

The projected timing of abrupt ecological disruption from climate change

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As anthropogenic climate change continues the risks to biodiversity will increase over time, with future projections indicating that a potentially catastrophic loss of global biodiversity is on the horizon^{1–3}. However, our understanding of when and how abruptly this climate-driven disruption of biodiversity will occur is limited because biodiversity forecasts typically focus on individual snapshots of the future. Here we use annual projections (from 1850 to 2100) of temperature and precipitation across the ranges of more than 30,000 marine and terrestrial species to estimate the timing of their exposure to potentially dangerous climate conditions. We project that future disruption of ecological assemblages as a result of climate change will be abrupt, because within any given ecological assemblage the exposure of most species to climate conditions beyond their realized niche limits occurs almost simultaneously. Under a high-emissions scenario (representative concentration pathway (RCP) 8.5), such abrupt exposure events begin before 2030 in tropical oceans and spread to tropical forests and higher latitudes by 2050. If global warming is kept below 2 °C, less than 2% of assemblages globally are projected to undergo abrupt exposure events of more than 20% of their constituent species; however, the risk accelerates with the magnitude of warming, threatening 15% of assemblages at 4 °C, with similar levels of risk in protected and unprotected areas. These results highlight the impending risk of sudden and severe biodiversity losses from climate change and provide a framework for predicting both when and where these events may occur.

Climate change is projected to become a leading driver of biodiversity loss¹, but it is not clear when during this century ecological assemblages might suffer such losses, and whether the process will be gradual or abrupt. Existing biodiversity forecasts typically lack the temporal perspective needed to answer these questions because they indicate the number and locations of species threatened by climate change for just a snapshot of the future, often around the end of the century^{1–3}. These snapshots do not account for the temporally dynamic nature of ecological disruption expected as a result of climate change, often focus at the level of species rather than ecological assemblages, and can seem remote to decision-makers who are concerned with managing more immediate risks⁴. Indeed, many of the most sudden and severe ecological effects of climate change can occur when conditions become unsuitable for several co-occurring species simultaneously, causing catastrophic die-offs and abrupt ‘regime shifts’ in ecological assemblages^{5,6}.

Forecasting the temporal dynamics of climate-driven disruption of ecological assemblages thus requires quantifying the differences among species in the time at which their climate niche limits may be locally exceeded. Developing advance warnings of the risk of gradual or abrupt ecological disruption is an urgent priority^{7–9}. A temporal perspective is also important for adaptation. Reducing emissions and delaying the onset of exposure to dangerous climate conditions—even

by a few decades—could buy valuable time for ecological assemblages to adapt^{10,11}, potentially reducing the magnitude of ecological disruption. However, despite the clear importance of a temporal perspective in understanding and managing the threats of climate change to biodiversity, we lack a general understanding of the time at which species in ecological assemblages will be exposed to climate conditions beyond their niche limits.

The biodiversity climate horizon

To describe the projected timing of the exposure of species to climate conditions beyond their niche, we developed an approach based on species historical climate limits and future climate projections. The range of climate conditions, over both space and time, under which a species has been recorded in the wild demarcates the boundaries of its realized niche¹². The projected time in the future at which these bounds are exceeded owing to climate change at a site can therefore be thought of as representing a climate horizon, beyond which evidence for the ability of the species to persist in the wild is lacking. Over this horizon lies, at best, a sizeable increase in uncertainty about species survival and, at worst, local extinction¹³. For a given species assemblage, the cumulative percentage of species over time that have been locally exposed to climate conditions beyond their realized niche limits forms

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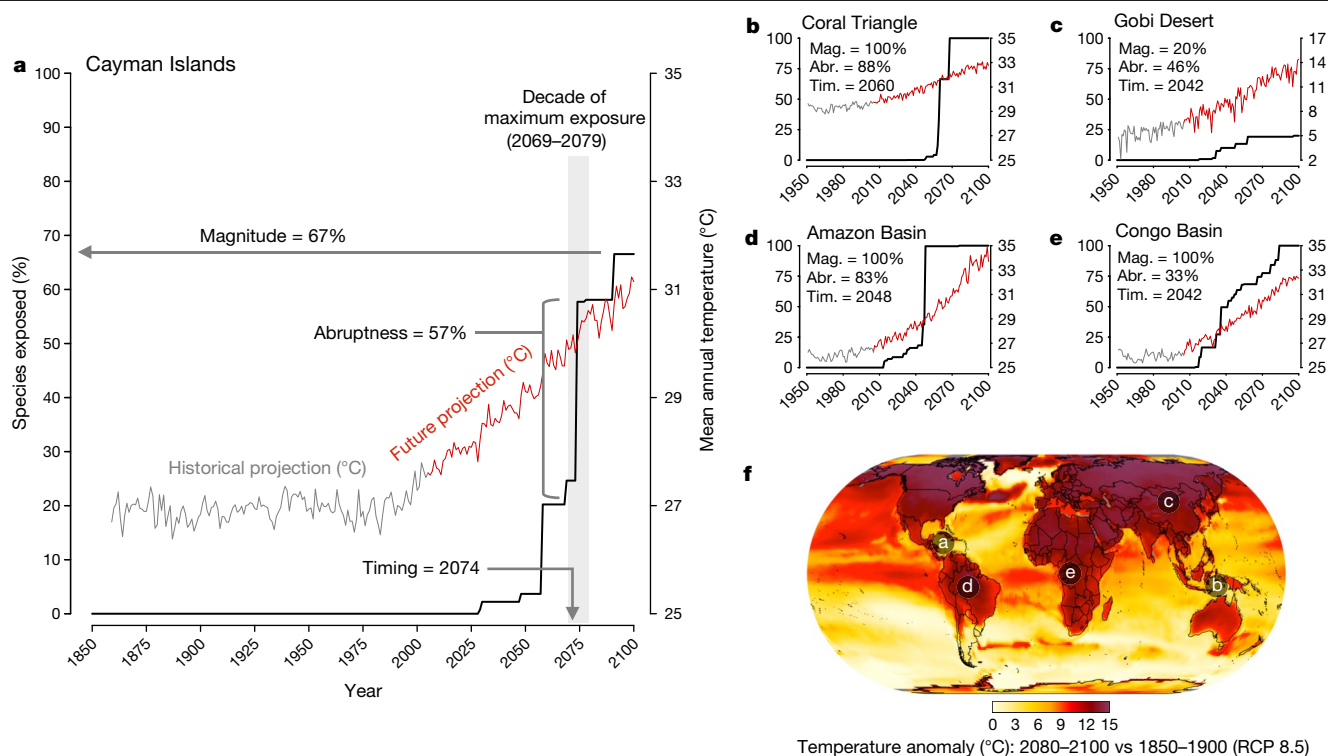


Fig. 1 | Biodiversity climate horizon profiles. a–e, Horizon profiles (solid black lines) indicate the cumulative percentage of species in an assemblage exposed to future temperatures (red lines) beyond their realized thermal niche over time. Iconic ecosystems provide examples of different profile shapes: **a**, Cayman Islands; **b**, Coral Triangle; **c**, Gobi Desert; **d**, Amazon Basin; **e**, Congo Basin. **f**, Map of temperature anomalies that shows the locations of the

ecosystems in **a–e**. Horizon profiles and temperature trends are shown for a single run of the Hadley Centre Global Environmental Model (HadGEM2) under a high greenhouse-gas-emissions scenario (RCP 8.5). The profiles differ in terms of timing, magnitude and abruptness. The grey lines show historical temperature projections at a site.

what we term the ‘horizon profile’ (Fig. 1). The shape of this horizon profile provides information on the potential for climate-driven disruption of species assemblages over time—especially the risk of early or abrupt disruption—that is not evident when focusing on individual climate snapshots.

We constructed horizon profiles for species assemblages globally, delimiting assemblages as the species occurring in 100-km grid cells based on expert-verified geographic range maps. A total of 30,652 species of birds, mammals, reptiles, amphibians, marine fish, benthic marine invertebrates, krill, cephalopods, and habitat-forming corals and seagrasses were included¹⁴ (Supplementary Table 1). We used climate projections throughout the twenty-first century from 22 climate models and 3 RCPs: strong mitigation (RCP 2.6), moderate mitigation (RCP 4.5) and a high-emissions scenario (RCP 8.5)¹⁵ (Supplementary Table 2). Given the importance of temperature as a driver of species metabolism and geographic ranges^{16–18}, we focus on mean annual temperature as the main proxy for climate. However, because species may be sensitive to other climate variables that may respond differently to greenhouse gas emissions, we also generated horizon profiles using maximum monthly temperatures and terrestrial annual precipitation (see Methods).

For each species at a site (that is, in a 100-km grid cell), we defined the local species exposure time as the year after which projected local temperatures consistently exceed—for at least 5 years—the maximum temperature experienced by the species across its geographic range during historical climate projections (1850–2005) (Supplementary Fig. 1). For species that breed annually or near-annually, 5 years represents a considerable number of breeding seasons at temperatures beyond which these species have never been recorded (a 20-year window yielded very similar results; Supplementary Figs. 2, 3). This

approach for quantifying exposure bears similarities to the concept of ‘time of emergence’ in climate science, defined as the time at which the signal of anthropogenic climate change at a location emerges from the envelope of historical climate variability^{19,20}. The key distinction is that we define exposure relative to the realized climatic niche limits of each species, rather than the historical conditions realized at a single site.

The shape of horizon profiles, and the potential ecological disruption that they imply, can vary substantially across assemblages (Fig. 1). To summarize each horizon profile, we focus on three key features: timing, the median year for an assemblage in which species exposure to unprecedented climate occurs; magnitude, the percentage of species locally exposed; and abruptness, the synchronicity in the timing of exposure among species in an assemblage, which is measured as the percentage of all species exposure times that occur in the decade of maximum exposure (Fig. 1a).

Timing, magnitude and abruptness of horizon profiles

Under RCP 8.5, 81% of terrestrial and 37% of marine assemblages are projected to have at least one species exposed to unprecedented mean annual temperatures (that is, beyond historical niche limits) before 2100. Despite the lower magnitude of warming, the magnitude of exposure is greatest in the tropics, where narrow historical climate variability²⁰ and shallow thermal gradients²¹ mean that many species occur close to their upper realized thermal limits throughout their geographic range. In total, 68% of terrestrial and 39% of tropical marine assemblages are projected to have more than 20% of their constituent species exposed to unprecedented temperatures by 2100, compared with 7% of terrestrial and 1% of marine assemblages outside the tropics (Fig. 2a). The Amazon, Indian subcontinent and Indo-Pacific regions

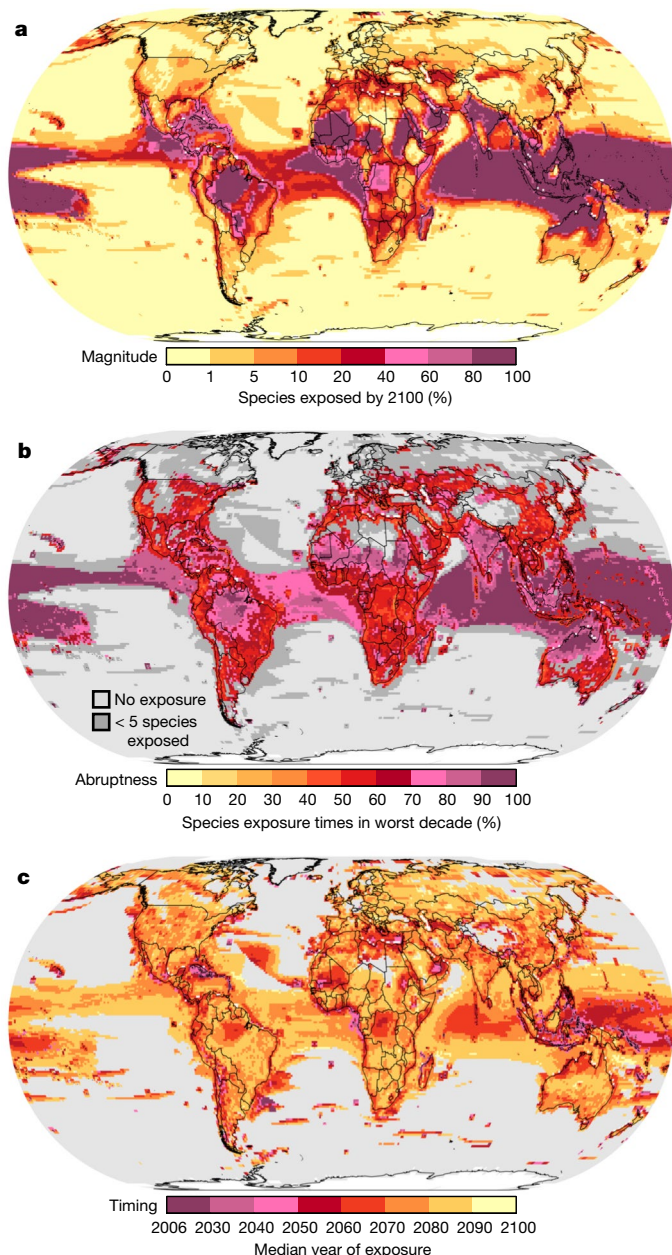


Fig. 2 | Global variation in the magnitude, abruptness and timing of horizon profiles. **a**, The magnitude of exposure is shown by the percentage of species in 100-km resolution grid cells (that is, assemblages) that are exposed to unprecedented temperature (that is, beyond the realized niche of each species) by 2100. **b**, Abruptness quantified as the percentage of species exposure times that occur within the decade of maximum exposure for each assemblage. **c**, Timing quantified as the median year of local species exposure conditional on being exposed by 2100, the end of the simulation. Maps show the median value across 22 climate models under RCP 8.5 (see Extended Data Fig. 1 for RCP 2.6 and RCP 4.5).

are most at risk, with more than 90% of species in any assemblage exposed to unprecedented temperatures by 2100 (Fig. 2a). Horizon profiles for mean annual temperature and maximum monthly temperature show strong correspondence (Extended Data Figs. 1, 2). By contrast, few species undergo prolonged exposure to unprecedented high or low annual precipitation before 2100 (Extended Data Figs. 1, 2), which is in agreement with the greater variability seen in projections of precipitation²². Thus, throughout we focus on exposure to changes in temperature.

The most notable feature of horizon profiles for local assemblages is their abruptness (Figs. 1, 2b). Under RCP 8.5, on average 71% (median) of local species exposure times for any given assemblage are projected to occur within a single decade (Fig. 3a, b), with the abruptness of exposure higher among marine assemblages (median abruptness 89%, Fig. 3a) than on land (median abruptness 61%, Fig. 3b). This pattern of highly synchronized species exposure within assemblages is robust to the choice of climate model (for RCP 8.5, median abruptness ranges from 60% to 79%; Extended Data Figs. 3, 4), emissions scenario (median abruptness 83% for RCP 2.6 and 72% for RCP 4.5), metric of abruptness (Extended Data Fig. 4), and when calculating exposure for maximum monthly temperature (median abruptness 68%) rather than mean annual temperature (Extended Data Figs. 1, 2). The same pattern of abruptness is also evident for horizon profiles constructed separately for each taxonomic group within local assemblages (Extended Data Fig. 4). Marine organisms—especially seagrasses, corals, cephalopods, marine reptiles and marine mammals—exhibit the most abrupt profiles, but it is the consistency of abruptness across groups, rather than the differences, that is most notable. Similarly, although the abruptness of exposure varies spatially—being greatest in the Amazon, Indian subcontinent, Sahel and Northern Australia, as well as tropical oceans—abrupt horizon profiles are the general rule both within the tropics (median abruptness 79%) and at higher latitudes (median abruptness 59%) (Fig. 2b).

This pervasive pattern of abrupt exposure arises primarily because co-occurring species often share similar realized thermal limits, rather than abruptness being dependent on higher rates of warming (Extended Data Fig. 5). This clustering of species-realized thermal limits can, in part, be explained by shared geographic barriers or, for tropical species, by the upper limits of temperatures available on Earth^{13,23}. However, even where these factors cannot explain the clustering of thermal limits because a high percentage of species have warmer temperatures available within 1,000 km of their range edge, assemblage exposure is still projected to occur abruptly (Extended Data Fig. 5); this suggests that other processes, such as ecological interactions²⁴ or evolutionary conservatism in fundamental niches^{25,26}, lead to similarity in realized niche limits^{16,27} and thus abruptness in the timing of exposure.

The synchronicity of species exposure within assemblages means that the timing of assemblage-level exposure events is well described by the median of species exposure times at a site (Extended Data Fig. 6). Under RCP 8.5, the global mean year of assemblage-level exposure is 2074 (± 11 years (s.d.)), but there is considerable variation in the timing of exposure across assemblages (Fig. 2c). In some locations—such as the Caribbean and the Coral Triangle—exposure is predicted to be underway already, with these hotspots of exposure expanding in spatial extent over time (Fig. 2c, Extended Data Fig. 7). By 2050, exposure spreads beyond ocean ecosystems to iconic terrestrial ecosystems, such as the Amazon, Indonesian and Congolese rainforests (Fig. 2c, Extended Data Fig. 7). Notably, the timing of these assemblage-level exposure events is not well predicted by the timing of local climate emergence (Spearman's ρ 0.29; Extended Data Fig. 5); in addition, the timing of abrupt exposure events lags behind local climate emergence by 42 years (± 12 years; mean \pm s.d.), indicating the potential time-lag between climate change and ensuing biotic responses.

The abrupt exposure of species within ecological assemblages has not been detected in earlier projections of climate-driven range loss and global species extinctions, which have implied a more gradual increase in risk to biodiversity^{2,3}. We find that the appearance of a gradual increase in risk can result from summarizing across local assemblages that differ in their projected timing of abrupt exposure (Fig. 3c, d, Extended Data Fig. 8). Although these global summaries mask the abrupt nature of exposure within local assemblages, they can highlight the importance of increased mitigation efforts in reducing and delaying the onset of unprecedented climate conditions. Compared to RCP 8.5, achieving RCP 2.6 delays exposure for the most at-risk species

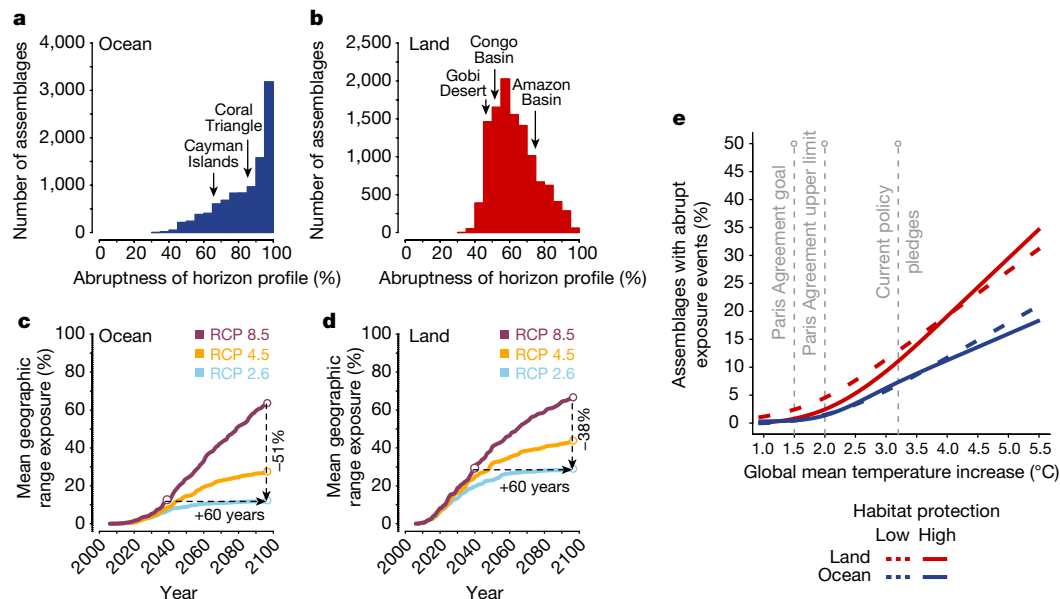


Fig. 3 | Abruptness of horizon profiles locally compared with globally, and the accelerating risk with global warming. **a, b**, The distribution in the projected abruptness of species exposure to unprecedented temperatures within marine (**a**) and terrestrial (**b**) assemblages. Selected assemblages from Fig. 1 are highlighted. Abruptness is quantified as the percentage of species exposure times that occur within the decade of maximum exposure, with results showing the median across climate models under RCP 8.5. **c, d**, Global horizon profiles for oceans (**c**) and land (**d**) show more gradual accumulation of species exposure to unprecedented temperatures. Dashed lines show how lowering emissions from RCP 8.5 to RCP 2.6 both reduces the median

by approximately 6 decades in the oceans (mean 58 years, range 46–65 years; Fig. 3c) and on land (mean 58 years, range 49–67 years; Fig. 3d), buying valuable time for species and ecosystems—and human societies that depend on them—to adapt to a warming climate.

The risk of abrupt exposure events

The abruptness of horizon profiles is positively correlated with the magnitude of exposure (Spearman's ρ 0.58; Extended Data Fig. 6), which indicates that exposure events involving larger fractions of species are projected to occur more abruptly. This near-simultaneous exposure among multiple species could have sudden and devastating effects on local biodiversity and ecosystem services. Catastrophic, multi-species coral die-offs caused by a record-breaking marine heatwave in 2016 are one recent example⁶. Although the 'safe limits' of species loss—at which ecosystem function can be maintained—remain uncertain, meta-analyses suggest a 20% decline in species diversity as one possible threshold^{28,29}. We therefore defined assemblages at risk of abrupt ecological disruption as those in which at least 20% of species are projected to undergo exposure to unprecedented temperatures within the same decade. Restricting global warming to less than 2 °C above pre-industrial levels limits such abrupt assemblage exposure events to less than 2% of assemblages (Fig. 3e). However, beyond 2 °C warming, the area projected to undergo abrupt assemblage exposure expands rapidly, encompassing 15% of assemblages globally at 4 °C warming. Furthermore, the increase in abrupt exposure does not differ markedly for assemblages that are afforded high habitat protection (at least 20% protected area coverage of a grid cell), indicating that current protected areas are equally at risk from abrupt exposure (Fig. 3e).

The risk of abrupt exposure events differs across assemblages globally, with variability across individual climate projections increasing the total area at risk compared with median projections. For instance,

magnitude of exposure across climate models and substantially delays the timing of exposure, buying about 60 years for species and conservation plans to adapt to a warming climate (see Extended Data Fig. 8 for individual climate models). **e**, The percentage of species assemblages projected to experience high-magnitude and abrupt assemblage exposure (more than 20% of species exposed in a single decade) as a function of global mean temperature increase relative to pre-industrial levels (1850–1900). Curves are fitted from model runs ($n = 66$) across RCP 2.6, RCP 4.5 and RCP 8.5. 'Current policy pledges' refers to a scenario in which countries implement their current nationally determined contributions to 2030 and make no further emissions reductions.

even under RCP 2.6 (1.75 °C mean warming), 9% of assemblages are at some risk of abrupt exposure (Fig. 4a), and this increases to 35% of assemblages under RCP 8.5 (4.4 °C mean warming; Fig. 4b). The risk of abrupt assemblage exposure events is positively correlated with species richness (RCP 8.5, Spearman's ρ 0.29 (land) and 0.56 (ocean)), highlighting the increased risk of sudden ecological disruption in the world's most biodiverse ecosystems. Moreover, the risk of disruption of ecological function may be underestimated in this analysis because even if particular functional groups (for example, habitat-forming corals) suffer high levels of exposure, this may not be evident at the scale of entire assemblages if other groups are relatively less affected. When abrupt assemblage exposure events are instead defined at the level of major taxonomic groups, the area at risk expands further, encompassing 49% of species assemblages under RCP 8.5 (Fig. 4c, Extended Data Fig. 9). Our approach estimates how much of the original biodiversity of an assemblage is exposed to potentially dangerous climate conditions over time²⁸. We do not consider the potential for immigration of species from elsewhere to offset local biodiversity losses; however, abrupt assemblage-wide exposure is likely to cause substantial ecological disruption regardless of the rate at which new species arrive. Furthermore, in tropical lowlands and oceans—where projected exposure is greatest and species adapted to warmer environments are lacking—net declines in local biodiversity are expected²¹.

Crossing the biodiversity climate horizon

Although the horizon profile describes the accumulating number of co-occurring species that are exposed to conditions beyond their realized niche limits, this need not equate with a profile of local extinction. Species may have wider fundamental niche limits than realized niche limits^{13,30}, may avoid exposure in microclimatic refugia (however, see Extended Data Fig. 10) or through behavioural thermoregulation^{17,31},

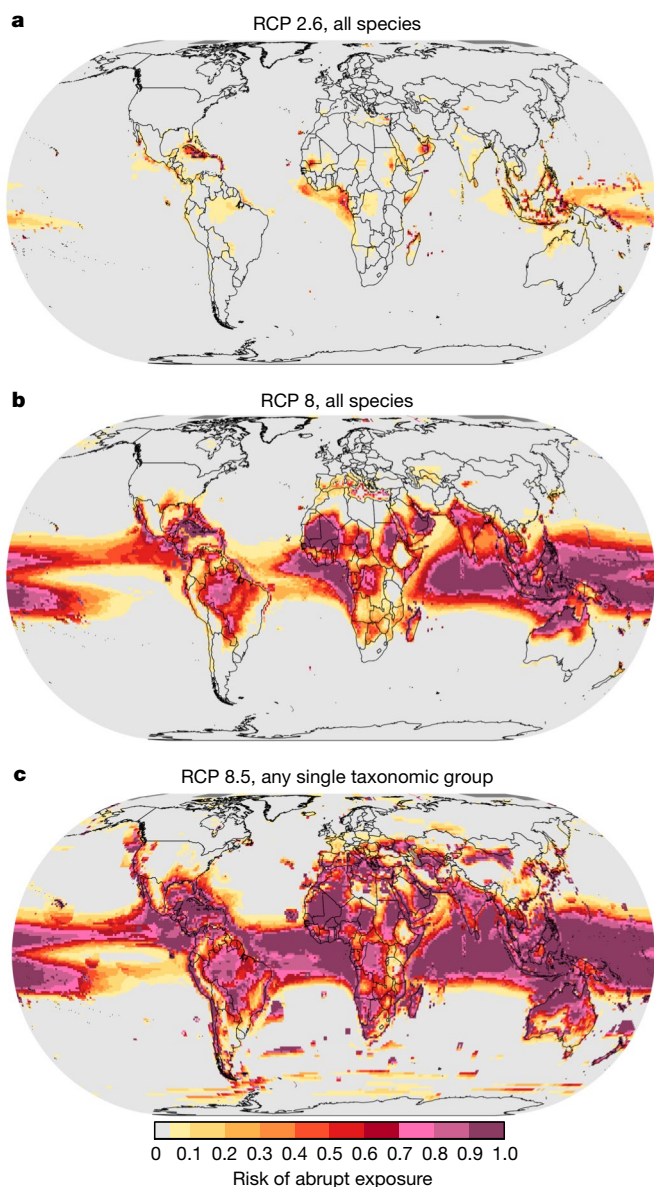


Fig. 4 | The risk of high-magnitude, abrupt assemblage exposure events. **a–c**, Risk is shown for all species under RCP 2.6 (**a**), all species under RCP 8.5 (**b**) and single taxonomic groups under RCP 8.5 (**c**). Risk is calculated as the proportion of 22 climate models in which an abrupt exposure event is projected to occur before 2100. Assemblages that avoid abrupt exposure events across all 22 models are in grey. In **a, b**, abrupt exposure events are defined as when more than 20% of all species in an assemblage are exposed in a single decade. In **c**, abrupt exposure events are defined when any single group of organisms (for example, amphibians or corals) within an assemblage experiences the exposure of more than 20% of its constituent species in a single decade, highlighting the widespread risk of abrupt ecological disruption.

or may evolve to tolerate new conditions¹⁰. In these cases, the timing of abrupt assemblage exposure events could be considered an ‘ignorance horizon’—the time beyond which local extinctions are not inevitable but evidence for the ability of species to persist in the wild is largely absent¹³. Thus, at the very least, our results show that within 30 years, continued high emissions will drive a sudden shift across many ecological assemblages to climate conditions under which we have almost no knowledge of the ability of their constituent species to survive. We caution that the timing and magnitude of this exposure may occur earlier and be larger than we anticipate, because our analysis does not consider changes in extreme events⁹, effects of warming on local

habitat (for example, melting sea ice), covariation between climate variables³², or that populations may be locally adapted³³.

Furthermore, to the extent that species-realized historical thermal limits do reflect fundamental limits to persistence, then the occurrence of abrupt exposure events marks the crossing of an ‘ecological horizon’ beyond which catastrophic and coordinated species losses are expected. These abrupt events—projected to spread from ocean (for example, coral reef) to land (for example, rainforest) ecosystems by 2050 under high emissions—risk sudden disruption to ecosystems and their capacity to maintain current levels of biodiversity and functioning. Evidence from laboratory-based and field-based studies indicates this is a credible risk, particularly for tropical terrestrial ectotherms and for marine organisms for which projected abruptness is most pronounced and for which realized geographic range boundaries most closely match thermal tolerance limits^{16,18,30,34}. Indeed, warming over recent decades has already been associated with marked population declines and local extinctions^{6,35,36}—even among endotherms, which are widely assumed to be less sensitive to warming but may be particularly vulnerable to climate-driven disruption of trophic interactions^{37,38}. For those ecosystems for which exposure is projected within the next few decades, the capacity for species to adapt would appear limited. A priority for future research is to refine estimates of the timing and consequences of exposure, including for regions in which factors other than temperature may more strongly constrain species ranges, and for which the emergence of novel climates has closest analogues deep in Earth’s history³⁹.

Considering the temporal dynamics of the exposure of biodiversity to climate change provides an early warning of the potential for abrupt ecological disruption. Averting—or at least delaying—the crossing of this ecological horizon is possible for most assemblages, and requires massive and rapid reductions in greenhouse gas emissions. Our results also highlight the urgency of targeted management responses, including establishing monitoring sites in exposed regions, establishing new protected areas in refugia, and investigating the potential of assisted migration and adaptation.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41586-020-2189-9>.

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Methods

Biodiversity data

We used expert-verified range maps for 30,652 species from the International Union for Conservation of Nature (IUCN)¹⁴ and BirdLife International⁴⁰, including birds, mammals, reptiles, amphibians, marine fish, benthic marine invertebrates, and habitat-forming corals and seagrasses (Supplementary Table 1). To further increase coverage of open-ocean assemblages, our sample includes additional data on krill⁴¹ and cephalopods⁴², reflecting the availability of expert range maps for oceanic species⁴³. We used only breeding ranges for terrestrial species. We excluded marine species that are restricted to depths greater than 200 m (the lower limit of the epipelagic zone), as these species are less likely to respond to changes in sea surface temperature. Range maps were converted to 100-km-resolution equal-area grid cells—the finest resolution justifiable for these data globally without incurring false presences^{44,45}. Expert range maps provide comprehensive information on the global geographic distributions of species⁴⁶, but our results should be interpreted in the context of known data limitations. For some groups, species coverage is incomplete and is biased towards commercial species (for example, cephalopods), whereas others have been comprehensively assessed for only a subset of clades (for example, fish) and the species included in our study thus represent a non-random subset of global biodiversity (Supplementary Table 1). For instance, insects and plants may on average be more at risk of geographic range loss due to climate change than are terrestrial vertebrates², but we did not assess exposure for these groups because range maps (expert or otherwise) are not available globally. As such, both very short-lived and long-lived terrestrial taxa may be underrepresented in our sample. Furthermore, although many IUCN range maps consider occurrence data from historical records, others may underestimate climate niche limits where longer-term historical records are unavailable and recent geographic range contractions have occurred in part due to reasons other than climate change⁴⁷.

Data on marine and terrestrial protected areas were downloaded from the World Database on Protected Areas (<http://protectedplanet.net/>; accessed 21 March 2018). The maps, originally in polygon format, were resampled to a 1-km resolution before further analysis. We considered 100-km-resolution grid cells highly protected if at least 20% of the grid cell was inside protected areas.

Climate model data

We used temperature and precipitation projections from 22 General Circulation and Earth System Models developed for the Coupled Model Intercomparison Project 5 (CMIP5) (Supplementary Table 2). For each model, we downloaded a single projection for mean monthly precipitation (mm), near-surface temperature (K) and sea surface temperature (K) for the historical run (1850–2005), as well as RCP 2.6, RCP 4.5 and RCP 8.5 scenarios for the years 2006–2100 or 2006–2300, when available. Model output was downloaded from <https://esgf-node.llnl.gov/projects/esgf-llnl/> (accessed 5 June 2017). In our main analysis, we focus on the dynamics of exposure according to mean annual temperature (MAT), calculated by averaging monthly values. However, we also repeated our analysis using the temperature of the hottest month, hereafter denoted maximum monthly temperature (MMT), and, for terrestrial assemblages, total annual precipitation (mm), calculated by summing precipitation values across months (see Supplementary Information). Note that the identity of the hottest month can vary both across sites and between years within a site. Given that CMIP5 models use different spatial grids, and to match the resolution of species geographic range data, climate model data were regridded to a 100-km resolution grid using an area-weighted mean interpolation. Climate data interpolation was performed in CDO⁴⁸ and R⁴⁹.

We calculated species exposure times for each assemblage using individual climate simulations, as opposed to ensembles or multi-model

averages, because individual simulation runs include variance in climatic time series due to internal climate variability such as the timing of El Niño/Southern Oscillation events^{22,50}. This internal variability is a key component of the uncertainty in the timing of exposure, and is smoothed out if using multi-model averages as input into the analysis. By calculating species exposure events using individual model simulation runs and then summarizing across models, we capture the uncertainty in the timing of exposure due to both internal climate variability and climate model uncertainty (that is, uncertainty about climate physics across models), in line with ‘time of emergence’ analyses from climate science¹⁹. Throughout, we report multi-model medians in each of our summary metrics.

Defining species-realized niche limits

Species experience variability in climatic conditions across both space and time, but this temporal variability is ignored when using time-averaged climate conditions (for example, Worldclim data⁵¹) to estimate species-realized niches. To address this, we estimated species-realized niche limits using the climate projections from the historical run of each climate model (1850–2005), which includes the influence on climate of observed changes in radiative forcing due to natural factors such as volcanic eruptions, as well as anthropogenic emissions and land-use changes⁵². Thus, in the case of MAT, we calculated the maximum MAT experienced across the species geographic range over both space and time ($T_{\max_{\text{MAT}}}$, see Supplementary Information). To prevent estimates of $T_{\max_{\text{MAT}}}$ being inflated by either extreme outliers in the temperature time series or from the overestimation of species ranges⁴⁴, we excluded outlier temperature values within each grid cell, defined as those more than three standard deviations from the mean. After we had selected the maximum temperature for each cell, we excluded outlier temperature values across each species range, defined as those more than three standard deviations above the mean range value. The $T_{\max_{\text{MAT}}}$ value for each species was then set as the maximum of the remaining values (Supplementary Fig. 1). We used an identical procedure to calculate T_{\max} using MMT ($T_{\max_{\text{MMT}}}$). For precipitation, species may be exposed to either drying or wetting conditions and so we calculated both the minimum (P_{\min}) and maximum (P_{\max}) precipitation values experienced by each species across its geographic range (see Supplementary Information).

Estimating species exposure times

Within each terrestrial ($n = 18,560$) and marine ($n = 37,333$) assemblage (that is, 100-km grid cell containing any terrestrial or marine species, respectively), we defined the time of local species exposure to unprecedented temperature (that is, the climate horizon) to be the year after which the MAT (or MMT) of the cell is projected to exceed the $T_{\max_{\text{MAT}}}$ (or $T_{\max_{\text{MMT}}}$) value of the species for at least five consecutive years. We note that using a higher number of consecutive years ($n = 20$ years) had little effect on the magnitude, timing or abruptness of exposure (Supplementary Figs. 2, 3).

For precipitation, we calculated the time of local species exposure as the year after which the precipitation of the cell is projected to be either greater or less than the P_{\max} and P_{\min} values, respectively, of the species for at least five consecutive years. Annual precipitation values are bounded at zero, and this could potentially lead to exposure being underestimated for locations projected to have historically received zero precipitation. To address this, we additionally defined exposure to occur when annual precipitation decreased to less than 15 mm for at least five consecutive years. Owing to the generally weaker trends and high variability in historical and future projected precipitation, we found that few species were exposed to unprecedented precipitation regardless of how exposure was defined (Extended Data Fig. 1). To show the importance of increasing temperatures as the primary driver of exposure, we compared patterns of exposure from MAT alone to those from MAT and precipitation combined, recording the earliest

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local exposure time of either MAT or precipitation for a species in an assemblage when it was exposed to both variables (Extended Data Fig. 2, see Supplementary Information).

We note that by using range-wide estimates of species niche limits, we may underestimate both the magnitude and the immediacy of exposure if populations are locally adapted³³. Unfortunately, information on the scale and strength of local adaptation is not generally available across species. Equally, our analysis does not attempt to model adaptive evolution, which may enable species to shift or expand their climatic niche limits over time. Nevertheless, our estimates of the timing of local exposure to unprecedented conditions may be relevant for understanding the potential for evolution to rescue populations from changing climates^{10,11}.

Horizon profiles

When species exposure times had been calculated for an assemblage, we constructed a horizon profile indicating the cumulative percentage of species that are locally exposed to conditions beyond their realized niche limits. We used the following metrics to summarize the temporal dynamics of biodiversity exposure. First, we calculated the magnitude of exposure as the percentage of species in the assemblage exposed over the course of the twenty-first century. Second, the abruptness of exposure for an assemblage was calculated as the percentage of all exposure times that occur in the decade of maximum exposure. We identified the decade of maximum exposure using a moving window of ten years. We also calculated an alternative metric of abruptness based on the Shannon entropy index⁵³, which quantifies the evenness in the distribution of exposure times across all decades of the horizon profile (Extended Data Fig. 4). In contrast to our original abruptness metric, lower values of the Shannon entropy index indicate a more abrupt profile. We therefore rescaled the Shannon entropy index by the maximum possible entropy value per assemblage, subtracted these values from 1 and then multiplied by 100 to give an index that ranged between 0 and 100, where a value of 100 indicates that all exposure times occur in a single decade and a value of 0 corresponds to an equitable distribution of exposure times across decades. Abruptness was calculated only for assemblages in which five or more species were exposed, to avoid idiosyncrasies due to small sample sizes. Third, the timing of exposure for each assemblage was calculated as the median of the times of local species exposure events. Species not exposed before the end of the twenty-first century were excluded from this calculation. We repeated our analysis using alternative metrics of timing, including the mean year of exposure and the mid-point of the decade of maximum exposure, obtaining very similar results (Extended Data Fig. 6). For each of these exposure metrics we report the median value across the 22 climate models for a given climate scenario, and quantify uncertainty as the standard deviation (Extended Data Fig. 3). The greatest uncertainty in projected effects involves the magnitude of exposure along the boundaries of the tropics. This arises because of variation among models in the magnitude of warming, which alters the spatial extent of regions exposed to unprecedented temperatures. By contrast, variation among models in the timing and abruptness of exposure is relatively small and does not exhibit any clear spatial structure.

We compared the median timing of species exposure within assemblages to the timing of local climate emergence, defined as the year after which future local temperatures are projected to exceed the maximum historical (1850–2005) conditions at a site^{19,20}. Timing of emergence was calculated using an identical procedure to that used to calculate the timing of exposure, excluding outlying values from the time series when quantifying the maximum historical temperature at a site and considering emergence only when temperatures exceed the historical maximum for at least five consecutive years. The time of local climate emergence at a site is therefore identical to the time of local exposure for a species occupying a single grid cell. In the absence of perfect adaptation to local climates, a time-lag is therefore expected between

local climate emergence and the median timing of exposure, because species typically persist under a broader range of conditions than is present in any single site.

Spatial scale

We modelled species-realized niche limits using climate projections at 100-km grain size, matching the resolution of expert geographic range maps^{44,45}. However, individual grid cells at this resolution may contain (potentially substantial) spatial climatic heterogeneity, thus potentially underestimating variability in species niche limits and potentially overestimating the abruptness of assemblage exposure dynamics. To investigate this possibility, we tested whether the abruptness of horizon profiles across terrestrial assemblages is related to the range in the MAT within each grid cell, using spatially interpolated temperature data for the period 1970–2000 available at 1-km resolution⁵¹. We found that abruptness is negatively correlated with the spatial heterogeneity in temperature within a cell (Spearman's $\rho = -0.29$), so that assemblages with higher spatial heterogeneity in temperatures (for example, tropical mountains), exhibit more gradual exposure profiles than those with low heterogeneity in temperatures (for example, tropical lowlands) (Extended Data Fig. 10). This result has two important implications. First, it suggests that—despite the relatively coarse grain size—our analysis still identifies those assemblages in which variation in realized niche limits among species is expected to be greatest (that is, grid cells containing substantial spatial climatic heterogeneity) as having the most gradual exposure profiles. Second, it suggests that, although incorporating finer-scale climate data may further reduce the lowest abruptness values estimated across assemblages (that is, making relatively gradual horizon profiles more gradual), it is unlikely to alter the key conclusion that assemblage exposure to climate warming occurs abruptly, because the most abrupt horizon profiles occur in assemblages in which there is little fine-scale climatic heterogeneity (Extended Data Fig. 10). These results support the robustness of our overall conclusions regarding the dynamics of exposure, but it is clear that increasing the spatial resolution at which species niche limits and assemblages are defined would enable a more precise quantification of the timing of species exposure to changing climates, and should be a priority for future research.

Horizon profiles can be calculated either for a single assemblage or for a set of assemblages combined, such as a biome or the entire globe. In addition to examining the dynamics within assemblages, we generated global horizon profiles, describing the total cumulative exposure of all populations (that is, species by site combinations) across marine and terrestrial assemblages (Fig. 3c, d). To avoid exposure dynamics being driven by the small number of species with the largest geographic ranges, we weighted each species by the inverse of its geographic range size. This range-size-weighted exposure profile ensures that each species contributes equally to exposure dynamics, and is mathematically equivalent to calculating the mean percentage geographic range exposure across species. Unweighted global horizon profiles show qualitatively similar patterns (Extended Data Fig. 8).

Risk of abrupt exposure events

We identified those assemblages projected to undergo abrupt and high-magnitude exposure events, defined as at least 20% of resident species exposed within a single decade before the end of the twenty-first century. Across the set of 66 climate model runs from the 3 RCP scenarios, we fit a generalized additive model to estimate the percentage of assemblages projected to undergo abrupt exposure events as a function of mean global warming at the end of the century (2080–2100) relative to pre-industrial conditions (1850–1900). We fit separate models for sites with either low or high (that is, greater than 20% in protected areas) levels of habitat protection. We forced the regression through the origin, thus assuming no abrupt exposure events would occur if temperatures remained stable at pre-industrial conditions. Because

the identity of assemblages projected to undergo abrupt exposure events may vary across model runs, the actual area at risk of abrupt exposure may be substantially greater than expected under any single climate simulation. For each assemblage, we therefore calculated the probability of an abrupt exposure event across the 22 climate models within each emissions scenario. We did this for assemblages consisting of all species, as well as for each group of organisms separately.

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

All datasets used here are publicly available. Expert verified range maps are available from <https://www.iucnredlist.org/resources/spatial-data-download> and <http://datazone.birdlife.org/species/requestdis>. Climate change projections for RCP 8.5, RCP 4.5 and RCP 2.6 for CMIP5 are available from <https://esgf-node.llnl.gov/search/cmip5/>. Maps of projected risk to biodiversity from climate change are available to view at <https://climatehorizons.users.earthengine.app/view/biodiversity-risk>.

Code availability

Computer code used in the analysis is available on request from the corresponding author. Code and data that were used to make Figs. 2–4 is available at Figshare (<https://doi.org/10.6084/m9.figshare.11814633>).

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Author contributions A.L.P., C.H.T. and C.M. conceived the study, processed the species and climate data, performed the analysis and wrote the manuscript. All authors read and approved the final manuscript.

Competing interests The authors declare no competing interests.

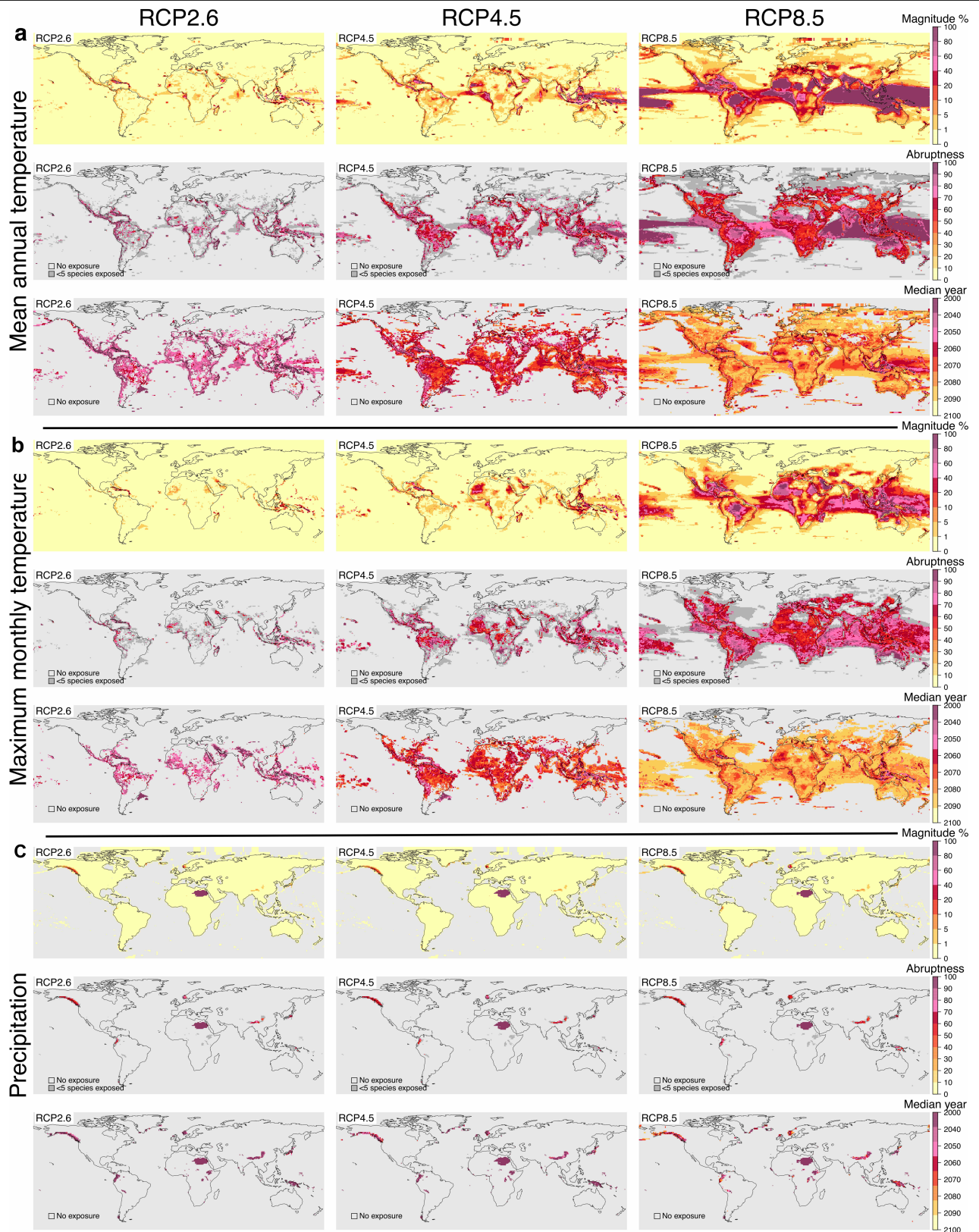
Additional information

Supplementary information is available for this paper at <https://doi.org/10.1038/s41586-020-2189-9>.

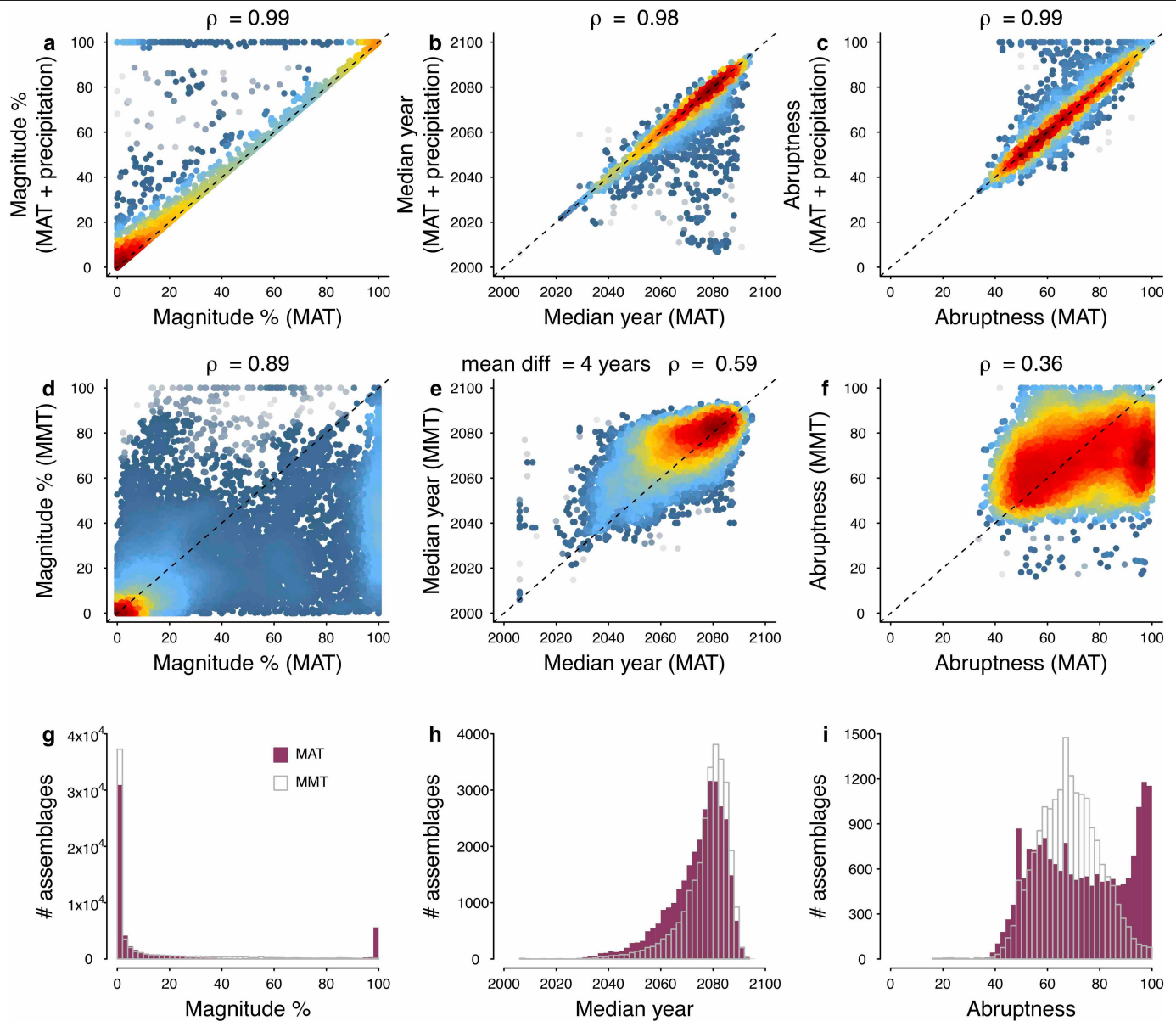
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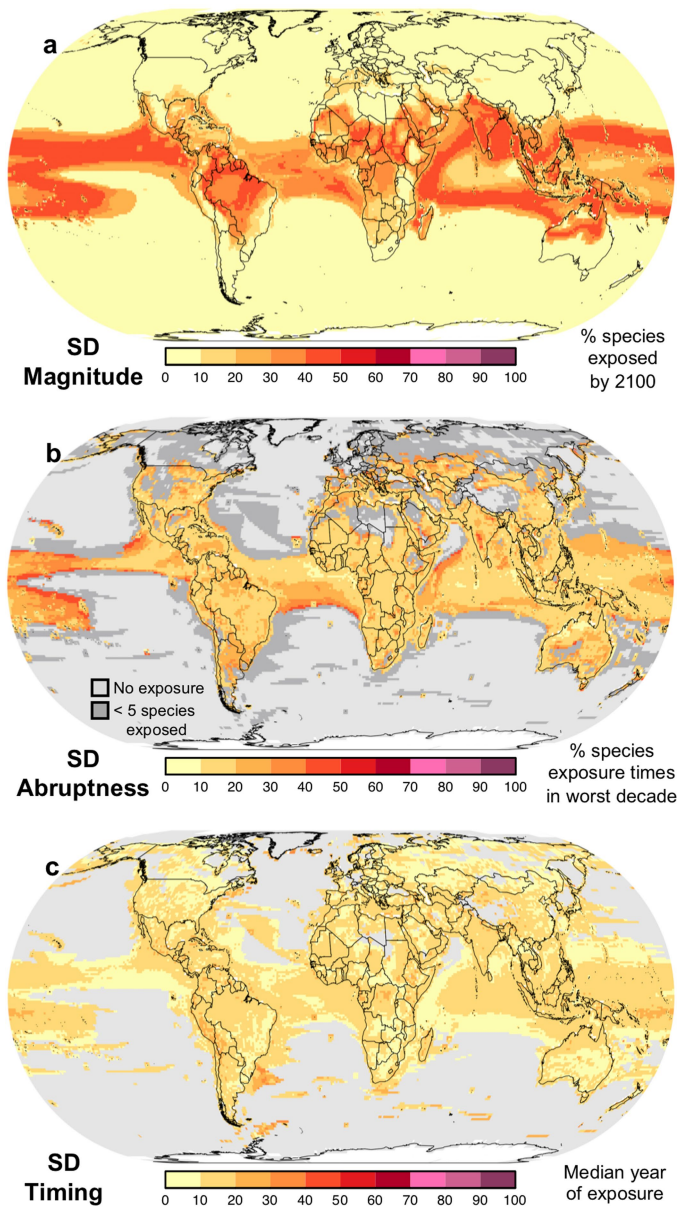


Extended Data Fig. 1 | Spatial distribution of the magnitude, abruptness and timing of assemblage exposure for alternative climate variables. a–c, Shown is the median value across 22 CMIP5 climate models for MAT (a), MMT (b) and precipitation (c) under RCP 2.6, RCP 4.5 and RCP 8.5.

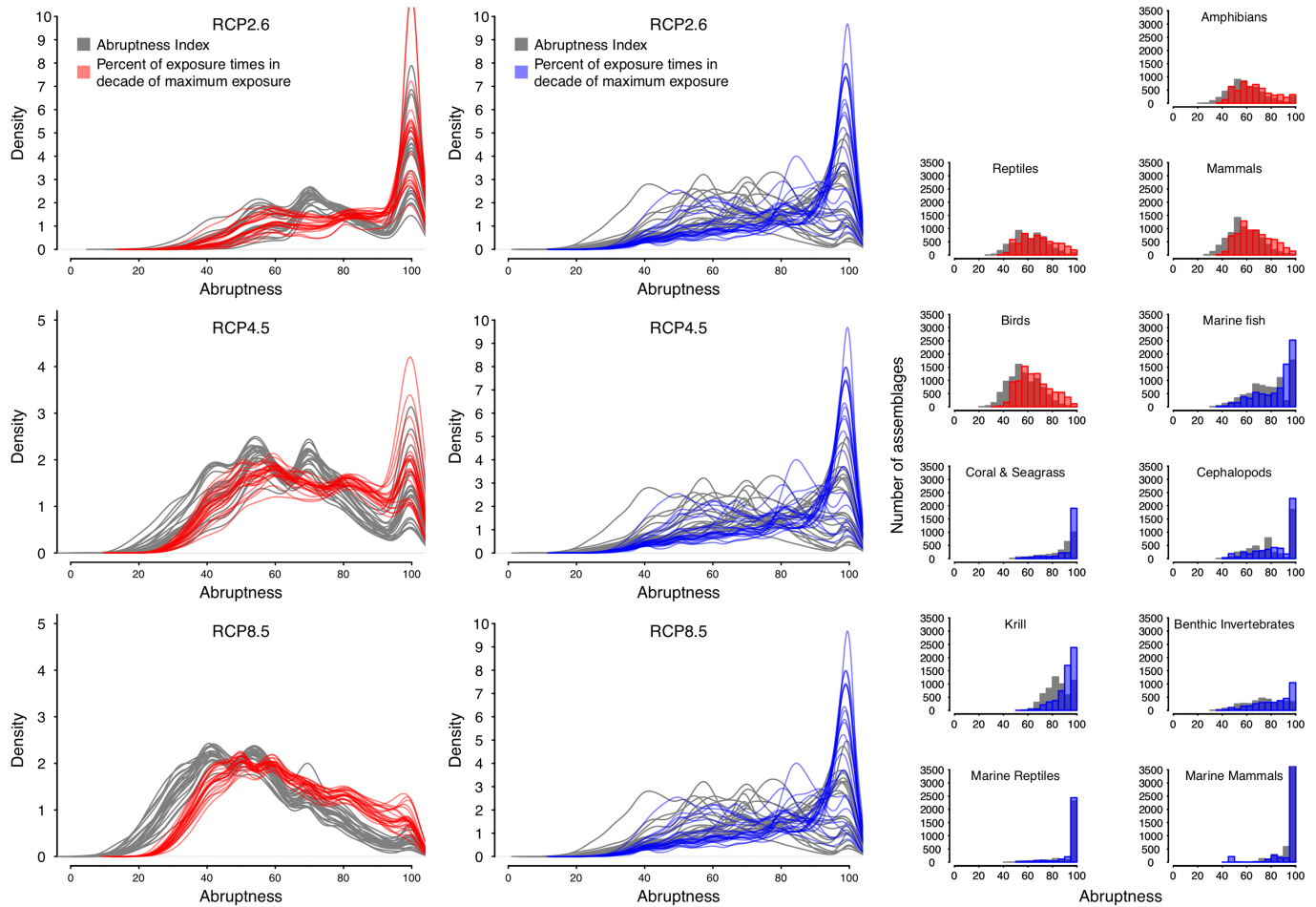


Extended Data Fig. 2 | Comparing the magnitude, timing and abruptness of assemblage exposure across alternative climate variables. **a–c**, Patterns of exposure to both MAT and precipitation combined are very similar to patterns of exposure to MAT only, highlighting the importance of changes in temperature in driving exposure. **d–i**, Patterns of exposure to unprecedented temperatures show both similarities and differences depending on whether temperature is quantified using MAT or MMT. More species are exposed and exposure occurs earlier for MAT compared with MMT, but spatial variation in the magnitude (**d, g**) and timing (**e, h**) of exposure are strongly correlated

between temperature variables. Variation in the abruptness of assemblage exposure is less strongly correlated between MAT and MMT (**f**), but both variables confirm the abruptness of projected exposure (**i**). Values are the median across 22 CMIP5 climate models under RCP 8.5, with hotter colours indicating a higher density of points. Points falling along the dashed 1:1 line indicate a perfect correspondence between metrics. The correlation between metrics (Spearman's ρ), and the mean difference in the timing of exposure (years), is shown.

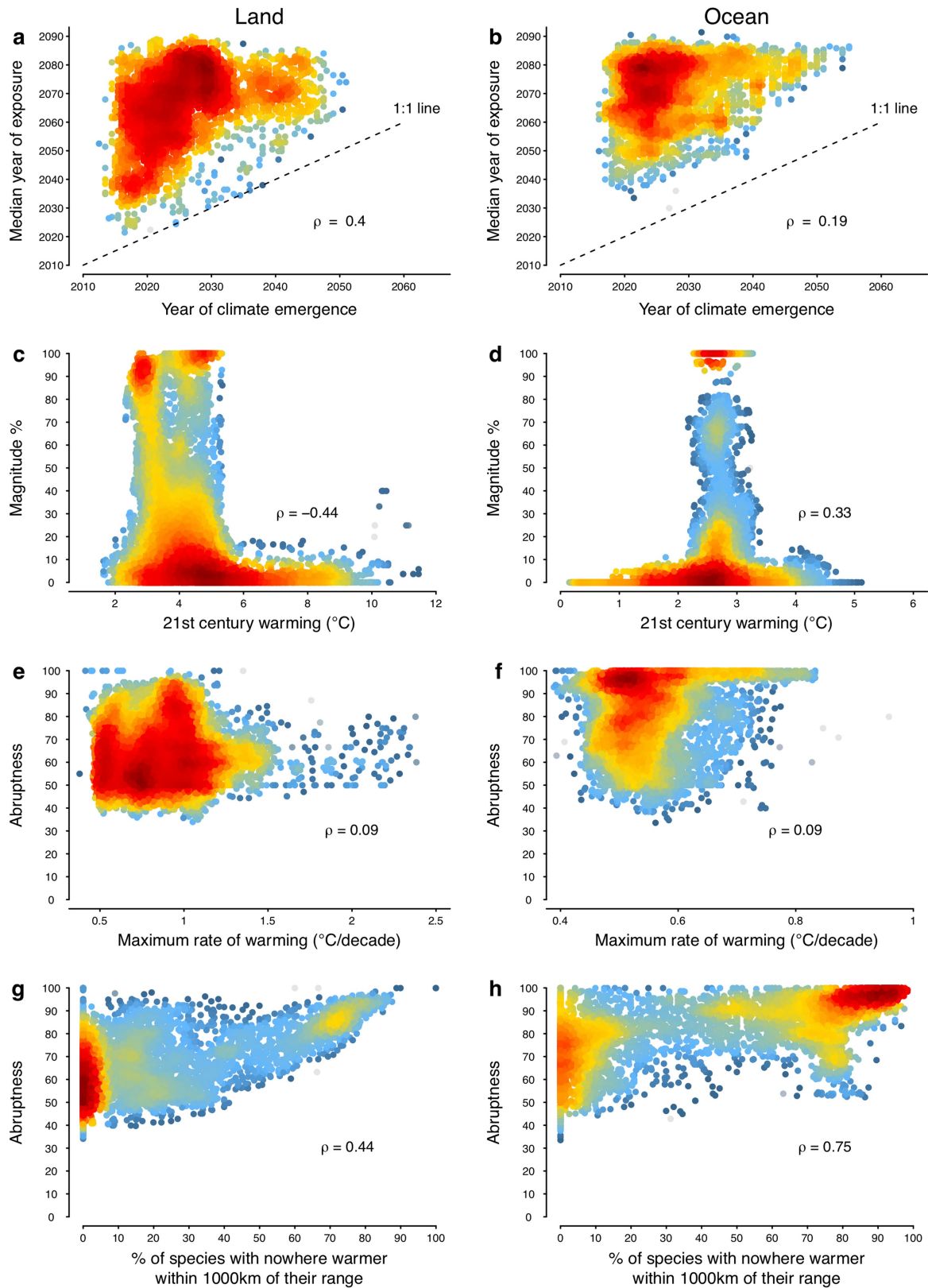


Extended Data Fig. 3 | Uncertainty in species local exposure metrics across 22 CMIP5 climate models under RCP 8.5. Uncertainty (standard deviation, SD) in the magnitude of exposure is greatest around the boundaries of the tropics, with little geographic variation in uncertainty in timing or abruptness.



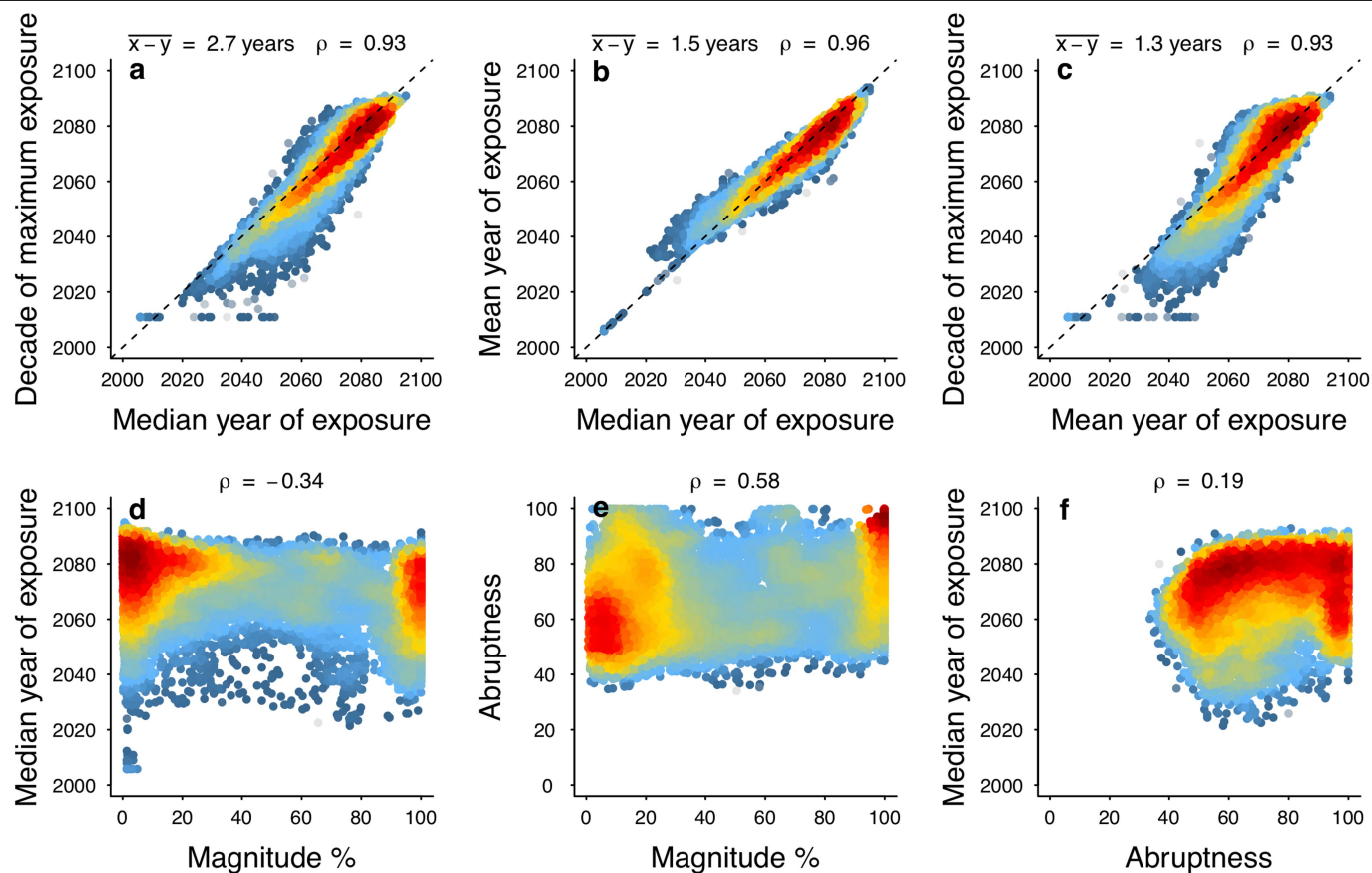
Extended Data Fig. 4 | Abruptness of horizon profiles. Density plots (left) show the distribution of abruptness values for different CMIP5 climate models ($n = 22$, lines) and RCPs on land (red) and in the ocean (blue). Histograms (right) show the median abruptness across climate models under RCP8.5 for each group of organisms. Abruptness is calculated as the percentage of exposure times occurring within the decadal window of maximum exposure (colours).

Abruptness is also shown for an alternative metric based on the Shannon entropy index (grey) with values scaled between 0 and 100, indicating the most gradual and the most abrupt distribution of exposure times possible for a given assemblage, respectively. Exposure is consistently abrupt across climate models, RCP scenarios, metrics and organism groups.



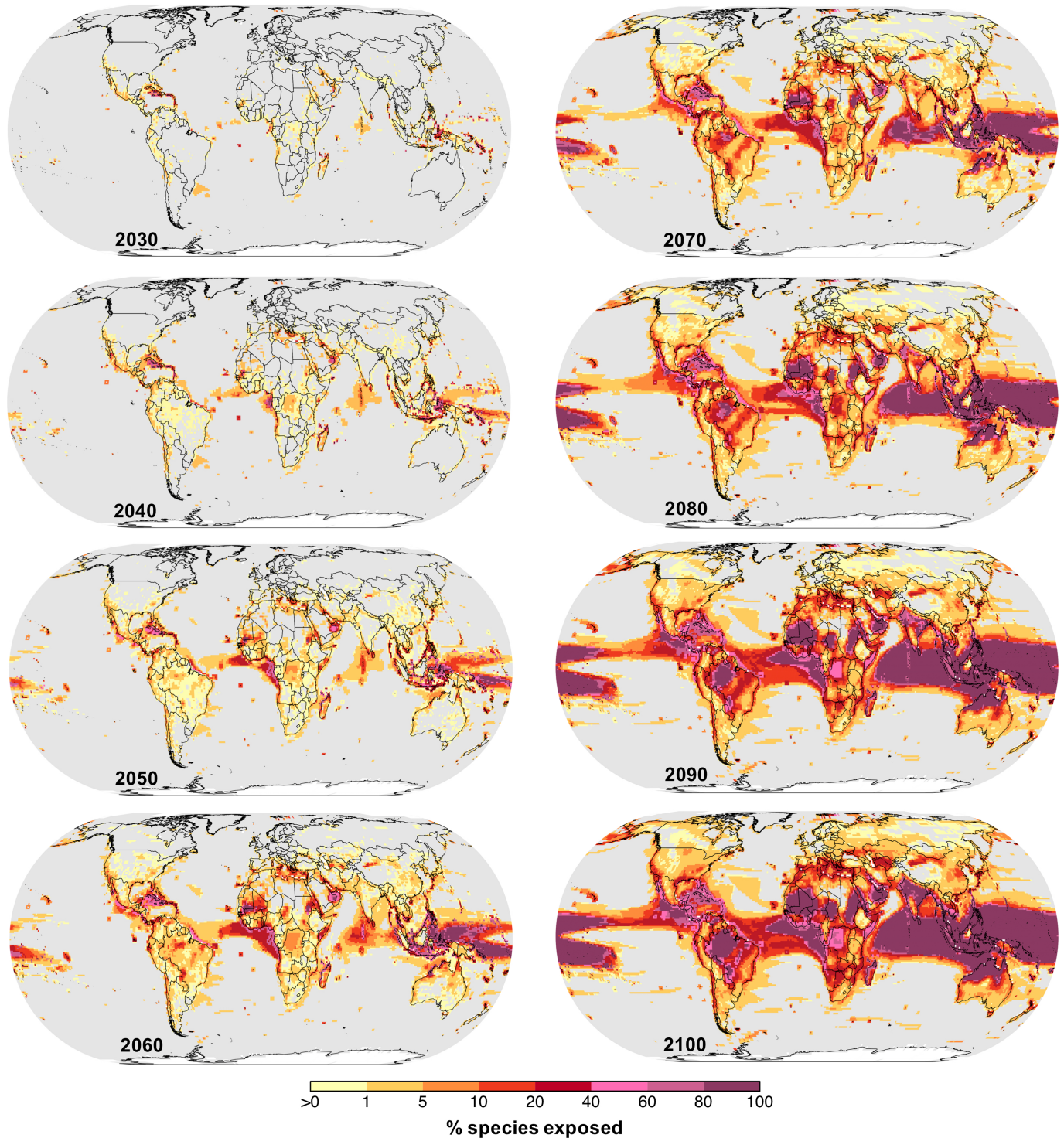
Extended Data Fig. 5 | Predicting the timing, magnitude and abruptness of local species exposure. a–h, On land (left) and in the ocean (right) the median timing of exposure (a, b) is weakly correlated (Spearman's ρ) with the timing of local climate emergence. The magnitude of exposure (c, d) is weakly correlated with the magnitude of warming between the start (2000–2020) and the end (2090–2100) of the twenty-first century. The abruptness of exposure

(percentage of local species exposure times that occur in the decade of maximum exposure) is only partly correlated with the maximum rate of warming (maximum difference in mean temperature between successive decades) (e, f) or the percentage of species with nowhere warmer within 1,000 km of their range (g, h). Values are the median across 22 CMIP5 climate models under RCP 8.5. Hotter colours indicate a higher density of points.



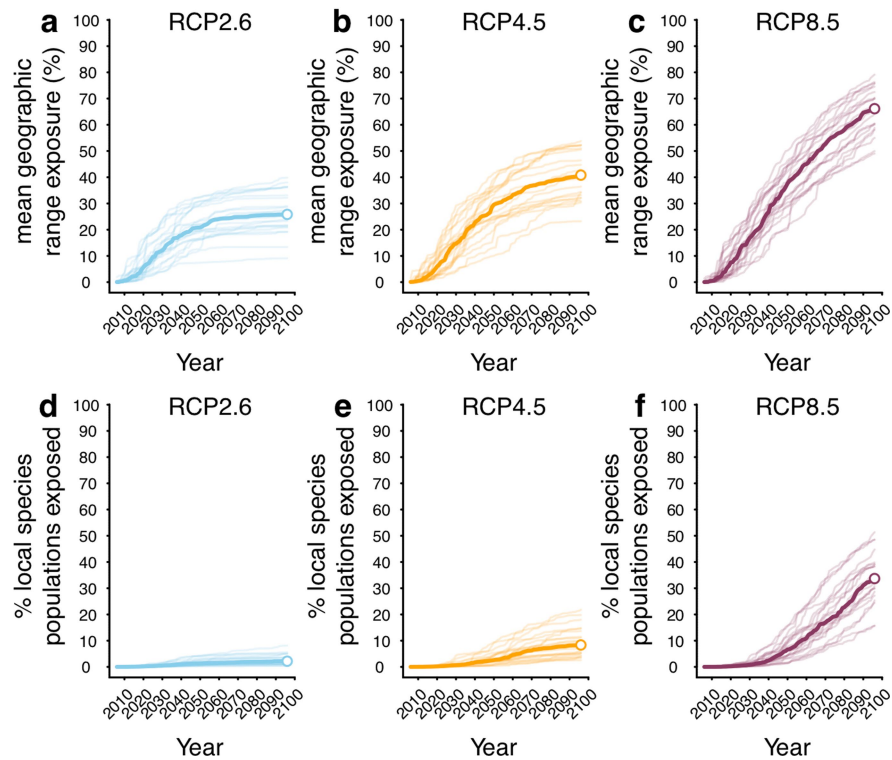
Extended Data Fig. 6 | The different dimensions of climate risk to species assemblages. a–c, Bivariate plots showing the strong correlation among alternative metrics for the timing of local assemblage exposure: the median year of local species exposure, the mean year of local species exposure and the mid-point of the decadal window of worst (that is, maximum) local species exposure. d–f, Bivariate plots showing the weaker correlation between the

magnitude, abruptness and timing of exposure across assemblages. Values are the median across 22 CMIP5 climate models under RCP 8.5, with hotter colours indicating a higher density of points. In a–c, points falling along the dashed 1:1 line indicate a perfect correspondence between metrics. The correlation between metrics (Spearman's ρ) is shown, as well as (for a–c) the mean difference in the timing of exposure (years).



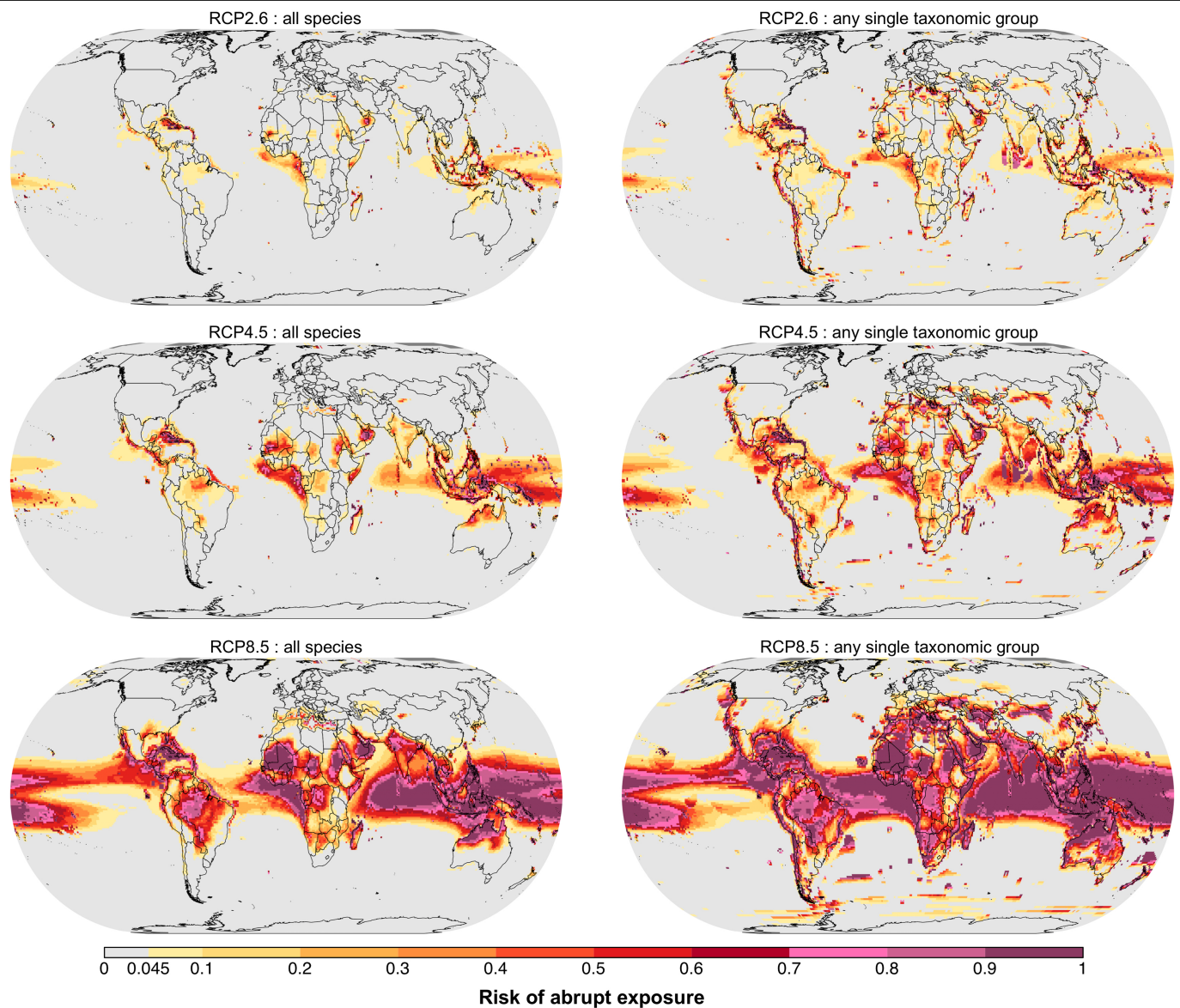
Extended Data Fig. 7 | Accumulation of exposure to unprecedented temperatures at decadal time snapshots from 2030 to 2100. Light grey indicates zero local species exposure. Maps show the median across 22 CMIP5

climate models under RCP 8.5, highlighting the immediate onset of exposure in the tropics that spreads to higher latitudes later in the century.



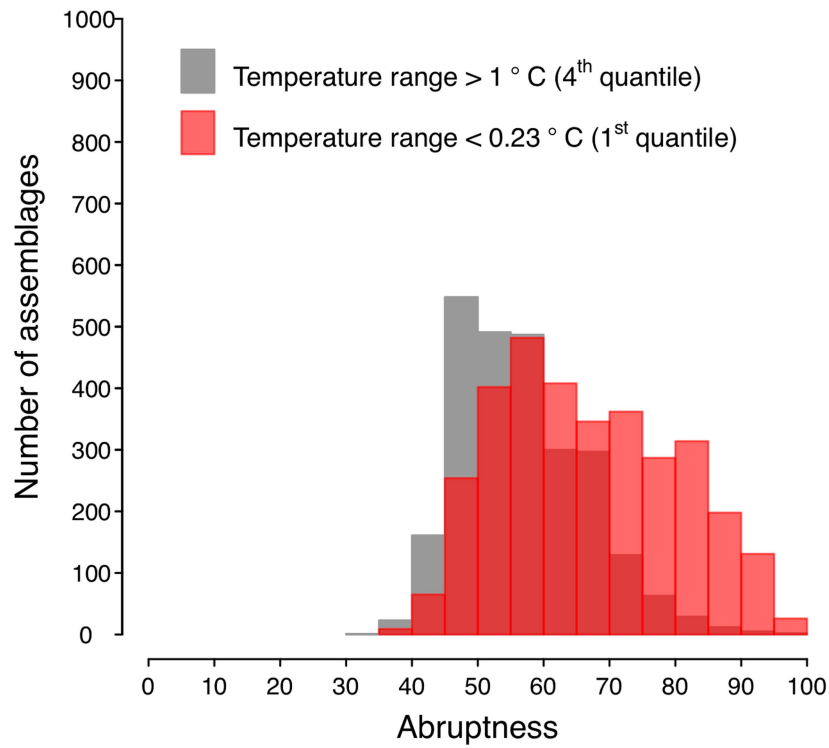
Extended Data Fig. 8 | The global biodiversity horizon profile. **a–d**, The cumulative exposure to unprecedented temperatures of all local species populations (that is, species X site aggregated across all sites) increases smoothly over time at the global scale. Global horizon profiles are shown when species are weighted by the inverse of their geographic range size (equivalent

to the mean percentage of the geographic range exposed) (**a, b**) or are given equivalent weighting (**d–f**). In **d–f**, dynamics are dominated by species with many local populations (that is, large geographic ranges). Variability in exposure across 22 climate models (thin lines) is shown for each RCP scenario (median, thick line).



Extended Data Fig. 9 | The global distribution in the risk of high-magnitude and abrupt assemblage exposure events under different representative concentration pathways. Maps show the probability of abrupt exposure calculated across 22 CMIP5 climate models. The risk of abrupt exposure was calculated on the basis of all species in an assemblage (left column) and for each

group of organisms separately (right column). The maps highlight the greater risk of abrupt exposure events under intermediate (RCP 4.5) and especially under high (RCP 8.5) emission pathways, and when considering taxonomic groups separately.



Extended Data Fig. 10 | Abruptness of horizon profiles for terrestrial vertebrates in 100-km grid cells with low or high spatial temperature heterogeneity. Red, low heterogeneity; grey, high heterogeneity. Abruptness is calculated as the percentage of species exposure times in the decade of maximum exposure. Temperature heterogeneity is the range in temperatures

at 1-km resolution within each 100-km cell. Assemblages with abrupt exposure have lower temperature heterogeneity, which suggests that quantifying species niches at finer spatial resolutions is unlikely to alter the abrupt nature of assemblage exposure dynamics.

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Data collection No software was used in the data collection process

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All datasets used are publicly available. We used expert verified range maps for 30,652 species from the International Union for Conservation of Nature (<https://www.iucnredlist.org/resources/spatial-data-download>) and BirdLife International (<http://datazone.birdlife.org/species/requestdis>) including: birds, mammals, reptiles, amphibians, marine fish, benthic marine invertebrates, and habitat forming corals and seagrasses. Climate change projections for RCPs 8.5, 4.5, and 2.6 for the Coupled Model Intercomparison Project 5 (CMIP5) are available from <https://esgf-node.llnl.gov/search/cmip5/>. Results data to make Figures 2-4 is available at figshare (10.6084/m9.figshare.11814633).

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Study description	Future climate projections from earth system models are combined with information on species geographic distributions (n=30,652 species) to estimate species realised thermal niche limits and project the timing of future exposure to conditions beyond their niche.
Research sample	We used expert verified range maps for 30,652 species from the International Union for Conservation of Nature (https://www.iucnredlist.org/resources/spatial-data-download) and BirdLife International (http://datazone.birdlife.org/species/requestdis), including; birds, mammals, reptiles, amphibians, marine fish, benthic marine invertebrates, and habitat forming corals and seagrasses. This sample reflects availability of geographic range data for each organisms group globally.
Sampling strategy	The sample size reflects availability of geographic range data for each organisms group. These sample sizes make up the majority of species in each major taxonomic group included in the study.
Data collection	All data used here is already published and was downloaded from public data portals
Timing and spatial scale	The data on species distributions we use represents more than a century of collecting efforts and observations by scientists, naturalists and the public. The climate data we use is generated by simulations from computer models of the earth system. Both kinds of data are accurate to ~100km resolution and are available globally.
Data exclusions	We excluded marine species restricted to depths >200m to focus on the effects of sea surface temperatures on shallow water species. To prevent estimates of maximum temperature being inflated by either extreme outliers in the temperature time series or from the overestimation of species ranges we excluded outlier temperature values within each grid cell, defined as those more than three standard deviations from the mean. Once we had selected the maximum temperature for each cell, we excluded outlier temperature values across each species range, defined as those more than three standard deviations above the mean range value.
Reproducibility	This is not an experimental study so experimental replication was not attempted. All data used in our analysis is publicly available. The results can be reproduced using the publicly available data and the analysis code is available on request from the authors. Code and results data to reproduce Figures 2-4 is available at figshare (10.6084/m9.figshare.11814633).
Randomization	No randomization was required. Our study was not experimental, but based on observed biodiversity and climate patterns.
Blinding	Our study was not experimental and so blinding is not relevant
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<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Involved in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging