The projected timing of abrupt ecological disruption from climate change
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The projected timing of abrupt ecological disruption from climate change

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13   As anthropogenic climate change continues, the risks to biodiversity will increase
14   over time, with future projections indicating a potentially catastrophic loss of global
15   biodiversity on the horizon[1–3]. However, our understanding of how this climate-
16   driven disruption of biodiversity will unfold over time is limited because
17   biodiversity forecasts typically focus on individual snapshots of the future. Here, we
18   use annual projections (1850-2100) of temperature and precipitation across
19   >30,000 marine and terrestrial species' ranges to estimate the timing of species
20   exposure to potentially dangerous climate conditions. We project that future
21   disruption of ecological assemblages from climate change will be abrupt, because
22   within any given ecological assemblage the exposure of most species to climate
23   conditions beyond their realised niche limits occurs near simultaneously. Under a
24   high emissions scenario (RCP8.5), such abrupt exposure events begin before 2030 in
25   tropical oceans and spread to tropical forests and higher latitudes by 2050. Below
26   2°C global warming, <2% of assemblages globally are projected to undergo abrupt
27   exposure events of >20% of their constituent species, but the risk accelerates with
28   the magnitude of warming, threatening 15% of assemblages at 4°C, with similar
29   levels of risk in protected and unprotected areas. These results highlight the
30   impending risk of sudden and severe biodiversity losses from climate change and
31   provide a framework for predicting both when and where these events may occur.
32
33

Introduction

Climate change is projected to become a leading driver of biodiversity loss[1], 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 century[1–3]. 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 risks[4]. 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 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 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 niche[12]. 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 extinction[13]. 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 seagrasses[14] (Supplementary Table 1). We used climate projections throughout the 21st century from 22 climate models and three Representative Concentration Pathways (RCPs):

80   strong mitigation (RCP2.6), moderate mitigation (RCP4.5), and a high emissions scenario
81   (RCP8.5)[15] (Supplementary Table 2). Given the importance of temperature as a driver of
82   species metabolism and geographic ranges[16–18], we focus on mean annual temperature as
83   the main proxy for climate. However, because species may be sensitive to other climate
84   variables that may respond differently to greenhouse gas emissions, we also generated
85   horizon profiles using maximum monthly temperatures and terrestrial annual
86   precipitation (see Methods).
87   For each species at a site (i.e., 100km grid cell), we defined the local species
88   exposure time as the year after which projected local temperatures *consistently* exceed, for
89   at least five years, the maximum temperature experienced by the species across its
90   geographic range during historical climate projections (1850–2005) (Supplementary Fig.
91   1). For species that breed annually or near-annually, five years represents a significant
92   number of breeding seasons at temperatures beyond which they have never been recorded
93   (a 20-year window yielded very similar results (Supplementary Figs. 2 and 3)). This
94   approach for quantifying exposure bears similarities to the concept of 'time of emergence'
95   in climate science, defined as the time at which the signal of anthropogenic climate change
96   at a location emerges from the envelope of historical climate variability[19,20]. The key
97   distinction is that we define exposure relative to each species' realised climatic niche limits
98   rather than the historical conditions realised at a single site.
99   The shape of horizon profiles, and the potential ecological disruption they imply, can
100   vary substantially across assemblages (Fig. 1). To summarize each horizon profile, we focus
101   on three key features: (1) timing, the median year for an assemblage when species
102   exposure to unprecedented climate occurs; (2) magnitude, the percentage of species locally
103   exposed; and (3) abruptness, the synchronicity in the timing of exposure among species in
104   an assemblage, measured as the percentage of all species exposure times that occur in the
105   decade of maximum exposure (Fig. 1a).
106
107   **Timing, magnitude and abruptness of horizon profiles**
108   Under RCP8.5, 81% of terrestrial and 37% of marine assemblages are projected to have at
109   least one species exposed to unprecedented mean annual temperatures (i.e., beyond
110   historical niche limits) before 2100. Despite the lower magnitude of warming, the
111   magnitude of exposure is greatest in the tropics, where narrow historical climate
112   variability[20] and shallow thermal gradients[21], result in many species occurring near their
113   upper realised thermal limits throughout their geographic range. In total, 68% of terrestrial
114   and 39% of tropical marine assemblages are projected to have >20% of their constituent
115   species exposed to unprecedented temperatures by 2100, compared to 7% of terrestrial
116   and 1% of marine assemblages outside the tropics (Fig. 2a). The Amazon, Indian
117   subcontinent and Indo-Pacific regions are most at risk, with >90% of species in any
118   assemblage exposed to unprecedented temperatures by 2100 (Fig. 2a). Horizon profiles for
119   mean annual and maximum monthly temperatures show strong correspondence (Extended
120   Data Figs. 1 and 2). In contrast, few species undergo prolonged exposure to unprecedented
121   high or low annual precipitation before 2100 (Extended Data Figs. 1 and 2), in agreement
122   with greater variability in precipitation projections[22]. Thus, throughout we focus on
123   exposure to changes in temperature.
124   The most striking feature of horizon profiles for local assemblages is their
125   abruptness (Figs. 1 and 2b). Under RCP8.5, on average 71% (median) of local species

4

126 exposure times for any given assemblage are projected to occur within a single decade (Fig.
127 3a-b), with the abruptness of exposure higher among marine assemblages (median
128 abruptness = 89%, Fig. 3a) than on land (median abruptness = 61%., Fig. 3b). This pattern
129 of highly synchronized species exposure within assemblages is robust to the choice of
130 climate model (RCP8.5 median abruptness ranges from 60% to 79%, Extended Data Figs. 3
131 and 4), emissions scenario (median abruptness = 83% for RCP2.6 and 72% for RCP4.5),
132 metric of abruptness (Extended Data Fig. 4), and when calculating exposure for maximum
133 monthly (median abruptness = 68%) rather than mean annual temperatures (Extended
134 Data Figs. 1 and 2). The same pattern of abruptness is also evident for horizon profiles
135 constructed separately for each taxonomic group within local assemblages (Extended Data
136 Fig. 4). Marine organisms, especially seagrasses, corals, cephalopods, marine reptiles and
137 mammals exhibit the most abrupt profiles, but it is the consistency of abruptness across
138 groups rather than the differences that is most notable. Similarly, although abruptness for
139 assemblages varies spatially, being greatest in the Amazon, Indian subcontinent, Sahel and
140 Northern Australia, as well as tropical oceans, abrupt horizon profiles are the general rule
141 both within the tropics (median abruptness = 79%) and at higher latitudes (median
142 abruptness = 59%) (Fig. 2b).
143   This pervasive pattern of abrupt exposure arises primarily because co-occurring
144 species often share similar realised thermal limits, rather than abruptness being dependent
145 on higher rates of warming (Extended Data Fig. 5). Clustering of species realised thermal
146 limits can, in part, be explained by shared geographic boundaries or, for tropical species, by
147 the upper limits of temperatures available on Earth[13,23]. However, even for assemblages
148 where this is not the case because a high percentage of species have warmer temperatures
149 available within 1000km of their range edge, assemblage exposure is still projected to
150 occur abruptly (Extended Data Fig. 5), suggesting that other processes, such as ecological
151 interactions[24] or evolutionary conservatism in fundamental niches[25,26], lead to similarity in
152 realised niche limits[16,27] and thus abruptness in the timing of exposure.
153   The synchronicity of species exposure within assemblages means the timing of
154 assemblage-level exposure events is well-described by the median of species exposure
155 times at a site (Extended Data Fig. 6). Under RCP8.5, the global mean year of assemblage-
156 level exposure is 2074 (±11 years s.d.), but there is considerable variation in the timing of
157 exposure across assemblages (Fig. 2c). In some locations—such as the Caribbean and Coral
158 Triangle—exposure is predicted to be already underway, with these hotspots of exposure
159 expanding in spatial extent over time (Fig. 2c, Extended Data Fig. 7). By 2050, exposure
160 spreads beyond ocean ecosystems to iconic terrestrial ecosystems, such as the Amazon and
161 Congolese rainforests (Fig. 2c, Extended Data Fig. 7). Notably, the timing of these
162 assemblage-level exposure events is not well predicted by the timing of local climate
163 emergence (Spearman's ρ = 0.29; Extended Data Fig. 5). And the timing of abrupt exposure
164 events lags behind local climate emergence by 42 years (mean±12 years s.d.), indicating the
165 potential time-lag between climate change and ensuing biotic responses.
166   We find that the appearance of a gradual increase in risk to biodiversity globally can
167 result from summarising across local assemblages that differ in their projected timing of
168 abrupt exposure (Figs. 3c-d, Extended Data Fig. 8). Although these global summaries mask
169 the abrupt nature of exposure within local assemblages, they can highlight the importance
170 of increased mitigation efforts in reducing and delaying the onset of unprecedented climate
171 conditions. Compared to RCP8.5, achieving RCP2.6 delays exposure for the most at risk

172   species by circa six decades in the oceans (mean = 58 years, range = 46-65 years, Fig. 3c)
173   and on land (mean = 58 years, range = 49-67 years, Fig. 3d), buying valuable time for
174   species and ecosystems, and human societies that depend upon them, to adapt to a
175   warming climate.
176
177   **The risk of abrupt exposure events**
178   The abruptness of horizon profiles is positively correlated with the magnitude of exposure
179   (Spearman's ρ = 0.58; Extended Data Fig. 6), indicating a form of double jeopardy, whereby
180   exposure events involving larger fractions of species are projected to occur more abruptly.
181   This near-simultaneous exposure among multiple species could have sudden and
182   devastating effects on local biodiversity and ecosystem services. Catastrophic, multi-
183   species coral die-offs caused by a record-breaking marine heatwave in 2016 are one recent
184   example[6]. Although it remains uncertain where "safe limits" of species loss for maintaining
185   ecosystem function are located, meta-analyses suggest a 20% decline in species diversity as
186   one possible threshold[28,29]. We therefore defined assemblages at risk of abrupt ecological
187   disruption as those where at least 20% of species are projected to undergo exposure to
188   unprecedented temperatures within the same decade. Holding warming to <2°C above pre-
189   industrial levels limits such abrupt assemblage exposure events to <2% of assemblages
190   (Fig. 3e). However, beyond 2°C warming the area projected to undergo abrupt assemblage
191   exposure expands rapidly, encompassing 15% of assemblages globally for 4°C warming.
192   Furthermore, the increase in abrupt exposure does not differ markedly for assemblages
193   afforded high habitat protection (≥20% protected area coverage of a grid cell), indicating
194   that current protected areas are equally at risk from abrupt exposure (Fig. 3e).
195   The risk of abrupt exposure events differs across assemblages globally, with variability
196   across individual climate projections increasing the total area at risk compared to median
197   projections. For instance, even under RCP2.6 (1.75°C mean warming), 9% of assemblages
198   are at some risk of abrupt exposure (Fig. 4a), increasing to 35% of assemblages under
199   RCP8.5 (4.4°C mean warming; Fig. 4b). The risk of abrupt assemblage exposure events is
200   positively correlated with species richness (RCP8.5, Spearman's ρ = 0.29 (land) and 0.56
201   (ocean)), highlighting the increased risk of sudden ecological disruption in the world's
202   most biodiverse ecosystems. Moreover, the risk of disruption of ecological function may be
203   underestimated in this analysis because even if particular functional groups (e.g., habitat
204   forming corals) suffer high levels of exposure, this may not be evident at the scale of entire
205   assemblages if other groups are relatively less affected. When abrupt assemblage exposure
206   events are instead defined at the level of major taxonomic groups, the area at risk expands
207   further, encompassing 49% of species assemblages under RCP8.5 (Fig. 4c, Extended Data
208   Fig. 9). Our approach estimates how much of an assemblage's original biodiversity is
209   exposed to potentially dangerous climate conditions over time[28]. We do not consider the
210   potential for immigration of species from elsewhere to offset local biodiversity losses, but
211   abrupt assemblage-wide exposure is likely to precipitate substantial ecological disruption
212   regardless of the rate at which new species arrive. Furthermore, in tropical lowlands and
213   oceans, where projected exposure is greatest, and warmer adapted species are lacking, net
214   declines in local biodiversity are expected[21].
215
216   **Crossing the biodiversity climate horizon**

217   While the horizon profile describes the accumulating number of co-occurring species
218   exposed to conditions beyond their realised niche limits, this need not equate with a profile
219   of local extinction. Species may have wider fundamental than realised niche limits[13,30], may
220   avoid exposure in microclimatic refugia (but see Extended Data Fig. 10) or via behavioural
221   thermoregulation[17,31], or may evolve to tolerate novel conditions[10]. In these cases, the
222   timing of abrupt assemblage exposure events could be considered an 'ignorance horizon',
223   marking the time beyond which local extinctions are not inevitable but evidence for the
224   ability of species to persist in the wild is largely absent[13]. Thus, at the very least, our results
225   show that within 30 years, continued high emissions will drive a sudden shift across many
226   ecological assemblages to climate conditions under which we have almost no knowledge of
227   the ability of their constituent species to survive. Furthermore, we caution that the timing
228   and magnitude of this exposure may occur earlier and be larger than we anticipate, because
229   our analysis does not consider changes in extreme events[9], effects of warming on local
230   habitat (e.g. melting sea ice), covariation between climate variables[32], or that populations
231   may be locally adapted[33].
232   To the extent that species realised historical thermal limits do reflect fundamental
233   limits to persistence then the occurrence of abrupt exposure events marks the crossing of
234   an 'ecological horizon' beyond which catastrophic and coordinated species losses are
235   expected. These abrupt events—projected to spread from ocean (e.g., coral reef) to land
236   (e.g., rainforest) ecosystems by 2050 under high emissions—risk sudden disruption to
237   ecosystems and their capacity to maintain current levels of biodiversity and functioning.
238   Evidence from lab and field-based studies indicates this is a credible risk, particularly for
239   tropical terrestrial ectotherms and for marine organisms for which projected abruptness is
240   most pronounced and for which realised geographic range boundaries most closely match
241   thermal tolerance limits[16,18,30,34]. Indeed, warming over recent decades has already been
242   associated with drastic population declines and local extinctions[6,35,36], even amongst
243   endotherms which are widely assumed to be less sensitive to warming but may be
244   particularly vulnerable to climate driven disruption of trophic interactions[37,38]. For those
245   ecosystems where exposure is projected within the next few decades, the capacity for
246   species to adapt would appear limited. A priority for future research is to refine estimates
247   of the timing and consequences of exposure, including where factors other than
248   temperature may more strongly constrain species ranges, and where the emergence of
249   novel climates has closest analogues deep in Earth's history[39].
250   Considering the temporal dynamics of biodiversity exposure to climate change
251   provides an early warning system of the potential for abrupt ecological disruption.
252   Averting, or at least delaying, the crossing of this ecological horizon is possible for most
253   assemblages, and requires massive and rapid reductions in greenhouse gas emissions.
254   Elsewhere, our results highlight the urgency of targeted management responses, including
255   establishing monitoring sites in exposed regions, new protected areas in refugia, and the
256   potential for assisted migration and adaptation.
257

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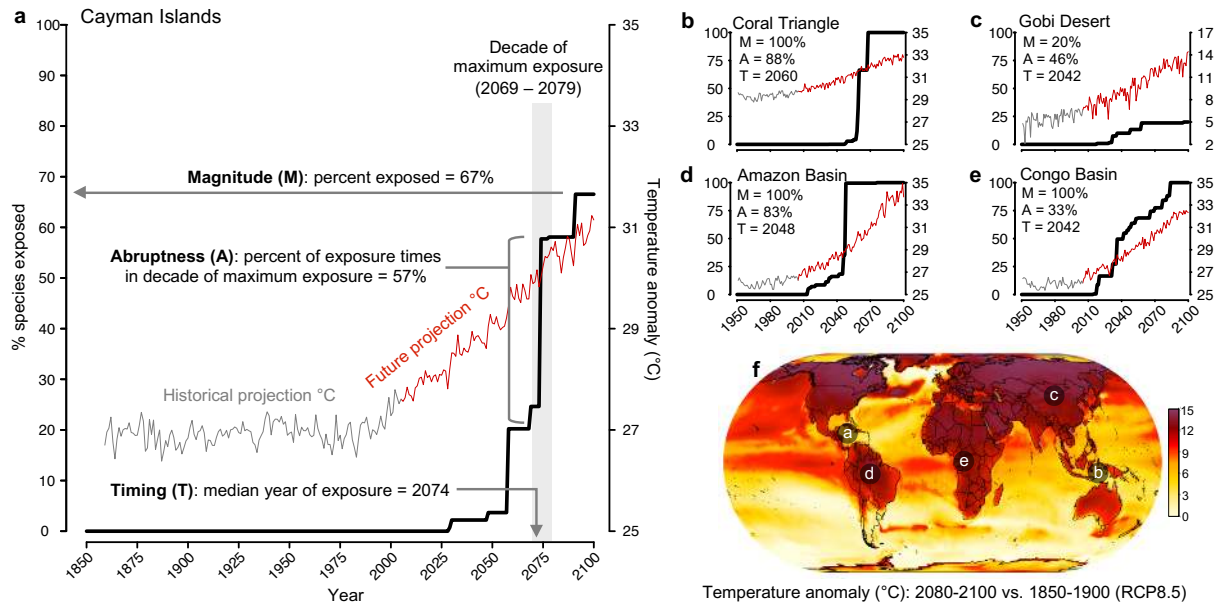
342
343 **Figure 1. Biodiversity climate horizon profiles.** Profiles (solid black lines) indicate the
344 cumulative percent of species in an assemblage exposed to future temperatures (red line)
345 beyond their realised thermal niche over time. Iconic ecosystems provide examples of
346 different profile shapes; **a**, Cayman Islands, **b**, Coral Triangle, **c**, Gobi Desert, **d**, Amazon Basin
347 and **e**, Congo Basin (see **f**, map of temperature anomalies for locations). Horizon profiles and
348 temperature trends are shown for a single run of the Hadley Centre Global Environmental
349 Model (HadGEM2) under a high greenhouse gas emissions scenario (RCP8.5). Timing,
350 magnitude and abruptness define differences among profiles. Grey line shows historical
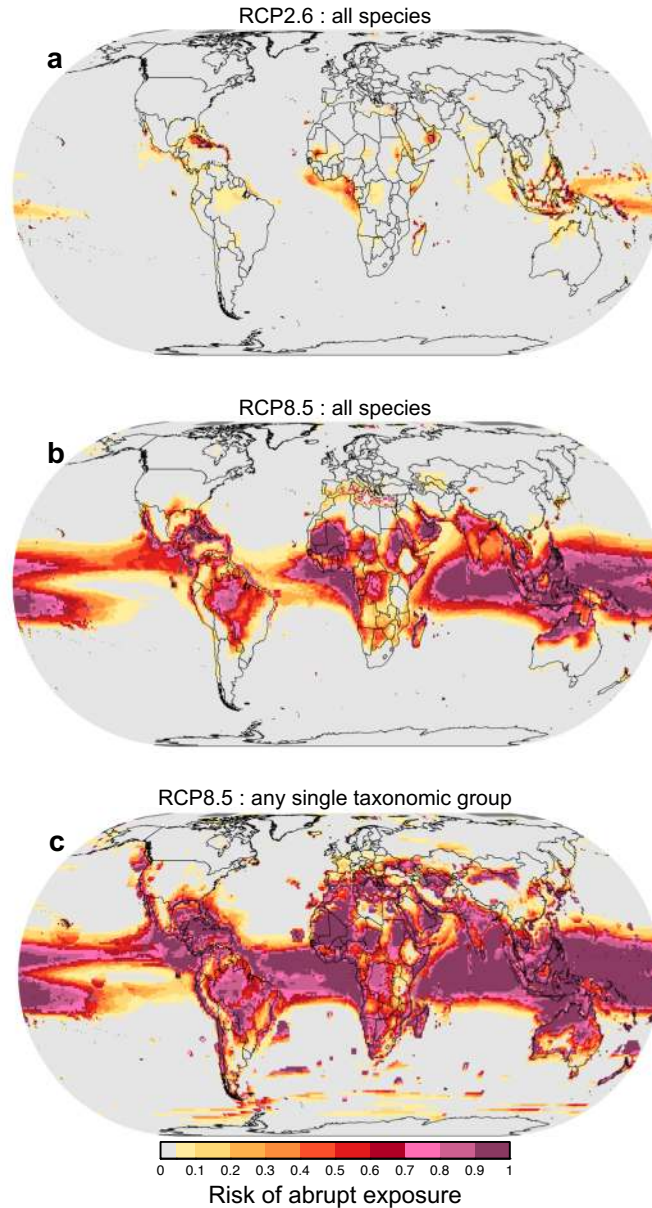351 temperature projections at a site.

352
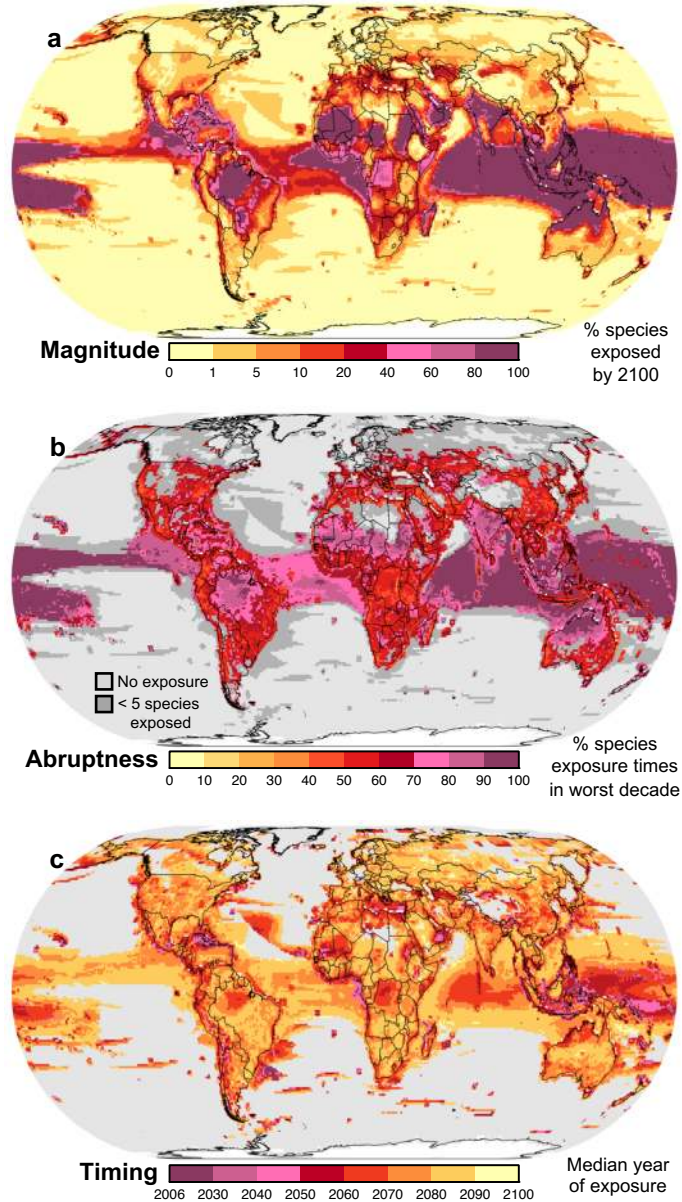
Figure 2. Global variation in the magnitude, abruptness and timing of horizon profiles. a, magnitude of exposure indicating the percent of species in 100km resolution grid cells (i.e., assemblages) exposed to unprecedented temperature (i.e., beyond each species' realised niche) by 2100. **b**, abruptness 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).

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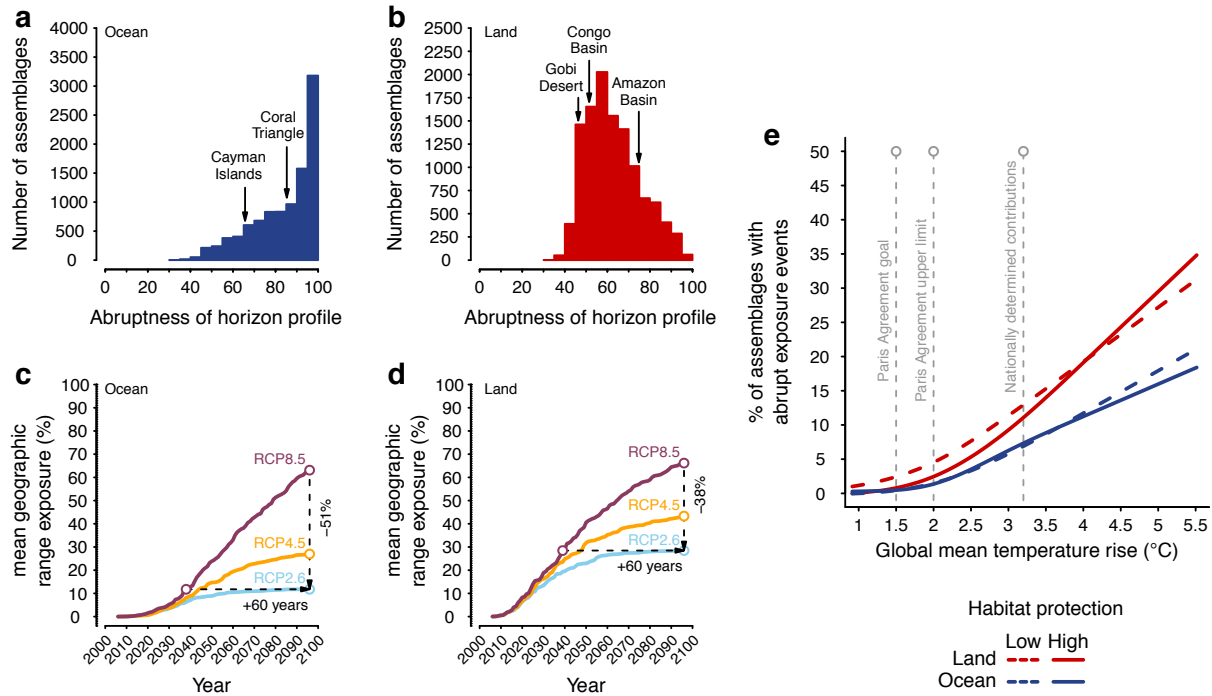
Figure 3. Abruptness of horizon profiles locally versus globally, and accelerating risk with global warming. The distribution in the projected abruptness of species exposure to unprecedented temperatures within marine and terrestrial assemblages (**a**,**b**). Selected assemblages from Fig. 1 are highlighted. 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 (**c,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 ~60 years for species and conservation plans to adapt to a warming climate (see Extended Data Fig. 8 for individual climate models). **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.

12

RCP2.6 : all species

RCP8.5 : all species

RCP8.5 : any single taxonomic group

0   0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9   1
Risk of abrupt exposure

376

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.

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386

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 International[40], 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 krill[41] and cephalopods[42], reflecting the availability of expert range maps for oceanic species[43]. 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 distributions[46], 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 vertebrates[2], 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 change[47].

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,

432 climate model data were regridded to a 100-km resolution grid using an area-weighted
433 mean interpolation. Climate data interpolation was done in CDO[48] and R[49].
434   We calculated species exposure times for each assemblage using individual climate
435 simulations, as opposed to ensembles or multi-model averages, because individual
436 simulation runs include variance in climatic time series due to internal climate variability
437 such as the timing of El Niño–Southern Oscillation events[22,50]. This internal variability is a
438 key component of the uncertainty in the timing of exposure, and is smoothed out if using
439 multi-model averages as input into the analysis. By calculating species exposure events
440 using individual model simulation runs and then summarising across models, we capture
441 the uncertainty in the timing of exposure due to both internal climate variability and
442 climate model uncertainty (i.e., uncertainty about climate physics across models), in line
443 with 'time of emergence' analyses from climate science[19]. Throughout, we report multi-
444 model medians in each of our summary metrics.
445
446 **Defining species realised niche limits.** Species experience variability in climatic
447 conditions across both space and time but this temporal variability is ignored when using
448 time-averaged climate conditions (e.g., Worldclim data[51]) to estimate species realised
449 niches. To address this, we estimated species realised niche limits using the climate
450 projections from the historical run of each climate model (1850–2005), which includes the
451 influence on climate of observed changes in radiative forcing due to natural factors such as
452 volcanic eruptions, as well as anthropogenic emissions and land use changes[52]. Thus, in the
453 case of MAT, we calculated the maximum MAT experienced across the species geographic
454 range over both space and time ($Tmax_{MAT}$, see Supplementary Information). To prevent
455 estimates of $Tmax_{MAT}$ being inflated by either extreme outliers in the temperature time
456 series or from the overestimation of species ranges[44], we excluded outlier temperature
457 values within each grid cell, defined as those more than three standard deviations from the
458 mean. Once we had selected the maximum temperature for each cell, we excluded outlier
459 temperature values across each species range, defined as those more than three standard
460 deviations above the mean range value. The $Tmax_{MAT}$ value for each species was then set as
461 the maximum of the remaining values (Supplementary Fig. 1). We used an identical
462 procedure to calculate Tmax using MMT ($Tmax_{MMT}$). For precipitation, species may be
463 exposed to either drying or wetting conditions and so we calculated both the minimum
464 (Pmin) and maximum (Pmax) precipitation value experienced by each species across its
465 geographic range (see Supplementary Information).
466
467 **Estimating species exposure times.** Within each terrestrial (n = 18560) and marine (n =
468 37333) assemblage (i.e. 100 km grid cell containing any terrestrial or marine species
469 respectively), we defined the time of local species exposure to unprecedented temperature
470 (i.e. the 'climate horizon') to be the year after which the MAT (or MMT) of the cell is
471 projected to exceed the species's $Tmax_{MAT}$ (or $Tmax_{MMT}$) value for at least five consecutive
472 years. We note that using a higher number of consecutive years (n = 20 years) had little
473 effect on the magnitude, timing or abruptness of exposure (Supplementary Figs. 2 and 3).
474   For precipitation, we calculated the time of local species exposure as the year after
475 which the precipitation of the cell is projected to be either above or below the species'
476 Pmax and Pmin values respectively for at least five consecutive years. Annual precipitation
477 values are bounded at zero and this could potentially lead to exposure being

478 underestimated for locations projected to have historically received zero precipitation. To
479 address this, we additionally defined exposure when annual precipitation fell below 15mm
480 for at least five consecutive years. Due to the generally weaker trends and high variability
481 in historical and future projected precipitation, we found that few species were exposed to
482 unprecedented precipitation regardless of how exposure was defined (Extended Data Fig.
483 1). To show the importance of increasing temperatures as the primary driver of exposure,
484 we compared patterns of exposure from MAT alone to those from MAT and precipitation
485 combined, recording the earliest local exposure time of either MAT or precipitation for a
486 species in an assemblage when it was exposed to both variables (Extended Data Fig. 2g-i,
487 see Supplementary Information).
488   We note that by using range-wide estimates of species niche limits, we may
489 underestimate both the magnitude and immediacy of exposure if populations are locally
490 adapted[33]. Unfortunately, information on the scale and strength of local adaptation is not
491 generally available across species. Equally, our analysis does not attempt to model adaptive
492 evolution, which may enable species to shift or expand their climatic niche limits over time.
493 Nevertheless, our estimates of the timing of local exposure to unprecedented conditions
494 may be relevant for understanding the potential for evolution to rescue populations from
495 changing climates[10,11].
496
497 **Horizon profiles**. Once species exposure times had been calculated for an assemblage we
498 constructed a horizon profile indicating the cumulative percentage of species locally
499 exposed to conditions beyond their realised niche limits. We used the following metrics to
500 summarise the temporal dynamics of biodiversity exposure. First, we calculated the
501 magnitude of exposure as the percent of species in the assemblage exposed over the course
502 of the 21st century. Second the abruptness of exposure for an assemblage was calculated as
503 the percent of all exposure times that occur in the decade of maximum exposure. We
504 identified the decade of maximum exposure using a moving window of ten years. We also
505 calculated an alternative metric of abruptness based on the Shannon-entropy index[53],
506 which quantifies the evenness in the distribution of exposure times across all years of the
507 horizon profile (Extended Data Fig. 4). In contrast to our original abruptness metric, lower
508 values of the Shannon-entropy index indicate a more abrupt profile. We therefore rescaled
509 the Shannon-entropy index by the maximum possible entropy value per assemblage,
510 subtracted these values from 1 and then multiplied by 100 to give an index ranging
511 between 0 and 100, where a value of 100 indicates that all exposure times occur in a single
512 decade and a value of 0 corresponds to an equitable distribution of exposure times across
513 years. Abruptness was only calculated for assemblages where five or more species were
514 exposed to avoid idiosyncrasies due to small sample sizes. Third, the timing of exposure for
515 each assemblage was calculated as the median of the times of local species exposure
516 events. Species not exposed before the end of the 21st century were excluded from this
517 calculation. We repeated our analysis using alternative metrics of timing, including the
518 mean year of exposure and the mid-point of the decade of maximum exposure, obtaining
519 very similar results (Extended Data Fig. 6). For each of these exposure metrics we report
520 the median value across the 22 climate models for a given climate scenario, and quantify
521 uncertainty as the standard deviation (Extended Data Fig. 3). The greatest uncertainty in
522 projected impacts involves the magnitude of exposure along the boundaries of the tropics.
523 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.

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 resolution[51]. We found that abruptness is negatively correlated with the spatial heterogeneity in temperature within a cell (Spearman's ρ = -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 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 (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 pre-industrial 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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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.

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 https://www.iucnredlist.org/resources/spatial-data-download and

672   http://datazone.birdlife.org/species/requestdis. Climate change projections for RCPs 8.5,
673   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
675   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.
692 Values are the median across 22 CMIP5 climate models under RCP8.5, with hotter colors
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
718 species with nowhere warmer within 1000km of their range. Values are the median across
719 22 CMIP5 climate models under RCP8.5. Hotter colors indicating a higher density of points.

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 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 exposure (years).

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 later in the century.

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 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 populations (i.e. large geographic ranges). Variability in exposure across 22 climate models (thin lines) is shown for each RCP scenario (median, thick line).

Extended Data figure 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 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 especially high (RCP8.5) emission pathways, and when considering taxonomic groups separately

Extended Data figure 10. Abruptness of horizon profiles for terrestrial vertebrates in 100km grid cells with low (red, 1st quantile) or high (grey, 4th quantile) spatial temperature heterogeneity. Abruptness is calculated as the % of species exposure times in the decade of maximum exposure. Temperature heterogeneity is the range in temperatures at 1km resolution within each 100km cell. Assemblages with abrupt exposure have lower temperature heterogeneity suggesting that quantifying species niches at finer spatial resolutions is unlikely to alter the abrupt nature of assemblage exposure dynamics.