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Improving the interpretability of climate landscape metrics: an ecological risk analysis of Japan's Marine Protected Areas

Running head: Ecologically-coherent climate landscape metrics

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Keywords: climate change, ecological coherence, climate analogues, connectivity, stability, Japan, marine protected areas

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1 **Abstract**

2 Conservation efforts strive to protect significant swaths of terrestrial, freshwater and marine
3 ecosystems from a range of threats. As climate change becomes an increasing concern, these
4 efforts must take into account how resilient protected spaces will be in the face of future
5 drivers of change such as warming temperatures. Climate landscape metrics, which signal the
6 spatial magnitude and direction of climate change, support a convenient initial assessment of
7 potential threats to and opportunities within ecosystems to inform conservation and policy
8 efforts where biological data are not available. However, inference of risk from purely
9 physical climatic changes is difficult unless set in a meaningful ecological context. Here, we
10 aim to establish this context using historical climatic variability, as a proxy for local
11 adaptation by resident biota, to identify areas where current local climate conditions will
12 remain extant and future regional climate analogues will emerge. This information is then
13 related to the processes governing species' climate-driven range edge dynamics,
14 differentiating changes in local climate conditions as promoters of species range contractions
15 from those in neighbouring locations facilitating range expansions. We applied this approach
16 to assess the future climatic stability and connectivity of Japanese waters and its network of
17 marine protected areas (MPAs). We find 88% of Japanese waters transitioning to climates
18 outside their historical variability bounds by 2035, resulting in large reductions in the amount
19 of available climatic space potentially promoting widespread range contractions and
20 expansions. Areas of high connectivity, where shifting climates converge, are present along
21 sections of the coast facilitated by the strong latitudinal gradient of the Japanese archipelago
22 and its ocean current system. While these areas overlap significantly with areas currently
23 under significant anthropogenic pressures, they also include much of the MPA network that
24 may provide stepping-stone protection for species that must shift their distribution due to
25 climate change.

26 **Keywords:** climate change, climate analogues, stability, connectivity, conservation, protected
27 areas

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30 **Introduction**

31 The multiple anthropogenic pressures threatening our globe, along with the challenges these
32 pressures pose, require nations to act to protect both terrestrial, freshwater and marine
33 biodiversity and ecosystems, thereby safeguarding the goods and services they provide for
34 future generations (United Nations Convention on Biological Diversity (UNCBD), 1992). For
35 marine management, this commitment necessitates a global, holistic, ecosystem-based
36 approach that recognizes the interactive and cumulative impacts of human activities on the
37 world’s oceans (Halpern *et al.*, 2010). However, considerable uncertainty still exists
38 concerning the effective adaptation of marine management techniques in response to climate
39 change (Craig, 2012). Although the effects of climate change are multifaceted and interact
40 with local and regional stressors (Hoegh-Guldberg & Bruno, 2010), the dynamic alteration
41 of global marine ecosystems through the reshuffling of biodiversity patterns will be a key
42 challenge facing conservation management in the near future (Jones & Cheung, 2014, García
43 Molinos *et al.*, 2016).

44 Climate landscape metrics (CLMs) provide simple, direct measures of the magnitude of
45 change and shifts in local climatological conditions (Garcia *et al.*, 2014). For example,
46 climate analogues identify where sites with climate conditions comparable to those of the
47 present day are likely to be found in the future (Williams & Jackson, 2007), while the
48 velocity of climate change captures the spatial displacement of isotherms over time (Loarie *et*
49 *al.*, 2009). CLMs thus offer a simple and convenient tool by which researchers can inform
50 conservation practitioners of the risks climate change poses to biodiversity (IPCC, 2014),
51 particularly where species-specific ecological and biological data, which may be required by
52 more sophisticated approaches, are lacking (Garcia *et al.*, 2014). Furthermore, by focusing on
53 complimentary spatiotemporal climatic features, CLMs offer a robust initial analysis of the
54 potential threats to and opportunities for biodiversity based on projected changes in climate.
55 For example, Ordonez *et al.* (2016) recently used a combination of CLMs to assess the
56 novelty, displacement and divergence of global terrestrial climate conditions to determine the
57 likelihood of the formation of novel species assemblages. However, these approaches rely on
58 simple attribution between potential ecological responses and physical climatic changes
59 based on direct equivalence. This limits the interpretability of CLMs for risk assessment.
60 Placing these metrics in a more meaningful ecological context will improve their
61 interpretability as surrogates of ecological risk caused by future climate change (Hamann *et*

62 *al.*, 2015). We argue that even in the absence of specific ecological or biological data, such
63 contextualization is still possible when ecologically informed rules are used to define these
64 metrics. Here, we propose a new approach to CLMs that adds ecological interpretability by
65 addressing four shortcomings of current approaches: (i) the assumption of equal, fixed
66 ecological responses to given changes in climatic conditions, (ii) the lack of differentiation
67 between the opposing processes of range contractions and expansions, (iii) the use of
68 spatially unrestricted responses overlooking the type and scale of ecological responses being
69 inferred, and (iv) the need for incorporating the spatial connectivity between present and
70 future climates. These items are introduced in more detailed below.

71 The assumption that resident biota are equally sensitive and exposed to the same change in
72 climatic conditions is implicit in analogue-based approaches that define similar conditions by
73 reference to a fixed, common climatic threshold (Ordonez & Williams, 2013, Hamann *et al.*,
74 2015, Dobrowski & Parks, 2016). However, the same change in climate is likely to have
75 very different effects on two species depending on the capacities of those species to withstand
76 that change. Where physiological information is not available, one alternative is to define
77 non-analogue conditions as those beyond the bounds of historical climatic variability specific
78 to a given locality (Mora *et al.*, 2013). Such definition focuses on the role of climatic
79 variability in shaping the physiological plasticity of populations through adaptation and
80 acclimatization (Pörtner & Farrell, 2008), as well as the plausible assumption that responses
81 to climate change are increasingly likely as conditions move beyond those that local biota are
82 adapted to (Ainsworth *et al.*, 2016). This is particularly true for endemic (range-restricted)
83 species or populations at the edges of a species' distribution, which are usually at or closer to
84 their physiological tolerance limits (Foden *et al.*, 2013, Bates *et al.*, 2014).

85 Second, changes in climatic conditions are invariably interpreted as the minimum distance
86 required by a species to remain in an analogue environment. These interpretations can
87 involve the climatically (Williams *et al.*, 2007) or geographically (Hamann *et al.*, 2015)
88 closest analogue, or the analogue with the climatically less exposed dispersal route
89 (Dobrowski & Parks, 2016). However, these approaches do not appropriately capture the
90 opposing mechanisms driving range edge dynamics (Bates *et al.*, 2014). For a given locality,
91 climate change represents both a threat and an opportunity for resident populations,
92 depending on whether the focus is placed on changes in local climate conditions that make a
93 site climatically unsuitable or on the opening of neighbouring locations to a species. These

94 two processes can be easily implemented in an analogue analysis, and allow for an
95 interpretation of results in terms of range contractions and expansions of hypothetical species
96 respectively (Fig. 1).

97 Third, the search for analogues is treated as spatially unrestricted within a given geographical
98 extent that often ranges from continental to global (Koven, 2013, Dobrowski & Parks, 2016,
99 Ordonez *et al.*, 2016). As a result, these analogues have little relationship to the usually much
100 more spatially constrained movements of species. More meaningful searches can be made by
101 limiting the pool of available analogues to those located within the distance that a species can
102 be expected to cover over a given time period (Fig. 1). In the absence of specific dispersal
103 information, climate-related range shifts that have been reported for broad taxonomic groups
104 can be used for this purpose (Table S1). This restriction should be dependent on the type of
105 response considered (Bates *et al.*, 2014); for example, unlike range contractions, expansions
106 are active responses that require dispersal into and colonization of new, climatically suitable
107 habitats.

108 A final major critique of climate analogues is that they do not account for how a location is
109 climatically connected to its future analogue spatially or temporally. Identifying the potential
110 links between present and future climate analogues is arguably just as important as knowing
111 of their existence in terms of understanding how biodiversity patterns may shift (McGuire *et al.*
112 *et al.*, 2016). Most existing studies consider simple Euclidean connections between source and
113 destination, which minimizes travel distance (Ordonez & Williams, 2013, Hamann *et al.*,
114 2015, Ordonez *et al.*, 2016). However, this approach overlooks the effect of geographic
115 features (Burrows *et al.*, 2014), and it can underestimate climate risk if species depart from
116 the minimum distance path in search of routes less exposed to changes in climate (McGuire
117 *et al.*, 2016) or other non-climatic factors such as habitat conditions (McGuire *et al.*, 2016). A
118 least-cost path analysis offers an elegant solution to these problems (Dobrowski & Parks,
119 2016, McGuire *et al.*, 2016); however, it still assumes a single unidirectional source-to-
120 destination pathway. Alternatively, we use a randomized shortest path analysis in this study
121 (Saerens *et al.*, 2009). The incorporation of a random element into the calculation of the
122 shortest path allows for a degree of network exploration that translates into movement
123 probabilities conditioned by underlying resistance layers (see Methods). This reflects the
124 reality that a species' knowledge of its surroundings is necessarily partial (Saerens *et al.*,

2009); where the location of the future climate analogue and the optimal route to reach it are *a priori* unknown.

In the following, we first explain the technical approach and inferences used to analyse climate analogues in the context of ecological risk assessment. We then provide a case study to illustrate how this method can be used in a management context to assess the future climatic stability and connectivity of marine waters under Japanese influence, irrespective of political constraints, and their potential implications for the existing MPA network (Fig. 1). We also discuss how the flexibility of the methodology allows incorporating the effect of other non-climatic interacting factors such as surface currents and habitat permeability influencing ecological responses to climate change.

Materials and Methods

Data sets

Climate data. We used simulated historical (1986-2005) and projected (2026-2035) bias-corrected (Yara *et al.*, 2011) monthly mean sea surface temperatures (SSTs) from the MIROC4h model (Sakamoto *et al.*, 2012), currently the highest resolution model ($0.281^{\circ} \times 0.188^{\circ}$) for ocean components developed for the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Maynard *et al.*, 2015). Developed by Japanese research institutions, the bias-corrected SST product has been shown to accurately reproduce historical observed SSTs for the region (Takao *et al.*, 2015). Given the type and scale of the analysis considered, the need for high resolution data outweighed the MIROC4h's limitations regarding timescale and climate scenarios. Projections are available only up to 2035 for the Representative Concentration Pathway (RCP) 4.5, which results in a stabilization after 2100 without an overshoot and a global median temperature increase of 2.4°C above pre-industrial levels by 2100 (Rogelj *et al.*, 2012). However, differences among the RCPs are minor until mid-century (van Vuuren *et al.*, 2011), thus projected effects on marine biodiversity are comparable (García Molinos *et al.*, 2016). Furthermore, although long-term projections offer important complementary insights, near-term analyses are of evident practical use in short-term human decision-making processes (Chapman *et al.*, 2014). To characterize maritime climate conditions, we used a composite thermal metric (see below) based on three annual temperature parameters (annual mean, and minimum and maximum monthly SST).

Surface currents and directional agreement with spatial thermal gradients. Median current directions were calculated from 1985-2005 daily surface current data (0.1 x 0.1° resolution) sourced from the MOVE/MRI.COM ocean data assimilation system (Usui *et al.*, 2006) and aggregated to the MIROC4h resolution. Median instead of mean values were used to avoid bias introduced by extreme daily values. We then estimated the agreement between SST spatial gradients as in Burrows *et al.* (2011), and currents as the cosine of the difference in angle, ranging from 1 (a perfect match) to -1 (opposite directions) (Fig. S1a). The corresponding isotropic conductance matrix for each temperature parameter was finally defined as the pairwise mean agreement value between a focal cell and each of its neighbours. A value of 1 was added to avoid negative conductance values. We used this index to account for the role of ocean currents in mediating expansions under climate change (see below).

Seascape permeability. We used the cumulative human impact index developed by Halpern *et al.* (2015), aggregated to the MIROC4h resolution, as an indicator of seascape permeability. This index reflects cell-average habitat vulnerability-weighted stressor intensities (19 individual stressors excluding the SST component to avoid confounding effects), with higher values representing higher intensities (Fig. S1b).

Climate analogue definition

We first calculated both the regional (between time-period comparisons of each grid cell with all others) and local (within-cell between time-period comparisons) climate anomalies as Euclidian distances (ED) in climate space (Ohlemüller *et al.*, 2006):

$$ED_{i,j} = \sqrt{\sum_{k=1}^m (\bar{x}_{k,i} - \bar{x}_{k,j})^2} \quad [1]$$

where i and j represent the focal (baseline) and target (future) cells within the study region ($i = j$ for local anomalies), m is the set of parameters defining their climate, and $\bar{x}$ is the corresponding mean of each k parameter under baseline (1986-2005) and future (2026-2035) conditions. From equation [1], we calculated a Euclidean-based analogue threshold based on the variability in historical focal climate conditions (within 1.5 standard deviations of the mean):

$$ED_t = \sqrt{\sum_{k=1}^m (\bar{x}_{k,i} - (\bar{x}_{k,i} + 1.5 * SD_{k,i}))^2} = \sqrt{\sum_{k=1}^m (1.5 * SD_{k,i})^2} \quad [2]$$

We used this threshold to define the distance bounds beyond which future thermal conditions were considered non-analogous (i.e., surpassed baseline climate variability at a locality; $ED_{i,j} > ED_t$). A factor of 1.5 was used to conservatively define the non-analogous condition (comparable to either the 7th or 93rd percentile rank), reflecting a high probability that said condition was either significantly below or above average current climate conditions (see Fig. S2 for sensitivity analysis of results using alternative factors).

Analogue search algorithm

We first defined the potential pool of future climate analogues relevant to each cell by calculating present-to-future differences in thermal conditions compared to other cells using equations [1] and [2]. This analysis was performed both with and without restricting the analogue search to the continental shelf edge as a coarse filter reflecting shallow (coastal and shelf) habitat availability. We set the shelf limit at the 200-m isobath, which is associated with strong ecotone changes (Spalding *et al.*, 2007), using the ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009). Resulting changes in climate were then analysed as two contrasting analogue searches (Fig. 2) mimicking climate-driven range edge dynamics (Bates *et al.*, 2014). For each grid cell we first search for the geographically closest location with future climatic conditions analogous to those currently existing at the location of interest (associated with potential range contractions of resident biota; Fig. 2a). The search for the geographically closest future analogue (Hamann *et al.*, 2015) was preferred over the climatically closest analogue (Williams *et al.*, 2007) because the latter can produce large overestimations of risks where suitable climatic analogues are found at shorter distances than the climatically closest analogue. Where no climate analogues were available, the climatically closest non-analogue was used instead. We then repeated the search algorithm but this time targeting cells initially under non-analogue conditions that were projected to become climate analogues for the focal cell in the future (interpreted as potential range expansions; Fig. 2b). Analogue distance and velocities were set to null (no response) for those cells for which all neighbouring cells within the threshold distance were currently climatically available, or for which no future analogues were found among those cells currently subject to non-analogous conditions. Contrary to range contractions, which are driven by the local effect of climate change on the physiological performance of resident populations, range expansions depend on the dispersion and settlement of organisms from edge populations into climatically suitable environments as they become available. To reflect this, we set analogue search

distance thresholds to coincide with the range of reported mean expansion rates for main taxonomic marine groups and their corresponding zonation (Table S1), namely regional oceanic (30 km/year) and coastal/shelf waters (6 km/year). Nevertheless, a maximum search distance was needed to define range contractions to avoid ecologically spurious results (selection of analogues from distant unrelated cells). We defined this as 300 km (8.6 km/year), or approximately the 95th percentile of reported global rates of range contraction for marine taxa (Poloczanska *et al.*, 2013).

Upon detection of the target analogue cell, geographical distances and bearings with the focal cell were recorded. To reflect the fact that expansions grow over the full set of thermally favourable environments within a range, expansion distances and bearings from each focal cell were calculated to the centre of mass of all future analogue cells within the search distance. We used least-cost distances in lieu of the more common great-circle distances (Williams *et al.*, 2007, Hamann *et al.*, 2015), to incorporate the biogeographical effect imposed by land and depth boundaries as well as other non-climatic factors influencing dispersal (see below).

Cost path analysis

We estimated future climatic connectivity between each focal cell and its corresponding future analogue using a randomized shortest path analysis (Saerens *et al.*, 2009) based on circuit theory and random walks (McRae *et al.*, 2008). In this approach, a probability distribution of the set of possible paths to follow for each node is first constrained to a fixed degree of randomness for the whole network. Probabilities are assigned using finite, first-order Markov chains for each node in the network, and the amount of associated randomness is estimated using the Shannon entropy of the probability distribution for the set of possible paths to follow (transition probabilities) from the node. The problem is then stated as a global optimization problem. We use this to find an optimal policy (the set of transition probabilities in each node) that minimizes the expected accumulated cost from source to destination given a predefined degree of randomness controlled by the parameter $T \geq 0$, which varies in theory between 0 (deterministic least-cost path) and ∞ (random walk). We arbitrarily used $T = 10$ to calculate the randomized shortest paths. A sensitivity analysis showed that our results were consistent for alternative values of T (Fig. S3).

A cost path analysis requires us to define a conductance model that represents the ease of movement across the seascape from one cell to its neighbours. We used two different models: (a) a model based solely on spatial temperature gradients (Fig. S4a) and used to determine passive responses elicited by local changes in climate (range contractions; Fig. 2a), and (b) a model that also accounts for the spatial agreement between thermal gradients and mean ocean current direction (Fig. S4b) as well as seascape permeability (Fig. S4c) to determine active responses motivated by changes in neighbouring climate conditions (range expansions; Fig. 2b).

Species that track thermal niches in a warming environment are expected to follow a route that minimizes the energetic cost of dispersal. This is equivalent to finding the optimal least-cost path given a conductance layer defined by a spatial temperature gradient. One possible approach to this is optimization based on the cost of moving through areas of dissimilar climate over time (Dobrowski & Parks, 2016) assuming that movement is less costly the closer the climate conditions of the cells that need to be crossed are, or will be in the future, to those existing at the locality of origin. Though this approach is attractive because it expresses costs in terms of absolute climatic exposure, it implicitly assumes “optimum” existing origin conditions that are worsened by any climate change, irrespective of the sign. We take an alternative approach that is more relevant to range edge dynamics by considering cost as contingent upon the sign of the difference. This approach assumes that for species responding to climate change, the tendency will be to move toward those cells that offer a greater gain via a temperature change with the opposite sign, i.e., towards cooler conditions under warming, following the most unidirectional temperature gradient (Nuñez *et al.*, 2013, McGuire *et al.*, 2016). The thermal conductance layer between each focal cell and its eight immediate neighbours was therefore defined using the mean spatial temperature gradient between the baseline (1986-2005) and future (2026-2035) conditions as well as the following anisotropic (i.e., conductance from cell i to j is not the same as from j to i) equation:

$$C_{SST} = 3 + SST_{focal} - SST_{neighbour} \quad [3]$$

This equation determines the most unidirectional rate of change in temperature (warm to cold) and the steepest thermal gradient (fastest gain in temperature for a given distance travelled), thus reflecting the most likely movement of a species tracking a thermal niche in a warming ocean. The constant value is an off-set to avoid negative conductance values.

We then defined the isotropic conductance matrices for the directional agreement between ocean currents and thermal gradients for each individual temperature parameter as the pairwise mean agreement value between a focal cell and each of its neighbours. A value of 1 was added to avoid negative conductance values (i.e., the index ranges from -1 to 1). Similarly, we defined isotropic conductance matrices for seascape permeability as the inverse of the pairwise mean cumulative human impact index value between a focal cell and each of its neighbours. This increasing stressor intensity to increasingly limit the capacity of movement through a cell.

All resulting conductance matrices were scaled and corrected to account for diagonal neighbours and map distortion introduced by the geographic projection. The two final composite seascape conductance models were then constructed as the mean of the individual conductance matrices for each temperature parameter (contraction model), and those of ocean surface currents and landscape permeability (expansion model).

Assessing climatic stability and connectivity under future climate change

We implemented the methods described above into several complementary analogue-based CLMs defining different climatic components of a landscape. Future local and regional climate stability was estimated by looking at how much (climate anomalies) and how fast (climate velocity) current climate conditions are projected to change into the future (Table 1). Climate velocities were estimated by dividing the resulting least-cost path distance by 35 years, the amount of time between the midpoint of both periods (1995-2030), and interpreted as expected responses (range contractions and expansions) of local biota shifting their distribution range in response to climate change. Our climate velocity metric is hence similar to that termed the minimum exposure distance velocity by Dobrowski and Parks (2016) in that a least-cost path analysis was used to define the optimal path; however, the two terms differ in how analogues are defined and searched for and in how least-cost paths are routed between source and destination analogues (see below).

Climate connectivity was assessed based on the passage density (Table 1) between each cell and its future (non-)analogue using randomized shortest paths ($T = 10$). This yielded the number of passages not reciprocated by transitions in the opposite direction (i.e., net number of transitions over each cell connection). This passage density can be considered equivalent to the likelihood of the cell passage between two localities (van Etten & Hijmans, 2010).

High density areas thus represent important thermal pathways connecting current and future climates within a region and are therefore likely to concentrate climate-migrant species tracking a warming ocean by shifting their ranges.

All cost-path calculations were performed using the *gdistance* package in the R statistical environment (van Etten, 2014).

Case Study

As an example, we apply the described methodology to analyse the future maritime climate stability and connectivity of Japan. We focus here on a regional assessment of all marine waters under Japanese influence, irrespective of their political situation, and its corresponding network of MPAs (Fig. 1). The Japanese archipelago covers latitudes from the subtropical to temperate zones and support high marine biodiversity (155,542 species, including 1,872 endemic species, according to a recent estimate; Fujikura *et al.*, 2010), including many species that reach their northern or southern limits in these waters (Yamano *et al.*, 2011). Therefore, the distribution of Japan's MPA network along this latitudinal gradient (Fig. S1) should *a priori* confer good connectivity between protected areas for species that must shift their distribution as a result of climate change.

Spatial and descriptive MPA data were extracted from the World Database on Protected Areas (WDPA, www.protectedplanet.net September 2015) by filtering all sites classified as "marine" for the Japanese territory ($n = 517$ sites). Internationally inscribed/approved sites (Ramsar and World Heritage sites) were not included because they are also designated nationally. For the purposes of this study, we considered the MPA network to be the multi-part polygon encompassing all patches of protected seascape within Japanese waters (Fig. S1). Terrestrial areas within coastal MPAs were discarded by masking the MPA dataset with a standardized high resolution EEZ boundary (VLIZ, 2014), resulting in a total of 489 MPAs.

Results and Discussion

87.8% of Japanese territorial waters are projected to experience local, non-analogue composite thermal environments by 2035 relative to baseline conditions, with 19.6% and 67.4% of non-analogue cells developing composite anomalies of less than 0.5 and 1°C above historical variability bounds, respectively (Fig. 3c). Projected remnant local climates are concentrated primarily in oceanic waters off the south-eastern coast of Japan (Fig. 3c), an

area influenced by the interannual bimodal fluctuation of the north-flowing warm Kuroshio Current (Qiu & Miao, 2000). This area exhibited strong baseline variability (Fig. 3a) and the lowest projected changes in composite thermal conditions (Fig. 3b); it is also subject to the extension of the Kuroshio Current into the Pacific Ocean (Fig. 1). In contrast, the most extreme, novel local climate conditions were identified across a latitudinal band (35-40°N) stretching off the Sanriku coast (north-eastern Japan) into the Pacific (Fig. 3c) where the Kuroshio and the south-flowing cold Oyashio Current fronts converge (Fig. 1). This mixing region, which is characterized by steep temperature gradients with frequent, intense small- to meso-scale eddies (Yasuda, 2003), was projected to experience the largest local changes in compound thermal conditions (Fig. 3b), resulting in future climates well beyond current baseline variability levels ($>1.5\text{-}2^{\circ}\text{C}$; Fig. 3c). Remnant climates were mostly oceanic: non-analogue local thermal environments developed for most (95.1%) of the Japanese coastal/shelf waters, especially along central/northern Japan (Fig. 3c). Spatial heterogeneity in projected local climate stability was nevertheless high for individual temperature parameters (Fig. S5). Regionally, however, the vast majority of local climate environments within Japanese waters were projected to be remnants (i.e., an available future climate analogue that falls within historical variability bounds; Fig. S6).

We found that significantly greater climate velocities (Fig. 4a-d) were related to changes in neighbouring thermal conditions rather than those related to changes in local conditions, both for continental shelf (medians of 3.63 and 1.78 km/year, respectively; Brunner-Munzel test statistic $t_{\text{bm}} = 23.3$, $\text{df} = 1749.8$; $p < 0.0001$) and regional (10.34 and 2.38 km/year, respectively; $t_{\text{bm}} = 318.73$, $\text{df} = 13807$; $p < 0.0001$) waters. Overall, directions of shift were consistent with a movement towards higher latitudes (see rose plots in Fig. 3a-d). Biogeographical shifts in marine ectotherms have been reported as being equally responsive globally (Sunday *et al.*, 2012) but significantly faster (nearly 5 times on average (Poloczanska *et al.*, 2013)) at leading rather than trailing edges; curiously, this was the same ratio found for regional analogue responses in the present study. In general, high velocity regions overlapped for both types of responses in shallow waters (Fig. 4a-b), particularly at several locations where tropical and temperate species currently meet their northern and southern distribution limits and recent range shifts have been documented (Fig. 1). This suggests that observed changes are likely to continue and will overlap spatially in the coming decades.

Connectivity is a primary goal in conservation planning (Lavorel *et al.*, 2015) because the exchange of organisms, materials and energy across land and seascapes influences population, community and ecosystem structures and functioning (Olds *et al.*, 2016), as well as communities' resilience against disturbances (Olds *et al.*, 2012). Therefore, climate-driven changes in spatial and temporal connectivity patterns have crucial implications for conservation planning (Munday *et al.*, 2009), particularly the design and placement of protected areas (McLeod *et al.*, 2009). Regions where climates from different localities converge represent "climate corridors" (Burrows *et al.*, 2014) that serve not only as core connectivity areas between present and future climates but also as transit routes where biotic interactions between climate migrants and resident biota are likely to be more intense, potentially promoting high rates of community turnover via species replacement (Magurran *et al.*, 2015, García Molinos *et al.*, 2016). Such effects are likely to be more profound where high passage densities (Table 1, Fig. 4e-h) overlap areas experiencing rapid changes in local/neighbouring climate conditions (i.e., high climate velocities). This is the situation along most of the south-western and north-eastern coasts of Japan, where passage densities are typically above the 75th percentile of all Japanese shelf waters (Fig. 4e-f). Furthermore, high-connectivity (above the 50th percentile) coastal areas appear to be exposed to significantly higher levels of other human impacts (Fig. S1b) than low-connectivity areas, both in terms of changes in local (median cumulative human impact index of 3.45 against 2.7; $t_{bm} = 20.52$, $df = 5223.9$; $p < 0.0001$) and neighbouring (3.64 against 2.66; $t_{bm} = 31.73$, $df = 4887.6$; $p < 0.0001$) thermal conditions. This highlights the importance of using holistic approaches to maintain the connectivity of coastal marine ecosystems (Le Corre *et al.*, 2012).

While our results highlight the potential strengths and weaknesses of the existing MPA network in the face of climate change (Fig. 5), a detailed analysis of these points is beyond the scope of this study. In general, grid cells within MPAs were projected to exhibit more rapid changes in local thermal anomalies than cells outside protected areas (Fig. 5c), with few cells ($4.1 \pm 13.9\%$) exhibiting future conditions within historical climate variability bounds (Fig. 5a green bars). This suggests a significant, widespread risk of species range contractions within currently protected areas, particularly considering the high number of endemic species currently found along their southern (warm edge) distribution edges in Japanese waters (Yamano *et al.*, 2011). Nevertheless, the closest analogues of a large proportion ($31.4 \pm 34.5\%$) of these shifting climates existed within other MPA cells (Fig. 5a orange bars). At the

402 same time, the rapid changes in regional thermal anomalies also resulted in almost one-fifth
403 of grid cells within MPAs ($17.3 \pm 21.8\%$ overall; Fig. 5b) developing future analogue
404 climatic conditions for current climates both within and outside the MPAs, thus indicating
405 opportunities for species range expansions. This was particularly evident in northern Japan
406 (Hokkaido, Fig. 5b), where the future climates in MPA cells were generally analogous to
407 current climates outside of MPAs (Fig. 5b light and mid-blue bars), indicating that these
408 MPAs are likely to experience shifting species distributions from across the broader region.
409 However, along the southern edge of mainland Japan, future climates were generally
410 analogous to current conditions within the studied MPAs (Fig. 5b dark blue bars).

411 Though limited in time and based only on projected climate data from a single model and
412 RCP scenario, these results nevertheless demonstrate how the method used here can provide
413 information on the stability and connectivity of future climate land and seascapes. These data
414 can be better interpreted in ecological terms and thus more readily incorporated into
415 management and conservation decisions than CLMs data derived from other existing
416 methods. For example, existing conservation demands on MPA networks call for
417 “ecologically representative and well connected systems of protected areas”, i.e., Target 11 of
418 the Convention on Biological Diversity (United Nations Convention on Biological Diversity
419 (UNCBD), 1992). Our connectivity analysis indicates that this seems to be the case for the
420 Japanese MPA network overall because the more or less even coastal alignment along the
421 well-defined latitudinal gradient of the archipelago (Fig. S1) provides a stepping-stone
422 system of protection for species shifting their distribution due to climate change. The
423 incorporation of climate change into marine spatial planning and resource management is
424 urgently needed to ensure the long-term sustainability and adaptive management of marine
425 systems (Pershing *et al.*, 2015). Where knowledge is partial or non-existent, simple coarse-
426 filter quantitative approaches such as CLMs are valuable for integrating climate change into
427 conservation planning, provided these approaches are ecologically relevant (Magris *et al.*,
428 2014). Furthermore, the present case study also demonstrates the advantages of this type of
429 analysis for the marine environment, where climate analogue analyses have not, to the best of
430 our knowledge, previously occurred. Together with climate effects, the present method
431 allows for the direct incorporation of the effects of other non-climatic factors such as
432 coastlines, oceanographic features (surface currents) and seascape permeability (existing non-

climatic human impacts) into the analysis. This flexibility allows such approaches to be easily integrated into prioritization protocols (Yamakita *et al.*, 2015).

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Author contributions

J.G.M. conceived and designed research. S.T., and N.H.K. provided the climatological and ocean current data, respectively. J.G.M. conducted the analysis and wrote the first draft of the paper. All authors contributed to the discussion of ideas with significant input to the final manuscript.

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Figure Captions

Figure 1. Study area and Japanese network of marine protected areas (MPAs). The inset provides a schematic of the main ocean surface current systems together with the approximate areas with documented range shifts (expansions and/or contractions) for species of corals and seaweeds. Note the bimodal onshore/offshore paths of the Kuroshio Current south of Japan that alternate on interannual scales.

Figure 2. Flow chart of the decision process to differentiate an analogue search based on (a) changes in local climate conditions that make the site climatically unsuitable, which are interpreted ecologically as the potential for range contractions, or (b) changes in neighbouring climates currently under non-analogue conditions that result in their future availability, which are associated with potential range expansions. Non-analogue conditions were defined as those beyond the bounds of the historical (1986-2005) composite climate variability at each cell based on the standard deviation of each temperature parameter (see Materials and Methods).

Figure 3. Projected local climate stability. (a) Climate analogue threshold for composite local thermal conditions defined from the baseline (1986-2005) standard deviation of all temperature parameters (see Methods; for individual SST parameters see Fig. S2). (b) Euclidean distances between baseline and future (2026-2035) composite mean thermal conditions. Higher distances indicate increasing dissimilarity between future local climates and current conditions. (c) Local composite thermal anomalies resulting from the difference between (a) and (b). Blueish/brownish colours indicate remnant/novel local climatic conditions where anomalies are projected to stay within/surpass background climate variability at each locality. The black contour defines the territorial waters considered in this study.

Figure 4. Future regional climate stability and connectivity. (a-d) Projected climate velocity in response to changes in (a, c) local (range contractions) and (b, d) neighbouring (range expansions) composite thermal conditions, and (e-h) resulting climate connectivity between current and future analogues for (a, b, e, f) shelf-restricted (200-m isobath) and (c, d, g, h) regional (unrestricted) waters. Silhouettes give reported global or regional (*) median expansion rates of different marine taxa for comparison. Inset rose plots provide a summary of the bearings from current localities to the corresponding future analogues. Connectivity (e-h) expressed as density of passage generated using randomized shortest paths between each cell and its corresponding future climate analogue. Colour breaks are set at 5% percentile increments for the subset of cells within the study region (black contour line).

Figure 5. Projected climatic stability and connectivity of the Japanese network of marine protected areas (MPAs). Summary (4x4° sectors) of the anticipated ecological responses to (a) changes in local climate conditions (range contractions), and (b) changes in neighbouring climate conditions (range

expansions). Proportions involve the total number of protected cells (i.e., including part or all of an MPA) by sector. Note that the size of the bars among sectors is not comparable as the number of protected cells differs. (c) Violin and box-plots for the area-weighted mean cell values of the different stability/connectivity metrics (Table 1) for the MPA network (“MPA”, $n = 489$), and those corresponding to unprotected cells (“Rest”, $n = 679$) within Japanese shelf waters (< 200 m depth). Asterisks indicate level of statistical significance for differences ($* < 0.05$, $** < 0.01$, $*** < 0.001$; Brunner-Munzel Test for stochastic equality in sample distributions).

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Tables

651 Table 1. Climate seascape metrics used to characterize the climatic stability and connectivity of the
652 Japanese waters under projected future climate change.

Metric	Definition	Interpretation	Property
Local climate anomalies (Fig. 2c)	Difference between the climate analogue threshold at a given locality (grid cell), based on baseline variability, and the Euclidean distance in climate space between current baseline (1986-2005) and future (2026-2035) local climatic conditions.	Estimate of the magnitude and type of climatic change expected in a locality. Negative values representing locally-novel future climatic conditions (i.e., beyond the bounds of local historical variability).	Stability
Regional climate anomalies (Fig. S6)	Difference between the climate analogue threshold at each cell and the Euclidean distance in climate space between its current baseline climatic conditions and the future conditions of its geographically closest climate analogue or, in its absence, the climatically closest non-analogue.	Provides an estimate of the magnitude and type of climatic change expected regionally. Negative values represent the development of novel regional climatic conditions.	Stability
Climate velocity (Fig. 4a-d)	Least-cost path distance (km) between the focal cell and its future target analogue, calculated by reference to biogeographical boundaries and processes linking range shift dynamics to climate change (see Methods), divided by the time interval between midpoints of the two periods (35 yr).	Speed (km/yr) at which hypothetical species will need to move to either (a) remain within current climatic conditions (i.e., changes in local climate conditions), or (b) exploit new environments becoming climatically suitable in the future (i.e., changes in neighbouring conditions).	Stability
Passage density (Fig. 4e-h)	Cumulative sum of passage probabilities at each cell corresponding to all climate trajectories that circulate over that cell linking present and future closest climatic analogue for (a) changes in local climate conditions or (b) changes in neighbouring conditions. A probability of passage is defined using randomized shortest paths as the total number of trajectories crossing through a cell that are not reciprocated by a passage in the opposite direction (see Methods).	High densities represent important thermal pathways connecting current and future climates within a region, therefore likely to concentrate climate-migrant species. Areas with null density correspond to climatically stable (i.e., remnant static climates), and/or isolated (i.e., not representing climate analogues for other localities) regions.	Connectivity

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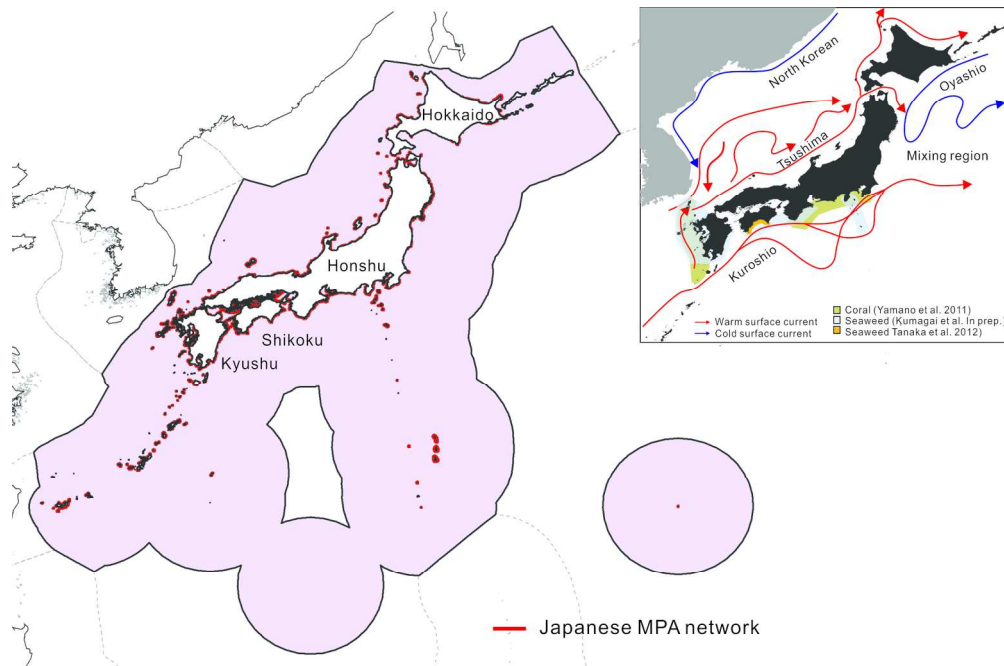


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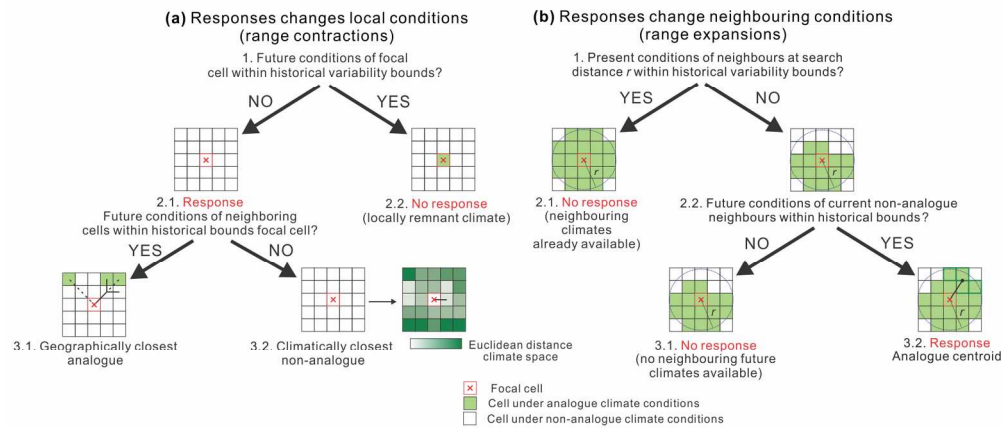


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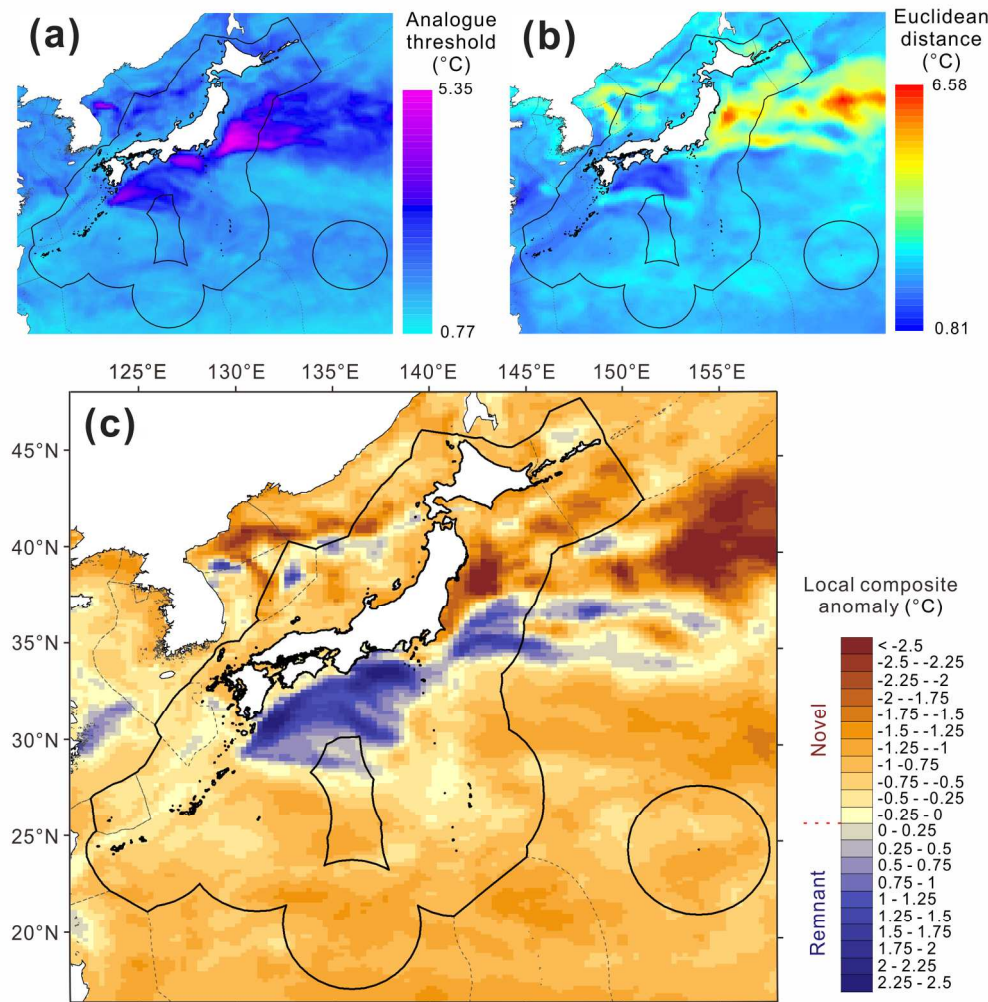


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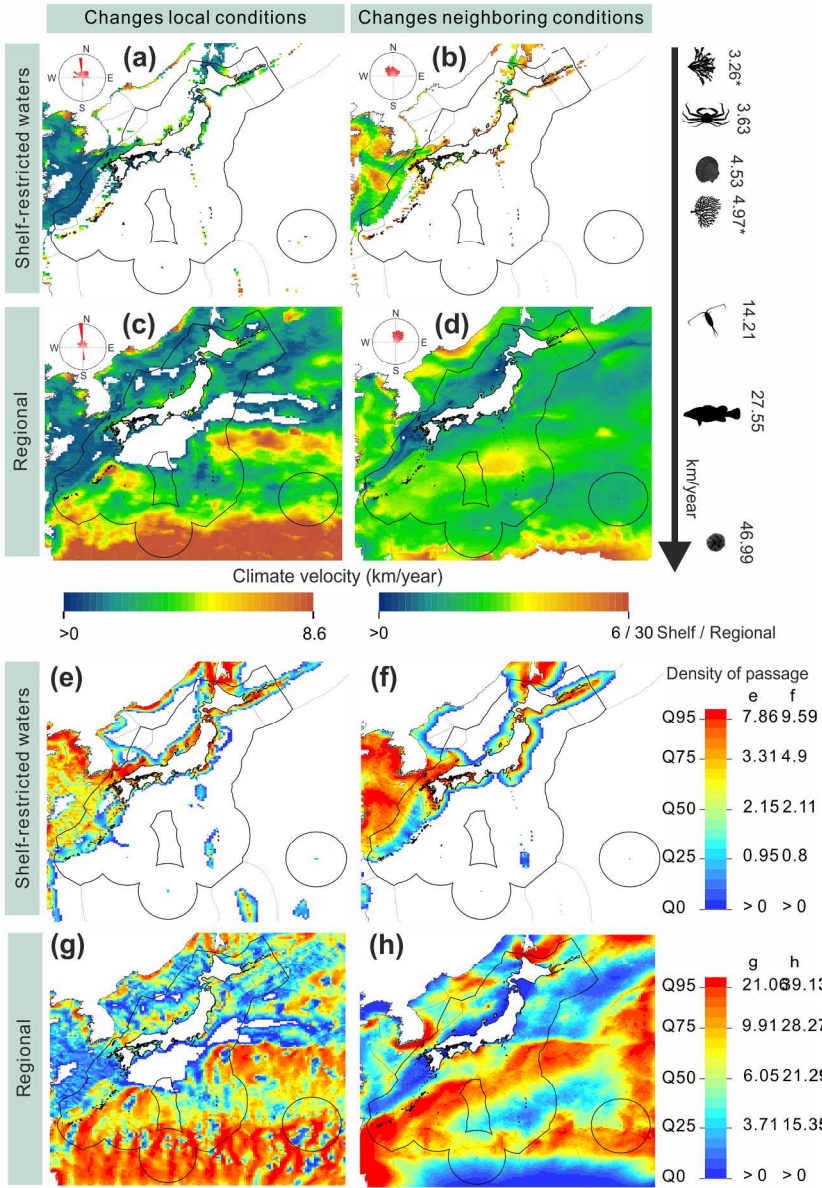


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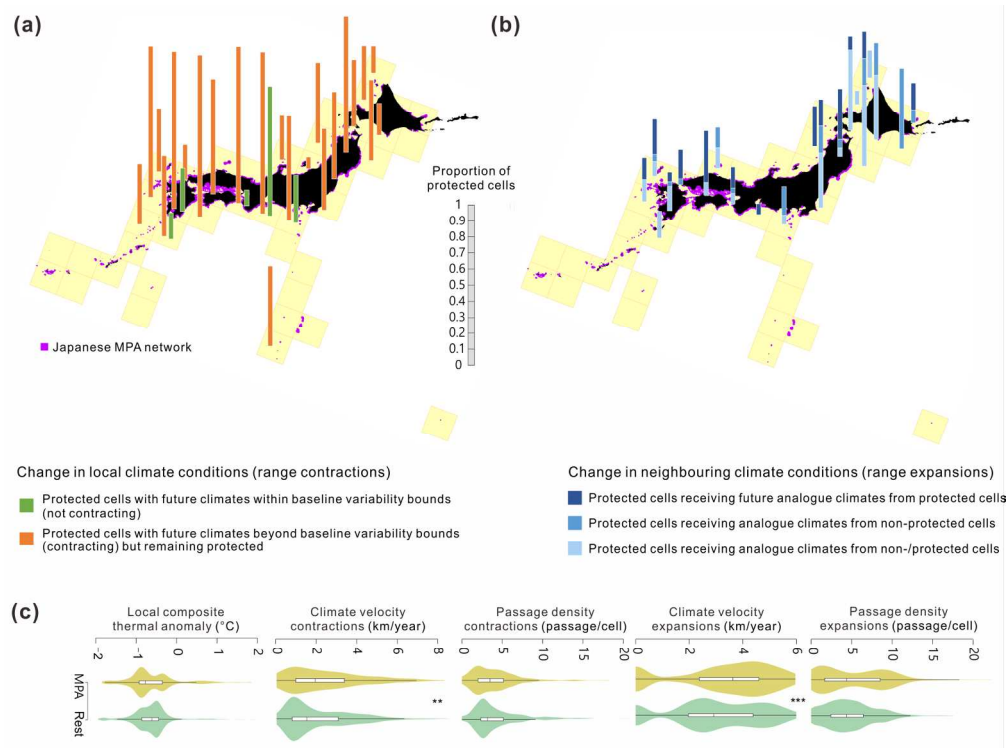


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