Received: 15 July 2022 | Revised: 20 January 2023 | Accepted: 9 March 2023

DOI: 10.1002/eap.2852

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

A metric-based framework for climate-smart conservation planning

Kristine Camille V. Buenafe[1,2,3,4] | **Daniel C. Dunn**[1,5] | **Jason D. Everett**[2,6,7] | **Isaac Brito-Morales**[8,9] | **David S. Schoeman**[10,11] | **Jeffrey O. Hanson**[12] | **Alvise Dabalà**[1,2,13,14] | **Sandra Neubert**[2,15] | **Stefano Cannicci**[3,4] | **Kristin Kaschner**[16] | **Anthony J. Richardson**[2,6]

[1]School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Queensland, Australia

[2]School of Mathematics and Physics, The University of Queensland, Brisbane, Queensland, Australia

[3]Department of Biology, University of Florence, Florence, Italy

[4]The Swire Institute of Marine Science and Area of Ecology and Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong, China

[5]Centre for Biodiversity and Conservation Science (CBCS), The University of Queensland, Brisbane, Queensland, Australia

[6]Commonwealth Scientific and Industrial Research Organization (CSIRO) Environment, Queensland Biosciences Precinct (QBP), St Lucia, Queensland, Australia

[7]Centre for Marine Science and Innovation (CMSI), The University of New South Wales, Sydney, New South Wales, Australia

[8]Betty and Gordon Moore Center for Science, Conservation International, Arlington, Virginia, USA

[9]Marine Science Institute, University of California Santa Barbara, Santa Barbara, California, USA

[10]Ocean Futures Research Cluster, School of Science, Technology and Engineering, University of the Sunshine Coast, Maroochydore, Queensland, Australia

[11]Centre for African Conservation Ecology, Department of Zoology, Nelson Mandela University, Gqeberha, South Africa

[12]Department of Biology, Carleton University, Ottawa, Ontario, Canada

[13]Systems Ecology and Resource Management, Department of Organism Biology, Faculté des Sciences, Université Libre de Bruxelles – ULB, Brussels, Belgium

[14]Ecology and Biodiversity, Laboratory of Plant Biology and Nature Management, Biology Department, Vrije Universiteit Brussel – VUB, Brussels, Belgium

[15]Institute of Computer Science, Leipzig University, Leipzig, Germany

[16]Department of Biometry and Environmental Systems Analysis, Albert-Ludwigs-University of Freiburg, Freiburg im Breisgau, Germany

Correspondence
Kristine Camille V. Buenafe
Email: k.buenafe@uqconnect.edu.au

Funding information
Erasmus Joint Master Degree Program by the European Commission; National Science Foundation (NSF), Grant/Award Number: 2029710; Nature Conservancy of Canada (NCC)

Abstract
Climate change is already having profound effects on biodiversity, but climate change adaptation has yet to be fully incorporated into area-based management tools used to conserve biodiversity, such as protected areas. One main obstacle is the lack of consensus regarding how impacts of climate change can be included in spatial conservation plans. We propose a climate-smart framework that prioritizes the protection of climate refugia—areas of low climate exposure and high biodiversity retention—using climate metrics. We explore

Handling Editor: Éva E. Plaganyi

four aspects of climate-smart conservation planning: (1) climate model ensembles; (2) multiple emission scenarios; (3) climate metrics; and (4) approaches to identifying climate refugia. We illustrate this framework in the Western Pacific Ocean, but it is equally applicable to terrestrial systems. We found that all aspects of climate-smart conservation planning considered affected the configuration of spatial plans. The choice of climate metrics and approaches to identifying refugia have large effects in the resulting climate-smart spatial plans, whereas the choice of climate models and emission scenarios have smaller effects. As the configuration of spatial plans depended on climate metrics used, a spatial plan based on a single measure of climate change (e.g., warming) will not necessarily be robust against other measures of climate change (e.g., ocean acidification). We therefore recommend using climate metrics most relevant for the biodiversity and region considered based on a single or multiple climate drivers. To include the uncertainty associated with different climate futures, we recommend using multiple climate models (i.e., an ensemble) and emission scenarios. Finally, we show that the approaches we used to identify climate refugia feature trade-offs between: (1) the degree to which they are climate-smart, and (2) their efficiency in meeting conservation targets. Hence, the choice of approach will depend on the relative value that stakeholders place on climate adaptation. By using this framework, protected areas can be designed with improved longevity and thus safeguard biodiversity against current and future climate change. We hope that the proposed climate-smart framework helps transition conservation planning toward climate-smart approaches.

KEYWORDS
climate resilience, environmental decision making, Marxan, MPAs, prioritizr, spatial prioritization, systematic conservation planning

INTRODUCTION

Climate change is a major threat to biodiversity (IPCC, 2021). Although protected areas have long been used to safeguard biodiversity (Bates et al., 2019), climate change reduces their effectiveness by exposing biodiversity to a suite of environmental changes, including warming, changes in rainfall, increasing ocean acidification, and deoxygenation (Bruno et al., 2018). Climate warming primarily drives species range shifts (Chaudhary et al., 2021; Lenoir et al., 2020; Parmesan & Yohe, 2003) and changes in communities (Burrows et al., 2019), which can cause species to move beyond boundaries of protected areas (Heikkinen et al., 2020; Loarie et al., 2009). Thus, protected area design needs to explicitly account for climate exposure and species retention (Doxa et al., 2022; Harris et al., 2019). However, there is currently little consensus on how to implement this goal (Tittensor et al., 2019; Wilson et al., 2020).

Climate-smart conservation planning is a relatively new concept that deals with the design of protected area systems robust to climate change (Jones et al., 2016; Santos et al., 2020; Tittensor et al., 2019). It could be achieved with a range of different approaches (Reside et al., 2018; Santos et al., 2020; Wilson et al., 2020) that use climate projections or cover risk and uncertainty (Figure 1). Examples include: (1) protecting ecologically- and economically-important species (Green et al., 2009; Lombard et al., 2007; Patrizzi & Dobrovolski, 2018); (2) conserving heterogeneous environments to hedge against uncertainty in climate change predictions (Green et al., 2009; Walsworth et al., 2019); and (3) ensuring redundancy in preserved areas to minimize risk (Green et al., 2009; Magris et al., 2014). Although these approaches can protect important species and critical habitats, protection against current threats does not equate to protection against impacts of climate change (Bates et al., 2019; Bruno et al., 2018).

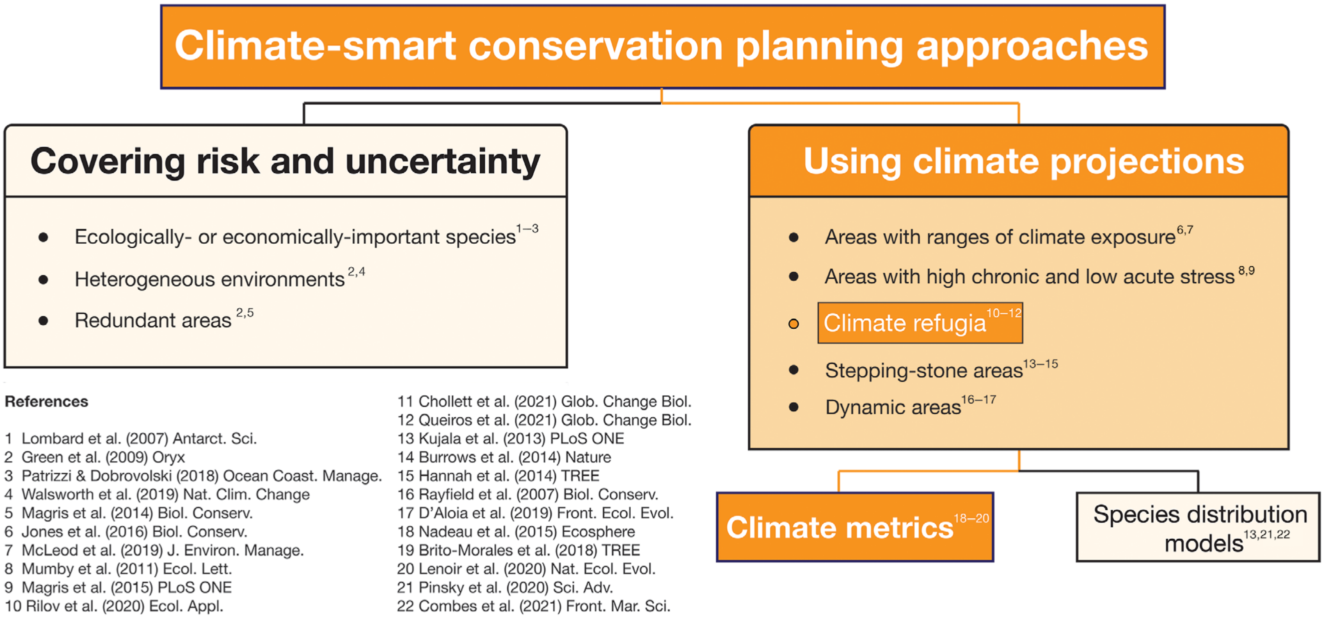


FIGURE 1 Range of approaches to climate-smart conservation planning. Highlighted route in orange represents the climate-smart conservation planning framework explored.

To explicitly address impacts of climate change, future climate projections are now used to identify important areas to consider in planning for climate change (Figure 1). These important "climate-smart" areas are defined differently across varying approaches. Climate-smart areas could refer to areas of high chronic but low acute thermal stress (Magris et al., 2015; Mumby et al., 2011). Others propose to ensure representation and protection of a range of areas, from low to high climate exposure (Jones et al., 2016; McLeod et al., 2019). Stepping-stone protected areas (Burrows et al., 2014; Hannah et al., 2014; Kujala et al., 2013) and/or dynamic closures (D'Aloia et al., 2019; Rayfield et al., 2008) could be designed and established to improve current protected area systems by making them more robust to climate change. Here, we define climate-smart areas as areas where climate is projected to remain relatively stable or where climate change might pose less of a threat to biodiversity. These areas are considered climate refugia (Chollett et al., 2022; Keppel et al., 2015; Morelli et al., 2016, 2020; Queirós et al., 2021; Rilov et al., 2020).

The most common approach to identifying climate-smart areas is to use species distribution models to approximate distribution shifts under climate change and incorporate these into the design of protected areas (Araújo et al., 2011; Combes et al., 2021; Kujala et al., 2013; Pacifici et al., 2015; Pinsky, Selden, & Kitchel, 2020). By using species distribution models, conservation practitioners can couple changes in climate to the biological response of organisms when identifying priority areas (Kujala et al., 2013; Thuiller et al., 2005). While this approach can account for species-specific responses to climate change, it can be time-consuming and data-intensive to incorporate species distribution models for thousands of species into large-scale conservation planning (e.g., regional or global) (Bellard et al., 2012; Pacifici et al., 2015) and it works best for well-studied species (Guisan et al., 2013; Porfirio et al., 2014; Robinson et al., 2011, 2017).

Climate metrics offer a simple and tractable alternative for incorporating the potential impacts of climate change into the design of protected area systems (Brito-Morales et al., 2018; Garcia et al., 2014; Nadeau et al., 2015; Stralberg et al., 2020). Although this approach does not explicitly link organismal response to the changing environmental conditions brought about by climate change (Garcia et al., 2014), climate metrics serve as robust generic proxies for species-specific responses (Burrows et al., 2019; Lenoir et al., 2020; Pinsky, Selden, & Kitchel, 2020). These proxies could inform a pragmatic approach to designing regional and/or global climate-smart spatial plans that consider hundreds to thousands of species, especially where species-specific information is lacking. Climate metrics are based on projected changes in environmental conditions, including temperature (e.g., García Molinos et al., 2016), rainfall (e.g., Wu et al., 2011), or dissolved oxygen concentration (e.g., Bopp et al., 2013; Bruno et al., 2018). Such metrics can be used to identify climate refugia (Sandel et al., 2011) that can be incorporated in spatial prioritization—the structured process of identifying protected areas for conservation (Harris et al., 2019). By designing protected area systems that safeguard climate refugia, conservation efforts can help ensure protection of biodiversity in future (Brito-Morales et al., 2022; Doxa et al., 2022; Jones et al., 2016).

Here, we provide a framework for designing climate-smart spatial plans based on climate metrics. We begin by describing the framework, detailing four key climate-smart aspects that could influence spatial plans: viz. climate models; emission scenarios; climate metrics; and approaches to identifying climate refugia. We then apply the framework to the Western Pacific and compare the resulting climate-smart spatial plans. Finally, we provide recommendations for practitioners to apply our framework to terrestrial, freshwater, estuarine, and marine systems.

THE CLIMATE-SMART FRAMEWORK

Our framework comprises three steps (Figure 2): (1) selecting climate projections, which involves deciding on the climate models, emission scenarios, and climate variables; (2) calculating climate metrics from model outputs; and (3) choosing an approach to identifying refugia based on climate metrics. Climate refugia could then be incorporated into a spatial prioritization using a range of decision-support tools (Moilanen et al., 2009), including *Marxan* (Ball et al., 2009), *Zonation* (Moilanen et al., 2009), and the *prioritizr* R package (Hanson et al., 2021). Although each decision-support tool uses different algorithms, they share several characteristics, including requiring: (1) a planning domain; (2) a cost layer; (3) conservation features with corresponding representation targets; and (4) an objective function (Moilanen et al., 2009). We next discussed the three steps in our framework.

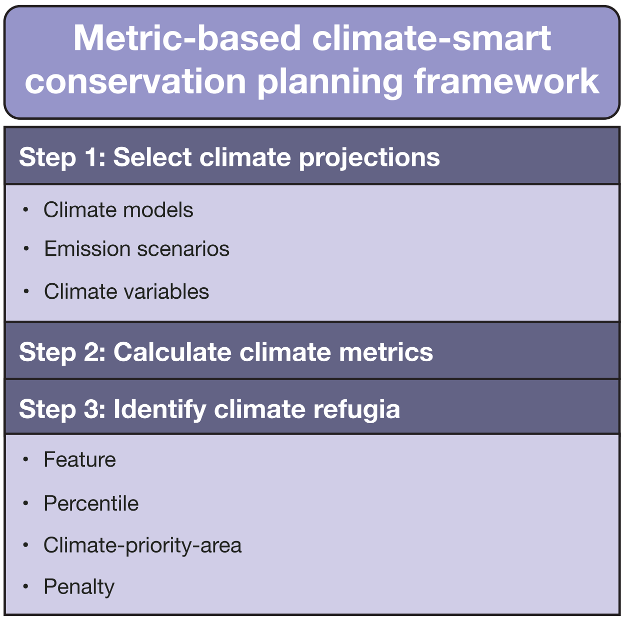


FIGURE 2 Climate-smart conservation planning framework. Model outputs are extracted based on the selected climate projections (*Select climate projections*) and are used to calculate climate metrics (*Calculate climate metrics based on climate model outputs*) to identify climate refugia (*Identify climate refugia*). These climate refugia can then be incorporated in a spatial prioritization, generating climate-smart spatial plans.

Select climate projections

Climate-smart conservation planning first requires selecting climate variables based on outputs from climate models under different emission scenarios.

Climate models

There are dozens of global climate models available (CMIP6; https://esgf-node.llnl.gov), each with slightly different approaches to modeling underlying physical, chemical, and biological processes. This variation will produce different future projections for environmental variables under any particular emission scenario (Gu et al., 2015; Raäisaänen, 2007). Therefore, using a single model in climate-smart reserve design will not adequately encompass uncertainties in future conditions (Makino et al., 2015). A common solution is to use multiple models, creating a model ensemble (Porfirio et al., 2014; Tegegne et al., 2020), in one of two ways: (1) a multi-model-ensemble using outputs of individual models separately; and (2) an ensemble mean (or median) that represents all models with a single layer. Temperature is the most-used variable to describe impacts of climate change because it is the primary climate driver in many ecosystems (Lenoir et al., 2020; Pinsky et al., 2019; Poloczanska et al., 2013), and there is higher confidence in its projection than for other climate variables (Raäisaänen, 2007). Rainfall (Wu et al., 2011), dissolved oxygen (Bopp et al., 2013; Pinsky, Selden, & Kitchel, 2020), net primary production (Wu et al., 2011), and ocean pH (Kroeker et al., 2013) are other variables used to describe impacts of climate change on biodiversity.

Emission scenarios

Climate models project different climate futures when forced under different emission scenarios (Makino et al., 2015). Climate futures range from scenarios assuming low emissions of greenhouse gasses such as SSP1-2.6 (an optimistic future that successfully limits warming to 2°C compared to pre-industrial temperatures) to high-emission scenarios such as SSP5-8.5 (a pessimistic future where the world continues to require more fossil fuels)

(O'Neill et al., 2017). As our climate future is uncertain, it is best practice to include multiple emission scenarios (Harris et al., 2014; Makino et al., 2015).

Calculate climate metrics based on climate model outputs

Projections from climate models can then be used to calculate climate metrics. Depending on how the climate metrics are defined and calculated, they can measure acute exposure, chronic exposure, relative exposure, biodiversity retention, and/or effects of multiple climate drivers on ecosystems. Here we presented some examples of metrics that fall under these categories.

Metrics of chronic exposure

Projected rates of change in temperature, precipitation, ocean acidification, and oxygen can all be considered metrics of chronic exposure, reflecting the degree of exposure to gradual climate change (IPCC, 2021; Wilson et al., 2020). Although temperature-derived metrics are the most commonly used (Wilson et al., 2020), other metrics could be more pertinent for particular ecosystems, such as changes in precipitation for tropical forests (Cornelissen, 2011; McCain & Colwell, 2011), rates of ocean acidification for coral reefs (McLeod et al., 2013), and rates of ocean deoxygenation for shallow benthic areas or hypoxic areas (Breitburg et al., 2018).

Metrics of acute exposure

Acute-exposure metrics provide insight into discrete anomalous events, such as wildfires, cyclones, and heatwaves (e.g., Foresta et al., 2016; Magris et al., 2015). Heatwaves are prolonged anomalously warm events (Hobday et al., 2016), increasing in severity with climate change (Oliver et al., 2019). On land, heatwaves and drought decrease photosynthetic activity and induce plant stress (Wang et al., 2019). In the ocean, marine heatwaves (MHWs) cause coral bleaching, species migrations, and mass mortalities (Eakin et al., 2019). There are many metrics describing heatwave frequency, intensity, effect, and duration (Hobday et al., 2016; Wohlfahrt et al., 2018).

Metrics of relative exposure

Relative-exposure metrics scale the change in the climate variable relative to its variation. For example, the relative climate exposure index scales the change in a climate variable such as temperature to its seasonal range (Brito-Morales et al., 2022) and the climate hazard metric scales it to its historical variability (Levin et al., 2020). Relative-exposure metrics are different from simple-exposure metrics because they consider that species inhabiting more variable environments might be less susceptible to gradual environmental change.

Metrics of retention

Metrics that infer the retention of biodiversity describe range shifts in response to climate change and are often temperature-derived (Chen et al., 2011; Lenoir et al., 2020; Pinsky et al., 2013). In terrestrial ecosystems, other drivers can influence range shifts (Mair et al., 2014; McCain & Colwell, 2011; Sunday et al., 2012). Thermal affinities and thermal tolerance limits have been used to infer species and community shifts (Burrows et al., 2019; Sunday et al., 2014, 2012). Climate velocity also serves as a proxy for shifts in species distributions (Loarie et al., 2009; VanDerWal et al., 2013) because it relates to the speed and direction that a species at a given point in space would need to move to remain in the same thermal conditions as the climate changes (Burrows et al., 2011; Loarie et al., 2009). Areas of slow climate velocity are expected to have high biodiversity retention (Brito-Morales et al., 2018; Burrows et al., 2011; Loarie et al., 2009; Sandel et al., 2011).

Combining multiple climate metrics

Climate refugia can be identified using information from multiple metrics (Carroll et al., 2017; Garcia et al., 2014; Rojas et al., 2022). One approach would be to define climate refugia separately for each climate metric (Brito-Morales et al., 2022). Other studies use an array of climate variables and indices to define a single metric used to identify climate-smart areas (Boyce et al., 2022; Rojas et al., 2022). For example, the climate risk index proposed by Boyce et al. (2022) incorporates several indices based on current, future, and innate responses of species to climate change into a single metric that can also be used to define areas of high climate risk.

Identify climate refugia

There are several ways of identifying climate refugia by creating climate layers and including them in spatial prioritization. We described four different approaches below:

(1) feature; (2) percentile; (3) climate-priority-area; and (4) penalty approaches. The first three approaches yield binary climate layers across the planning domain, while the fourth approach preserves the continuous nature of the metrics (Figure 3). To convert continuous climate metrics to binary layers, percentile thresholds should be chosen by practitioners, depending on the local context and objectives of their conservation plan.

The feature approach

The simplest approach is to consider climate refugia based only on climate variables, ignoring biodiversity (Arafeh-Dalmau et al., 2021). Areas of low exposure and/or high retention can be determined by setting a threshold for identifying the range of climate metric values used to classify areas as climate refugia (Figure 3). Using the threshold, the climate refugia of the entire planning domain are identified. This contributes a single additional layer to the spatial prioritization for each climate metric considered (a total of $J+1$ features in the prioritization, where $J =$ number of biodiversity features).

The percentile approach

The percentile approach identifies climate refugia for each biodiversity feature (Brito-Morales et al., 2022). The distribution of each biodiversity feature is intersected with the climate metric layer. Using the chosen threshold, the distribution available for protection is restricted to solely its climate-smart areas (i.e., climate refugia) in the prioritization (a total of J features, with each biodiversity feature intersected with the same climate metric; Figure 3).

The climate-priority-area approach

This approach identifies the most stable climate refugia for each biodiversity feature (i.e., climate-priority areas) and gives it higher prioritization by setting a higher target than the remainder of the distribution range of a species (Figure 3). The climate-priority-area approach is thus a variant of the percentile approach that focuses protection on high-value climate refugia and enables key areas outside of climate refugia to be included in the solution (a total of $2J$ features in the prioritization). This approach also results in the conservation of a greater diversity of future climate conditions.

The penalty approach

The penalty approach seeks to minimize climate exposure and/or maximize biodiversity retention while still minimizing the cost of the solution. This approach treats the climate metric as a linear penalty in the spatial prioritization (Figure 3), where solutions that have higher (or lower, depending on the climate metric) total penalties are penalized to discourage the selection of less climate-smart areas.

$$\text{Penalty} = \sum_{i=1}^{I} P \times D_i \times X_i, \tag{1}$$

where P is the penalty scaling, D_i is the penalty data per planning unit i in the planning domain I, and X_i is the decision variable (i.e., selected or not selected in the spatial plan) per planning unit i.

Choosing thresholds

Choosing percentile thresholds, akin to assigning representation targets for the biodiversity features, could be done through area-based policy targets (e.g., 30% following the 30×30 international targets set by the CBD; CBD, 2020, 2022; Zhao et al., 2020), expert-based thresholds (e.g., following IUCN conservation status; Brito-Morales et al., 2022), or population-viability analyses (e.g., Taylor et al., 2017). The chosen percentile thresholds determine how strict the definition of a climate refugium is. More-demanding thresholds (e.g., lowest 5th percentile of climate warming, highest 5th percentile of ocean acidification) restrict climate refugia to the most climate-smart areas, whereas less-demanding thresholds (e.g., lowest 40th percentile of climate warming, highest 40th percentile of ocean acidification) include moderately climate-smart areas.

Depending on the approach, the chosen threshold can influence: (1) the allowable targets for the biodiversity features; (2) the number of selected areas; and (3) how climate-smart the spatial plan would be. It will be impossible to have targets greater than the threshold. For example, by defining climate refugia as areas within the lowest 30th percentile of climate warming, the distributions of the biodiversity features are now limited to only 30% of the original distribution (i.e., the top 30% climate-smart areas). Hence, when applying this threshold, it would not be possible to protect more than 30% of the biodiversity features' distribution. Choosing more-demanding thresholds will also lead to larger but more climate-smart spatial plans (Appendix S2). Therefore, if protecting against climate change is considered a high

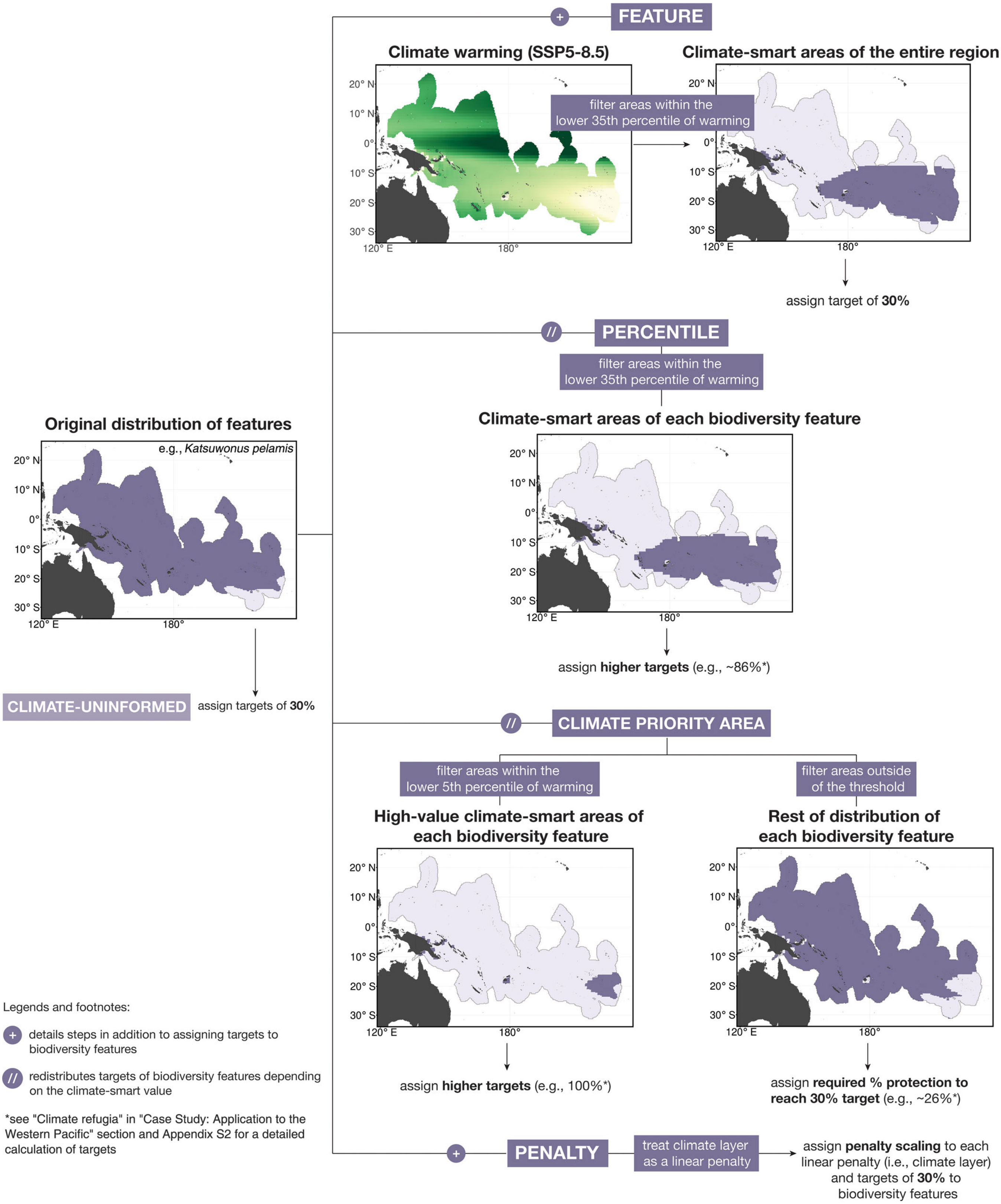


FIGURE 3 Workflows of the different approaches to identifying climate refugia. Feature, percentile, and climate-priority-area approaches use the climate metric data to create binary layers using a percentile threshold. The feature approach creates a single layer. The percentile and climate-priority-area approaches consider each of the biodiversity features' distributions. The penalty approach maintains the continuous nature of the climate metric data and retains the original distributions of the biodiversity features.

priority, practitioners should consider choosing more-demanding thresholds at the expense of selecting more areas for protection. Notably, choosing a higher penalty scaling puts more weight on avoiding areas of higher penalties (i.e., less climate-smart areas) and will thus lead to more climate-smart but more costly spatial plans when using the penalty approach (Appendix S2: Section S1).

CASE STUDY: APPLICATION TO THE WESTERN PACIFIC

We used the case study to: (1) illustrate the utility of the proposed climate-smart framework in spatial prioritization; (2) assess the relative effect on spatial plans of varying the climate models, emission scenarios, climate metrics, and approaches to identifying climate refugia; and (3) develop key recommendations. Although this is a marine application, our methodology could also be applied to other systems.

Spatial prioritization

The planning domain was the epipelagic layer of the Western Pacific, with 42,543 planning units, each covering 670 km^2, using the Mollweide equal-area projection (Appendix S3: Figure S1A). We used current distribution maps from AquaMaps (Kaschner et al., 2019) with uniform representation targets of 30%, resulting in 8716 biodiversity features in the region. Although our framework can be applied using various decision-support tools, we used the *prioritizr* R package (Hanson et al., 2021). All analyses were undertaken in the R statistical computing environment (version 4.1.1; R Core Team, 2022) (Appendix S3: Section S1).

Climate projections

Historical daily temperature data (1982–2015) were downloaded from the National Oceanographic and Atmospheric Administration (NOAA) ¼° Daily Optimum Interpolation Sea Surface Temperature (OISST; Huang et al., 2020). Projections (2015–2100) from the climate models forced by several emission scenarios were downloaded at daily or monthly resolution (depending on the climate metric) from the Coupled Model Intercomparison Project Phase 6 (CMIP6; https://esgf-node.llnl.gov/). We re-gridded and reprojected all climate projections using area-weighted bilinear interpolation (Brito-Morales et al., 2022) with the Climate Data Operators (CDO) software (Schulzweida, 2022) and the R statistical computing environment (version 4.1.1; R Core Team, 2022).

Emission scenarios

To test how using climate projections forced under different emission scenarios influenced the resulting spatial plans, we created and compared spatial plans using three emission scenarios (Shared Socioeconomic Pathways or SSPs; SSP1-2.6, SSP2-4.5, and SSP5-8.5; O'Neill et al., 2017).

Climate models

As different climate models suggest different environmental futures, the aim here was to highlight methods of including multiple climate models in spatial prioritization. We used five climate models: (1) CanESM5 (Swart et al., 2019a, 2019b, 2019c); (2) CMCC-ESM2 (Lovato et al., 2021a, 2021b, 2021c); (3) GFDL-ESM4 (John et al., 2018a, 2018b, 2018c); (4) IPSL-CM6A-LR (Boucher et al., 2019a, 2019b, 2019c); and (5) NorESM2-MM (Bentsen et al., 2019a, 2019b, 2019c). We created spatial plans using both a model ensemble comprising outputs from individual models (Appendix S3: Figure S2) and an ensemble mean (Appendix S3: Figure S1C–T).

Climate metrics

To investigate the effect of using different climate metrics on spatial plans, we developed separate plans based on five climate metrics that are considered relevant for the marine planning domain: (1) rate of climate warming; (2) rate of ocean acidification; (3) rate of ocean deoxygenation; (4) climate velocity (based on temperature); and (5) sum of annual cumulative MHW intensity. Examples of appropriate terrestrial metrics could be temperature- and precipitation-derived metrics (Araújo et al., 2011; Heikkinen et al., 2020).

Rates of climate warming, ocean acidification, and ocean deoxygenation are chronic-exposure metrics. For each, we defined and prioritized protection of areas characterized by low exposure to climate impacts (i.e., climate refugia as areas of low rates of warming, acidification, and deoxygenation). These metrics were calculated as the slope of the linear regression of projected mean annual values from each climate model output (Δ magnitude $year^{-1}$, 2015–2100).

Despite climate warming, climate velocity, and the sum of annual cumulative MHW intensity all being calculated from temperature, they are fundamentally different metrics. Areas of slow climate velocity are areas of high biodiversity retention and were prioritized for protection (Arafeh-Dalmau et al., 2021; Stralberg et al., 2020). These climate refugia are more likely to retain their current environmental conditions, and consequently, their biodiversity (Brito-Morales et al., 2018). Climate velocity (km year^{-1}) was calculated as the ratio of the temporal gradient (°C year^{-1}, 2015–2100) to the spatial gradient (°C km^{-1}, 2015–2100) of temperature using the *VoCC* R package (García Molinos et al., 2019; Appendix S3: Section S2). However, climate velocity can be calculated based on other variables such as rainfall (Brito-Morales et al., 2018; Heikkinen et al., 2020).

We used the sum of cumulative MHW intensity to measure long-term exposure to acute warming events (Hobday et al., 2016). As the frequency and magnitude of temperature anomalies vary non-linearly through time depending on the emission scenario (Frölicher et al., 2018; Oliver et al., 2019), impacts are better represented by the sum of intensities than by the rate of change. We calculated this metric using the *heatwaveR* R package (Schlegel & Smit, 2021) following MHW equations (Hobday et al., 2016; Appendix S3: Section S3) and expressed it as total degree days, representing the sum of the annual temperature anomalies.

To demonstrate the use of different climate metrics in the climate-smart spatial plan, for each planning unit, we calculated the geometric mean of all five climate metrics to derive one combined climate-smart metric. This approach assumes equal weighting among the different metrics. Each metric was rescaled to 0–100 where higher values represent more climate-smart areas.

Climate refugia

Our aim was to demonstrate the use of each of the four approaches in identifying climate refugia and investigate whether these yielded different climate-smart spatial plans. Comparable 30% representation targets were assigned to all biodiversity features, regardless of approach (CBD, 2020, 2022).

For the spatial plans designed using the feature approach, we included climate refugia as an additional feature. These refugia are identified by selecting climate-smart areas of the entire planning domain. Selected areas within the lower 35th percentile represent: (1) slow warming; (2) low MHW intensity; and (3) slow velocity, and those within the upper 35th percentile represent: (1) low rate of change in ocean acidification (i.e., smallest decreases in ocean pH); (2) low rate of ocean deoxygenation (i.e., smallest decreases in ocean deoxygenation); and (3) high combined climate-smart metric scores (Figure 3). Since we are restricting the original area of a particular layer, its representation target of 30% is expected to change:

$$R = \frac{T}{P}, \tag{2}$$

where R is the new representation target and is dependent on T—the original representation target—and P—the proportion identified as climate-smart areas. To maintain the original representation target of 30%, we used Equation (2) to calculate the target of the additional feature representing the climate-smart areas of the entire planning domain (i.e., upper or lower 35th percentile of the chosen climate metric; Appendix S2: Section S2).

We used the same 35th percentile thresholds for spatial plans designed using the percentile approach. However, unlike the feature approach, the climate refugia identified using the percentile approach are specific to each feature. This means that the original area of each feature is restricted to the distribution of their climate refugia (Figure 3). We modify Equation (2) to:

$$R_j = \frac{T_j}{P_j} \; \forall j \in J, \tag{3}$$

where R is the new representation target of feature j (in the set of all features J) and is dependent on T—the original representation target of feature j—and P—the proportion identified as climate-smart areas. We calculated R for each feature using Equation (3) to maintain the original representation target of 30% for all features (Appendix S2: Section S2).

The climate-priority-area approach splits each biodiversity feature into two: (1) high-value climate-smart areas (i.e., climate-priority areas); and (2) non-climate-priority areas (Figure 3). Since climate-priority areas (CPA) and non-climate-priority areas (NCPA) of the same feature are considered separately, the number of biodiversity features included in the prioritization is doubled. Climate-priority areas and non-climate-priority areas of the same feature have different targets:

$$T_{\text{Total},j} = \left(P_{\text{CPA},j} \times T_{\text{CPA},j}\right) + \left(P_{\text{NCPA},j} \times T_{\text{NCPA},j}\right) \; \forall j \in J, \tag{4}$$

where $T_{\text{Total},j}$ represents the total target assigned to feature j (in the set of all features J). $T_{\text{Total},j}$ depends on the targets and proportions of feature j identified as climate-priority areas ($T_{\text{CPA},j}$ and $P_{\text{CPA},j}$, respectively) and non-climate-priority areas ($T_{\text{NCPA},j}$ and $P_{\text{NCPA},j}$, respectively). Here, we assigned higher targets (i.e., 100%) and more-demanding thresholds (i.e., 5th percentile) to climate-priority areas to prioritize their protection. To maintain the original representation target of 30% (T_{Total}) for all features, we rearranged Equation (4) to calculate the target (T_{NCPA}) for non-climate-priority areas (i.e., 95th percentile) of each feature (Appendix S2: Section S3):

$$T_{\mathrm{NCPA},j} = \frac{T_{\mathrm{total},j} - \left(P_{\mathrm{CPA},j} \times T_{\mathrm{CPA},j}\right)}{P_{\mathrm{NCPA},j}} \; \forall j \in J. \tag{5}$$

The penalty approach utilizes the same biodiversity features and their 30% representation targets. Instead, the climate metric is included in the prioritization as a linear penalty. We used the median of the climate metric as the penalty scaling, P (see Equation 1).

Comparing spatial prioritizations

To illustrate differences among the climate-smart solutions, we used a simplified configuration for comparison (unless otherwise specified), viz. the ensemble-mean for warming forced under SSP 5-8.5 using the percentile approach. We used the Cohen's Kappa Coefficient (McHugh, 2012) to quantify the degree of agreement between designs. We also reported how well these approaches met the target of 30% protection for each of the biodiversity features.

To identify how different options affected the resulting climate-smart spatial plans, we also completed prioritizations for every possible combination of the climate-smart aspects (three scenarios, five models and the ensemble-mean, five metrics and the combined climate-smart metric, and four approaches). We compared all 432 plans by extracting the solutions (selected/not selected data across all planning units), creating a Jaccard dissimilarity matrix, and visualizing the matrix using a non-metric multidimensional scaling (nMDS) ordination following Dexter et al. (2018) to interpret the results of the ordination despite the high stress value (Appendix S4: Figure S2).

RESULTS

Spatial plans for the Western Pacific Ocean varied substantially, depending on the chosen climate models, emission scenarios, climate variables, climate metrics, and approach used to identify climate refugia.

Climate models: Multi-model-ensemble versus an ensemble-mean

Spatial plans designed using individual climate models differed from each other and from the spatial plan designed using the ensemble mean (Figure 4; Appendix S5: Figure S1). Only 23.0% of the planning domain was common to all individual solutions (Figure 4b) and protecting these common areas alone would lead to unmet targets in 19.9% of the biodiversity features (Figure 4d). The degree of agreement between spatial plans using different climate models was similar (Figure 4c). Although the ensemble mean did not cover the full range of climate projections for all models, the spatial plan of the ensemble mean covered areas of intermediate climate warming across all models (Figure 4e).

Emission scenarios: Single versus multiple

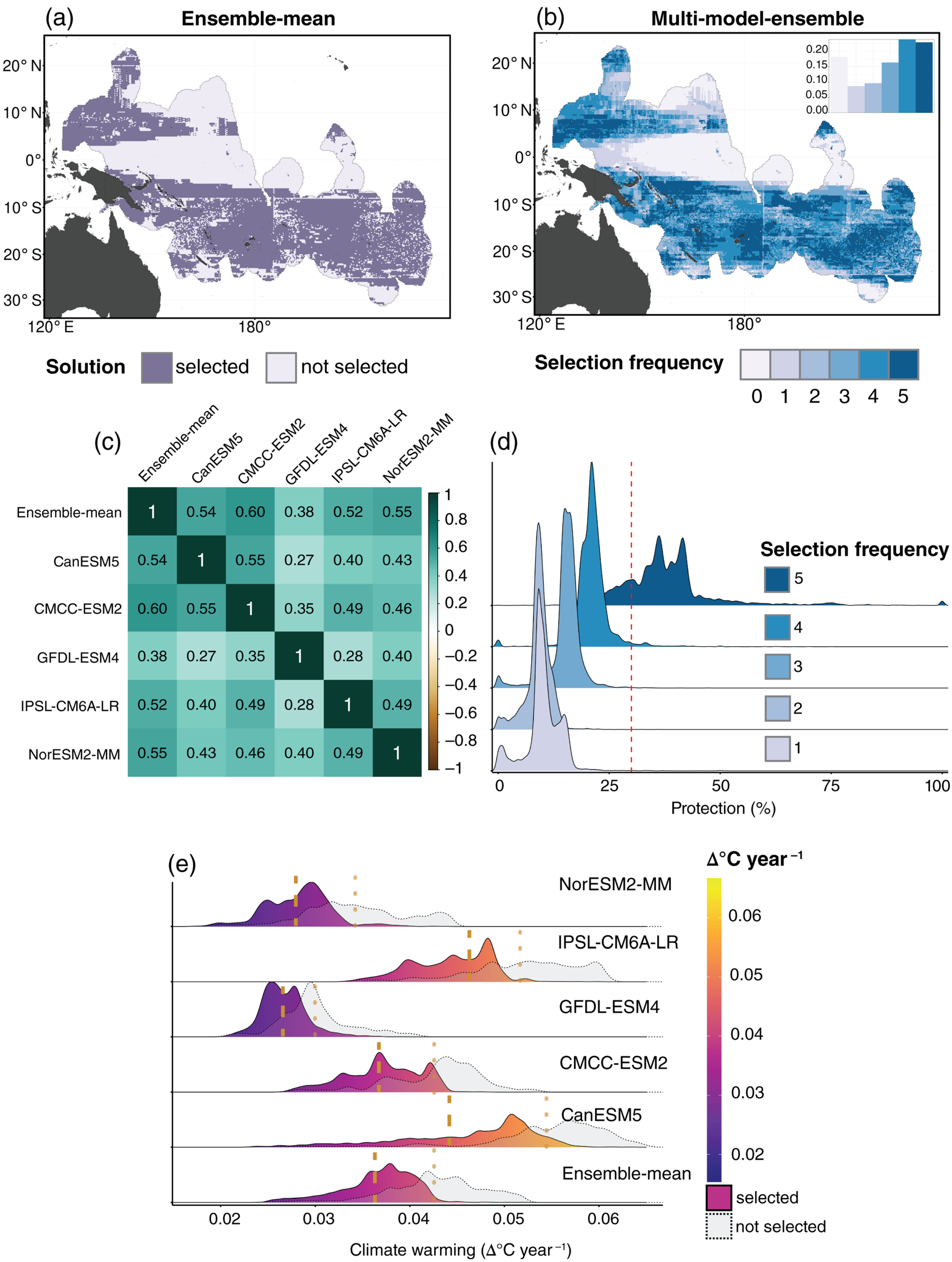
Spatial plans created using the three emission scenarios had similar spatial configurations but had slightly different areas required to meet targets (Figure 5). About 33.5% of the planning domain was common to solutions (Figure 5d) and protecting only these areas would meet the targets for 97.1% of the biodiversity features (Figure 5f). There was general agreement between the different plans (Figure 5e). As expected, the climate warming in planning units selected for conservation fell in the slowest tail of warming in the planning domain and was slowest in SSP1-2.6 and fastest in SSP 5-8.5 (Figure 5g).

Utility of different climate metrics

Configurations of the spatial plans created using different metrics contrasted strongly (Figure 6), although solutions based on warming, deoxygenation, and, to a lesser extent, MHW were relatively similar (Figure 6h). These three spatial plans were similar to the spatial plan designed using a combined climate-smart metric (Figure 6h). Unlike solutions created with different scenarios and models, selected areas common for all metrics constituted only 9.6% of the planning domain (Figure 6g), suggesting the spatial plans are quite different. Protecting these areas would result in unmet targets in 36.0% of the biodiversity features (Figure 6i).

Identify climate refugia: Trade-offs among approaches

Climate-smart conservation planning was sensitive to the approach chosen to identify climate refugia (Figure 7). Despite using the same climate metric, only 5.9% of the planning domain was common across all approaches (Figure 7e). Protecting only these common areas resulted



	Ensemble-mean	CanESM5	CMCC-ESM2	GFDL-ESM4	IPSL-CM6A-LR	NorESM2-MM
Ensemble-mean	1	0.54	0.60	0.38	0.52	0.55
CanESM5	0.54	1	0.55	0.27	0.40	0.43
CMCC-ESM2	0.60	0.55	1	0.35	0.49	0.46
GFDL-ESM4	0.38	0.27	0.35	1	0.28	0.40
IPSL-CM6A-LR	0.52	0.40	0.49	0.28	1	0.49
NorESM2-MM	0.55	0.43	0.46	0.40	0.49	1

FIGURE 4 Legend on next page.

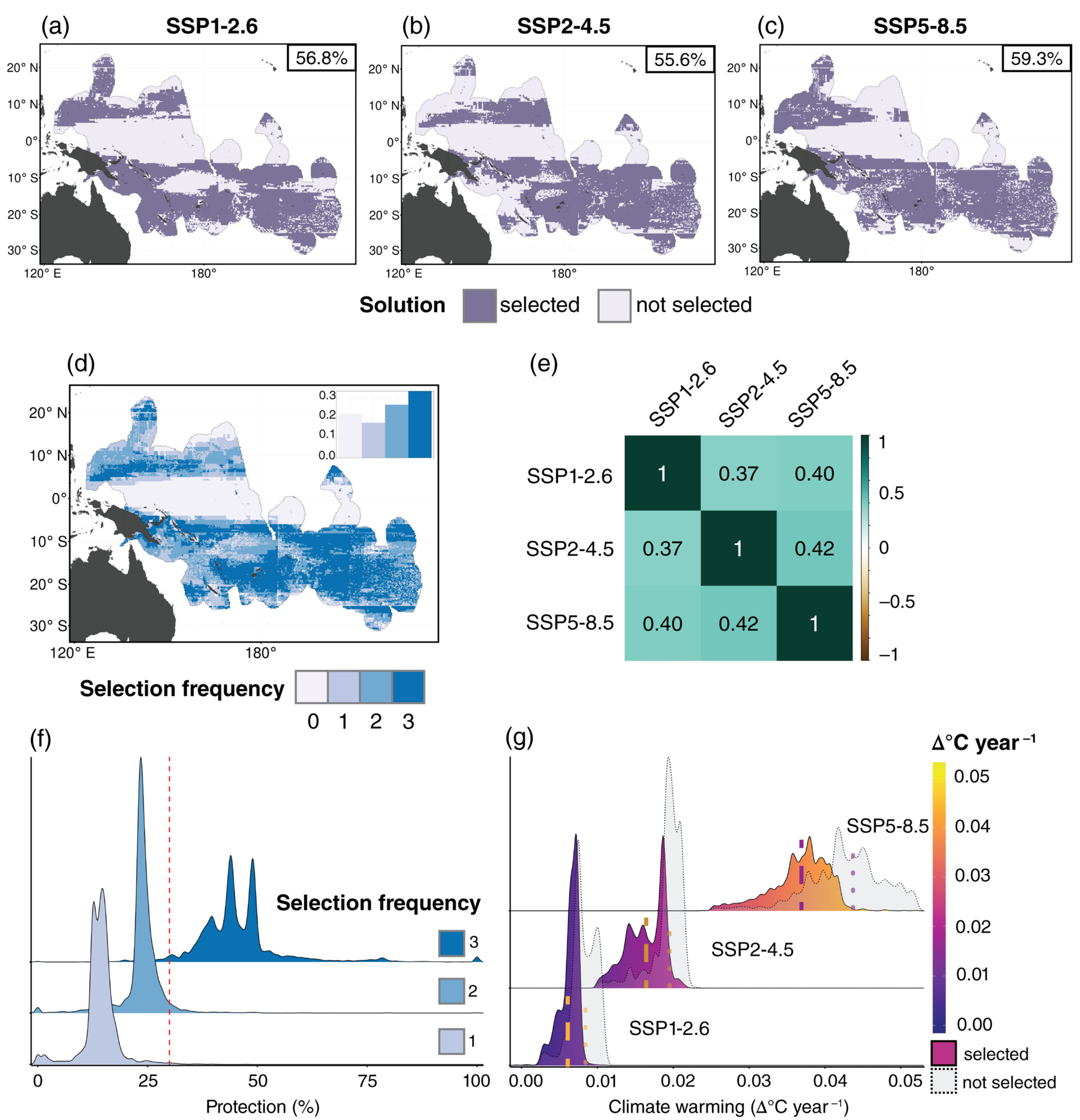


FIGURE 5 Incorporating different emission scenarios. Spatial plans (with % area selected in top right) designed using climate warming forced under: (a) SSP1-2.6; (b) SSP2-4.5; and (c) SSP5-8.5. (d) Selection frequency plot showing areas selected across scenarios with an inset histogram showing selection proportion. (e) Cohen's Kappa coefficient matrix, showing correspondence between solutions. (f) Kernel density estimates of the % protection of the biodiversity features across selection frequencies (dashed line represents the 30% protection target). (g) Kernel density estimates of the degree of climate warming in the solutions. Colored polygons represent the warming in selected planning units; gray polygons represent warming of areas not selected for protection. The dashed and dotted lines represent the mean warming for each scenario across planning units that were selected and not selected, respectively.

FIGURE 4 Using the climate model ensemble mean or the multi-model-ensemble. (a) Spatial plan created using the ensemble mean. (b) Selection frequency plot using the multi-model-ensemble with an inset histogram showing selection proportion across models. (c) Cohen's Kappa coefficient matrix, showing correspondence between solutions. (d) Kernel density estimates of the % protection of the biodiversity features across selection frequencies (dashed line represents the 30% protection target). (e) Kernel density estimates of the degree of climate warming in the solutions. Colored polygons represent the warming in selected planning units; gray polygons represent warming of areas not selected for protection. The dashed and dotted lines represent the mean warming for each model across planning units that were selected and not selected, respectively.

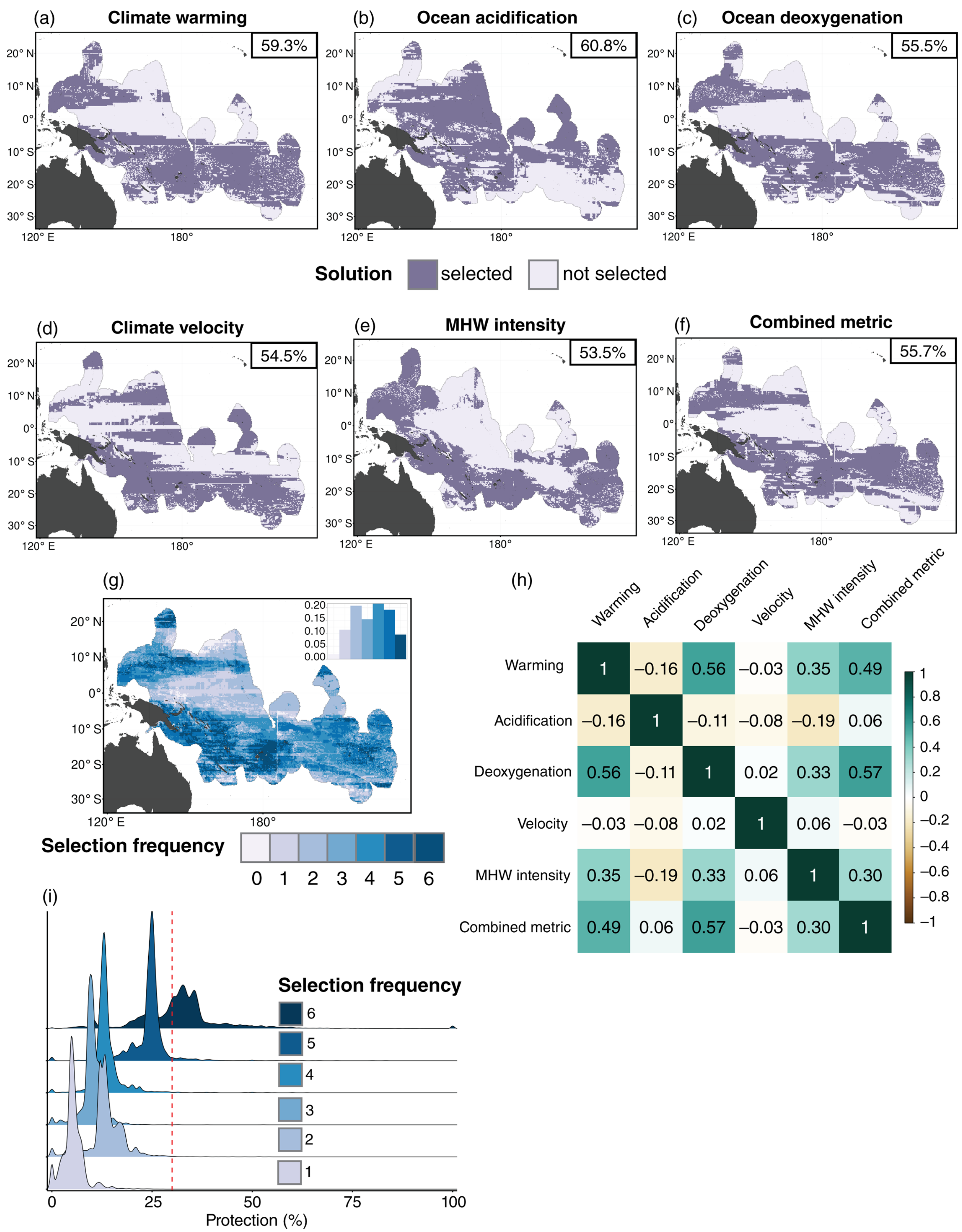


FIGURE 6 Legend on next page.

in unmet targets for 98.5% of the biodiversity features (Figure 7g). Each approach resulted in relatively dissimilar spatial plans, but the climate-priority-area approach is the most dissimilar (Figure 7f). The percentile approach yielded a spatial plan with the most area selected. The penalty approach yielded the smallest spatial plan, with the climate-priority-area approach following closely. Biodiversity features were afforded the greatest protection in the percentile approach and the least protection in the climate-priority-area approach (Figure 7h). The percentile approach was the most effective at selecting planning units of slower rates of warming and leaving out planning units of higher rates of warming (Figure 7i). These observations were generally reflected in spatial designs using the other metrics (Figures 8 and 9). For all climate metrics, the percentile approach was the most effective at leaving less climate-smart planning units out of the solution. However, the approach most effective at selecting more climate-smart planning units varied across the metrics. The percentile approach also afforded the greatest protection to the biodiversity features across all metrics and the climate-priority-area approach consistently provided the least protection.

In our sensitivity analyses for the percentile, feature, and climate-priority-area approaches, there was an inverse relationship between the area selected in the solution and the resulting climate warming (Appendix S2: Figure S1). For both the feature and percentile approaches, choosing more-demanding thresholds (i.e., lower percentile thresholds) resulted in larger areas of protection (Appendix S2: Figure S1A–D) because these approaches restricted the area considered for the planning domain and for each biodiversity feature, respectively. The opposite was observed in the climate-priority-area approach because the sensitivity analysis was conducted with a constant 100% target afforded to the high-value climate refugia identified by the percentile thresholds (Appendix S2: Figure S1E,F). Hence, higher percentile thresholds resulted in larger areas that will always be selected for protection. The analysis for the penalty approach did not show an inverse relationship between cost and climate-smart performance (Appendix S2: Section S1; Figure S1G,H).

Overall importance of different climate-smart aspects

The nMDS ordinations of 432 different spatial plans showed that the chosen metric and approach to identifying climate refugia influenced the resulting climate-smart spatial plans more than the climate model or emission scenario (Figure 10). This was evident in how metrics (Figure 10c) and approaches to identifying climate refugia (Figure 10d) have more distinct standard deviation ellipses on ordinations. Their points were also clumped across different regions of the two-dimensional space. By contrast, the climate models (Figure 10a) and emission scenarios (Figure 10b) had more overlapping ellipses and their points were more evenly distributed across the two-dimensional space. Solutions using the ensemble mean reasonably represented the solutions based on individual models (Figure 10a).

Configurations of solutions across scenarios showed overlapping ellipses, suggesting they were similar (Figure 10b). Of the five explored climate metrics, warming, ocean deoxygenation, and MHW intensity were similar (Figure 10c). Solutions designed using the combined metric clustered closer to these three metrics. Among approaches to identifying climate refugia, solutions using the percentile approach were the most tightly clustered. Solutions using the feature, penalty, and climate-priority-area were increasingly dissimilar from each other and from other approaches (Figure 10d). Within each approach, the chosen metric considerably influenced the resulting spatial plan, showing that approaches were sensitive to the metrics (Appendix S4: Figure S1). Although ordination stress exceeded 0.20, the structure we observed is significantly different from the structures of 1000 independent permutations of the dataset ($p < 0.05$; Appendix S4: Figure S2).

DISCUSSION

We developed a climate-smart framework for designing protected areas, focusing on climate refugia and accounting for uncertainty associated with climate models and emission scenarios. By applying this framework to our case study, we found that among all aspects of designing

FIGURE 6 Using different climate metrics. Spatial plans (with % area selected in top right) designed with the percentile approach using: (a) Climate warming (Δ°C year^{-1}); (b) Ocean acidification (ΔpH year^{-1}); (c) Ocean deoxygenation ($\Delta[O_2]$ year^{-1}); (d) Climate velocity (km year^{-1}); (e) Marine heatwave (MHW) intensity (total degree days); and (f) Combined climate-smart metric. (g) Selection frequency plot showing areas selected across different metrics with an inset histogram showing selection proportion. (h) Cohen's Kappa coefficient matrix, showing correspondence between solutions. (i) Kernel density estimates of the % protection of the biodiversity features across approaches (dashed line represents the 30% protection target).

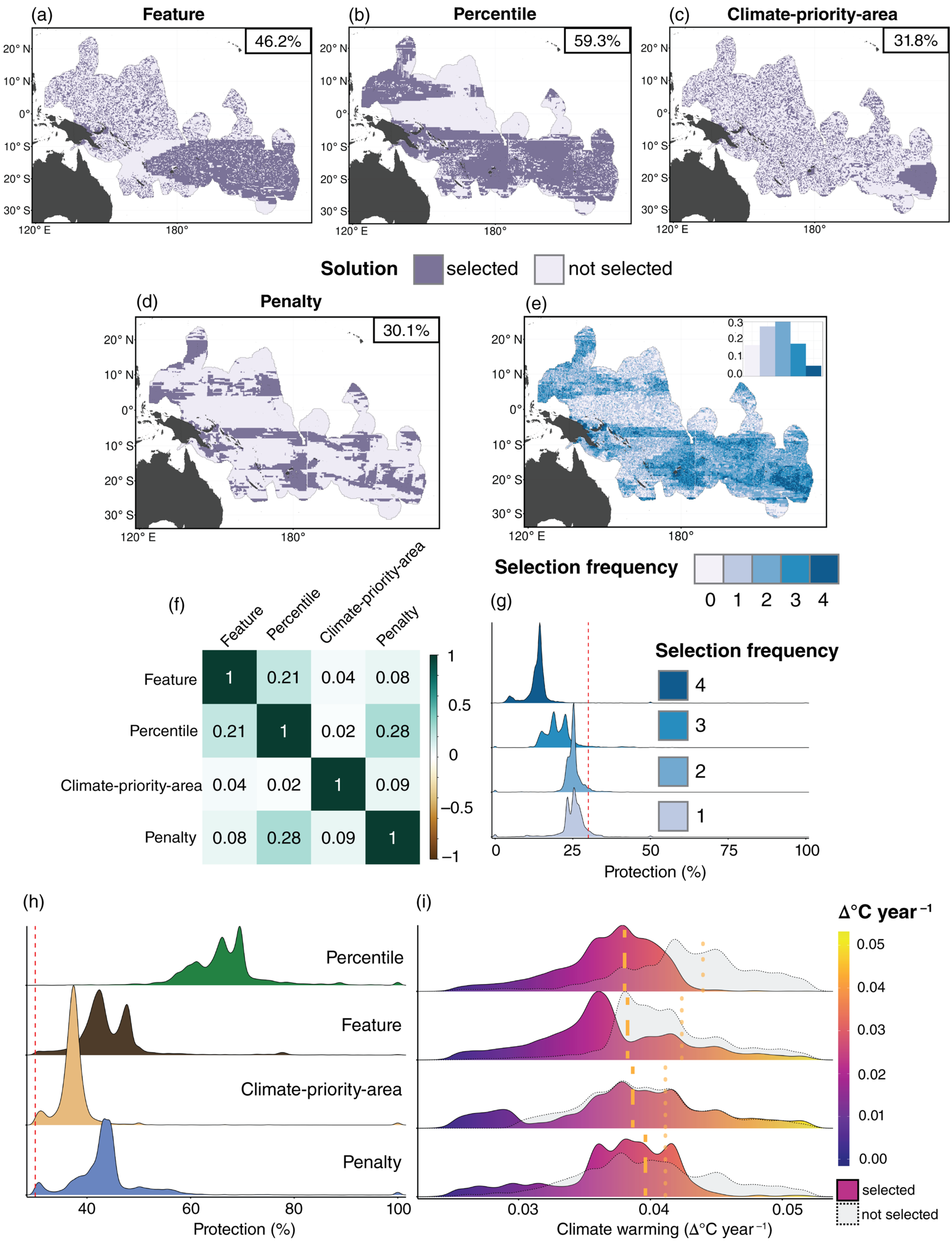


FIGURE 7 Legend on next page.

climate-smart protected area systems, the choice of climate metrics, and approaches to identifying climate refugia had the largest impact on the configuration of spatial plans. The choice of climate models and emission scenarios had smaller impacts on the resulting climate-smart spatial plan. Based on the strengths and weaknesses of the options explored for each aspect of the framework (Table 1), we outline core recommendations for climate-smart conservation planning.

Capturing model and emission uncertainty

Our results show that using different model outputs and emission scenarios influenced spatial plans in a modest way. Some conservation studies use outputs from a single model (e.g., Magris et al., 2015; Patrizzi & Dobrovolski, 2018) and a single scenario (e.g., Stralberg et al., 2020), but these designs underestimate the uncertainty inherent in planning for climate change. Thus, unless there are compelling reasons—that is, a particular climate model is known to perform particularly well in the region and there is more certainty about our climate future—we suggest using a model ensemble (e.g., Chollett et al., 2022; Martins et al., 2021; Nadeau et al., 2015; Tegegne et al., 2020) and incorporating multiple emission scenarios (e.g., Araújo et al., 2011; Brito-Morales et al., 2022; Chollett et al., 2022).

Using the ensemble mean is less onerous (Oliver et al., 2019; Stralberg et al., 2020) than using multiple models directly (Gu et al., 2015; Porfirio et al., 2014), although an ensemble median might be more appropriate to avoid potential bias from models with higher climate sensitivity (Hausfather et al., 2022). Using the multi-model-ensemble increases complexity of the prioritization dramatically but would be more suitable for regions characterized by extreme or conflicting climate projections from models included in the ensemble. Since the spatial plan created using the ensemble mean captured most of the areas selected using the multi-model-ensemble, capturing the generic climate signal using the ensemble mean appeared reasonable for our case study.

Selecting climate metrics

We found that different climate metrics result in markedly different spatial plans. Consideration of climate change in conservation planning has typically focused on temperature (Magris et al., 2015; Nadeau et al., 2015; Wilson et al., 2020). However, we show that protecting areas exposed to high climate warming does not always result in protecting climate refugia defined by other variables (Bruno et al., 2018). In fact, even different climate metrics derived from the same variable (e.g., climate velocity calculated from temperature) produce different results. We found that climate warming solutions were most similar to those for ocean deoxygenation, presumably because of the temperature dependence of gas solubility (Deutsch et al., 2015; Pörtner & Knust, 2007). Warming also exacerbates negative effects of ocean deoxygenation by increasing metabolic demands (Pörtner & Knust, 2007), suggesting synergistic impacts.

Given the influence of the climate metrics on the resulting spatial plan, the metrics used to define climate refugia should be carefully considered based on their unique attributes and relevance to the ecosystem (e.g., Table 2 summarizes this for the case study). Using a climate metric based on a single climate variable may not sufficiently account for how climate change will affect some ecosystems (Reside et al., 2018). Further, incorporating multiple metrics in climate-smart conservation planning may be useful (Harvey et al., 2013; VanDerWal et al., 2013) in protecting a system of climate-smart areas that will be more resilient to different aspects of climate change (Garcia et al., 2014; Magris et al., 2015).

In our case study, we chose to create a combined metric, weighing the five individual metrics equally. Since the spatial plans designed using climate warming, ocean deoxygenation, and—to some extent—MHW intensity were similar, this resulted in the spatial plan designed using the combined metric resembling those three spatial plans. We chose this method to demonstrate how information from different climate variables and/or metrics

FIGURE 7 Exploring approaches of identifying and protecting climate refugia. Spatial plans (with % area selected in top right) designed using the following approaches: (a) Feature; (b) Percentile; (c) Climate-priority-area; and (d) Penalty. (e) Selection frequency plot showing areas selected across approaches with an inset histogram showing selection proportion. (f) Cohen's Kappa coefficient matrix, showing correspondence between solutions. (g) Kernel density estimates of the % protection of the biodiversity features across selection frequencies (dashed line represents the 30% protection target). (h) Kernel density estimates of the % protection of the biodiversity features across approaches (dashed line represents the 30% protection target). (i) Kernel density estimates of the degree of climate warming in the solutions. Colored polygons represent the warming in selected planning units; gray polygons represent warming of areas not selected for protection. The dashed and dotted lines represent the mean warming for each approach across planning units that were selected and not selected, respectively.

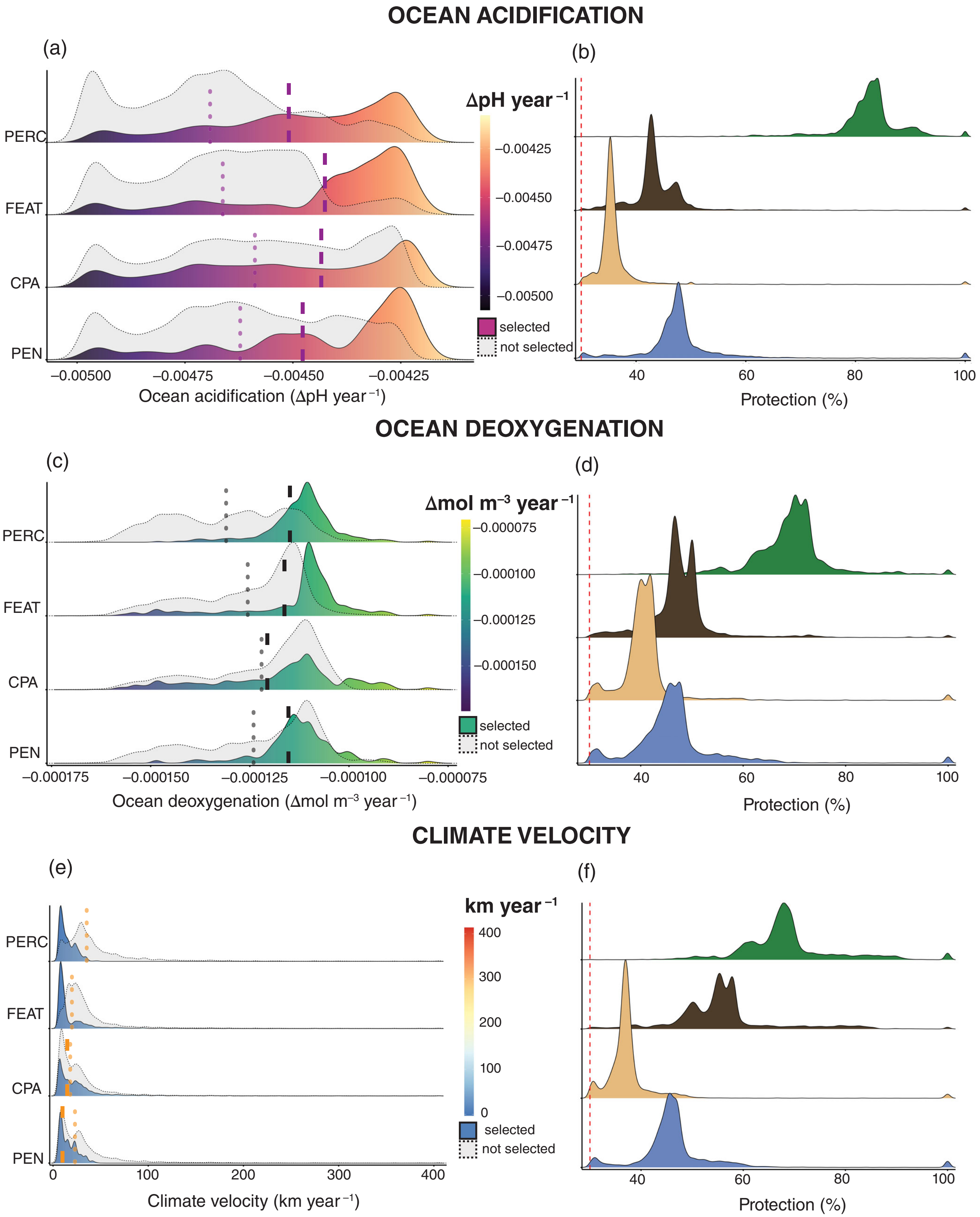


FIGURE 8 Performance of different approaches across metrics. (a, b) Ocean acidification (ΔpH year^{-1}); (c, d) Ocean deoxygenation ($\Delta[O_2]$ year^{-1}); and (e, f) Climate velocity (km year^{-1}). The plots on the left of each of the metrics show the kernel density estimates of the metric values in the solutions. Colored polygons represent values of different climate metrics. Grayed polygons represent values for areas not selected for protection. The dashed and dotted lines represent the mean and median (for velocity) values across planning units that were selected and not selected, respectively. The plots on the right of each of the five metrics show the kernel density estimates of the % protection of the biodiversity features (dashed line represents the 30% protection target). CPA, climate-priority-area; FEAT, feature; PEN, penalty; PERC, percentile.

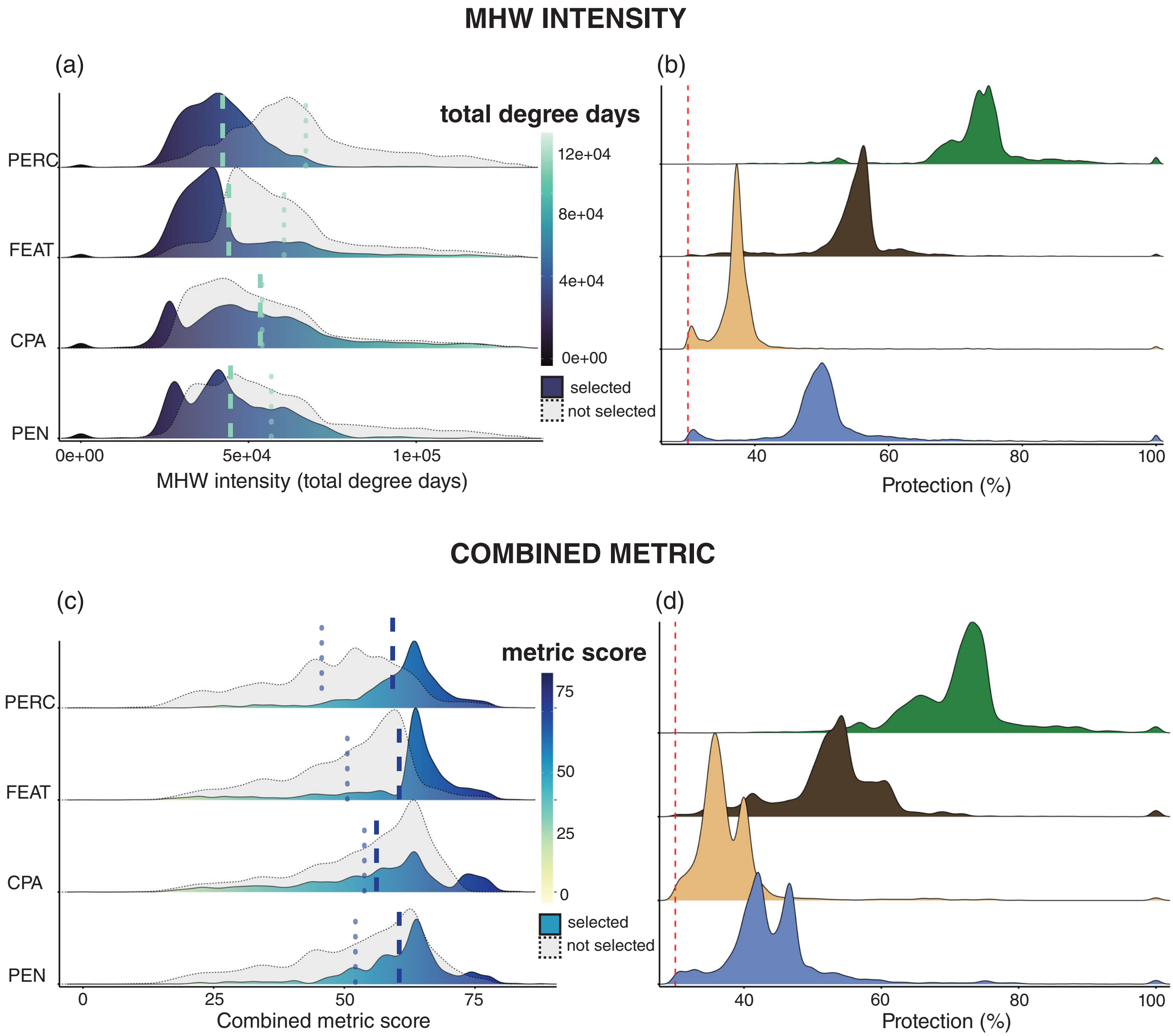


FIGURE 9 Performance of different approaches across metrics. (a, b) Marine heatwave (MHW) intensity (total degree days); and (c, d) Combined metric. The plots on the left of each of the metrics show the kernel density estimates of the metric values in the solutions. Colored polygons represent values of different climate metrics. Grayed polygons represent values for areas not selected for protection. The dashed and dotted lines represent the mean values across planning units that were selected and not selected, respectively. The plots on the right of each of the five metrics show the kernel density estimates of the % protection of the biodiversity features (dashed line represents the 30% protection target). CPA, climate-priority-area; FEAT, feature; PEN, penalty; PERC, percentile.

can be incorporated into a conservation plan. However, for particular ecosystems, practitioners might suggest that some metrics should have greater weights as they may represent more important environmental drivers. A more practical solution may be to explore how using a few relevant climate metrics would be included in the analysis (Garcia et al., 2014). Then, when possible, explore ways of condensing these into a metric that incorporates information from multiple climate variables or climate metrics (e.g., Boyce et al., 2022).

Prioritizing protection of climate refugia

Each of the four ways of identifying climate refugia and prioritizing their protection has its advantages and disadvantages (Table 1), resulting from the trade-off between climate-smart performance and efficiency of meeting biodiversity targets. The better the climate-smart performance of the approach (i.e., likely increased climate resilience), the less efficient the spatial plan will be in meeting representation targets and thus the larger

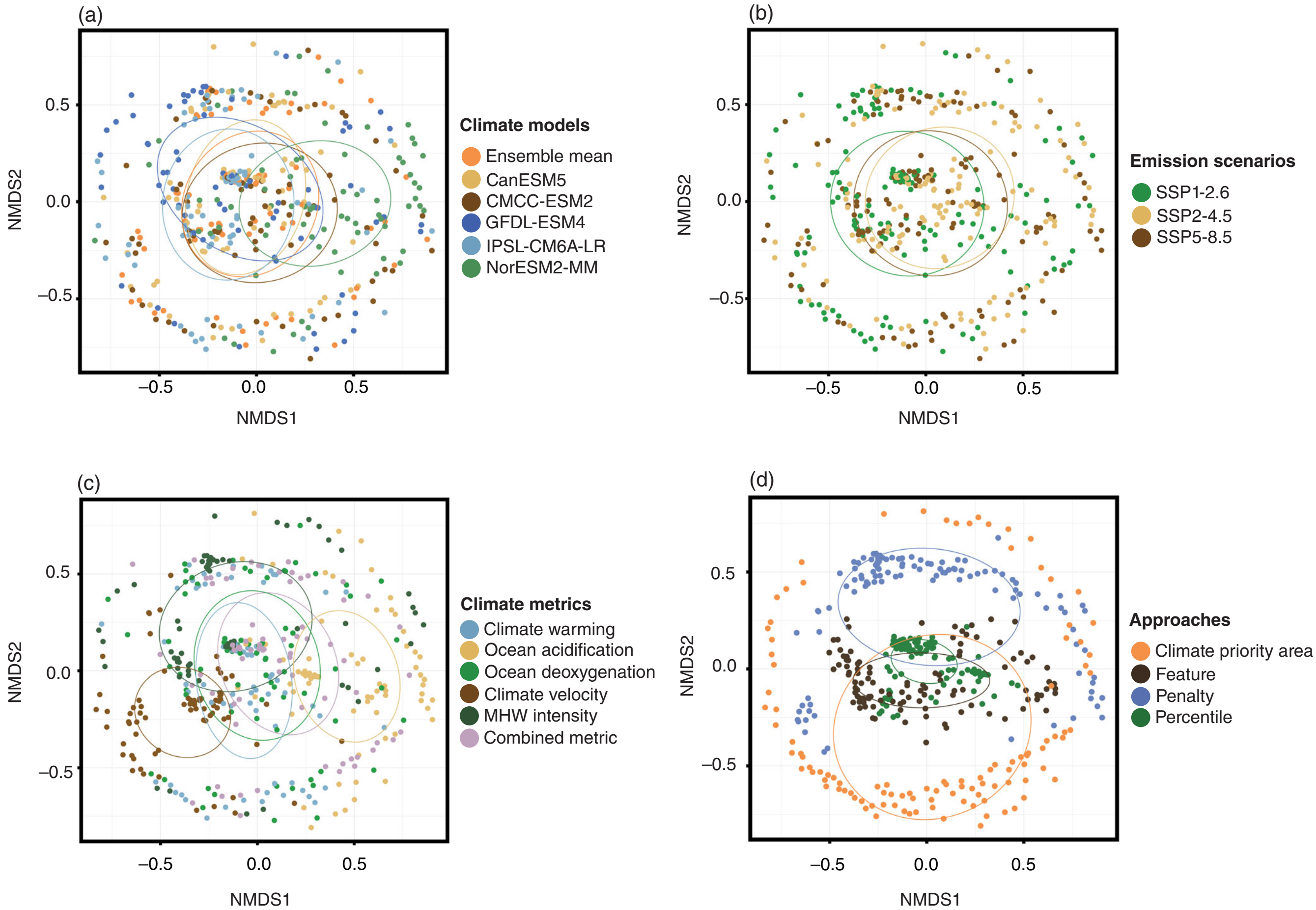


FIGURE 10 Non-metric multidimensional scaling (nMDS) ordination plots comparing 432 spatial plans across all combinations of options considered. Solutions by (a) scenario, (b) individual climate models and the ensemble-mean, (c) climate metrics, and (d) approaches to identifying refugia. Stress = 0.27. Number of iterations = 1000. Ellipses represent the standard deviation of the solutions.

protected area needed. Since each of the approaches requires carefully selecting thresholds or scaling penalty values to parameterize the trade-offs (Appendix S2), we recommend consulting with stakeholders and conducting calibration and sensitivity analysis to identify spatial plans that strike the right balance. To help understand trade-offs between each of the four approaches, we synthesize our findings below.

The feature approach is the simplest but lacks ecological relevance. This approach protects the climate-smart areas of the entire planning domain regardless of whether the area has any biodiversity value or not (Arafeh-Dalmau et al., 2021). Choosing less-demanding percentile thresholds decreases the area of the solution and climate-smart performance.

The percentile approach is the most climate-smart and provides the biodiversity features the greatest protection, but it was extremely costly in terms of the area selected. This is because the prioritization considers only the climate-smart areas of the biodiversity features for protection (Brito-Morales et al., 2022), which limits possible areas for selection and decreases the efficiency of the approach. Similar to the feature approach, choosing less-demanding thresholds decreases the area of the solution and climate-smart performance.

The climate-priority-area approach represents a modified version of the percentile approach and addresses its limitations. It is the most ecologically relevant approach as it prioritizes the protection of high-value climate-smart areas (i.e., climate-priority areas) while still providing a degree of protection to non-climate-smart areas. The resulting climate-smart spatial plan was only slightly more expensive than the climate-uninformed solution (i.e., a solution that does not consider climate change; Appendix S6: Figure S1). Additionally, this approach also yielded the prioritization with the greatest cost-efficiency—among all four approaches—for meeting representation targets. This is likely because this approach ensures that prioritizations select high-value climate refugia for different biodiversity features (similar to the percentile approach), without restricting their distribution (unlike the percentile approach). As such, this approach is among the least

TABLE 1 Overview of the options explored under each climate-smart aspect.

Climate-smart aspect		Strengths	Weaknesses	Utility and cautions
Emission scenarios	Single	Easy to implement and interpret results	Offers a single solution but ignores uncertainty associated with different futures	Focuses conservation efforts on one climate scenario
	Multiple	Produces a suite of solutions to a conservation problem	Involves more analyses and is more complex	Established as "best practice" (Harris et al., 2014; Jones et al., 2016); Captures variability and uncertainty of different scenarios (Brito-Morales et al., 2022; Makino et al., 2015; O'Neill et al., 2017)
Ensemble	Multi-model ensemble	Shows variability across climate models	Increases complexity as the no. climate models in an ensemble grows	Areas selected frequently across climate models more confidently identify climate refugia; Captures more uncertainty associated with models (Tegegne et al., 2020)
	Ensemble-mean (or median)	More easily used in more elaborate analyses	Offers one solution but loses information from individual climate models, especially when there are extreme climate projections that can bias the ensemble mean or median	Used in indicative spatial planning (Brito-Morales et al., 2022; Stralberg et al., 2020); Focuses on a generic climate signal from the ensemble rather than subtle variation introduced by each model; Provides a reasonable representation of the climate models in the ensemble
Metric	Based on a single climate variable	Produces results that are easier to interpret; Involves less assumptions	May not include interactions of different variables and their effects on the solution	Focuses conservation efforts on a particular impact of climate change; Can use a well-known driver of climate change (e.g., temperature) (Wilson et al., 2020)
	Integrated	Includes interactions of different drivers	Assumptions may increase with an increasing no. variables involved (e.g., using equal weighting versus varied weighting)	Can use multiple, relevant drivers of climate change, especially when they are not correlated or similar (e.g., warming versus acidification)
Approach	Feature	Adds a single layer to the prioritization; Intermediate in terms of climate-smart performance and area selected; Intermediate protection afforded to biodiversity features	Not species-specific; Uses a binary climate layer, leading to some loss of information	Protects refugia that do not necessarily have any biodiversity value (Arafeh-Dalmau et al., 2021); Requires a user-inputted percentile threshold to identify climate-smart areas; Representation target depends on the percentile threshold chosen

(Continues)

TABLE 1 (Continued)

Climate-smart aspect	Strengths	Weaknesses	Utility and cautions
Percentile	Identifies species-specific (or feature-specific) climate refugia; Most climate-smart approach; Approach where biodiversity features are afforded the greatest protection	Complex approach to implement; Restricts the distribution of each feature to the climate-smart areas; Discards any part of the distribution not considered climate refugia; Depending on threshold used, can potentially result in extremely costly solutions; Uses a binary climate layer, leading to some loss of information	Protects climate refugia only when they have biodiversity value (Brito-Morales et al., 2022); Requires a user-inputted percentile threshold to identify climate-smart areas; Representation target depends on the percentile threshold chosen
Climate-priority-area	Identifies high-value species-specific (or feature-specific) climate refugia; Preferentially protects high-value climate-smart areas and still protects the rest of the distribution; Little difference in area compared to a climate-uninformed spatial plan; Results in smaller spatial plans	Complex approach to implement; Uses a binary climate layer, leading to some loss of information; Relatively low climate-smart performance; Approach where biodiversity features are afforded the least protection	Modified percentile approach; Protects high-value climate-refugia only when they have biodiversity value; Requires both a user-inputted percentile threshold to identify high-value climate-smart areas and a target for these areas
Penalty	Does not require additional processing of feature distribution data; Intermediate protection afforded to biodiversity features; Selects the same total area as a climate-uninformed spatial plan	Modifies the objective function; Not species-specific; By preserving the continuous nature of the climate metric, assumes a linear relationship between the climate metric and impacts of climate change; Relatively poor climate-smart performance	Requires a user-inputted penalty scaling that requires calibration

climate-smart of the approaches. Aside from choosing a percentile threshold to identify high-value climate refugia, a target must also be assigned to it. Choosing more-demanding thresholds while still assigning a 100% target to these priority areas decreases the area of the solution and climate-smart performance.

The penalty approach is the least climate-smart approach because it does not account for species-specific impacts of climate change, and—by preserving the continuous nature of climate metrics—allows the selection of areas of intermediate climate exposure. In our case study, it resulted in the smallest area (i.e., % of the planning domain most similar to the climate-uninformed solution). Further, the trade-off between higher penalty scaling and both area and climate-smart performance was not evident in the sensitivity analysis for this approach. This is because our case study used equal-sized planning units and a uniform cost layer. When using different-sized planning units or a non-uniform cost layer (e.g., where costs are derived from land or ocean value), conservation planning exercises will need to calibrate trade-offs between the cost layer and the climate-smart penalties to ensure that the resulting prioritization is not too costly (Cohon et al., 1979).

Caveats

Our analysis has several caveats that should be noted. First, to explore the different climate-smart aspects of spatial planning, we simplified the spatial plans, but any real-world application would likely include: (1) a non-uniform cost layer representing the opportunity costs of closing an area for protection; (2) targets reflecting the threat status or

TABLE 2 Summary of climate metrics used in the case study.

Climate metric	Attributes	Utility
Climate warming	Most similar with spatial plans using ocean deoxygenation; Selected a considerably large area for protection	Chronic-exposure metric; Temperature is the most common driver of climate change used in climate-smart conservation planning (Wilson et al., 2020)
Ocean acidification	Most dissimilar to other climate metrics; Selected a relatively large area for protection	Chronic-exposure metric; Generally, negatively impacts ecosystems; however, its impact can also be positive or neutral for some species (Harvey et al., 2013; Kroeker et al., 2013); Can be influenced by anthropogenic activities other than climate change (Harvey et al., 2013)
Ocean deoxygenation	Most similar with spatial plans using climate warming; Intermediate in terms of total area selected for protection	Chronic-exposure metric; Directly correlated with temperature (Deutsch et al., 2015; Pörtner & Knust, 2007); Some organisms may be insensitive to small declines, but all suffer physiological stress once oxygen levels decline past a hypoxic threshold (Bopp et al., 2013)
Climate velocity (using temperature)	Spatial plans are dissimilar to climate warming despite being both calculated from temperature; Calculation involves both temporal and spatial gradients of temperature; More computationally complex than using climate warming	Retention metric; Established as a robust proxy of observed range shifts (Lenoir et al., 2020); Can be calculated from variables other than temperature (Brito-Morales et al., 2018); Could inform how long a reserve remains effective in protecting biodiversity within its boundaries (Loarie et al., 2009)
Sum of cumulative MHW intensity	More data intensive since it requires daily data; Measures discrete warming events; More computationally complex than using climate warming	Acute-exposure metric of discrete warming events (Hobday et al., 2016); Useful for protecting species susceptible to discrete warming events (Magris et al., 2015)
Combined metric	Weighs all metrics equally; Most similar to climate warming and ocean deoxygenation, and, to some extent, MHW intensity	Integrated or combined metrics that involve multiple climate drivers (e.g., Boyce et al., 2022) can be useful for protecting regions against these drivers as well as their interactions

Abbreviation: MHW, marine heatwave.

area of the distribution of a species; (3) greater emphasis on the selection of biodiversity features; and (4) boundary penalties to reduce fragmentation of the resulting spatial plans. Second, we created spatial plans using simple climate metrics. However, refugia could also be identified using integrated metrics calculated form multiple climate indices or multiple climate variables (e.g., Boyce et al., 2022; Rojas et al., 2022) that could account for species' predicted movements based on species distribution models (Kujala et al., 2013; Pinsky, Rogers, et al., 2020 but see Lee-Yaw et al., 2022) and could be included in a single prioritization (Kujala et al., 2013). Last, we considered a large planning domain and a relatively coarse spatial resolution, which might not be applicable to conservation planning conducted at finer spatial scales, especially on land (Bellard et al., 2012; Wilson et al., 2020). Nevertheless, because impacts of climate change on ecosystems are more evident at larger spatial scales (Edgar et al., 2014), regional or global spatial planning could determine climate-resilient priority areas that then inform conservation planning at more local scales. Thus, rather than ignoring climate change at finer scales, successful planning could be achieved by complementing local, bottom-up conservation planning with regional, climate-smart conservation planning that identifies key areas for protection (Gaymer et al., 2014).

KEY RECOMMENDATIONS FOR CLIMATE-SMART CONSERVATION PLANNING

1. Practitioners should use their expert knowledge of the region and its species to choose the appropriate metrics and approach to identifying climate refugia because these two choices are most influential in the configuration of resultant climate-smart spatial plans.
2. Incorporate model outputs from an ensemble of models to encompass model uncertainty.
3. It may be sufficient to use the ensemble-mean (or median) to represent the generic climate signal from the ensemble rather than subtle variation introduced by each model—especially when the ensemble consists of

multiple models (e.g., >5)—to greatly reduce complexity imposed by directly using multiple models. However, using multiple models individually (i.e., multi-model-ensemble) would be best used if a region is characterized by extreme or conflicting climate projections from a model/s that could render the ensemble mean less reliable.
4. To account for multiple climate drivers, we suggest combining the selected relevant climate information into a single climate-smart metric before including them in the prioritization. This is especially important for conservation exercises that select climate metrics that would result in different configurations when used individually.
5. Carefully choose the approach to identifying climate refugia based on how important climate change is in the prioritization, as different approaches produce strikingly different solutions. Generally, the more climate-smart the approach, the larger the area needed for protection. The climate-priority-area approach represents a good tradeoff because it protects the core high-value climate refugia while still affording some protection for the rest of the species' distributions and not resulting in unnecessarily large spatial plans.

Our proposed framework identifies and prioritizes the protection of climate refugia. This climate-smart approach protects areas important to biodiversity today and will still likely be important in the future (e.g., Chollett et al., 2022; Morelli et al., 2020). Although the focus of the framework is on climate refugia, recommendations of using a range of emission scenarios, model ensembles, and appropriate metrics could just as easily be applied to other climate-smart conservation planning methods. Instead of prioritizing protection of low-exposure and high-retention climate refugia, our framework could be generalized in many ways to: protect areas of high chronic but low acute thermal stress (Magris et al., 2014); ensure a range of areas, from low to high climate exposure, are protected (Jones et al., 2016; McLeod et al., 2019; Tittensor et al., 2019); and design dynamic closures and stepping-stone protected areas (D'Aloia et al., 2019; Hannah et al., 2014; Tittensor et al., 2019). In fact, large protected areas that prioritize protection of climate refugia can be supplemented by smaller stepping-stone protected areas and dynamic closures to make a network more climate-smart (Morelli et al., 2020; Tittensor et al., 2019). Further, although the case study did not consider connectivity, it is an important aspect to consider when developing climate-smart spatial plans (Beger et al., 2022; Berglund et al., 2012; Christie et al., 2010; Wilson et al., 2020). There are different approaches developed to promote connectivity (Beger et al., 2022) that could be incorporated by modifying our proposed framework.

The complexity of conservation planning is increased by adding the uncertainty of climate change into spatial prioritization. This is one reason why there has been little consensus on methods for climate-smart conservation planning, and why protection against climate change has not yet been fully incorporated in conservation planning (O'Regan et al., 2021). Our proposed framework helps close this gap. We suggest that using climate metrics that identify low-exposure, high-retention climate refugia is an informative and simpler approach than building many species distribution models for biodiversity features to inform a climate-smart spatial plan. We hope that this framework will be a valuable addition to the conservation practitioner's toolkit in a range of ecosystems.

AUTHOR CONTRIBUTIONS

Kristine Camille V. Buenafe, Daniel C. Dunn, Jason D. Everett, Isaac Brito-Morales, David S. Schoeman, Jeffrey O. Hanson, and Anthony J. Richardson conceived the ideas and designed methodology. Kristine Camille V. Buenafe, Jason D. Everett, David S. Schoeman, Isaac Brito-Morales, Alvise Dabalà, and Sandra Neubert analyzed the data. Kristine Camille V. Buenafe and Anthony J. Richardson led the writing of the manuscript. All authors contributed critically and significantly to the manuscript drafts, and all gave their approval for publication.

ACKNOWLEDGMENTS

Kristine Camille V. Buenafe and Alvise Dabalà were supported by the Erasmus Joint Master Degree Program in Tropical Biodiversity and Ecosystems (EMJMD TROPIMUNDO), which is funded by the European Commission (EC). Jeffrey O. Hanson was supported by Environment and Climate Change Canada (ECCC) and Nature Conservancy of Canada (NCC). Isaac Brito-Morales was supported by the National Science Foundation (NSF) no. 2029710. Open access publishing facilitated by The University of Queensland, as part of the Wiley - The University of Queensland agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used for the case study are available at Zenodo (Buenafe et al., 2023). The global AquaMaps data (Kaschner et al., 2019) were retrieved as described in Appendix S1. The global daily and monthly future model projections (Bentsen et al., 2019a, 2019b, 2019c; Boucher et al., 2019a, 2019b, 2019c; John et al., 2018a, 2018b, 2018c; Lovato et al., 2021a, 2021b, 2021c; Swart et al., 2019a, 2019b, 2019c) were downloaded from Coupled Model Intercomparison Project Phase 6 (CMIP6) through the Earth System Grid Federation (ESGF) as described in Appendix S1. The historical sea surface temperatures were downloaded from the National Oceanic and Atmospheric Administration (NOAA)'s Optimum Interpolation SST (OISST) product (Huang et al., 2020) where the entire global dataset from 1981-present can be downloaded as a netCDF and must be spliced temporally and spatially as needed. All scripts used to conduct the case study are published at Zenondo (Buenafe et al., 2023). To ensure that the code runs smoothly, use the updated versions of R and all Comprehensive R Archive Network (CRAN) packages declared in the repository. We used R version 4.1.1 (R Core Team, 2022). To aid in interpretation, we have created a Shiny App that can be accessed on Zenodo along with the other code. This Shiny App briefly explains the climate-smart conservation planning framework and allows the user to compare solutions created from different options of the climate-smart aspects explored in this paper.

ORCID

Kristine Camille V. Buenafe https://orcid.org/0000-0002-1643-5557
Isaac Brito-Morales https://orcid.org/0000-0003-0073-2431

REFERENCES

Arafeh-Dalmau, N., I. Brito-Morales, D. S. Schoeman, H. P. Possingham, C. J. Klein, and A. J. Richardson. 2021. "Incorporating Climate Velocity into the Design of Climate-Smart Networks of Marine Protected Areas." *Methods in Ecology and Evolution* 12(10): 1969–83. https://doi.org/10.1111/2041-210X.13675.

Araújo, M. B., D. Alagador, M. Cabeza, D. Nogués-Bravo, and W. Thuiller. 2011. "Climate Change Threatens European Conservation Areas." *Ecology Letters* 14(5): 484–92. https://doi.org/10.1111/j.1461-0248.2011.01610.x.

Ball, I. R., H. P. Possingham, and M. E. Watts. 2009. "Marxan and Relatives: Software for Spatial Conservation Prioritization." In *Spatial Conservation Prioritization*. Oxford: Oxford University Press.

Bates, A. E., R. S. C. Cooke, M. I. Duncan, G. J. Edgar, J. F. Bruno, L. Benedetti-Cecchi, I. M. Côté, et al. 2019. "Climate Resilience in Marine Protected Areas and the 'Protection Paradox.'." *Biological Conservation* 236: 305–14. https://doi.org/10.1016/j.biocon.2019.05.005.

Beger, M., A. Metaxas, A. C. Balbar, J. A. McGowan, R. Daigle, C. D. Kuempel, E. A. Treml, and H. P. Possingham. 2022. "Demystifying Ecological Connectivity for Actionable Spatial Conservation Planning." *Trends in Ecology & Evolution* 37(12): 1079–91. https://doi.org/10.1016/j.tree.2022.09.002.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. "Impacts of Climate Change on the Future of Biodiversity." *Ecology Letters* 15(4): 365–77. https://doi.org/10.1111/j.1461-0248.2011.01736.x.

Bentsen, M., D. J. L. Oliviè, Ø. Seland, T. Thomas, G. Ada, L. S. Graff, J. B. Debernard, et al. 2019a. "NCC NorESM2-MM Model Output Prepared for CMIP6 ScenarioMIP ssp126." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8250.

Bentsen, M., D. J. L. Oliviè, Ø. Seland, T. Thomas, G. Ada, L. S. Graff, J. B. Debernard, et al. 2019b. "NCC NorESM2-MM Model Output Prepared for CMIP6 ScenarioMIP ssp245." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8255.

Bentsen, M., D. J. L. Oliviè, Ø. Seland, T. Thomas, G. Ada, L. S. Graff, J. B. Debernard, et al. 2019c. "NCC NorESM2-MM Model Output Prepared for CMIP6 ScenarioMIP ssp585." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8321.

Berglund, M., M. N. Jacobi, and P. R. Jonsson. 2012. "Optimal Selection of Marine Protected Areas Based on Connectivity and Habitat Quality." *Ecological Modelling* 240: 105–12. https://doi.org/10.1016/j.ecolmodel.2012.04.011.

Bopp, L., L. Resplandy, J. C. Orr, S. C. Doney, J. P. Dunne, M. Gehlen, P. Halloran, et al. 2013. "Multiple Stressors of Ocean Ecosystems in the 21st Century: Projections with CMIP5 Models." *Biogeosciences* 10(10): 6225–45. https://doi.org/10.5194/bg-10-6225-2013.

Boucher, O., S. Denvil, G. Levavasseur, C. Anne, C. Arnaud, F. Marie-Alice, Y. Meurdesoif, et al. 2019a. "IPSL IPSL-CM6A-LR Model Output Prepared for CMIP6 ScenarioMIP ssp126." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.5262.

Boucher, O., S. Denvil, G. Levavasseur, C. Anne, C. Arnaud, F. Marie-Alice, Y. Meurdesoif, et al. 2019b. "IPSL IPSL-CM6A-LR Model Output Prepared for CMIP6 ScenarioMIP ssp245." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.5264

Boucher, O., S. Denvil, G. Levavasseur, C. Anne, C. Arnaud, F. Marie-Alice, Y. Meurdesoif, et al. 2019c. "IPSL IPSL-CM6A-LR Model Output Prepared for CMIP6 ScenarioMIP ssp585." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.5271.

Boyce, D. G., D. P. Tittensor, C. Garilao, S. Henson, K. Kaschner, K. Kesner-Reyes, A. Pigot, et al. 2022. "A Climate Risk Index for Marine Life." *Nature Climate Change* 12(9): 854–62. https://doi.org/10.1038/s41558-022-01437-y.

Breitburg, D., L. A. Levin, A. Oschlies, M. Grégoire, F. P. Chavez, D. J. Conley, V. Garçon, et al. 2018. "Declining Oxygen in the Global Ocean and Coastal Waters." *Science* 359(6371): eaam7240. https://doi.org/10.1126/science.aam7240.

Brito-Morales, I., J. G. Molinos, D. S. Schoeman, M. T. Burrows, E. S. Poloczanska, C. J. Brown, S. Ferrier, et al. 2018. "Climate Velocity Can Inform Conservation in a Warming World." *Trends in Ecology & Evolution* 33(6): 441–57. https://doi.org/10.1016/j.tree.2018.03.009.

Brito-Morales, I., D. S. Schoeman, J. D. Everett, C. J. Klein, D. C. Dunn, J. G. Molinos, M. T. Burrows, et al. 2022. "Towards Climate-Smart, Three-Dimensional Protected Areas for Biodiversity Conservation in the High Seas." *Nature Climate Change* 12: 1–6. https://doi.org/10.1038/s41558-022-01323-7.

Bruno, J. F., A. E. Bates, C. Cacciapaglia, E. P. Pike, S. C. Amstrup, R. van Hooidonk, S. A. Henson, and R. B. Aronson. 2018. "Climate Change Threatens the World's Marine Protected Areas." *Nature Climate Change* 8(6): 499–503. https://doi.org/10.1038/s41558-018-0149-2.

Buenafe, K. C. V., D. C. Dunn, J. D. Everett, I. Brito-Morales, D. S. Schoeman, J. O. Hanson, A. Dabalà, et al. 2023. "Climate-Smart SPFramework: Climate-Smart Conservation Planning

Framework." Version 2.1.0. https://doi.org/10.5281/zenodo.7747545.

Burrows, M. T., A. E. Bates, M. J. Costello, M. Edwards, G. J. Edgar, C. J. Fox, B. S. Halpern, et al. 2019. "Ocean Community Warming Responses Explained by Thermal Affinities and Temperature Gradients." *Nature Climate Change* 9(12): 959–63. https://doi.org/10.1038/s41558-019-0631-5.

Burrows, M. T., D. S. Schoeman, L. B. Buckley, P. Moore, E. S. Poloczanska, K. M. Brander, C. Brown, et al. 2011. "The Pace of Shifting Climate in Marine and Terrestrial Ecosystems." *Science* 334(6056): 652–5. https://doi.org/10.1126/science.1210288.

Burrows, M. T., D. S. Schoeman, A. J. Richardson, J. G. Molinos, A. Hoffmann, L. B. Buckley, P. J. Moore, et al. 2014. "Geographical Limits to Species-Range Shifts Are Suggested by Climate Velocity." *Nature* 507(7493): 492–5. https://doi.org/10.1038/nature12976.

Carroll, C., D. R. Roberts, J. L. Michalak, J. J. Lawler, S. E. Nielsen, D. Stralberg, A. Hamann, B. H. Mcrae, and T. Wang. 2017. "Scale-Dependent Complementarity of Climatic Velocity and Environmental Diversity for Identifying Priority Areas for Conservation under Climate Change." *Global Change Biology* 23(11): 4508–20. https://doi.org/10.1111/gcb.13679.

CBD. 2020. "Update of the Zero Draft of the Post-2020 Global Biodiversity Framework." CBD/POST2020/PREP/2/1. https://www.cbd.int/doc/c/3064/749a/0f65ac7f9def86707f4eaefa/post2020-prep-02-01-en.pdf.

CBD. 2022. "Kunming-Montreal Global Biodiversity Framework: Draft Decision Submitted by the President." CBD/COP/15/L.25. https://www.cbd.int/doc/c/e6d3/cd1d/daf663719a03902a9b116c34/cop-15-l-25-en.pdf.

Chaudhary, C., A. J. Richardson, D. S. Schoeman, and M. J. Costello. 2021. "Global Warming Is Causing a more Pronounced Dip in Marine Species Richness around the Equator." *Proceedings of the National Academy of Sciences* 118(15): e2015094118. https://doi.org/10.1073/pnas.2015094118.

Chen, I.-C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. "Rapid Range Shifts of Species Associated with High Levels of Climate Warming." *Science* 333(6045): 1024–6. https://doi.org/10.1126/science.1206432.

Chollett, I., X. Escovar-Fadul, S. R. Schill, A. Croquer, A. M. Dixon, M. Beger, E. Shaver, V. P. McNulty, and N. H. Wolff. 2022. "Planning for Resilience: Incorporating Scenario and Model Uncertainty and Trade-Offs when Prioritizing Management of Climate Refugia." *Global Change Biology* 28(13): 4054–68. https://doi.org/10.1111/gcb.16167.

Christie, M. R., B. N. Tissot, M. A. Albins, J. P. Beets, Y. Jia, D. M. Ortiz, S. E. Thompson, and M. A. Hixon. 2010. "Larval Connectivity in an Effective Network of Marine Protected Areas." *PLOS ONE* 5(12): e15715. https://doi.org/10.1371/journal.pone.0015715.

Cohon, J. L., R. L. Church, and D. P. Sheer. 1979. "Generating Multiobjective Trade-Offs: An Algorithm for Bicriterion Problems." *Water Resources Research* 15(5): 1001–10. https://doi.org/10.1029/WR015i005p01001.

Combes, M., S. Vaz, A. Grehan, T. Morato, S. Arnaud-Haond, C. Dominguez-Carrió, A. Fox, et al. 2021. "Systematic Conservation Planning at an Ocean Basin Scale: Identifying a Viable Network of Deep-Sea Protected Areas in the North Atlantic and the Mediterranean." *Frontiers in Marine Science* 8: 611358. https://doi.org/10.3389/fmars.2021.611358.

Cornelissen, T. 2011. "Climate Change and its Effects on Terrestrial Insects and Herbivory Patterns." *Neotropical Entomology* 40(2): 155–63.

D'Aloia, C. C., I. Naujokaitis-Lewis, C. Blackford, C. Chu, J. M. R. Curtis, E. Darling, F. Guichard, et al. 2019. "Coupled Networks of Permanent Protected Areas and Dynamic Conservation Areas for Biodiversity Conservation under Climate Change." *Frontiers in Ecology and Evolution* 7: 00027. https://doi.org/10.3389/fevo.2019.00027.

Deutsch, C., A. Ferrel, B. Seibel, H.-O. Pörtner, and R. B. Huey. 2015. "Climate Change Tightens a Metabolic Constraint on Marine Habitats." *Science* 348(6239): 1132–5. https://doi.org/10.1126/science.aaa1605.

Dexter, E., G. Rollwagen-Bollens, and S. M. Bollens. 2018. "The Trouble with Stress: A Flexible Method for the Evaluation of Nonmetric Multidimensional Scaling." *Limnology and Oceanography: Methods* 16(7): 434–43. https://doi.org/10.1002/lom3.10257.

Doxa, A., V. Almpanidou, S. Katsanevakis, A. M. Queirós, K. Kaschner, C. Garilao, K. Kesner-Reyes, and A. D. Mazaris. 2022. "4D Marine Conservation Networks: Combining 3D Prioritization of Present and Future Biodiversity with Climatic Refugia." *Global Change Biology* 28(15): 4577–88. https://doi.org/10.1111/gcb.16268.

Eakin, C. M., H. P. A. Sweatman, and R. E. Brainard. 2019. "The 2014–2017 Global-Scale Coral Bleaching Event: Insights and Impacts." *Coral Reefs* 38(4): 539–45. https://doi.org/10.1007/s00338-019-01844-2.

Edgar, G. J., R. D. Stuart-Smith, T. J. Willis, S. Kininmonth, S. C. Baker, S. Banks, N. S. Barrett, et al. 2014. "Global Conservation Outcomes Depend on Marine Protected Areas with Five Key Features." *Nature* 506(7487): 216–20. https://doi.org/10.1038/nature13022.

Foresta, M., M. L. Carranza, V. Garfì, M. Di Febbraro, M. Marchetti, and A. Loy. 2016. "A Systematic Conservation Planning Approach to Fire Risk Management in Natura 2000 Sites." *Journal of Environmental Management* 181(October): 574–81. https://doi.org/10.1016/j.jenvman.2016.07.006.

Frölicher, T. L., E. M. Fischer, and N. Gruber. 2018. "Marine Heatwaves under Global Warming." *Nature* 560(7718): 360–4. https://doi.org/10.1038/s41586-018-0383-9.

García Molinos, J., D. S. Schoeman, C. J. Brown, and M. T. Burrows. 2019. "VoCC: An r Package for Calculating the Velocity of Climate Change and Related Climatic Metrics." *Methods in Ecology and Evolution* 10(12): 2195–202. https://doi.org/10.1111/2041-210X.13295.

Garcia, R. A., M. Cabeza, C. Rahbek, and M. B. Araújo. 2014. "Multiple Dimensions of Climate Change and their Implications for Biodiversity." *Science* 344(6183): 1247579. https://doi.org/10.1126/science.1247579.

Gaymer, C. F., A. V. Stadel, N. C. Ban, P. Francisco Cárcamo, J. I. Jr., and L. M. Lieberknecht. 2014. "Merging Top-Down and Bottom-up Approaches in Marine Protected Areas Planning: Experiences from around the Globe." *Aquatic Conservation: Marine and Freshwater Ecosystems* 24(S2): 128–44. https://doi.org/10.1002/aqc.2508.

Green, A., S. E. Smith, G. Lipsett-Moore, C. Groves, N. Peterson, S. Sheppard, P. Lokani, et al. 2009. "Designing a Resilient Network of Marine Protected Areas for Kimbe Bay, Papua New Guinea." *Oryx* 43(4): 488–98. https://doi.org/10.1017/S0030605309990342.

Gu, H., Y. Zhongbo, J. Wang, G. Wang, T. Yang, J. Qin, C. Yang, X. Feng, and C. Fan. 2015. "Assessing CMIP5 General Circulation Model Simulations of Precipitation and Temperature over China." *International Journal of Climatology* 35(9): 2431–40. https://doi.org/10.1002/joc.4152.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, et al. 2013. "Predicting Species Distributions for Conservation Decisions." *Ecology Letters* 16(12): 1424–35. https://doi.org/10.1111/ele.12189.

Hannah, L., L. Flint, A. D. Syphard, M. A. Moritz, L. B. Buckley, and I. M. McCullough. 2014. "Fine-Grain Modeling of Species' Response to Climate Change: Holdouts, Stepping-Stones, and Microrefugia." *Trends in Ecology & Evolution* 29(7): 390–7. https://doi.org/10.1016/j.tree.2014.04.006.

Hanson, J. O., R. Schuster, N. Morrell, M. Strimas-Mackey, B. P. M. Edwards, M. E. Watts, P. Arcese, J. Bennett, and H. P. Possingham. 2021. "Prioritizr: Systematic Conservation Prioritization in R." https://CRAN.R650project.org/package=prioritizr.

Harris, L. R., S. Holness, S. Finke, G. Kirkman, and K. Sink. 2019. "Systematic Conservation Planning as a Tool to Advance Ecologically or Biologically Significant Area and Marine Spatial Planning Processes." In *Maritime Spatial Planning* 71–96. Cham: Palgrave Macmillan.

Harris, R. M. B., M. R. Grose, G. Lee, N. L. Bindoff, L. L. Porfirio, and P. Fox-Hughes. 2014. "Climate Projections for Ecologists." *WIREs Climate Change* 5(5): 621–37. https://doi.org/10.1002/wcc.291.

Harvey, B. P., D. Gwynn-Jones, and P. J. Moore. 2013. "Meta-Analysis Reveals Complex Marine Biological Responses to the Interactive Effects of Ocean Acidification and Warming." *Ecology and Evolution* 3(4): 1016–30. https://doi.org/10.1002/ece3.516.

Hausfather, Z., K. Marvel, G. A. Schmidt, J. W. Nielsen-Gammon, and M. Zelinka. 2022. "Climate Simulations: Recognize the 'Hot Model' Problem." *Nature* 605(7908): 26–9. https://doi.org/10.1038/d41586-022-01192-2.

Heikkinen, R. K., N. Leikola, J. Aalto, K. Aapala, S. Kuusela, M. Luoto, and R. Virkkala. 2020. "Fine-Grained Climate Velocities Reveal Vulnerability of Protected Areas to Climate Change." *Scientific Reports* 10. https://www.nature.com/articles/s41598-020-58638-8: 1678.

Hobday, A. J., L. V. Alexander, S. E. Perkins, D. A. Smale, S. C. Straub, E. C. J. Oliver, J. A. Benthuysen, et al. 2016. "A Hierarchical Approach to Defining Marine Heatwaves." *Progress in Oceanography* 141: 227–38. https://doi.org/10.1016/j.pocean.2015.12.014.

Huang, B., C. Liu, V. Banzon, E. Freeman, G. Graham, B. Hankins, T. Smith, and H.-M. Zhang. 2020. "Improvements of the Daily Optimum Interpolation Sea Surface Temperature (DOISST) Version 2.1." *Journal of Climate* 34: 2923–39. https://doi.org/10.1175/JCLI-D-20-0166.1.

IPCC. 2021. "Summary for Policymakers." In *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou. Cambridge: Cambridge University Press.

John, J. G., C. Blanton, C. McHugh, R. Aparna, R. Kristopher, H. Vahlenkamp, W. Chandin, et al. 2018a. "NOAA-GFDL GFDL-ESM4 Model Output Prepared for CMIP6 ScenarioMIP ssp126." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8684.

John, J. G., C. Blanton, C. McHugh, R. Aparna, R. Kristopher, H. Vahlenkamp, W. Chandin, et al. 2018b. "NOAA-GFDL GFDL-ESM4 Model Output Prepared for CMIP6 ScenarioMIP ssp245." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8686.

John, J. G., C. Blanton, C. McHugh, R. Aparna, R. Kristopher, H. Vahlenkamp, W. Chandin, et al. 2018c. "NOAA-GFDL GFDL-ESM4 Model Output Prepared for CMIP6 ScenarioMIP ssp585." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.8706.

Jones, K. R., J. E. M. Watson, H. P. Possingham, and C. J. Klein. 2016. "Incorporating Climate Change into Spatial Conservation Prioritisation: A Review." *Biological Conservation* 194: 121–30. https://doi.org/10.1016/j.biocon.2015.12.008.

Kaschner, K., K. Kesner-Reyes, C. Garilao, J. Segschneider, J. Rius-Barile, T. Rees, and R. Froese. 2019. "AquaMaps: Predicted Range Maps for Aquatic Species." https://www.aquamaps.org.

Keppel, G., K. Mokany, G. W. Wardell-Johnson, B. L. Phillips, J. A. Welbergen, and A. E. Reside. 2015. "The Capacity of Refugia for Conservation Planning under Climate Change." *Frontiers in Ecology and the Environment* 13(2): 106–12. https://doi.org/10.1890/140055.

Kroeker, K. J., R. L. Kordas, R. Crim, I. E. Hendriks, L. Ramajo, G. S. Singh, C. M. Duarte, and J.-P. Gattuso. 2013. "Impacts of Ocean Acidification on Marine Organisms: Quantifying Sensitivities and Interaction with Warming." *Global Change Biology* 19(6): 1884–96. https://doi.org/10.1111/gcb.12179.

Kujala, H., A. Moilanen, M. B. Araújo, and M. Cabeza. 2013. "Conservation Planning with Uncertain Climate Change Projections." *PLOS ONE* 8(2): e53315. https://doi.org/10.1371/journal.pone.0053315.

Lee-Yaw, J. A., J. L. McCune, S. Pironon, and S. N. Sheth. 2022. "Species Distribution Models Rarely Predict the Biology of Real Populations." *Ecography* 2022(6): e05877. https://doi.org/10.1111/ecog.05877.

Lenoir, J., R. Bertrand, L. Comte, L. Bourgeaud, T. Hattab, J. Murienne, and G. Grenouillet. 2020. "Species Better Track Climate Warming in the Oceans than on Land." *Nature Ecology & Evolution* 4(8): 1044–59. https://doi.org/10.1038/s41559-020-1198-2.

Levin, L. A., C.-L. Wei, D. C. Dunn, D. J. Amon, O. S. Ashford, W. W. L. Cheung, A. Colaço, et al. 2020. "Climate Change Considerations Are Fundamental to Management of Deep-sea Resource Extraction." *Global Change Biology* 26(9): 4664–78. https://doi.org/10.1111/gcb.15223.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462(7276): 1052–5. https://doi.org/10.1038/nature08649.

Lombard, A. T., B. Reyers, L. Y. Schonegevel, J. Cooper, L. B. Smith-Adao, D. C. Nel, P. W. Froneman, et al. 2007. "Conserving Pattern and Process in the Southern Ocean: Designing a Marine Protected Area for the Prince Edward Islands." *Antarctic Science* 19(1): 39–54. https://doi.org/10.1017/S0954102007000077.

Lovato, T., D. Peano, and M. Butenschön. 2021a. "CMCC CMCC-ESM2 Model Output Prepared for CMIP6 ScenarioMIP ssp126." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.13250.

Lovato, T., D. Peano, and M. Butenschön. 2021b. "CMCC CMCC-ESM2 Model Output Prepared for CMIP6 ScenarioMIP ssp245." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.13252.

Lovato, T., D. Peano, and M. Butenschön. 2021c. "CMCC CMCC-ESM2 Model Output Prepared for CMIP6 ScenarioMIP ssp585." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.13259.

Magris, R. A., S. F. Heron, and R. L. Pressey. 2015. "Conservation Planning for Coral Reefs Accounting for Climate Warming Disturbances." *PLOS ONE* 10(11): e0140828. https://doi.org/10.1371/journal.pone.0140828.

Magris, R. A., R. L. Pressey, R. Weeks, and N. C. Ban. 2014. "Integrating Connectivity and Climate Change into Marine Conservation Planning." *Biological Conservation* 170(2): 207–21. https://doi.org/10.1016/j.biocon.2013.12.032.

Mair, L., J. K. Hill, R. Fox, M. Botham, T. Brereton, and C. D. Thomas. 2014. "Abundance Changes and Habitat Availability Drive Species' Responses to Climate Change." *Nature Climate Change* 4(2): 127–31. https://doi.org/10.1038/nclimate2086.

Makino, A., C. J. Klein, H. P. Possingham, H. Yamano, Y. Yara, T. Ariga, K. Matsuhasi, and M. Beger. 2015. "The Effect of Applying Alternate IPCC Climate Scenarios to Marine Reserve Design for Range Changing Species." *Conservation Letters* 8(5): 320–8. https://doi.org/10.1111/conl.12147.

Martins, M. R., J. Assis, and D. Abecasis. 2021. "Biologically Meaningful Distribution Models Highlight the Benefits of the Paris Agreement for Demersal Fishing Targets in the North Atlantic Ocean." *Global Ecology and Biogeography* 30(8): 1643–56. https://doi.org/10.1111/geb.13327.

McCain, C. M., and R. K. Colwell. 2011. "Assessing the Threat to Montane Biodiversity from Discordant Shifts in Temperature and Precipitation in a Changing Climate." *Ecology Letters* 14(12): 1236–45. https://doi.org/10.1111/j.1461-0248.2011.01695.x.

McHugh, M. L. 2012. "Interrater Reliability: The Kappa Statistic." *Biochemia Medica* 22(3): 276–82.

McLeod, E., K. R. N. Anthony, A. Andersson, R. Beeden, Y. Golbuu, J. Kleypas, K. Kroeker, et al. 2013. "Preparing to Manage Coral Reefs for Ocean Acidification: Lessons from Coral Bleaching." *Frontiers in Ecology and the Environment* 11(1): 20–7. https://doi.org/10.1890/110240.

McLeod, E., K. R. N. Anthony, P. J. Mumby, J. Maynard, R. Beeden, N. A. J. Graham, S. F. Heron, et al. 2019. "The Future of Resilience-Based Management in Coral Reef Ecosystems." *Journal of Environmental Management* 233(3): 291–301. https://doi.org/10.1016/j.jenvman.2018.11.034.

Moilanen, A., K. Wilson, and H. Possingham. 2009. *Spatial Conservation Prioritization: Quantitative Methods and Computational Tools*. Oxford: Oxford University Press.

Molinos, G., B. S. Jorge, D. S. Halpern, C. J. Schoeman, W. K. Brown, P. J. Moore, J. M. Pandolfi, E. S. Poloczanska, A. J. Richardson, and M. T. Burrows. 2016. "Climate Velocity and the Future Global Redistribution of Marine Biodiversity." *Nature Climate Change* 6(1): 83–8. https://doi.org/10.1038/nclimate2769.

Morelli, T. L., C. W. Barrows, A. R. Ramirez, J. M. Cartwright, D. D. Ackerly, T. D. Eaves, J. L. Ebersole, et al. 2020. "Climate-Change Refugia: Biodiversity in the Slow Lane." *Frontiers in Ecology and the Environment* 18(5): 228–34. https://doi.org/10.1002/fee.2189.

Morelli, T. L., C. Daly, S. Z. Dobrowski, D. M. Dulen, J. L. Ebersole, S. T. Jackson, J. D. Lundquist, et al. 2016. "Managing Climate Change Refugia for Climate Adaptation." *PLOS ONE* 11(8): e0159909. https://doi.org/10.1371/journal.pone.0159909.

Mumby, P. J., I. A. Elliott, C. Mark Eakin, W. Skirving, C. B. Paris, H. J. Edwards, S. Enríquez, R. Iglesias-Prieto, L. M. Cherubin, and J. R. Stevens. 2011. "Reserve Design for Uncertain Responses of Coral Reefs to Climate Change." *Ecology Letters* 14(2): 132–40. https://doi.org/10.1111/j.1461-0248.2010.01562.x.

Nadeau, C. P., A. K. Fuller, and D. L. Rosenblatt. 2015. "Climate-Smart Management of Biodiversity." *Ecosphere* 6(6): art91. https://doi.org/10.1890/ES15-00069.1.

Oliver, E. C. J., M. T. Burrows, M. G. Donat, A. S. Gupta, L. V. Alexander, S. E. Perkins-Kirkpatrick, J. A. Benthuysen, et al. 2019. "Projected Marine Heatwaves in the 21st Century and the Potential for Ecological Impact." *Frontiers in Marine Science* 6: 00734. https://doi.org/10.3389/fmars.2019.00734.

O'Neill, B. C., E. Kriegler, K. L. Ebi, E. Kemp-Benedict, K. Riahi, D. S. Rothman, B. J. van Ruijven, et al. 2017. "The Roads Ahead: Narratives for Shared Socioeconomic Pathways Describing World Futures in the 21st Century." *Global Environmental Change* 42(1): 169–80. https://doi.org/10.1016/j.gloenvcha.2015.01.004.

O'Regan, S. M., S. K. Archer, S. K. Friesen, and K. L. Hunter. 2021. "A Global Assessment of Climate Change Adaptation in Marine Protected Area Management Plans." *Frontiers in Marine Science* 8: 711085. https://doi.org/10.3389/fmars.2021.711085.

Pacifici, M., W. B. Foden, P. Visconti, J. E. M. Watson, S. H. M. Butchart, K. M. Kovacs, B. R. Scheffers, et al. 2015. "Assessing Species Vulnerability to Climate Change." *Nature Climate Change* 5: 215–24.

Parmesan, C., and G. Yohe. 2003. "A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems." *Nature* 421(2): 37–42. https://doi.org/10.1038/nature01286.

Patrizzi, N. S., and R. Dobrovolski. 2018. "Integrating Climate Change and Human Impacts into Marine Spatial Planning: A Case Study of Threatened Starfish Species in Brazil." *Ocean and Coastal Management* 161: 177–88.

Pinsky, M. L., L. A. Rogers, J. W. Morley, and T. L. Frölicher. 2020. "Ocean Planning for Species on the Move Provides Substantial Benefits and Requires Few Trade-Offs." *Science Advances* 6(50): eabb8428. https://doi.org/10.1126/sciadv.abb8428.

Pinsky, M. L., A. M. Eikeset, D. J. McCauley, J. L. Payne, and J. M. Sunday. 2019. "Greater Vulnerability to Warming of Marine Versus Terrestrial Ectotherms." *Nature* 569(7754): 108–11. https://doi.org/10.1038/s41586-019-1132-4.

Pinsky, M. L., R. L. Selden, and Z. J. Kitchel. 2020. "Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities." *Annual Review of Marine Science* 12(1): 153–79. https://doi.org/10.1146/annurev-marine-010419-010916.

Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. "Marine Taxa Track Local Climate Velocities." *Science* 341(6151): 1239–42. https://doi.org/10.1126/science.1239352.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, et al. 2013. "Global Imprint of Climate Change on Marine Life." *Nature Climate Change* 3(10): 919–25. https://doi.org/10.1038/nclimate1958.

Porfirio, L. L., R. M. B. Harris, E. C. Lefroy, S. Hugh, S. F. Gould, G. Lee, N. L. Bindoff, and B. Mackey. 2014. "Improving the Use of Species Distribution Models in Conservation Planning and Management under Climate Change." *PLOS ONE* 9(11): e113749. https://doi.org/10.1371/journal.pone.0113749.

Pörtner, H. O., and R. Knust. 2007. "Climate Change Affects Marine Fishes through the Oxygen Limitation of Thermal Tolerance." *Science* 315(5808): 95–7. https://doi.org/10.1126/science.1135471.

Queirós, A. M., E. Talbot, N. J. Beaumont, P. J. Somerfield, S. Kay, C. Pascoe, S. Dedman, et al. 2021. "Bright Spots as Climate-Smart Marine Spatial Planning Tools for Conservation and Blue Growth." *Global Change Biology* 27(21): 5514–31. https://doi.org/10.1111/gcb.15827.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Raäisaänen, J. 2007. "How Reliable Are Climate Models?" *Tellus A: Dynamic Meteorology and Oceanography* 59(1): 2–29. https://doi.org/10.1111/j.1600-0870.2006.00211.x.

Rayfield, B., P. M. A. James, A. Fall, and M.-J. Fortin. 2008. "Comparing Static Versus Dynamic Protected Areas in the Québec Boreal Forest." *Biological Conservation* 141(2): 438–49. https://doi.org/10.1016/j.biocon.2007.10.013.

Reside, A. E., N. Butt, and V. M. Adams. 2018. "Adapting Systematic Conservation Planning for Climate Change." *Biodiversity and Conservation* 27(1): 1–29. https://doi.org/10.1007/s10531-017-1442-5.

Rilov, G., S. Fraschetti, E. Gissi, C. Pipitone, F. Badalamenti, L. Tamburello, E. Menini, et al. 2020. "A Fast-Moving Target: Achieving Marine Conservation Goals under Shifting Climate and Policies." *Ecological Applications* 30(1): e02009. https://doi.org/10.1002/eap.2009.

Robinson, L. M., J. Elith, A. J. Hobday, R. G. Pearson, B. E. Kendall, H. P. Possingham, and A. J. Richardson. 2011. "Pushing the Limits in Marine Species Distribution Modelling: Lessons from the Land Present Challenges and Opportunities." *Global Ecology and Biogeography* 20(6): 789–802. https://doi.org/10.1111/j.1466-8238.2010.00636.x.

Robinson, N. M., W. A. Nelson, M. J. Costello, J. E. Sutherland, and C. J. Lundquist. 2017. "A Systematic Review of Marine-Based Species Distribution Models (SDMs) with Recommendations for Best Practice." *Frontiers in Marine Science* 4: 00421. https://doi.org/10.3389/fmars.2017.00421.

Rojas, I. M., M. K. Jennings, E. Conlisk, A. D. Syphard, J. Mikesell, A. M. Kinoshita, K. West, et al. 2022. "A Landscape-Scale Framework to Identify Refugia from Multiple Stressors." *Conservation Biology* 36(1): e13834. https://doi.org/10.1111/cobi.13834.

Sandel, B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland, and J.-C. Svenning. 2011. "The Influence of Late Quaternary Climate-Change Velocity on Species Endemism." *Science* 334(6056): 660–4. https://doi.org/10.1126/science.1210173.

Santos, F., T. A. Catarina, F. Andrade, H. Calado, L. B. Crowder, C. N. Ehler, S. García-Morales, et al. 2020. "Integrating Climate Change in Ocean Planning." *Nature Sustainability* 3(7): 505–16. https://doi.org/10.1038/s41893-020-0513-x.

Schlegel, R., and A. J. Smit. 2021. "HeatwaveR: Detect Heatwaves and Cold-Spells." https://cran.r-project.org/web/packages/heatwaveR/index.html.

Schulzweida, U. 2022. "CDO (Climate Data Operators) User Guide (2.1.0)." https://doi.org/10.5281/zenodo.7112925.

Stralberg, D., C. Carroll, and S. E. Nielsen. 2020. "Toward a Climate-Informed North American Protected Areas Network: Incorporating Climate-Change Refugia and Corridors in Conservation Planning." *Conservation Letters* 13(4): e12712. https://doi.org/10.1111/conl.12712.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. "Thermal Tolerance and the Global Redistribution of Animals." *Nature Climate Change* 2(9): 686–90. https://doi.org/10.1038/nclimate1539.

Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. "Thermal-Safety Margins and the Necessity of Thermoregulatory Behavior across Latitude and Elevation." *Proceedings of the National Academy of Sciences* 111(15): 5610–5. https://doi.org/10.1073/pnas.1316145111.

Swart, N. C., J. N. S. Cole, V. Kharin, L. Mike, F. Scinocca John, P. Gillett Nathan, J. Anstey, et al. 2019a. "CCCma CanESM5 Model Output Prepared for CMIP6 ScenarioMIP ssp126." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.3683.

Swart, N. C., J. N. S. Cole, V. Kharin, L. Mike, F. Scinocca John, P. Gillett Nathan, J. Anstey, et al. 2019b. "CCCma CanESM5 Model Output Prepared for CMIP6 ScenarioMIP ssp245." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.3685.

Swart, N. C., J. N. S. Cole, V. Kharin, L. Mike, F. Scinocca John, P. Gillett Nathan, J. Anstey, et al. 2019c. "CCCma CanESM5 Model Output Prepared for CMIP6 ScenarioMIP ssp585." Earth System Grid Federation. https://doi.org/10.22033/ESGF/CMIP6.3696.

Taylor, C., N. Cadenhead, D. B. Lindenmayer, and B. A. Wintle. 2017. "Improving the Design of a Conservation Reserve for a Critically Endangered Species." *PLOS ONE* 12(1): e0169629. https://doi.org/10.1371/journal.pone.0169629.

Tegegne, G., A. M. Melesse, and A. W. Worqlul. 2020. "Development of Multi-Model Ensemble Approach for Enhanced Assessment of Impacts of Climate Change on Climate Extremes." *Science of The Total Environment* 704(2): 135357. https://doi.org/10.1016/j.scitotenv.2019.135357.

Thuiller, W., S. Lavorel, M. B. Araújo, M. T. Sykes, and I. Colin Prentice. 2005. "Climate Change Threats to Plant Diversity in Europe." *Proceedings of the National Academy of Sciences* 102(23): 8245–50. https://doi.org/10.1073/pnas.0409902102.

Tittensor, D. P., M. Beger, K. Boerder, D. G. Boyce, R. D. Cavanagh, A. Cosandey-Godin, G. O. Crespo, et al. 2019. "Integrating Climate Adaptation and Biodiversity Conservation in the Global Ocean." *Science Advances* 5(11): eaay9969. https://doi.org/10.1126/sciadv.aay9969.

VanDerWal, J., H. T. Murphy, A. S. Kutt, G. C. Perkins, B. L. Bateman, J. J. Perry, and A. E. Reside. 2013. "Focus on Poleward Shifts in Species' Distribution Underestimates the Fingerprint of Climate Change." *Nature Climate Change* 3(3): 239–43. https://doi.org/10.1038/nclimate1688.

Walsworth, T. E., D. E. Schindler, M. A. Colton, M. S. Webster, S. R. Palumbi, P. J. Mumby, T. E. Essington, and M. L. Pinsky. 2019.

"Management for Network Diversity Speeds Evolutionary Adaptation to Climate Change." *Nature Climate Change* 9: 632–6.

Wang, X., B. Qiu, W. Li, and Q. Zhang. 2019. "Impacts of Drought and Heatwave on the Terrestrial Ecosystem in China as Revealed by Satellite Solar-Induced Chlorophyll Fluorescence." *Science of The Total Environment* 693(11): 133627. https://doi.org/10.1016/j.scitotenv.2019.133627.

Wilson, K. L., D. P. Tittensor, B. Worm, and H. K. Lotze. 2020. "Incorporating Climate Change Adaptation into Marine Protected Area Planning." *Global Change Biology* 26(6): 3251–67. https://doi.org/10.1111/gcb.15094.

Wohlfahrt, G., K. Gerdel, M. Migliavacca, E. Rotenberg, F. Tatarinov, J. Müller, A. Hammerle, T. Julitta, F. M. Spielmann, and D. Yakir. 2018. "Sun-Induced Fluorescence and Gross Primary Productivity during a Heat Wave." *Scientific Reports* 8(1): 14169. https://doi.org/10.1038/s41598-018-32602-z.

Wu, Z., P. Dijkstra, G. W. Koch, J. Peñuelas, and B. A. Hungate. 2011. "Responses of Terrestrial Ecosystems to Temperature and Precipitation Change: A Meta-Analysis of Experimental Manipulation." *Global Change Biology* 17(2): 927–42. https://doi.org/10.1111/j.1365-2486.2010.02302.x.

Zhao, Q., F. Stephenson, C. Lundquist, K. Kaschner, D. Jayathilake, and M. J. Costello. 2020. "Where Marine Protected Areas Would Best Represent 30% of Ocean Biodiversity." *Biological Conservation* 244: 108536. https://doi.org/10.1016/j.biocon.2020.108536.

SUPPORTING INFORMATION

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

How to cite this article: Buenafe, Kristine Camille V., Daniel C. Dunn, Jason D. Everett, Isaac Brito-Morales, David S. Schoeman, Jeffrey O. Hanson, Alvise Dabalà, et al. 2023. "A Metric-Based Framework for Climate-Smart Conservation Planning." *Ecological Applications* 33(4): e2852. https://doi.org/10.1002/eap.2852