern French Atlantic coast) also matched well with current observed absence data (Figures 2a and 3a, Figure S1). Fetch was the most important variable (explaining 35% of variance), suggesting that coastal exposure to wind-wave action, a local to regional scale feature, is a primary determinant of habitat suitability (Table S3 and Figure S7). Dynamic temperature variables and ocean variables had less influence on model predictions but were still critical to characterise broad-scale geographic range. In fact, sea surface and air temperature were the second and fourth most important variables, respectively, while salinity was the third most important variable (Table S3). See Figure S11 for variable response curves.

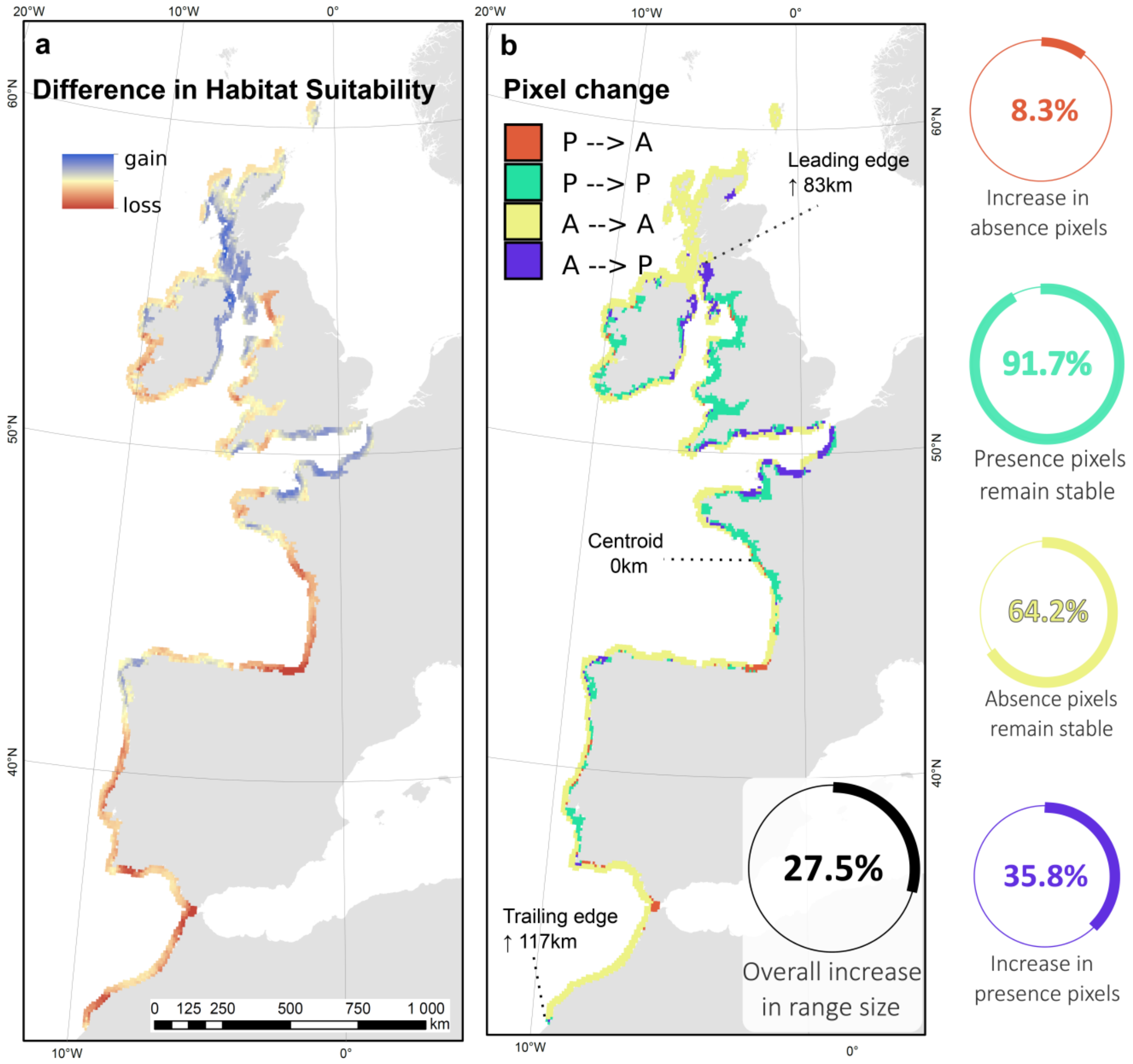

FIGURE 3 Predicted difference in habitat suitability and presence-absence patterns between current and future (RCP 4.5 2050) climatic conditions. a, Difference in habitat suitability between present and future, with blue colours indicating a future increase in habitat suitability, and red colours indicating a future loss in habitat suitability (yellow colours represent an absence of change). **b,** Change in presence/absence predictions between the present and future. Orange pixels (P -> A) = shift from current presence to future absence; green pixels (P -> P) = stable presence pixels; yellow pixels (A -> A) = stable absence pixels; violet pixels (A -> P) = shift from current absence to future presence. Predictions were

binarised using a max TSS threshold of 0.53. Leading edge = 95% quantile of the latitudinal range, Trailing edge = 5% quantile of the latitudinal range, centroid = range centre/optimum median.

3.2 | Broad-scale range changes

The ensemble model predicts a 27.5% increase in range size (Figure 3b), with future gains predicted to mostly occur around the Irish Sea, on both sides of the English Channel and along the coast of Galicia (Spain) (Figure 3a). Overall, we found large spatial heterogeneity in the proportion of pixels predicted to become suitable (35.8%), unsuitable (8.3%) and stable (91.7% of absence pixels and 64.2% of presence pixels) in the future (Figure 3b). This heterogeneity leads to an overall contraction of the latitudinal range owing to a greater retraction of the trailing edge relative to the extension of the leading edge (117 km vs. 83 km respectively; Table S4, Figure 3b). Although other local changes are visible, they are not captured by broad-scale range metrics.

3.3 | Within-range changes

The application of landscape metrics enabled us to identify 90 patches (both presences and absences) in the current time period, and 92 patches in the future. While mean habitat suitability per patch increased with latitude ($P<0.001$; $R^2=0.41$), 59% of the variability in patch suitability remained unexplained, highlighting departures from expectations (i.e. a global poleward shift).

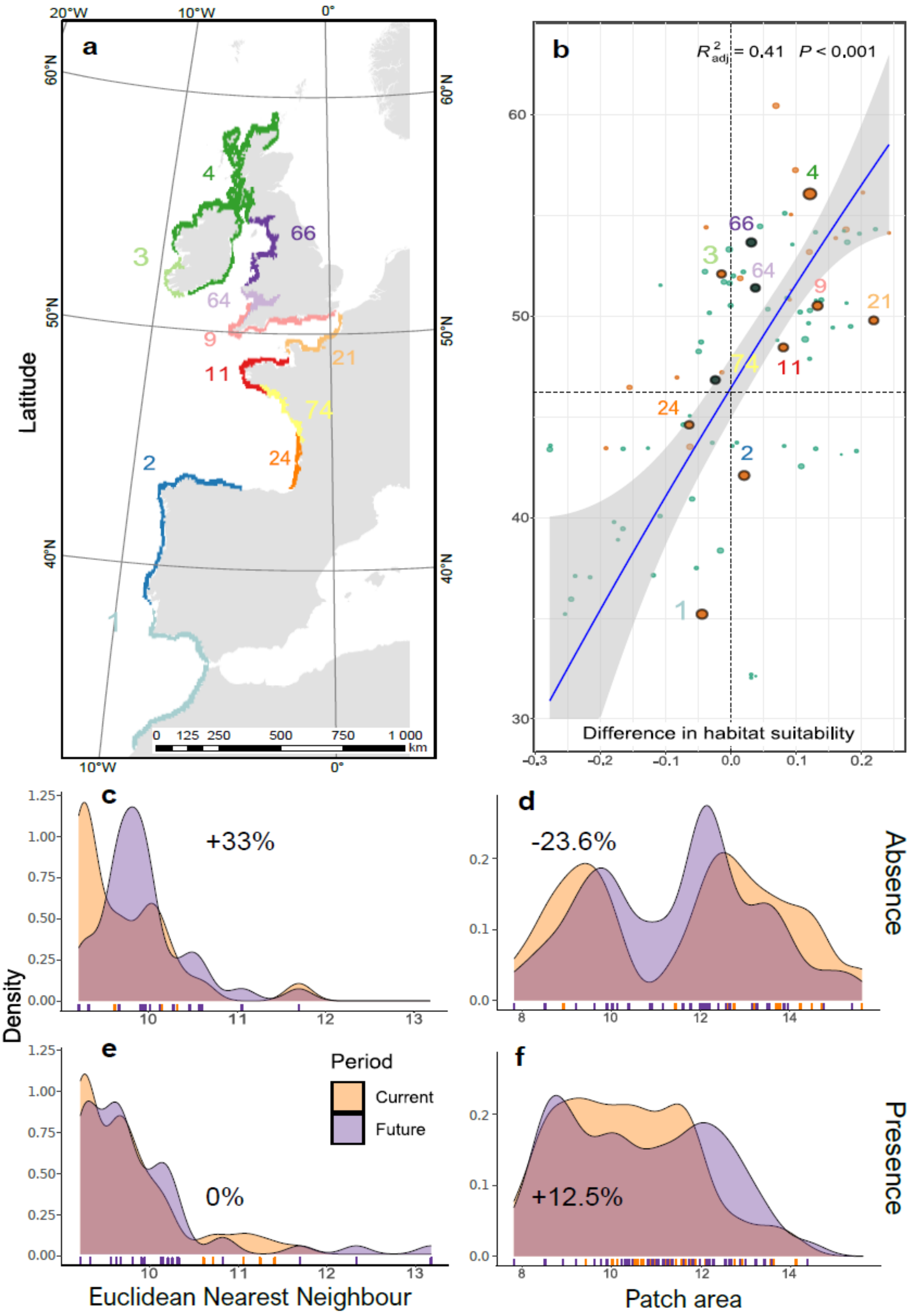

FIGURE 4 Overview of presence-absence patches and changes between time periods for selected patch and landscape metrics. a, Map of 2000-2019 presence/absence patches. Numbered regions map to their equivalent 'bubbles' in (b). **b,** Change in average patch habitat suitability between current (2000-2019) and future (RCP 4.5 2040-2049) as a function of latitude. Current presence patches are displayed in green whereas current absence patches are in orange. Bubble size indicates patch area. The horizontal dashed line points to the latitude at

which the predicted difference in habitat suitability switches from negative to positive. Latitude was treated as the independent variable but the axes were flipped for presentation purposes. Density plots highlighting changes in patch level Euclidean nearest neighbour (ENN) distance for both absence (**c**) and presence patches (**e**), whilst (**d**) and (**f**) show the change in patch area for absences and presences respectively. For each density plot, the proportional change between future and current median values, relative to the current period, are highlighted.

Despite an overall stability in the total number of patches between current and future conditions, presence patches are predicted to decrease from 65 to 56 (-14%), while absence patches are predicted to increase from 25 to 36 (+31%) (Figures S12 and S13). This does not however mean that absences are more prevalent in the future, owing to a global increase in the size of presence patches (+12.5%) combined with a decrease in the size of absence patches (-23.6%) (Figures 4d and 4f). The average distance (Euclidean nearest neighbour; Figures 4c and 4e) between patches is predicted to increase in the future for absences (+33%) but to remain stable for presences. The geographic distribution of presence and absence patches is also predicted to change. For instance, presence patches are predicted to coalesce poleward, with the formation of a large presence patch along the west coast of Britain and Ireland, while most equatorward patches are predicted to fragment (Figures 3b and 4e).

Future predictions show that patches can behave in one of four ways. Either presence and absence patches can expand, or patches of presence can appear in areas of absence and vice-versa. An example of each specific case is presented in Figure 5, with associated local-scale landscape metrics. Note that these metrics can be obtained within any section of the range. For instance, when considering the southwest coast of England, we predict that five presence patches will merge into one larger presence patch in the future owing to multiple absence pixels predicted to become suitable (Figure 5b). Focusing on this region, this change leads to a 400% increase in the Largest Patch Index (LPI), the largest presence patch dominating 20%

of this regional landscape under current conditions, and 100% under future conditions. In the current range centre (north Bay of Biscay), we predict a localised extirpation in the centre of a large presence patch (Figure 5c), increasing edge pixels between presence and absence patches and thus decreasing the percent of core area (-6%). In northern Spain and the southern Bay of Biscay, we predict the disappearance of small presence patches within a large absence area (Figure 5d), increasing the total area of absences by nearly 18% within this region (total class area metric). Finally, along the northwest Iberian Peninsula, numerous small areas of suitable habitat are predicted to appear in a currently large absence patch (Figure 5e), leading to a 1% decrease in aggregation index (from 86% under current conditions to 85% in the future).

4 | DISCUSSION

In this study, we aimed to illustrate how and to what extent broad-scale metrics, that mostly describe external range changes, can overlook the more nuanced internal range changes that can take place under climate change. For this purpose, we focused on changes predicted under current and future (2000-2019 vs. 2040-2049) environmental conditions for a species with a naturally discontinuous distribution: *Sabellaria alveolata.* We then investigated how broad-scale range metrics can be complemented by landscape metrics to better characterise the effect climate change can have on species geographic ranges. Overall, we found that broad-scale range metrics alone would have led to the conclusion that the study species is a climate change winner. Within-range changes provided additional insights by revealing that the range will become increasingly fragmented in its equatorward half in the future, with potential implications for local declines and extirpations. As *S. alveolata* underpins myriad ecosystem functions (Dubois et al., 2002; Jones et al., 2018) changes in its distribution (i.e. presence-absence, hence occupancy of suitable habitats) and abundance are likely to have adverse cascading effects on ecosystem services (Wethey et al., 2011).

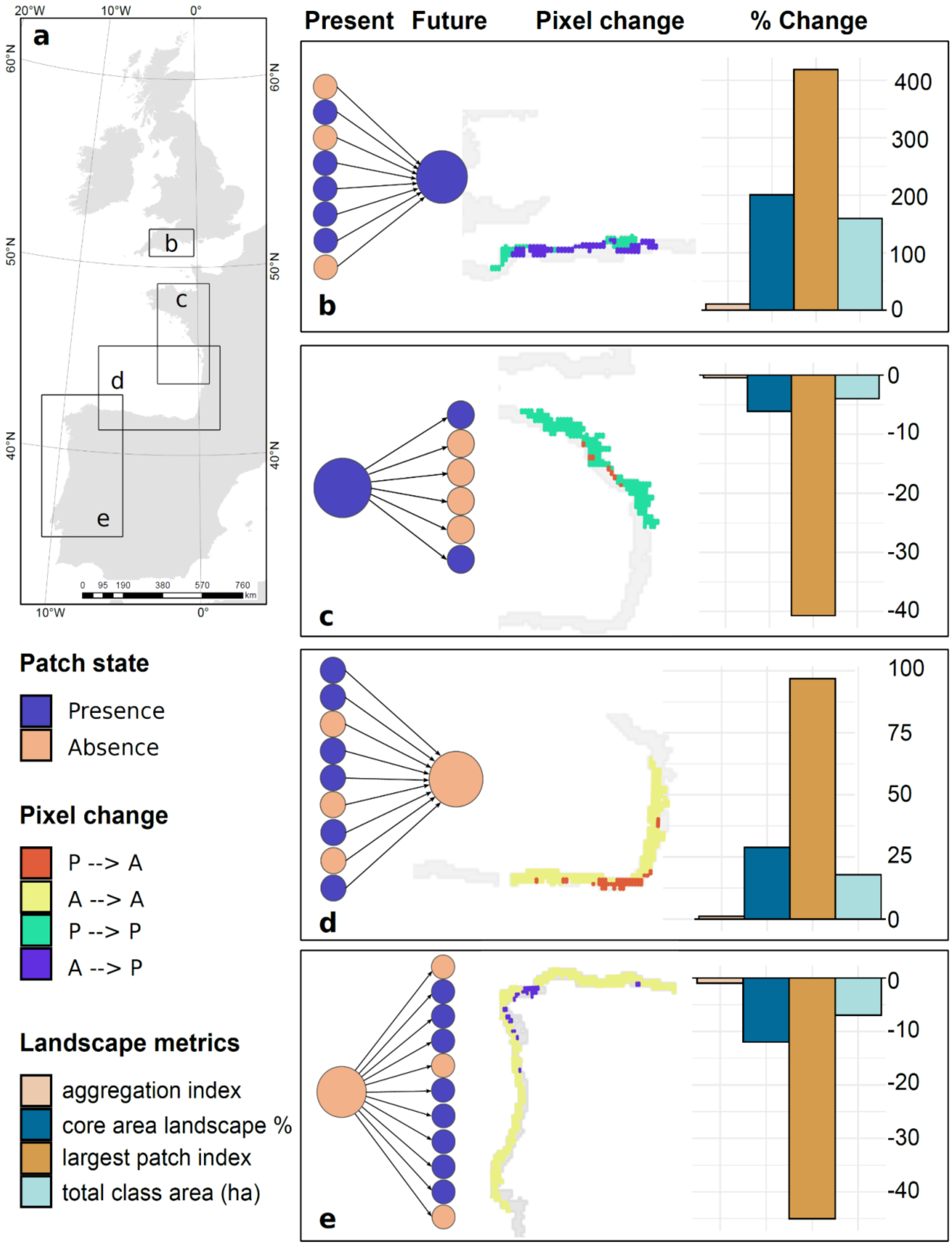

FIGURE 5 Examples of internal range change. The four types of patch transitions, with barplots of associated landscape metrics. **a,** Location of all four examples. **b,** Expansion of presence patches **c,** Absence patches appearing in a larger presence patch. **d,** Expansion of absence patches. **e,** Presence patches appearing in a large absence patch. The barplots represent relative changes in different landscape metrics relative to baseline metrics calculated

under current environmental conditions: negative values indicate a decrease of the metric in the future and positive values indicate the opposite. In all four examples, the coloured pixels define the landscape on which the metrics are computed. The largest patch index is the percentage of the landscape covered by the largest patch. The aggregation index describes the extent to which patches of the same class are aggregated. The total class area is the sum of the area of all patches of the same class. Finally, the core area landscape is the average of the percentage of core area (i.e. patch area without edge pixels) in relation to total patch area.

Despite the recognised ecological and economic value of ecosystem engineers in terms of biodiversity and ecosystem functioning (Ellison et al., 2005; Lemasson et al., 2017), to our knowledge, only a handful of studies have simultaneously considered terrestrial and marine environmental conditions to which coastal ecosystems are exposed (e.g. Lima et al., 2013; Boo et al., 2019); so far only one study has focused on an ecosystem engineer (Faroni-Perez, 2017). Our results confirm that both air and seawater temperatures are ultimate drivers of changes in sabellarid distribution (Faroni-Perez, 2017; Firth et al., 2015; Firth et al., 2021a), thus confirming its status as an indicator of climate change in Britain and Ireland (Mieszkowska et al., 2006). However, patterns of change are predicted to differ between biogeographic regions owing to the effect of other local factors (Firth et al., 2021a). For instance, our study suggests that the effect of temperature can be overridden by local and regional factors determined by coastline orientation, especially due to fetch.

While the overall increase of habitat suitability predicted by SDM would categorise *S. alveolata* as a climate change 'winner' (Somero, 2010), a closer look at SDM predictions highlights a more nuanced situation owing to a complex interplay of various factors. First, *S. alveolata* is predicted to reach the very north of Britain and Ireland by 2050, but in the longer-term future (e.g. the 2090s), its poleward expansion will be limited by the lack of continuous or connected landmass, as is the case for a number of other coastal species in northwest Europe (Philippart et al., 2011). Some longer-term colonisation of the outer islands of the

British Isles (Hebrides, Orkney, Shetland) might be possible, but may be dispersal-limited. This suggests that proximate factors such as habitat availability (supply of sand for tube building adjacent to hard substrata for adhesion) and dispersal ability may override the ultimate drive of climate change (Harley et al., 2006). Second, the predicted shrink of the latitudinal range (Figure 3b) indicates that the distribution will be mostly clustered in poleward regions but increasingly fragmented in equatorward regions (Figure 4), a process that could disrupt connectivity networks between isolated populations. This is particularly concerning in the equatorward part of *S. alveolata's* range given that it is currently located within the Canary Eastern Boundary Upwelling System, where a rapid warming at its trailing edge is occurring (0.60°C decade^{-1} off Mauritania), leading to speculation that an upwelling shutdown or geographic shift has already begun (Seabra et al., 2019). This pattern matches well with previous findings showing that leading (poleward) and trailing (equatorward) edges respond differently to climate change (Poloczanska et al., 2013). At the leading edge, larger occurrence patches could strengthen regional connectivity, which could favour inter-seeding between distant populations and enhance species regional resilience to local perturbations or extreme climatic events. In contrast, at the trailing edge, increased distance between presence patches could lead to a loss of genetic diversity in threatened former core areas of the range (Nicastro et al., 2013). Thus, while some presence patches located at the trailing edge are predicted to increase in habitat suitability (e.g. the patch located close to Morocco is predicted to increase from 0.53 to 0.57), their increasing isolation could actually lead to an increased extirpation risk. If this happens, the trailing edge would shift to southern Spain (Gulf of Cadiz), leading to a further range contraction of 500 km. Third, while trailing and leading edges are clearly identified by SDM predictions, our model further predicts a strong decrease in habitat suitability in the central part of the range along the French Atlantic coast (Figure 3b), a critical region for this species where it forms extensive reefs (surface cover (100s ha) and height (>1m)) (Curd et al., 2020). A decrease in habitat suitability in this region could lead to a break in connectivity between the equatorward and poleward parts of the range, should the gap between the two regions exceed the dispersal abilities of the species (Wort et al., 2019).

The three preceding points suggest that *S. alveolata* may not, at a global scale, be a climate change winner. Up until now, such detailed changes required expert knowledge and a deep understanding of the ecology of the focal species, which are very difficult to attain particularly in multi-species studies. We propose to use additional landscape metrics, transposable from one species to another, to adequately and generically describe the complex changes taking place within species ranges. While not replacing the critical value of expert-based interpretations, this approach could help pinpoint more complex changes than the ones reported with broad-scale range metrics. Overall, our results indicate that landscape metrics, and particularly the Euclidean nearest neighbour distance between patches of the same class, are valuable to identify vulnerable and isolated patches, and can help inform regional management strategies (e.g. promoting ecological connectivity among populations). For instance, the identification of isolated patches could be used to locate further work on larval dispersal and recruitment, along with genetic diversity studies to help understand how separate patches of presences are interconnected and therefore whether they are part of a metapopulation functioning. Such studies are of particular interest given the role of isolated populations in evolutionary processes (see Supplementary Text).

More generally, several landscape metrics could be used to describe the extent to which various patch properties (e.g. area, aggregation patterns) are predicted to change in the future. Similarly to global change metrics classically reported in SDMs studies, we encourage future studies to report such internal range metrics to better predict climate change effects on species ranges. Interestingly, these metrics can be calculated at different user-defined resolutions, giving the possibility to study changes taking place at different spatial scales (e.g. regional, global, Chase et al. 2018). The issue of scale is at the core of landscape ecology (Turner et al. 2005) and previous studies have reviewed its effects on landscape metrics (e.g. Newman et al. 2019). Applying landscape metrics to SDM outputs adds another layer of complexity, since the accuracy of SDM predictions also varies depending on the spatial resolution and the scale considered (e.g. Chauvier et al. 2022). Here, we defined a patch as a minimum of one isolated pixel because of the broad-scale nature of the study. For finer-scale studies, a given number of pixels per patch could be set as a threshold. The latter could be based on ecological knowledge (e.g. dispersal distance), or by setting arbitrary thresholds and subsequently conducting a sensitivity analysis. Beyond landscape metrics, the fact that patches and associated pixels are characterised by unique identifiers further makes it possible to study in more detail (e.g. regional or species-centred studies) how patches of presences and absences are predicted to fragment or coalesce in the future. For instance, despite the stable number of patches predicted in the future, multiple colonisation and extinction events are predicted throughout the range, leading to current patches (of presences or absences) either splitting into several patches or merging with existing patches (Figure 5, Figures S12 and S13, Table S5). The predicted merging of presence patches in southwest England suggests that greater dispersion among existing presence patches in this area could either foster a range expansion, or resilience increase. In the current range centre (north Bay of Biscay), we predict a localised extirpation in the centre of a large presence patch, leading to a future gap between two presence patches. Similarly, between trailing edge populations (northern Spain) and populations from the Bay of Biscay, we predict local extirpations of a potential key stepping-stone population within a large absence area, with potential implications for connectivity. Finally, the predicted appearance of several small patches of suitable habitat within a currently large absence patch along the northwest Iberian Peninsula reinforces the importance of conservation efforts covering small habitat areas, as integrating key fragments in coastal management could benefit long-term species persistence. Beyond population connectivity, the predicted changes in spatial configuration may alter ecosystem functioning and dynamics. Spatial configurations are intrinsically linked with regime stability or shifts (Kefi et al., 2014). Landscape metrics can provide information on internal range changes which can act as early warning signals of impending regime shifts (Nijp et al., 2019). Relatively simple statistical landscape metrics are therefore critical for conservation, and could perhaps even fuel other types of analysis aiming to understand spatial early warning signals as ecosystems approach a tipping point (Génin et al., 2018).

The extirpation of ecosystem engineers and the related cascading ecosystem effects are considered principal drivers of regime shifts in both marine and terrestrial realms (Estes et al., 2018; Wright, 2009). There are, however, also consequences when the range of an ecosystem engineer shifts due to climate change, enabling colonisation of individuals and persistence of populations into new areas. The potential gain of an extensive area of suitable habitat, in Britain and Ireland, could alter community structure and ecosystem processes, with ensuing positive and negative impacts (Bulleri et al., 2018; Wallingford et al., 2020). It is also possible that species inhabiting *S. alveolata* reefs will exhibit range extensions by using the new areas of reef occurrence as “stepping stones”, with climate change facilitating the dispersion of the associated biota into new territories (Dubois et al., 2002; Faroni-Perez 2017), aided by proliferating sea defences as a societal adaptational response to rising and stormier seas driven by climate change (Bugnot et al., 2021; Firth et al., 2015). As a biogenic habitat forming species, it could also promote the diversity and resilience of benthic fauna by providing improved environmental conditions in the face of climate change through facilitation or habitat cascades (Bulleri et al., 2018; Gribben et al., 2019). The duality of effects upon recipient communities underscores the importance of considering the ecological impacts of species exhibiting range-shifts, in terms of both the benefits and potential costs to associated biodiversity and ecosystem functioning and service provision (Wallingford et al., 2020). Despite fundamental differences between introduced non-native and naturally range-shifting species, they can impact communities via analogous mechanisms (Wallingford et al., 2020). Landscape metrics could therefore also be useful for invasion risk assessments at a spatial scale relevant to regional and local-scale management decisions, e.g. Marine Protected Areas.

Several studies have used landscape metrics as covariates in SDMs to improve model predictions (Hasui et al., 2017; Ortner & Wallentin 2020). The novelty in our approach lies in the application of landscape metrics to binary predictions obtained from SDMs (or any spatial model e.g. joint-SDMs or mechanistic models) in order to identify patches of absences and presences. This framework makes it possible to study the internal range structure of species and better characterise the evolution of species ranges in response to e.g. climate change, provided that predictions are robust (i.e. our approach does not circumvent the flaws inherent to spatial models and does not improve their accuracy). For instance, selected landscape metrics can either reinforce or hinder the conclusions drawn from global change metrics. Here, we have shown a global increase in the range area (+27%) but further found that this global increase was mostly due to one presence patch largely increasing in the northern part of the range (coalescing with other presence patches) while most other presence patches were collapsing. While providing some avenues regarding how changes in landscape metrics could be interpreted when applied to SDMs outputs, the choice of landscape metrics and their interpretation will ultimately depend on the study system and question. Here we focused on the effect of climate change; however SDMs have been used for many other purposes (Bellard et al. 2012) where the use of landscape metrics would still be valuable. For instance, patch size and nearest neighbour metrics can be used jointly to identify patches that will become increasingly isolated in the future and for which conservation actions may be needed.

5 | CONCLUSIONS

As Earth’s climate rapidly changes, individuals of a species must move, acclimate, adapt, or die. Range shifts are therefore key to species persistence (Muir et al., 2020). Beyond range size and boundaries, internal range structure metrics are needed to adequately describe species’ ranges and more accurately quantify how they will be affected in the future (Csergő et al., 2020), particularly for species with discontinuous distributions. Analysing which landscape-level processes scale up to structure biogeographic ranges of species has however remained largely unexplored. Recent work however provides evidence that population and species level responses to habitat change at the landscape scale are modulated by factors and processes occurring at macroecological scales, such as historical disturbance rates, distance to geographic range edges, and climatic suitability (Banks-Leite et al., 2022). Our results suggest that these landscape-scale processes may be key to understanding and predicting internal range reconfiguration in changing environments. Specifically, we showed that broad-scale SDM combining terrestrial and marine predictors, coupled with a selection of global and regional landscape metrics, can be used to more accurately describe the changes a widely distributed intertidal species will face. Fragmentation of occupied area or suitable habitat has already been identified as a better predictor of extinction risk than range size (Crooks et al., 2017), and we propose that metrics characterising different aspects of species range structure, such as the distance between patches of suitable habitat, may be useful to meet conservation targets.

Conservation efforts should be refocused to search for critical internal range structure thresholds, especially those acting as proximate factors. Environmental management often focuses on single sites and populations, which crucially do not consider the wider context.

Landscape metrics applied to SDM outputs are a robust, non-data-intensive method that can aid environmental managers with broad-scale spatial planning under climate change.

AUTHOR CONTRIBUTIONS

A.C., L.B.F. and S.F.D. conceived this research. M.C., M.V., A.B. and M.P.M. analysed species distribution data and developed the use of landscape metrics in combination with SDM outputs to better characterize changes in species internal range structure. L.M.B, M.T.B and J.A.M.G. provided the oceanographic data for wave, fetch and tide respectively. A.C., L.E.B., C.C., A.J.D., S.F.D., L.B.F., S.J.H., F.P.L., C.M., N.M. and R.S. contributed towards the species distribution data. A.C. wrote the first draft. A.C., M.C., L.B.F., S.F.D., A.B., M.V. and M.M. contributed equally to discussion of ideas and analyses. M.C., A.J.D., L.B.F. and S.J.H. provided substantial inputs on drafts and revisions of the paper. All authors commented on the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The *S. alveolata* records dataset is archived as a .csv file in the SEANOE data repository (https://doi.org/10.17882/72164). All sources of environmental predictors used for modelling are freely available and referenced in Table S1. The code that supports the findings of this study is available from https://github.com/Mathieu-Chevalier/SDM_landscape_metrics

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