1 The projected timing of abrupt ecological disruption from climate

2 change

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As anthropogenic climate change continues, the risks to biodiversity will increase over time, with future projections indicating a potentially catastrophic loss of global biodiversity on the horizon¹⁻³. However, our understanding of how this climatedriven disruption of biodiversity will unfold over time is limited because biodiversity forecasts typically focus on individual snapshots of the future. Here, we use annual projections (1850-2100) of temperature and precipitation across >30,000 marine and terrestrial species' ranges to estimate the timing of species exposure to potentially dangerous climate conditions. We project that future disruption of ecological assemblages from climate change will be abrupt, because within any given ecological assemblage the exposure of most species to climate conditions beyond their realised niche limits occurs near simultaneously. Under a high emissions scenario (RCP8.5), such abrupt exposure events begin before 2030 in tropical oceans and spread to tropical forests and higher latitudes by 2050. Below 2°C global warming, <2% of assemblages globally are projected to undergo abrupt exposure events of >20% of their constituent species, but 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.

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Introduction

Climate change is projected to become a leading driver of biodiversity loss¹, but when during this century might ecological assemblages suffer such losses, and will the process be gradual or abrupt? Existing biodiversity forecasts typically lack the temporal perspective needed to answer this question 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 century¹-³. These snapshots do not account for the temporally dynamic nature of ecological disruption expected due to climate change, often focus at the level of species rather than ecological assemblages, and can seem remote to decision-makers concerned with managing more immediate risks⁴. Indeed, many of the most sudden and severe ecological impacts of climate change can occur when conditions become unsuitable for multiple co-occurring species simultaneously, causing catastrophic die-offs and abrupt 'regime shifts' in ecological assemblages⁵,6.

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 priority⁷⁻⁹. 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 climate change threats 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 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, both over space and time, under which a species has been recorded in the wild demarcates the boundaries of its realised niche¹². The projected time in the future at which these bounds are exceeded due to climate change at a site can therefore be thought of as representing a climate horizon, beyond which evidence for the species' ability 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 exceeding their realised niche limits reveals 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 100km grid cells based on expert verified geographic range maps for 30,652 species of birds, mammals, reptiles, amphibians, marine fish, benthic marine invertebrates, krill, cephalopods and habitat forming corals and seagrasses¹⁴ (Supplementary Table 1). We used climate projections throughout the 21st century from 22 climate models and three Representative Concentration Pathways (RCPs):

strong mitigation (RCP2.6), moderate mitigation (RCP4.5), and a high emissions scenario (RCP8.5)¹⁵ (Supplementary Table 2). Given the importance of temperature as a driver of species metabolism and geographic ranges¹⁶⁻¹⁸, 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 (i.e., 100km grid cell), we defined the local species exposure time as the year after which projected local temperatures *consistently* exceed, for at least five 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, five years represents a significant number of breeding seasons at temperatures beyond which they have never been recorded (a 20-year window yielded very similar results (Supplementary Figs. 2 and 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 each species' realised climatic niche limits rather than the historical conditions realised at a single site.

The shape of horizon profiles, and the potential ecological disruption they imply, can vary substantially across assemblages (Fig. 1). To summarize each horizon profile, we focus on three key features: (1) timing, the median year for an assemblage when species exposure to unprecedented climate occurs; (2) magnitude, the percentage of species locally exposed; and (3) abruptness, the synchronicity in the timing of exposure among species in an assemblage, 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 RCP8.5, 81% of terrestrial and 37% of marine assemblages are projected to have at least one species exposed to unprecedented mean annual temperatures (i.e., 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, result in many species occurring near their upper realised thermal limits throughout their geographic range. In total, 68% of terrestrial and 39% of tropical marine assemblages are projected to have >20% of their constituent species exposed to unprecedented temperatures by 2100, compared to 7% of terrestrial and 1% of marine assemblages outside the tropics (Fig. 2a). The Amazon, Indian subcontinent and Indo-Pacific regions are most at risk, with >90% of species in any assemblage exposed to unprecedented temperatures by 2100 (Fig. 2a). Horizon profiles for mean annual and maximum monthly temperatures show strong correspondence (Extended Data Figs. 1 and 2). In contrast, few species undergo prolonged exposure to unprecedented high or low annual precipitation before 2100 (Extended Data Figs. 1 and 2), in agreement with greater variability in precipitation projections²². Thus, throughout we focus on exposure to changes in temperature.

The most striking feature of horizon profiles for local assemblages is their abruptness (Figs. 1 and 2b). Under RCP8.5, 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 (RCP8.5 median abruptness ranges from 60% to 79%, Extended Data Figs. 3 and 4), emissions scenario (median abruptness = 83% for RCP2.6 and 72% for RCP4.5), metric of abruptness (Extended Data Fig. 4), and when calculating exposure for maximum monthly (median abruptness = 68%) rather than mean annual temperatures (Extended Data Figs. 1 and 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 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 abruptness for assemblages 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 realised thermal limits, rather than abruptness being dependent on higher rates of warming (Extended Data Fig. 5). Clustering of species realised thermal limits can, in part, be explained by shared geographic boundaries or, for tropical species, by the upper limits of temperatures available on Earth^{13,23}. However, even for assemblages where this is not the case because a high percentage of species have warmer temperatures available within 1000km of their range edge, assemblage exposure is still projected to occur abruptly (Extended Data Fig. 5), suggesting that other processes, such as ecological interactions²⁴ or evolutionary conservatism in fundamental niches^{25,26}, lead to similarity in realised niche limits^{16,27} and thus abruptness in the timing of exposure.

The synchronicity of species exposure within assemblages means 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 RCP8.5, 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 Coral Triangle—exposure is predicted to be already underway, 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 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). And the timing of abrupt exposure events lags behind local climate emergence by 42 years (mean±12 years s.d.), indicating the potential time-lag between climate change and ensuing biotic responses.

We find that the appearance of a gradual increase in risk to biodiversity globally can result from summarising across local assemblages that differ in their projected timing of abrupt exposure (Figs. 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 RCP8.5, achieving RCP2.6 delays exposure for the most at risk

species by circa six 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 upon them, to adapt to a warming climate.

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The risk of abrupt exposure events

The abruptness of horizon profiles is positively correlated with the magnitude of exposure (Spearman's $\rho = 0.58$; Extended Data Fig. 6), indicating a form of double jeopardy, whereby 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, multispecies coral die-offs caused by a record-breaking marine heatwave in 2016 are one recent example⁶. Although it remains uncertain where "safe limits" of species loss for maintaining ecosystem function are located, 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 where at least 20% of species are projected to undergo exposure to unprecedented temperatures within the same decade. Holding warming to <2°C above preindustrial levels limits such abrupt assemblage exposure events to <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 for 4°C warming. Furthermore, the increase in abrupt exposure does not differ markedly for assemblages afforded high habitat protection (≥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 to median projections. For instance, even under RCP2.6 (1.75°C mean warming), 9% of assemblages are at some risk of abrupt exposure (Fig. 4a), increasing to 35% of assemblages under RCP8.5 (4.4°C mean warming; Fig. 4b). The risk of abrupt assemblage exposure events is positively correlated with species richness (RCP8.5, Spearman's $\rho = 0.29$ (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 (e.g., 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 RCP8.5 (Fig. 4c, Extended Data Fig. 9). Our approach estimates how much of an assemblage's original biodiversity 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, but abrupt assemblage-wide exposure is likely to precipitate substantial ecological disruption regardless of the rate at which new species arrive. Furthermore, in tropical lowlands and oceans, where projected exposure is greatest, and warmer adapted species are lacking, net declines in local biodiversity are expected²¹.

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Crossing the biodiversity climate horizon

While the horizon profile describes the accumulating number of co-occurring species exposed to conditions beyond their realised niche limits, this need not equate with a profile of local extinction. Species may have wider fundamental than realised niche limits^{13,30}, may avoid exposure in microclimatic refugia (but see Extended Data Fig. 10) or via behavioural thermoregulation^{17,31}, or may evolve to tolerate novel conditions¹⁰. In these cases, the timing of abrupt assemblage exposure events could be considered an 'ignorance horizon', marking 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. Furthermore, 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 (e.g. melting sea ice), covariation between climate variables³², or that populations may be locally adapted³³.

To the extent that species realised 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 (e.g., coral reef) to land (e.g., 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 lab 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 realised geographic range boundaries most closely match thermal tolerance limits^{16,18,30,34}. Indeed, warming over recent decades has already been associated with drastic population declines and local extinctions^{6,35,36}, even amongst 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 where 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 where factors other than temperature may more strongly constrain species ranges, and where the emergence of novel climates has closest analogues deep in Earth's history³⁹.

Considering the temporal dynamics of biodiversity exposure to climate change provides an early warning system 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. Elsewhere, our results highlight the urgency of targeted management responses, including establishing monitoring sites in exposed regions, new protected areas in refugia, and the potential for assisted migration and adaptation.

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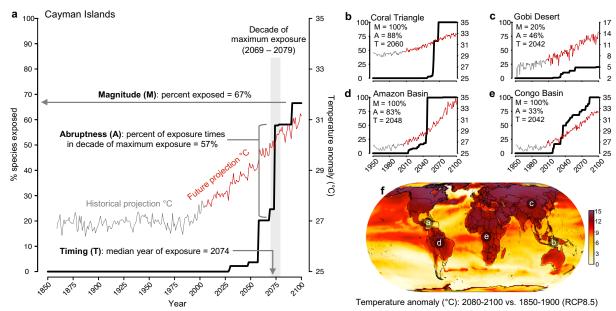


Figure 1. Biodiversity climate horizon profiles. Profiles (solid black lines) indicate the cumulative percent of species in an assemblage exposed to future temperatures (red line) beyond their realised thermal niche over time. Iconic ecosystems provide examples of different profile shapes; **a**, Cayman Islands, **b**, Coral Triangle, **c**, Gobi Desert, **d**, Amazon Basin and **e**, Congo Basin (see **f**, map of temperature anomalies for locations). 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 (RCP8.5). Timing, magnitude and abruptness define differences among profiles. Grey line shows historical temperature projections at a site.

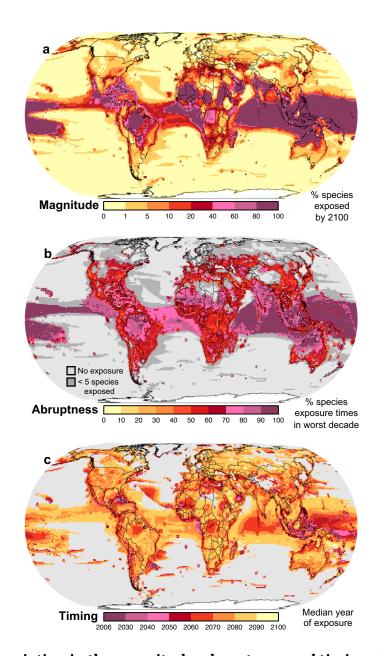


Figure 2. Global variation in the magnitude, abruptness and timing of horizon profiles. a, magnitude of exposure indicating the percent of species in 100km resolution grid cells (i.e., assemblages) exposed to unprecedented temperature (i.e., beyond each species' realised niche) by 2100. **b**, abruptness quantified as the percent of species exposure times occurring 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 RCP8.5 (see Extended Data Fig. 1 for RCPs 2.6 and 4.5).

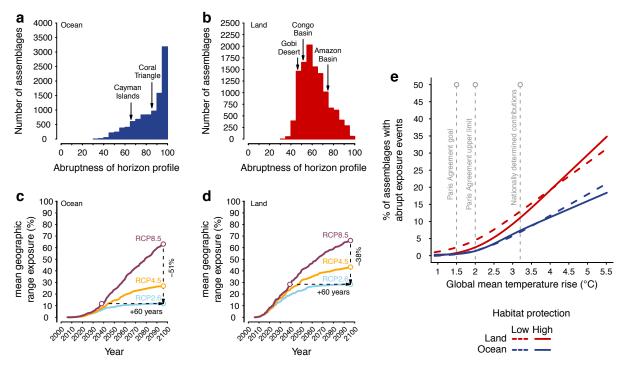


Figure 3. Abruptness of horizon profiles locally versus globally, and accelerating risk with global warming. The distribution in the projected abruptness of species exposure to unprecedented temperatures within marine and terrestrial assemblages (\mathbf{a} , \mathbf{b}). Selected assemblages from Fig. 1 are highlighted. Abruptness is quantified as the percent of species exposure times occurring within the decade of maximum exposure, with results showing the median across climate models under RCP8.5. Global horizon profiles for oceans and land (\mathbf{c} , \mathbf{d}) showing more gradual accumulation of species exposure to unprecedented temperatures. Dashed lines show how lowering emissions from RCP8.5 to RCP2.6 both reduces the median magnitude of exposure across climate models and substantially delays the timing of exposure, buying \sim 60 years for species and conservation plans to adapt to a warming climate (see Extended Data Fig. 8 for individual climate models). \mathbf{e} , the percent of species assemblages projected to experience high magnitude and abrupt assemblage exposure (>20% of species exposed in a single decade) as a function of global warming. Curves are fitted from model runs (n = 66) across RCP2.6, RCP4.5 and RCP8.5.

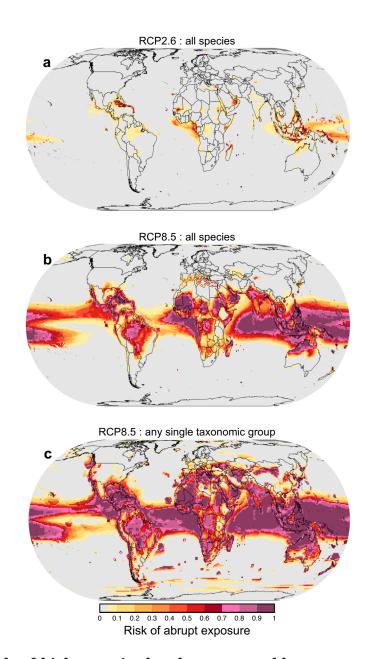


Figure 4. The risk of high magnitude, abrupt assemblage exposure events. Risk is calculated as the proportion of 22 climate models where an abrupt exposure event is projected to occur before 2100. Assemblages avoiding abrupt exposure events across all 22 models are in grey. In **a-b**, abrupt exposure events are defined as >20% of all species in an assemblage exposed in a single decade. In **c**, abrupt exposure events are defined when any single organism group (e.g., amphibians) within an assemblage exhibits the exposure of >20% of its constituent species in a single decade, highlighting the widespread risk of abrupt ecological disruption.

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 restricted to depths greater than 200 meters (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 species' global geographic distributions⁴⁶, but our results should be interpreted in the context of known data limitations. For some groups, species coverage is incomplete and biased towards commercial species (e.g. cephalopods), while others have been comprehensively assessed for only a subset of clades (e.g. 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 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, while 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 21st March 2018). The maps, originally in polygon format, were re-sampled to a 1km resolution prior to further analysis. We considered 100km 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 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 RCP2.6, RCP4.5 and RCP8.5 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 5th 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 '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 done 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 summarising across models, we capture the uncertainty in the timing of exposure due to both internal climate variability and climate model uncertainty (i.e., 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 realised 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 (e.g., Worldclim data⁵¹) to estimate species realised niches. To address this, we estimated species realised 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 ($Tmax_{MAT}$, see Supplementary Information). To prevent estimates of Tmax_{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. 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. The $Tmax_{MAT}$ value for each species was then set as the maximum of the remaining values (Supplementary Fig. 1). We used an identical procedure to calculate Tmax using MMT (Tmax $_{MMT}$). For precipitation, species may be exposed to either drying or wetting conditions and so we calculated both the minimum (Pmin) and maximum (Pmax) precipitation value experienced by each species across its geographic range (see Supplementary Information).

Estimating species exposure times. Within each terrestrial (n = 18560) and marine (n = 37333) assemblage (i.e. 100 km grid cell containing any terrestrial or marine species respectively), we defined the time of local species exposure to unprecedented temperature (i.e. the 'climate horizon') to be the year after which the MAT (or MMT) of the cell is projected to exceed the species's $Tmax_{MAT}$ (or $Tmax_{MMT}$) value 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 and 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 above or below the species' Pmax and Pmin values respectively 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 when annual precipitation fell below 15mm for at least five consecutive years. Due 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 local exposure time of either MAT or precipitation for a species in an assemblage when it was exposed to both variables (Extended Data Fig. 2g-i, see Supplementary Information).

We note that by using range-wide estimates of species niche limits, we may underestimate both the magnitude and 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. Once species exposure times had been calculated for an assemblage we constructed a horizon profile indicating the cumulative percentage of species locally exposed to conditions beyond their realised niche limits. We used the following metrics to summarise the temporal dynamics of biodiversity exposure. First, we calculated the magnitude of exposure as the percent of species in the assemblage exposed over the course of the 21st century. Second the abruptness of exposure for an assemblage was calculated as the percent 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 years 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 ranging 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 years. Abruptness was only calculated for assemblages where 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 21st 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 impacts 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. In 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 the timing of exposure, excluding outlying values from the time series when quantifying the maximum historical temperature at a site and only considering emergence 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.

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Spatial scale. We modelled species realised niche limits using climate projections at 100km 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 mean annual temperatures within each grid cell, using spatially interpolated weather data for the period 1970-2000 available at 1km 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 (e.g. tropical mountains), exhibit more gradual exposure profiles than those with low heterogeneity in temperatures (e.g. 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 where variation in realised niche limits among species is expected to be greatest (i.e. grid cells containing substantial spatial climatic heterogeneity) as having the most gradual exposure profiles. Second, it suggests that while incorporating finer-scale climate data may further reduce the lowest abruptness values estimated across assemblages (i.e. 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 where there is little finescale 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 (i.e. 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 % 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 21st century. Across the set of 66 climate model runs from the three RCP scenarios, we fit a generalised additive model (GAM) to estimate the % 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 preindustrial conditions (1850-1900). We fit separate models for sites with either low or high (i.e. >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 organism group separately.

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Contributions

- 656 A.L.P, C.H.T, 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.

658659 Competing interests

The authors declare no competing financial interests.

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Data availability

- All datasets used here are publicly available. Expert verified range maps are available from
- 671 https://www.iucnredlist.org/resources/spatial-data-download and

- 672 http://datazone.birdlife.org/species/requestdis. Climate change projections for RCPs 8.5,
- 4.5, and 2.6 for the Coupled Model Intercomparison Project 5 (CMIP5) are available from
- 674 https://esgf-node.llnl.gov/search/cmip5/. Computer code used in the analysis is available
- on request from the authors. Code and results data to make figures 2-4 is available at
- 676 figshare (10.6084/m9.figshare.11814633).

- 677 Extended Data figure 1. Spatial distribution of the magnitude, abruptness and timing,
- 678 of assemblage exposure for alternative climate variables. Results show the median
- 679 value across 22 CMIP5 climate models for mean annual temperature, maximum monthly
- 680 temperature, and precipitation under RCP2.6, RCP4.5 and RCP8.5.
- 681 Extended Data figure 2. Comparing the magnitude, timing and abruptness of
- 682 assemblage exposure across alternative climate variables. a-f, patterns of exposure to
- 683 unprecedented temperatures show both similarities and differences depending on whether
- 684 temperature is quantified using mean annual temperature (MAT) or maximum monthly
- 685 temperatures (MMT). More species are exposed and exposure occurs earlier for MAT
- 686 compared to MMT, but spatial variation in the magnitude (a, d) and timing (b, e) of
- 687 exposure are strongly correlated between temperature variables. Variation in the
- 688 abruptness of assemblage exposure is less strongly correlated between MAT and MMT (c),
- 689 but both variables confirm the abruptness of projected exposure (f). g-i, patterns of
- 690
- exposure to both MAT and precipitation combined are very similar to patterns of exposure
- 691 to only MAT, highlighting the primacy of changes in temperature in driving exposure.
- Values are the median across 22 CMIP5 climate models under RCP8.5, with hotter colors 692
- 693 indicating a higher density of points. In (a-c) and (g-i) points falling along the dashed 1:1
- 694 line indicate a perfect correspondence between metrics. The correlation between metrics
- 695 (Spearman's ρ), and the mean difference in the timing of exposure (years), is shown.
- 696 **Extended Data figure 3.** Uncertainty (standard deviation, SD) in species local exposure
- 697 metrics across 22 CMIP5 climate models under RCP8.5. Uncertainty in the magnitude of
- 698 exposure is greatest around the boundaries of the tropics with little geographic variation in
- 699 uncertainty in timing or abruptness.
- 700 **Extended Data figure 4. Abruptness of horizon profiles.** Density plots show the
- 701 distribution of abruptness values for different CMIP5 climate models (n = 22, lines) and
- 702 representative concentration pathways (RCPs) on land (red) and in the ocean (blue).
- 703 Histograms show the median abruptness across climate models under RCP8.5 for each
- 704 organism group. Abruptness is calculated as the percent of exposure times occurring
- 705 within the decadal window of maximum exposure (colors). Abruptness is also shown for an
- 706 alternative metric based on the Shannon-entropy index (grey) with values scaled between
- 707 0 and 100, indicating the most gradual and abrupt distribution of exposure times possible
- 708 for a given assemblage respectively. Exposure is consistently abrupt across climate models,
- 709 RCP scenarios, metrics and organism groups.
- 710 Extended Data figure 5. Predicting the timing, magnitude and abruptness of local
- 711 **species exposure.** On land (left) and in the ocean (right) the (a-b) median timing of
- 712 exposure is weakly correlated (Spearman's ρ) with the timing of local climate emergence.
- 713 The magnitude of exposure (**c-d**) is weakly correlated with the magnitude of warming
- 714 between the start (2000-2020) and the end (2090-2100) of the 21st Century. The
- 715 abruptness of exposure (% of local species exposure times occurring in the decade of
- 716 maximum exposure) is only partly correlated with (e-f) the maximum rate of warming
- 717 (maximum difference in mean temperature between successive decades) or (g-h) the % of
- species with nowhere warmer within 1000km of their range. Values are the median across 718
- 719 22 CMIP5 climate models under RCP8.5. Hotter colors indicating a higher density of points.

- 720 Extended Data figure 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 (i.e. maximum) local species exposure. **d-f**, Bivariate plots showing the weaker
- 725 correlation between the magnitude, abruptness and timing of exposure across
- assemblages. Values are the median across 22 CMIP5 climate models under RCP8.5, with
- hotter colors 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
- 730 exposure (years).

- 732 Extended Data figure 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 RCP8.5,
- highlighting the immediate onset of exposure in the tropics that spreads to higher latitudes
- 736 later in the century.
- 737 **Extended Data figure 8. The global biodiversity horizon profile.** The cumulative
- exposure to unprecedented temperatures of all local species populations (i.e. species X site
- 739 aggregated across all sites) increases smoothly over time at the global scale. Global horizon
- profiles are shown when (**a-b**) species are weighted by the inverse of their geographic
- range size (equivalent to the mean % geographic range exposed) or (**d-f**) are given
- equivalent weighting. In (**d-f**), dynamics are dominated by species with many local
- 743 populations (i.e. large geographic ranges). Variability in exposure across 22 climate models
- 744 (thin lines) is shown for each RCP scenario (median, thick line).
- 745 Extended Data figure 9. The global distribution in the risk of high-magnitude and
- abrupt assemblage exposure events under different representative concentration
- 747 **pathways**. Maps show the probability of abrupt exposure calculated across 22 CMIP5
- 748 climate models. The risk of abrupt exposure was calculated based on all species in an
- assemblage (left column) and for each organism group separately (right column). Maps
- highlight the greater risk of abrupt exposure events under intermediate (RCP4.5), and
- 751 especially high (RCP8.5) emission pathways, and when considering taxonomic groups
- 752 separately
- 753 Extended Data figure 10. Abruptness of horizon profiles for terrestrial vertebrates in
- 754 100km grid cells with low (red, 1st quantile) or high (grey, 4th quantile) spatial
- 755 **temperature heterogeneity**. Abruptness is calculated as the % of species exposure times
- 756 in the decade of maximum exposure. Temperature heterogeneity is the range in
- 757 temperatures at 1km resolution within each 100km cell. Assemblages with abrupt exposure
- have lower temperature heterogeneity suggesting that quantifying species niches at finer
- 759 spatial resolutions is unlikely to alter the abrupt nature of assemblage exposure dynamics.
- 760