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Climate change impacts the vertical structure of marine ecosystem thermal ranges

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Temperature drives global ocean patterns of biodiversity, shaping thermal niches through thresholds of thermal tolerance. Global warming is predicted to change thermal range bounds, yet research has primarily focused on temperature at the sea surface, while knowledge of changes through the depths of the water column is lacking. Here using daily observations from Ocean Sites and model simulations, we track shifts in ocean temperatures, focusing on the emergence of thermal ranges whose future lower bounds exceed current upper bounds. These emerge below 50 m depth as early as ~2040 with high anthropogenic emissions, yet are delayed several decades for reduced emission scenarios. By 2100, concomitant changes in both lower and upper boundaries can expose pelagic ecosystems to thermal environments never experienced before. These results suggest the redistribution of marine species might differ across depth, highlighting a much more complex picture of the impact of climate change on marine ecosystems.

Anthropogenic climate change impacts the world's oceans by warming significantly the upper layers^{1,2}. This heat content increase is projected to alter long-term well defined thermal niches driving species redistribution at a global scale^{3,4}. These changes are already affecting goods and services provided by the oceans⁵, and are projected to be amplified with rising greenhouse gas emissions. A close coupling between marine organisms' physiological thermal tolerances and environmental temperature^{6–9} suggests that distributional shifts can be predicted by tracking changes on the lower and upper bounds of the ecosystems' thermal ranges^{10,11}. Since the vertical structure of temperature in the ocean is rarely considered, current understanding on how and when climate change will drive changes in marine habitats is largely restricted to the ocean surface (e.g., ref. ^{4,12,13}). However, considering only the ocean surface offers a limited view of an ocean under anthropogenic pressure¹⁴, and broad scale studies on how species

distribution will be affected by changes in ecosystems' thermal ranges below the surface are lacking. In this framework, we aim to track the emergence of future changes in marine ecosystem thermal ranges across the water column by following the evolution of the vertical structure of ocean temperature.

Predicting changes in marine ecosystems due to variations in environmental temperature relies on the assumption that species' tolerance ranges reflect the magnitude of local temperature variability^{8,15}. Marine organisms tend indeed to live in thermal environments tolerable within their thermal tolerance limits^{7,16}. In an attempt to characterize organisms' thermal distribution, Stuart-Smith et al.¹⁰ used the 5th and 95th percentiles range of sea surface temperature. We extend this concept through the water column by considering the lower and upper limits of the thermal range to be represented by the environmental temperature minimum (Tmin) and maximum (Tmax). At each depth, Tmin and Tmax correspond to the annual 1st and 99th percentile as computed using the statistical distribution of daily records, respectively. Since both boundaries are warming or cooling differently across depth in response to climate change, marine organisms will confront transformed thermal environments in the future. In this regard, the level of dissimilarity with environmental conditions at which organisms are adapted to, or climate novelty^{17,18}, may provide a measure of the range of temperatures never experienced before. The ability of an organism to adapt to this novel thermal environment ultimately depends on the speed at which significant changes emerge^{13,19,20}. Therefore, our overarching objective is to understand where, when, and how global warming-induced changes over the water column in the environmental thermal range bounds, i.e., Tmin and Tmax, will take place in the future affecting current marine ecosystems.

We take advantage of comprehensive data sets of daily three-dimensional ocean temperatures from both the long-term Ocean Sites (OS) network and state-of-the-art Earth System Models (ESMs). We select six OS stations for which at least seven years of daily temperature observations from the surface to ~1000 m are available (Supplementary Table 1). We map them into polar, temperate, and tropical domains, and determine the surface area informed by each station by computing the level of similarity in daily temperature profiles using a p-value analysis (Fig. 1a, see Methods). A pattern of alternation of cooling and warming periods is seen over the time of available observations (Fig. 1b). In the two southernmost stations, these episodes predominantly consists on warming periods and last a few years. They last longer in the rest of the stations, at which these episodes end towards general warming. The first 400 m of the water

column at station CIS-1 ends towards general cooling, though warming anomalies dominate during most of the observational period. Though measurements' coverage is not complete along depth and time for some stations, we consider they allow us to confidently compute annual Tmin and Tmax, and extract trends to compare with ESM simulations.

Fifteen-member ensemble simulations were performed with CNRM-ESM2-1²¹ (see Methods) encompassing the historical period (1850-2014) followed by three future projections (2015-2100) that explore contrasted emission pathways²² developed for the sixth Coupled Model Inter-comparison Project²³ (CMIP6); a low (SSP1-2.6), a moderate (SSP2-4.5), and a high (SSP5-8.5) emission pathways. To test the robustness of our results, an ensemble of opportunity consisting of two additional ESMs following a single member SSP5-8.5 simulation is used (see Supplementary Table 2). At each OS location, we extract a subsample of the historical + SSP5-8.5 simulation that matches the observational period. Comparison between both data sets (Extended Data Fig. 1) show simulation deviates from observations at the northernmost stations, especially at station FRAM at which observations show a warming period before 2010 that may originate from an anomaly advection of North Atlantic waters northwards²⁴. This anomalous episode can also be behind the positive anomaly at station CIS-1.

Observations and model data are then used to compute profiles of Tmin and Tmax over the observational period. We derive the anomalies of the lower and upper thermal range boundaries by removing the mean temperature profile. These profiles are then employed to determine the magnitude of the thermal range across depth (Fig. 2), informing the vertical structure of current ecosystems' thermal environment. To assess that the vertical structure of the thermal environment is not biased by the short time period of available observations, we additionally compute these profiles for a 30 years subsample of model data at each station. A comparative analysis (see Supplementary Fig. 1) shows that observational period profiles are consistent with longer time span profiles. Thermal ranges decrease toward high and low latitudes⁸ being wider at temperate domains, where they average ~5° C across the first 1000 m depth, and toward deeper layers as the temperature interannual variability also declines. The largest amplitude of the thermal range takes place in the first 200 m of the water column (5.8° C on average) where most of the biota lives²⁵, while it narrows to below (1.4°C on average below 200 m).

Environmental thermal ranges can be represented by a combination of their breadth and their midpoint (Fig. 2, middle panels). Thermal breadth corresponds to the difference between Tmin and Tmax. Midpoint temperature (Tmidpoint) is computed as the arithmetic mean of Tmin and

Tmax. Thermal ranges show a wider breadth above 50 m that narrows rapidly with depth. Modelled thermal ranges are in agreement with observed counterparts, except for an underestimation at FRAM. Excluding FRAM, the agreement is further corroborated by Tmidpoint profiles ($R^2 > 0.8$). At MBARI, simulated thermal ranges as well as the Tmidpoint profile are warmer than derived from the observations, maybe due to the difficulties of ESMs to simulate eastern boundary regions as the California upwelling (see ref. ^{21,26,27}).

Concomitant changes in thermal range boundaries

Concomitant changes in thermal range lower and upper boundaries can be seen as a compound event²⁸ since they can result in several developments of the thermal range (Extended Data Fig. 2). Profiles of the linear trends of change for Tmin and Tmax following SSP5-8.5 (Fig. 2) show that the paces of change of current thermal ranges differ across depth. In fact, significant trends in Tmin and Tmax over recent years (Extended Data Fig. 3 and 4) may lead to various developments of the thermal ranges as depicted by the observations and as simulated by CNRM-ESM2-1. In general, warming trends are stronger than cooling trends thus resulting in warmer thermal ranges. Overlapping this warming, imbalanced warming of Tmax will result in wider thermal ranges while excess warming of Tmin will shrink the thermal range. As global warming trends are likely to increase^{29–31}, it is key to understand the time at which these changes may occur, pending on the level of future greenhouse gases emission and associated global warming levels.

Emergence of changes in current thermal ranges

We estimate when and where substantial changes in the thermal ranges may emerge from warming-induced changes in their bounds, by modifying the canonical approach of the Time of Emergence³² (ToE). We track the evolution of Tmin across the water column under the three contrasted scenarios with respect to the current (1990 to 2020) Tmidpoint and Tmax, considered as key thresholds for marine ecosystems. We also built a 5th-95th confidence interval for each ToE estimate accounting for internal climate variability, by using a distribution of 100 randomly selected 30 yearslong subsamples of the piControl simulation. When Tmin surpasses a first threshold (Tmidpoint), we consider that the shift of the thermal range may represent a *warning* to current ecosystems since Tmidpoint has been observed to align well with the temperature of maximum ecological success (see ref. ^{9,33}). Furthermore, when an ecosystem will be exposed to a Tmin that is warmer than the current Tmax, we consider that

organisms should deal with a completely *new thermal range* (see Fig. 3a). Since marine organisms are strongly sensitive to changes in their upper boundary (e.g., ref. ^{34,35}), we combine this analysis with tracking the timing at which the accumulation of heat in the ocean due to ocean warming causes T_{max} to exceed current natural variability, a threshold that can be up to 30% higher than current T_{max} . Altogether, these metrics provide a comprehensive view on how climate change will transform marine thermal environments.

The earliest times of emergence of T_{max} from current natural variability appear before mid-century (Fig. 3b). Consistently across scenarios, warmer T_{max} will affect the upper (0 – 50 m) and lower (50 – 200 m) epipelagic waters in the next few decades (firstly appearing from 2022 to 2053, depending on the station), though this warning will occur sooner (as early as during the present decade) in the mesopelagic waters (200 – 1000 m) of all stations. T_{max} -based times of emergence delay up to several decades when moderate and low emission scenarios are considered. However, this feature is less consistent at mesopelagic waters, where early emergence times are relatively independent from the scenario considered, possibly arising from warming commitment due to past emissions or to natural features of the ocean interior (see ref. ^{36,37}).

For T_{min} -based times of emergence, we find a rather good agreement across all stations in the first 200 m of the water column (Fig. 3b), with most T_{min} -driven changes in the thermal range appearing within lower epipelagic waters (50 – 200 m). This feature, broadly simulated by the three ESMs (see Supplementary Fig. 2), results from both the shape of current thermal ranges, and the rather homogeneous pattern of higher warming of T_{max} over T_{min} in these layers (Fig. 2). In the four northernmost stations, the emergence of these warnings are delayed in the deepest layers (> 700 m) as the rate of change of T_{min} decreases with depth, even though current thermal ranges are the narrowest of the vertical profile (see Fig. 2). At BATS, at which T_{min} and $T_{midpoint}$ are close across the mesopelagic layer, T_{min} crosses this threshold as early as the present decade. Small rates of change in the thermal ranges preclude this warning to emerge during this century at the mesopelagic layer of HOT-01 (see Extended Data Fig. 5), though they appear by ~2040 below 700 m depth as T_{min} warms more rapidly (see Fig. 2).

The emergence of T_{min} crossing current T_{max} follows a similar profile of that for $T_{midpoint}$, but with a delay of about two to four decades: all domains see emergence before 2080 for depths above 200 m, and before 2070 for depths below 200 m. Appearance occurs sooner in the tropics than in northern stations.

Consistently across all stations, T_{min} -based emergence times are delayed by several years when a moderate emission pathway is considered, and by up to decades when a low emission pathway is accounted for. In general, the emergence of T_{min} crossing current $T_{midpoint}$ occurs earlier for the high emission scenario than the emergence of T_{min} crossing current T_{max} for the moderate emission scenario, except at FRAM. However, taking into account the internal variability confidence intervals considered here, it is difficult to distinguish between the emergence times informed by different scenarios.

End-of-the-century thermal ranges

Under the high emission scenario, end-of-the-century (2080 to 2100) thermal ranges differ from those estimated over the historical period (1990 to 2014) (Fig. 4 and Extended Data Fig. 6). In general, both the lower and upper bounds will be warmer across the water column. Situations in which end-of-the-century T_{min} will be warmer than historical T_{max} occur at all stations within either the lower epipelagic or mesopelagic, or in both layers, in agreement with emergence times shown in Fig. 3. The only exceptions are found in the deepest levels of FRAM, and in most parts of the mesopelagic layer of HOT-01, where T_{max} and T_{min} are predicted to be slightly cooler.

We track novel thermal space at the end of the century using *Climate Novelty* (C_N , see Methods). This metric accounts for the difference between the historical and end-of-the-century period's thermal ranges, and gives insights of the range of temperatures that has never been experienced before for a particular environment. C_N profiles (Fig. 4) show most lower epipelagic and mesopelagic waters' thermal ranges will be >50% novel, consistently with previous studies (see ref. ³⁸ for climate velocity analysis). At HOT-01, C_N of mesopelagic waters indicates relatively low levels of novelty. Nonetheless, this station presents novel thermal ranges at the very deepest waters, in agreement with the emergence of T_{min} crossing T_{max} warnings (Fig. 3). At the upper epipelagic waters, the level of novelty is lower than 50% at all stations except FRAM, at which C_N is closer to this value. However, while the overall level of novelty experienced in the upper pelagic waters will be less than in the mesopelagic, organisms there already have to deal with large interannual thermal variability, and may be near the upper limits of their tolerance. As such, the emergence of warmer T_{max} (Fig. 3) along with the occurrence of short-term extreme events like marine heatwaves^{39,40} (MHW) will impact upper waters. In this respect, an analysis on MHW duration and intensity (Extended Data Fig. 7; see Supplementary Text) shows they will last longer (~2.6 days) and be more intense (>0.3°C) by 2100 at tropical

stations above 200 m considering SSP5-8.5.

Depending on the station and the layer considered, end-of-the-century thermal ranges will be warmer/cooler as a result of comparable warming/cooling of T_{min} and T_{max} (Fig. 4). They can also be warmer and narrower as a result of quicker warming of T_{min} , or warmer and wider by T_{max} warming more rapidly than T_{min} . Wider thermal ranges will result above 200 m at all stations under a high-emission scenario, with the only exception at CIS-1 due to an excess warming of T_{min} below 50 m (Extended Data Fig. 6). Below 200 m, the pace of warming of both bounds are comparable, generating both wide or narrow thermal ranges depending on the station. Both T_{min} and T_{max} changes as long as C_N profiles remain similar when considering a moderate emission scenario (SSP2-4.5) (Extended Data Fig. 8), but showing lower difference values between end-of-the-century and historical thermal range bounds. Considering a high mitigation scenario (SSP1-2.6), all stations show warming anomalies (Extended Data Fig. 9), except at station CIS-1 where both bounds will generally be cooler than the historical mean. Only developments at stations FRAM and K276 are consistent across all emission scenarios.

Implications of the work

Current research, mainly based on monthly surface data, suggest an expansion of marine ectotherms toward their poleward range boundaries as a response to the warming of the oceans^{41–43}. Our work reveals a much more complex picture, demonstrating the added-value of scrutinizing climate change perturbations on ecosystem thermal ranges across the water column with respect to surface data. We find that climate change will generate changes across the water column in the upper and lower thermal range bounds on six OS stations. If anthropogenic emissions continue to rise, we project that the upper bound of thermal ranges will emerge from current natural variability within the present decade, while the lower bound may cross the upper limit of current thermal ranges as early as ~2040 in pelagic waters. These changes can be delayed several decades with immediate emission reduction consistent with a high mitigation scenario, in line with results included in the last IPCC AR6 report⁴⁴, implying marine habitats are committed to change even if reaching net zero emissions by mid-century. In response to ocean warming, thermal ranges will mostly be warmer by 2100. Nonetheless, excess warming of T_{min} with respect to T_{max} will result in narrower thermal ranges, while excess warming of T_{max} with respect to T_{min} will result in wider thermal ranges (Extended Data Fig. 10). In the former case, new conditions will defy local adaptation of inhabitant organisms, possibly leading to the loss of ecosystems' habitability if species cannot adjust their

lifecycle to the contraction of their thermal environment. In the latter, possible spread of species from neighbour habitats may generate additional stresses by changing species interaction^{4,45}, especially at high-latitude stations where the range of tolerable temperature for marine ectotherms are narrow⁸, and the warming of temperate waters may increase the abundance of species at their poleward range boundaries⁴⁶. Furthermore, wider thermal ranges may challenge the capacity limits of species already exposed to large interannual thermal variability by the excess warming of current T_{max}. In addition, C_N profiles indicate that the thermal environment will be novel at several depth levels below upper layers, suggesting marine organisms living at depth might be impacted before upper waters thermal ranges undergo substantial changes; including the emergence of warmer T_{max} that appear sooner in mesopelagic waters.

Assuming organisms are adapted to current environmental conditions, such changes may lead to important rearrangements of marine habitats across latitude and depth⁴⁷ in the decades to come. Though the possibility of looking for refuge at depth may exist for some organisms (e.g.,^{41,48}), vertical rearrangements may be limited by the capacity of the organisms to acclimate to higher hydrostatic pressure⁴⁹, by high light requirements (e.g.,⁵⁰), or by deeper thermal ranges that are not suitable anymore. Our work indicates that the resilience of polar organisms, which are very sensitive to elevated temperatures^{51,52}, will be profoundly affected by substantial changes on current thermal ranges (C_N ~ 100% between 100 to 500 m depth) along with variations in the sea ice coverage (e.g., ref. ⁵³). In tropical regions, where some species live near their physiological limits⁵⁴, our results indicate marine organisms living at depth will be challenged sooner, as rapid warming of T_{min} in the mesopelagic layer will reduce their thermal environment. The reduced capacity of adaptation to warmer upper thermal boundaries of organisms living at these aseasonal regions^{46,55–57} will reinforce their vulnerability in the next decades by the emergence of T_{max} from current natural variability. In temperate areas, ectotherms like the *Atlantic Cod* may be affected by a warmer thermal environment above 200 m, where spawning takes place⁵⁸ and by changes in the vertical structure of their thermal range that may disrupt their daily vertical migration (e.g., ref. ⁵⁹). In addition, extreme events like MHWs are expected to increase (ref. ⁶⁰ and Extended Data Fig. 7; see Supplementary Text) with devastating effects on marine ecosystems (e.g., ref. ^{61–63}).

Anthropogenic climate change is pushing marine organisms to adapt to a less-oxygen acidified warmer ocean^{64,65}. These climatic impact drivers, along with numbers of anthropogenic stressors like fishing⁶⁶, acoustic pollution⁶⁷ or plastics⁶⁸, and extreme and compound events⁶⁹,

exacerbate marine ecosystems degradation. Our results add new insights on the timing of long-term global warming impacts acting throughout the water column, and suggest that future research should consider the three-dimensional extension of the thermal environment of marine organisms in the assessments of climate change impacts.

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Author Contributions Y.S.F. and R.S. conceived the study, developed the data sets, performed the computations and wrote the manuscript.

Competing interests The authors declare no competing interests.

Figure captions

Figure 1: Overview of the Ocean Sites (OS) stations. (a) Geographic location and period of the six available long-term OS stations. Colour code indicates how the OS stations are grouped into polar (blue), temperate (green) and tropical (orange) ocean domains. The shading indicates the ocean domains that are informed by each OS station. (b) Depth-time variations of daily ocean temperature anomalies over the observational period from the surface to 1000 m. Anomalies are computed by removing the daily climatological temperature to daily temperature. Red (blue) colours indicate warmer (cooler) daily temperature variations with respect to the daily climatological temperature. Blank space indicates lack of observational data.

Figure 2: Profiles of thermal ranges. Profiles of the lower (bluish) and upper (reddish) thermal range boundaries anomalies relative to temperature mean over the observational period, for both observations (shading) and model (lines). Model profiles are represented with (bold) and without (thin) applying the observational mask in space and time. Dashed lines demarcate the upper epipelagic, lower epipelagic and mesopelagic layers. Middle panels show profiles of thermal ranges' thermal midpoint (line) and breadth (shading) for observations (orange) and

281 model (grey). At right, profiles of the linear trends from 1990 to 2100 following SSP5-8.5 are
282 given for both thermal range boundaries.

283 **Figure 3: Emergence of climate change signals in thermal ranges.** (a) Schematic explaining
284 how the evolution of Tmin and Tmax may result in the emergence of substantial changes in
285 current thermal ranges. (b) Profiles of the timing of when future Tmin is warmer than current
286 Tmidpoint and Tmax. Confidence interval of the emergence of these thresholds is included by
287 accounting for climate variability. Profiles of the timing of when future Tmax exceeds the natural
288 variability of current Tmax are included. Dashed lines demarcate the upper epipelagic, lower
289 epipelagic and mesopelagic layers. Solid, dashed, dotted lines represent SSP5-8.5, SSP2-4.5,
290 SSP1-2.6.

291 **Figure 4: End-of-the-century thermal ranges.** Profiles illustrate anomalies for Tmin and Tmax
292 with respect to temperature mean over last years of the historical simulation (1990 to 2014) for
293 historical and end-of-the-century (2080 to 2100) periods, considering SSP5-8.5. Reddish
294 (bluish) shading areas indicate ocean layers where end-of-the-century Tmin and Tmax are
295 warmer (cooler) than the historical period. Dashed lines demarcate the water column into upper
296 epipelagic, lower epipelagic and mesopelagic. Middle panels *Climate Novelty* profiles represent
297 the novel environmental temperatures experienced with respect to the end-of-the-century
298 thermal range. Boxes indicate how changes in both boundaries have reshaped thermal ranges
299 under the three scenarios.

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Methods

Ocean Sites observations

The *Ocean Sites* (OS) network constitutes a worldwide effort to monitor ocean parameters through high-quality data extracted from long-term, high-frequency observations at several locations of the World ocean. Six OS stations, listed in Supplementary Table 1, were selected because of the availability of continuous daily measurements of ocean temperature and salinity across the water column for more than seven years, allowing a robust computation of thermal range boundaries (see below). All of the six stations provide data from the surface to about 1000 m depth, that have been resampled daily at each depth, and then interpolated into the vertical grid of CNRM-ESM2-1 (see below).

Observational data is accessible through <http://tds0.ifremer.fr/thredds/catalog/CORIOLIS-OCEANSITES-GDAC-OBS/DATA/>. Last accessed was in October 2020.

Simulations

This work exploits simulations from a state-of-the-art Earth system model, CNRM-ESM2-1²¹, that has been developed by the CNRM-CERFACS climate group for the sixth phase of the Coupled Model Inter-comparison Project (CMIP6²³). The ocean component of CNRM-ESM2-1 is NEMOv3.6⁷⁰, which resolves ocean dynamics on an eORCA1 grid⁷¹ with 75 vertical z-coordinate levels. This grid offers a horizontal resolution of about 1° with a grid refinement up to 0.3° in the tropics.

In this study, we performed five simulations with CNRM-ESM2-1: a 250 year-long pre-industrial control simulation (without anthropogenic forcing) to estimate the model's internal variability; and a historical simulation from 1850 to 2014 followed by three future scenarios from 2015 to 2100, which are used to derive present and future variations in temperature minimum and

maximum. For each simulation, an ensemble of 15 members has been performed in order to account for the influence of the internal variability in the computation of quantiles (see below).

These simulations were produced using the external forcing as recommended by CMIP6 for the pre-industrial state and the historical period. For the future scenarios we used contrasting pathways: a low (SSP1-2.6), moderate (SSP2-4.5), and high (SSP5-8.5) emission pathways as described in ref. ²².

All simulations provide daily outputs from the ocean surface to 4000 m for ocean temperature and salinity as well as oxygen, pH and net primary productivity. Here, we exploit only the first 47 vertical layers for ocean temperature and salinity in order to describe the first 1000 m depth of the water column. Finally, to ensure both observations and model data (historical + SSP5-8.5 simulation) cover exactly the same period, model data was selected to begin and end at the same date as observations.

Two additional ESMs (details on Supplementary Table 3) have been used in the study to assess the robustness of our results. This robustness analysis is based on a simple intercomparison where model properties (thermal range and ToE) are compared between each other using only a single realization for each model.

Model internal variability

As a consequence of the chaotic nature of processes in the Earth systems being simulated (ocean-atmosphere-land-biosphere-cryosphere), one of the main sources of uncertainties in climatic future projections is their internal variability⁷². One way to isolate these uncertainties is to generate an ensemble of model realizations⁷³. Here we make use of an ensemble of 15 members in order to minimise the influence of the internal variability in our computation. Each realization sampling different states of the model climate.

Ocean domains informed by Ocean Site stations

Though OS networks are located throughout the World ocean, our selection of OS stations is disproportionately located in the North Atlantic and North Pacific oceans (see Fig. 1 and Supplementary Table 1). To assess how large is the surface area of ocean domains informed by our six selected OS stations, we compute the level of similarity between daily profiles as

provided by observations and the model hindcast over the current period (1990 to 2020) using the statistical approach presented in ref. ⁷⁴. This approach compares simultaneously the mean and the daily variations of OS daily profiles with a neighbour grid-point model profile using a Chi-squared-based test. The test consists in comparing the cumulative sum of the Welch's t_z^2 ⁷⁵ across depth levels to an empirical Chi-squared distribution with 47 degrees of freedom (i.e., the number of depth levels). We use 10,000 random samples of this Chi-squared distribution to estimate the empirical distribution of the Chi-squared law. The distribution is then used to compute an empirical 'integrated' p-value that represents an objective metric to determine how far the two profiles are consistent between each other within the depth interval.

The empirical 'integrated' p-value allows us to quantify the match between profiles. We establish a threshold of 0.90 to consider a profile over a grid-cell consistent with the OS profile. For further analysis, stations were grouped into three ocean domains: polar, temperate and tropical waters.

Estimation of the environmental temperature range boundaries

The working definition of the ecosystem thermal range, or the environmental temperature range that experiences an ecosystem, employed in this work assumes that organisms track changes in environmental temperature^{7,11,76}, and that the magnitude of the local temperature variability reflect their ranges of temperature tolerance^{8,77}. As a consequence, we infer the vertical structure of ecosystem thermal ranges from their lower and upper limits, which are captured by the minimal and maximal environmental temperature across the water column, respectively.

Thanks to high-frequency data, we provide a robust yearly estimate of these bounds using the annual first (p01, Tmin) and last (p99, Tmax) percentiles of both model and observation temperature time-series at each depth level. Though this approach encompasses most of the range of temperature variability, it can yield more pessimistic projections as tolerance ranges can be wider than environmental thermal ranges^{15,55}, and as ectotherms display some plasticity to adapt to environmental temperatures that challenge their tolerance limits^{78,79}. Nonetheless, there is limited capacity of acclimation when long-term heating occurs⁸⁰, especially for tropical species⁸¹ and during reproductive stages⁸².

In order to minimize the influence of the internal climate variability when comparing model and data results, we estimate model annual percentiles by grouping the 15 ensemble members.

537 Thus, model percentile for thermal range is derived from a $365 \times 15 = 5475$ sample of daily outputs
538 at each depth.

539 The breadth of thermal ranges are estimated as the difference between T_{max} and T_{min} at each
540 depth level. Midpoint temperatures ($T_{midpoint}$) correspond to the arithmetic mean of T_{min} and
541 T_{max} , thus assuming normality in the distribution of T_{min} and T_{max} .

542 **Timing of crossing thermal range thresholds**

543 To track future changes in the thermal range boundaries, we employed a method inspired from
544 the well-established Time of Emergence (ToE) approach (see Supplementary Fig. 3 and 4). As
545 for the ToE approach, our method requires estimates of a climate change signal (S). We
546 estimate it using daily model outputs from 1990 to 2100 for an ensemble of 15 realizations from
547 CNRM-ESM2-1 that has been run following historical and low emission SSP1-2.6, moderate
548 emission SSP2-4.5, and high emission SSP5-8.5 pathways. For each pathway, we define S as
549 the smooth spline (four degrees of freedom) of the variation of T_{min} during the full simulation. In
550 general, the ToE approach is defined as the first year at which S surpasses twice the standard
551 deviation of the internal climate variability. Here, in contrast, we make use of different thresholds
552 that have a meaning for ecosystem functioning, which represent key characteristics of the
553 thermal range; $T_{midpoint}$ and T_{max} . These two thresholds are defined as the average of a
554 smooth spline (four degrees of freedom) of the variation of $T_{midpoint}$ and T_{max} during the past
555 30 years from today (1990 to 2020); a period considered to be representative of the current
556 period. We consider the emergence of substantial changes in the current range of temperatures
557 that defines the environmental conditions of a given habitat as the time at which the lower
558 boundary of this range (T_{min}) crosses in the future the current thresholds ($T_{midpoint}$ and
559 T_{max}).

560 We built a 5th-95th confidence interval for each ToE estimate accounting for the influence of the
561 internal climate variability. For that, we generate 100 30-yearslong samples selected randomly
562 from the piControl simulation. Then, we compute the annual T_{max} and $T_{midpoint}$ for these
563 samples, and remove the annual mean to them. Finally, we compute the 5th and 95th
564 percentiles of the statistical distribution of the 100 random T_{max} and $T_{midpoint}$ anomaly
565 samples.

566 We additionally compute the emergence of changes in the upper limit of the current thermal

range, i.e., T_{max} . Particularly, we estimate the time at which T_{max} crosses in the future a threshold defined as the current (1990 to 2020) upper boundary plus twice the standard deviation of the statistical distribution of the 100 random T_{max} anomaly samples from the piControl simulation (see above).

In order to illustrate that emergence times are not an artifact of the current shape of thermal ranges, we computed the trends of both boundaries during the 1990 to 2100 period following the historical + SSP5-8.5 simulation (third subpanels at Fig. 2). We have chosen this period as it represents the range of years for which we compute ToE. The shape of these profiles allow us to confirm that ToEs are the results of both the vertical structure of the thermal ranges, and the evolution of the lower and upper boundaries through time.

For illustration purposes, we illustrate how our approach works for four depth levels of HOT-01 station (Extended Data Fig. 5).

End-of-the-century environmental temperature ranges

End-of-the-century environmental temperature ranges provide a snapshot of the concomitant changes in thermal range boundaries resulting from climate change. We compute the end-of-the-century thermal ranges from daily data over the 2080 to 2100 period. Fig. 4 displays the end-of-the-century thermal range anomalies of both T_{min} and T_{max} with respect to the mean over 1990 to 2014, corresponding to the last years of the historical simulation. To compare with the historical profiles, we also include their anomalies. At each depth level, we assess the magnitude of the changes between the end-of-the-century and the historical profiles.

As changes in thermal range boundaries can evolve in both directions, and with a different pace, they may result in a re-arrangement of the vertical shape of the thermal range. To track if end-of-the-century thermal ranges are also wider or narrower, we compute the difference between T_{max} and T_{min} anomalies at each depth level (Extended Data Fig. 6, 8, and 9). If the difference is positive, thermal ranges will be wider, i.e., T_{max} warms more rapidly. If the difference is negative, thermal ranges will be narrower, i.e., T_{min} warms more rapidly. If differences are < 0.05 °C (i.e., level of uncertainty informed from the analysis of the internal variability of thermal range profiles in Extended Data Fig. 4), we consider no changes in the shape of thermal ranges will take place, i.e., only shifting toward warming or cooling is

projected. The three emission pathways are displayed in Extended Data Fig. 6, 8, and 9, respectively.

In Fig. 4 we have assigned a colour code for each of these developments. A depiction of these developments is provided in Extended Data Fig. 2.

We track novel thermal space resulting from changes in end-of-the-century thermal ranges that differ from historical period counterparts using *Climate Novelty* (C_N). As in previous approaches (e.g., ref. ^{17,18}), our metric approach accounts for the level of dissimilarity to baseline conditions. This metric accounts for the difference between the last years of the historical period, i.e., 1990 to 2014, and end-of-the-century thermal ranges at each depth. It takes the space gained/lost by the warming/cooling of T_{max} and T_{min} , and by the thermal space loss when future T_{min} surpasses current T_{max} . This metric is expressed as follows:

$$C_N = (\Delta_{max} + \Delta_{min} - \Delta_{mod})/ThBr ;$$

Where Δ_{max} corresponds to the difference between T_{max} at the end-of-the-century and at the historical period. Δ_{min} corresponds to the difference between T_{min} at the end-of-the-century and at the historical period. Δ_{mod} corresponds to the intersection of thermal space between future and historical thermal ranges, i.e., when end-of-the-century $T_{min} >$ historical T_{max} . $ThBr$ is the difference between T_{max} and T_{min} at the end of the century period. Thus, C_N informs of the range of environmental temperatures that has never been experienced before with respect to the thermal range at the end of the century. We express it in the manuscript as a percentage by multiplying by 100.

Data availability Interpolated data presented in the paper can be accessed via Zenodo at <https://doi.org/10.5281/zenodo.6940283>.

Code availability All code used in the current study is available from the corresponding author upon reasonable request.

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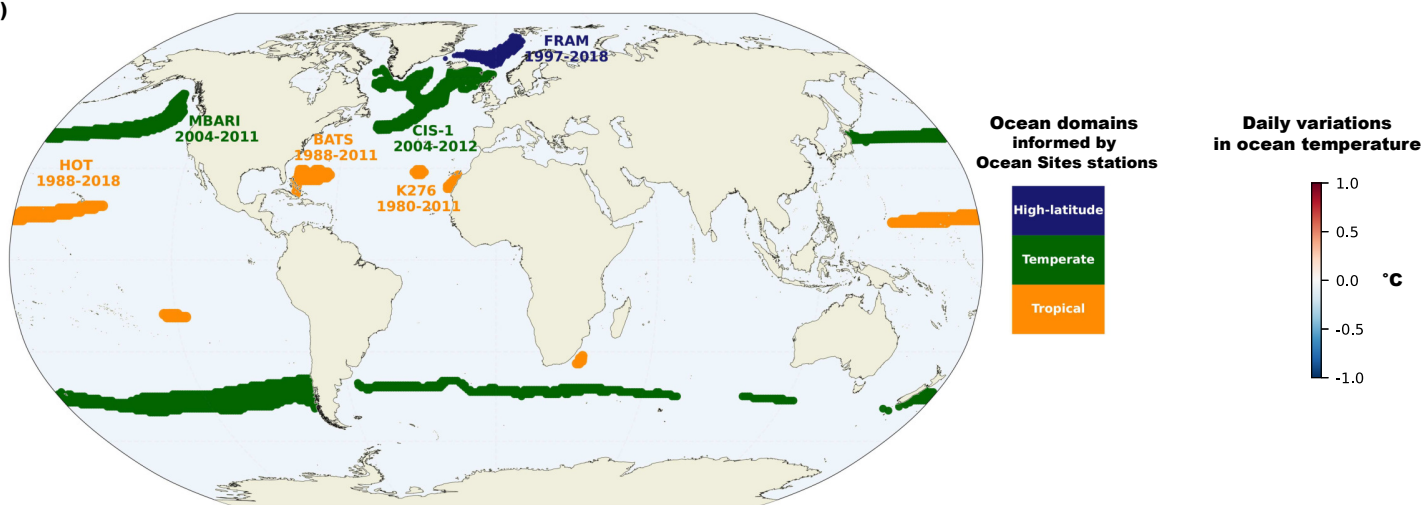
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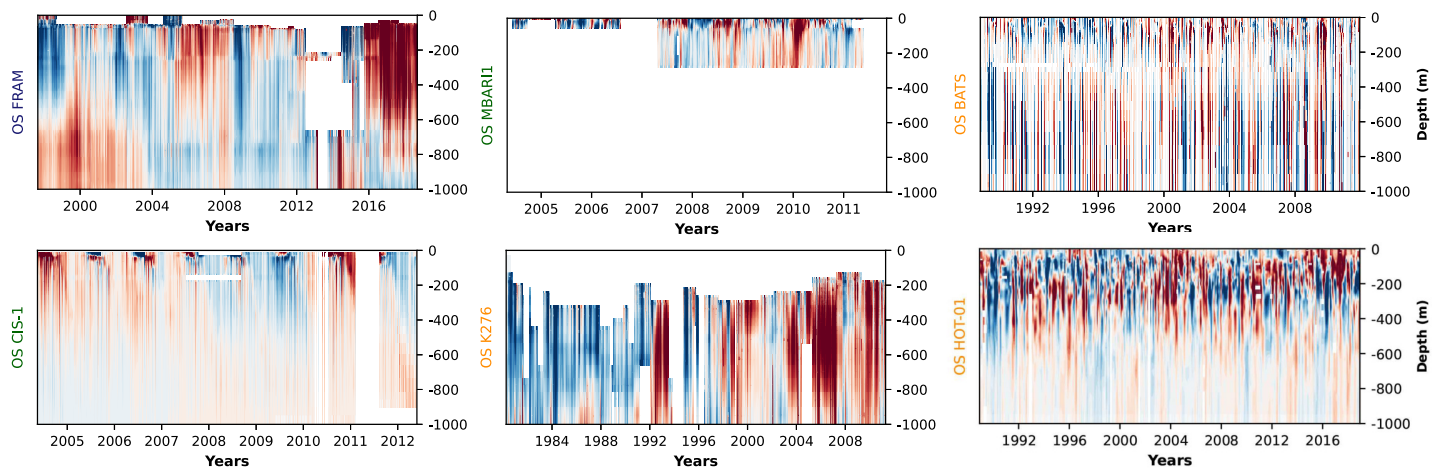
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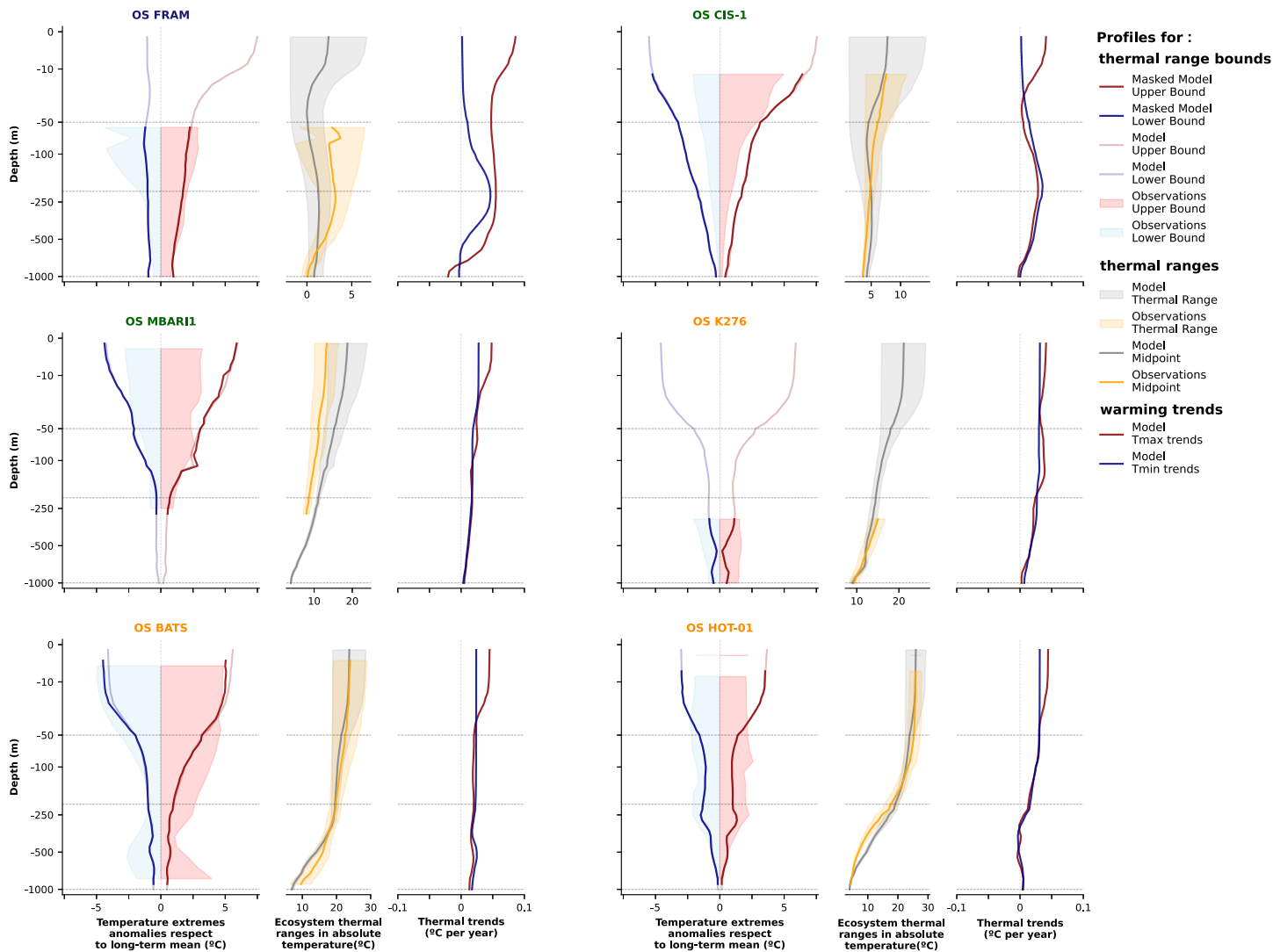
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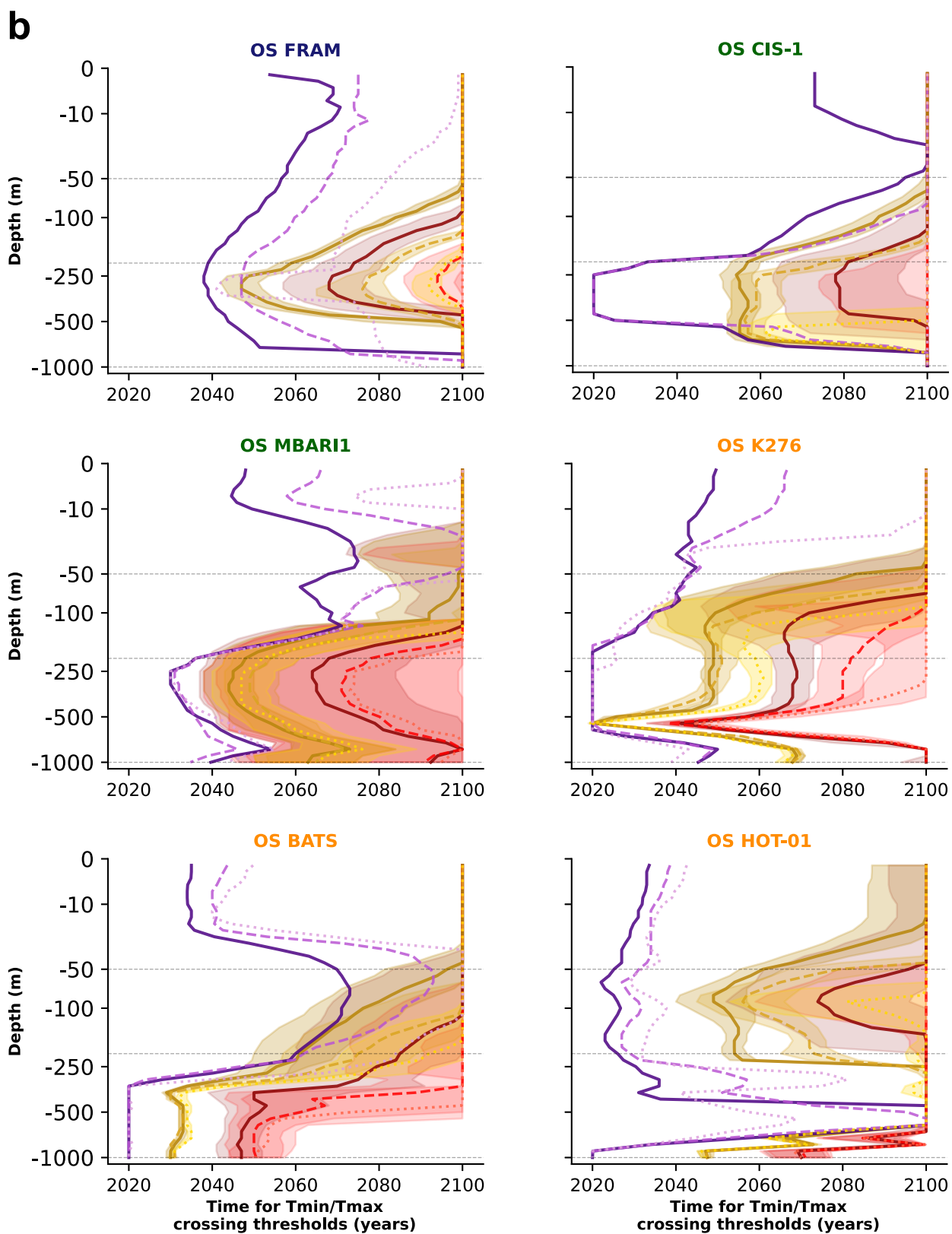
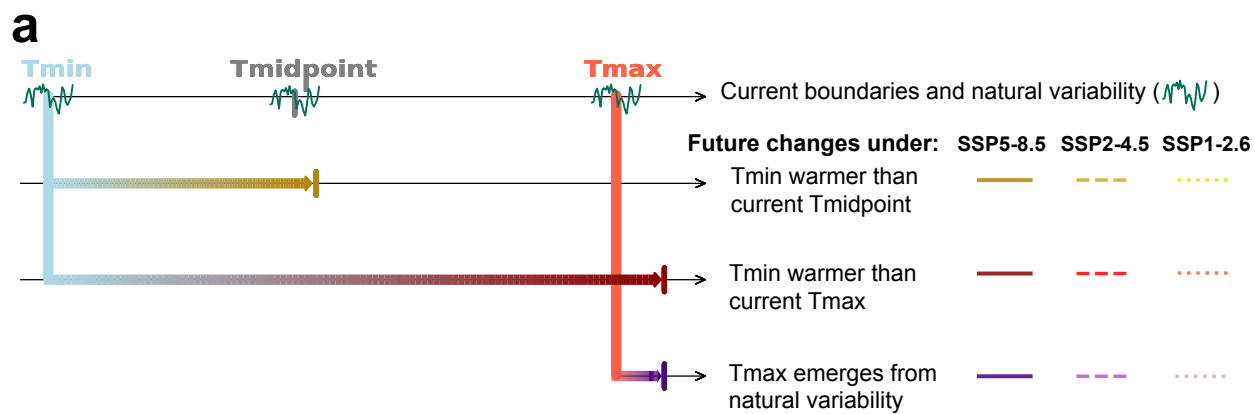
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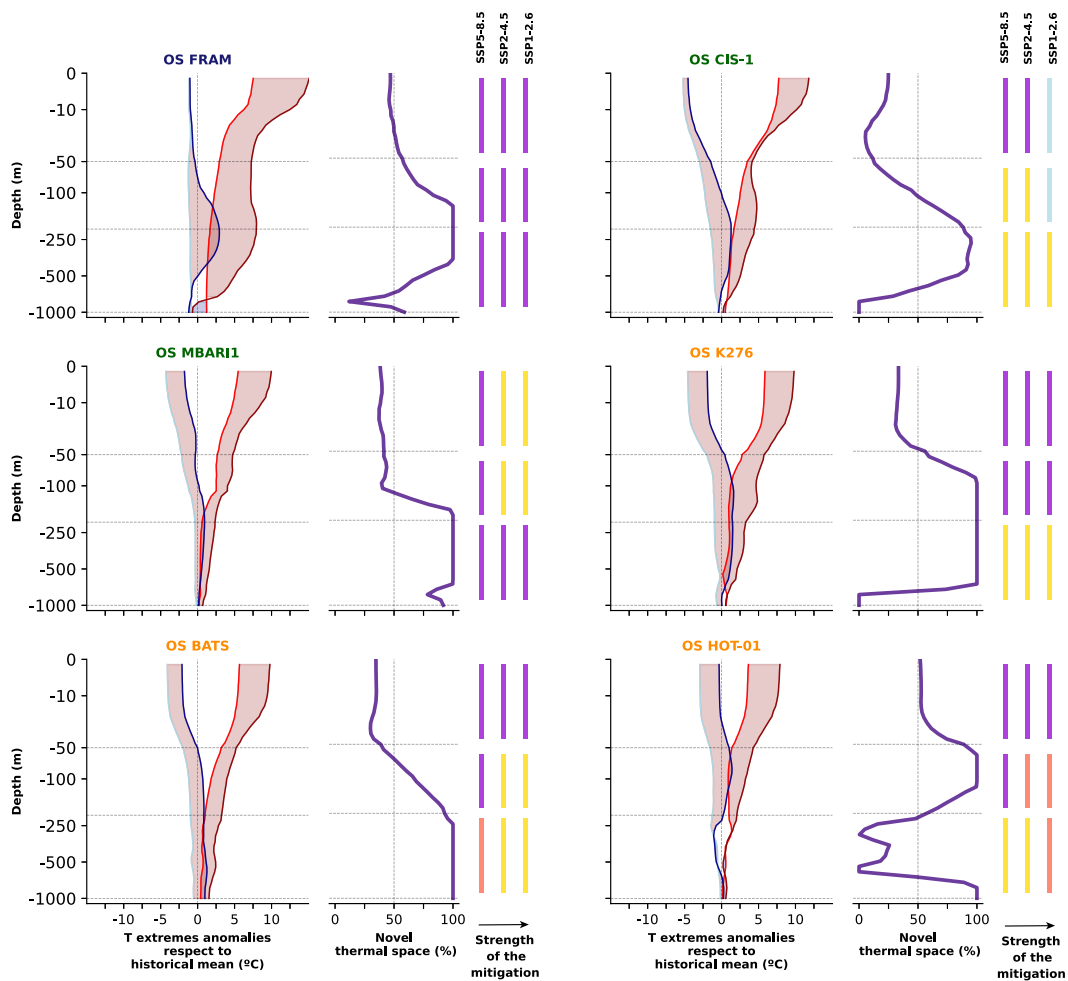


b)









Anomaly respect to historical (1990-2014) mean

- Historical Lower Bound
- Historical Upper Bound
- End-of-the-century (2080-2100) Lower Bound
- End-of-the-century (2080-2100) Upper Bound

Changes in thermal range

- End-of-the-century T extremes warmer than historical T extremes
- End-of-the-century T extremes cooler than historical T extremes
- Climate Novelty

Future changes in thermal range resulting from concomitant changes in both boudaries

- Cooler
- Warmer
- Warmer & Shrunk
- Warmer & Expanded