

1 **Title: Abrupt expansion of climate change risks for species globally**

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10 **Abstract**

11 **Climate change is already exposing species to dangerous temperatures driving**
12 **widespread population and geographic contractions¹⁻⁶. However, little is known**
13 **about how these risks of thermal exposure will expand across species existing**
14 **geographic ranges over time as climate change continues. Using geographic data for**
15 **~36,000 marine and terrestrial species and climate projections to 2100, we show**
16 **that the area of each species' geographic range at risk of thermal exposure will**
17 **expand abruptly. On average, >50% of the increase in exposure projected for a**
18 **species will occur in a single decade. This abruptness arises partly due to the rapid**
19 **pace of future projected warming but also because the greater area available at the**
20 **warm end of thermal gradients constrains species to disproportionately occupy sites**
21 **close to their upper thermal limit. These geographical constraints on the structure of**
22 **species ranges operate both on land and in the ocean and mean that, even in the**
23 **absence of amplifying ecological feedbacks, thermally sensitive species may be**
24 **inherently vulnerable to sudden warming driven collapse. With higher levels of**
25 **warming, the number of species passing these thermal thresholds, and at risk of**
26 **abrupt and widespread thermal exposure increases, doubling from <15% to >30%**
27 **between 1.5°C and 2.5°C of global warming. These results indicate that climate**
28 **threats to thousands of species are expected to expand abruptly in the coming**
29 **decades—highlighting the urgency of mitigation and adaptation actions.**

30 **Main text**

31 **Introduction**

32 Species are increasingly being exposed to dangerous temperatures, driving mass die-offs,
33 population declines, and contractions at the warm edges of their geographic range¹⁻⁷. As
34 global warming continues, the area over which species are adversely impacted by thermal
35 exposure will expand, increasing the risks of local and global extinctions^{8,9}, and disrupting
36 the functioning and stability of the ecosystems these species form and on which society
37 depends¹⁰.

38 Critical to understanding and managing these climate risks, is how the spatial
39 footprint of thermal exposure will expand across a species' geographic range over time.
40 Because climate change will unfold over decades to centuries, the expansion in the area over
41 which a species is at risk of thermal exposure may also be protracted¹¹. A gradual spread of
42 thermal risks would provide more time for species to adapt via dispersal¹² or evolution¹³,
43 and more opportunity to implement conservation interventions and adaptation policies
44 once the adverse effects of thermal exposure are first detected. While the gradual spread of
45 risk could pose a potential challenge for existing vulnerability assessments—which typically
46 consider population and range declines over much shorter time horizons (e.g. a single
47 decade^{14,15})—a greater concern is the possibility that future climate risks to species will
48 expand suddenly, impacting widespread areas across a species' geographic range almost
49 simultaneously¹⁶⁻¹⁸. An abrupt expansion in the area of a species' geographic range at risk of
50 thermal exposure, could overwhelm the ecological and evolutionary processes that might
51 otherwise provide resilience to species and ecosystems under more gradual environmental
52 change^{19,20}, and would limit the capacity for timely conservation actions²¹. Determining
53 whether there are thresholds of warming beyond which risks of thermal exposure to species
54 rapidly expand—and predicting where and when these thresholds will be crossed—is
55 essential for improved early warning systems to assist conservation and adaptation
56 planning, and for informing international policy to mitigate climate change.

57 To understand the risks to species from abrupt thermal exposure, we used global
58 climate models to project the cumulative area of individual species existing geographic
59 ranges that will be exposed to potentially dangerous temperatures up to 2100 (at ~100km

60 grid cell resolution, see Methods). Our analysis encompasses geographic data on 35,863
61 species, from both terrestrial ($n = 31,790$) and near-surface marine ($n = 4,073$)
62 environments, including: mammals, amphibians, reptiles, birds, corals, cephalopods, reef
63 fish, seagrasses and zooplankton (Extended Data Table 1). While species will be adversely
64 impacted by exposure to multiple abiotic and biotic variables we focus our analysis on
65 temperature, which provides a universal driver of species distributions across both marine²²
66 and terrestrial²³ realms, and thus a logical starting point for understanding the
67 spatiotemporal dynamics of climate change risks to species. We do not consider processes
68 of evolutionary adaptation, changes in phenology and behaviour or dispersal to new
69 locations. While these processes will determine the resilience of species to climate change,
70 here we focus on the first key step of understanding the spatial and temporal dynamics of
71 thermal exposure that will ultimately drive these biological responses.

72 The adverse impacts of thermal exposure (e.g. declines of fitness or increased
73 mortality) are likely to be driven by the increasing intensity and frequency of extreme
74 temperatures rather than changes in long term climate averages^{24,25}. Here we define thermal
75 exposure as the year after which the annual maximum monthly air or sea surface
76 temperatures in a grid cell consistently (for at least 5 consecutive years) exceeds the most
77 extreme monthly temperature experienced by a species across its geographic range over
78 recent history (1850-2014), hereafter, its 'upper realised thermal limit'¹⁰ (see Methods). We
79 focus on an intermediate greenhouse gas (GHG) emission scenario (SSP2-4.5),
80 corresponding to $\sim 2.5^{\circ}\text{C}$ global warming by the end of the century, relative to the pre-
81 industrial period (1850-1900). This is approximately the level of warming expected if
82 countries meet the 2030 targets in their nationally determined contributions (NDCs at the
83 time of CoP26)²⁶. We also explore how the dynamics of thermal exposure vary under both
84 lower (SSP1-2.6) and higher (SSP5-8.5) GHG emission scenarios and thus global warming
85 levels.

86 We quantified how gradually or abruptly the spatial extent of thermal exposure is
87 projected to expand over time using a moving window analysis to calculate the maximum
88 percent of grid cell exposure events occurring in any decade for each species (Extended Data
89 Fig. 1)¹⁰. We additionally calculated the magnitude of exposure, that is, the total proportion

90 of the species' geographic range exposed this century (Extended Data Fig. 1). Finally, we
91 calculated the timing of exposure in two ways: (i) the year of onset of exposure and (ii) the
92 median year of grid cell exposure, which for species undergoing abrupt exposure, captures
93 well the timing of these abrupt events (Extended Data Fig. 1). Together the abruptness,
94 magnitude and timing of exposure describe key independent dimensions of climate change
95 risk for a species.

96

97 **Results**

98 **Spatiotemporal dynamics of thermal exposure**

99 Species exhibit three distinct spatial patterns in the projected expansion of thermal
100 exposure, determined by the spatiotemporal dynamics of future warming and the
101 distribution of a species' geographic range across thermal gradients (Fig. 1). First, grid cells
102 in a species' geographic range projected to experience more rapid warming this century are
103 exposed earlier than those where warming is projected to occur more gradually (Extended
104 Data Fig. 2a). Second, grid cells with a small warming tolerance—defined here as the
105 difference between the 'current' temperature (2005-2014 mean) of a grid cell and the
106 species' rangewide upper realised thermal limit—are exposed earlier than grid cells where
107 the warming tolerance is larger (Extended Data Fig. 2b). Third, projected thermal exposure
108 will not occur gradually. Instead, over the coming decades, trends of increasing thermal
109 exposure are characterised by periods of relative stability punctuated by sudden pulses,
110 where large numbers of grid cells across a species' geographic range are exposed in a narrow
111 window of time, with these pulses occurring at different times for different species (Fig. 1).

112 An abrupt expansion in the area at risk of thermal exposure is a pervasive pattern
113 across species geographic ranges. On average, 57% (mean \pm 15% s.d.) of the exposure
114 projected for a species this century will occur in a single decade under SSP2-4.5, with similar
115 levels of abruptness under both higher and lower GHG emission pathways (Fig. 2a). Despite
116 the contrasting physical environments in which species occur, the expansion of thermal
117 exposure risks is projected to occur abruptly for both terrestrial (mean = 58% \pm 16% s.d.)
118 and marine species (mean = 51% \pm 11% s.d.), across all studied organism groups—from
119 reptiles to zooplankton—and regardless of whether species are widespread (> the median

120 range size of 34 grid cells; mean = 58% \pm 15% s.d.) or geographically rare (< 34 grid cells;
121 mean = 56% \pm 15% s.d.). Moreover, abrupt thermal exposure occurs regardless of whether
122 a species' geographic range is only partially (<25% grid cells; mean = 55% \pm 13% s.d.) or
123 widely exposed (\geq 75% grid cells; mean = 56% \pm 15% s.d.) and whether exposure on average
124 happens early (<2050; mean = 66% \pm 18% s.d.) or late (\geq 2050; mean = 53% \pm 13% s.d.) in
125 the century (Extended Data Fig. 3). Some degree of synchronicity in the timing of thermal
126 exposure among grid cells could arise by chance. However, for almost all species (88%), the
127 spatial extent of thermal exposure expands more abruptly than expected if exposure events
128 within a species' geographic range occur independently over time (Fig. 3j) (Methods).

129 The timing and magnitude of exposure varies substantially across species—while
130 some species are projected to experience minimal thermal exposure by the end of the
131 century, others experience an almost immediate onset of exposure that spreads across their
132 entire geographic range (Fig. 2b-c, Extended Data Fig. 3). Under SSP2-4.5, 52% of species are
133 projected to experience thermal exposure before 2050 (Fig. 2b), with 34% of species
134 exposed across at least 30% of their geographic range by the end of the century (Fig. 2c). The
135 time between the initial onset of thermal exposure for a species and the median year of
136 exposure across its geographic range is on average 12 years (mean \pm 12s.d), indicating that
137 once exposure commences there is only a limited window of time before the area at risk
138 expands abruptly (Fig. 2b).

139

140 **The drivers of abrupt thermal exposure**

141 One possible explanation for the pervasive abruptness of thermal exposure is that the
142 relatively coarse spatial grain size (100km) of global climate models underestimates spatial
143 variability in rates of warming and thus heterogeneity in the timing of future exposure
144 across grid cells. However, this seems unlikely because we found similar levels of
145 abruptness when repeating our analysis on a subset of species using regional climate
146 models that generate projections at a finer spatial resolution (20km) (Supplementary
147 Figure 1).

148 Another potential explanation is that abrupt thermal exposure is driven by the rapid
149 pace of future climate change—both in terms of the long-term warming 'press' and short-

150 term ‘pulses’ of extreme conditions²⁷—relative to the range of temperatures species have
151 occupied in recent history. To quantify the effect of rapid climate warming on future
152 exposure dynamics, we performed a computational experiment in which we manipulated
153 the future temperature time series (Fig. 3a-d) and recalculated the abruptness of projected
154 thermal exposure (Fig. 3e-h, see Methods).

155 First, smoothing the future temperature time series to remove extreme year-to-year
156 variability (Fig. 3b,f), results in a consistent reduction in projected abruptness from on
157 average 57% to 48% ($\pm 13\%$ s.d.) of grid cell exposure events for a species occurring within
158 a single decade (Fig. 3i). Second, smoothing and slowing the long-term warming trend—so
159 that the average warming across a species’ geographic range projected by 2100 is only
160 reached in 2500 (a factor of 5 downgrading of the warming trend, Fig. 3c,g)—results in a
161 further reduction in projected abruptness (mean abruptness = $22\% \pm 9\%$ s.d., Fig. 3i).
162 However, even after removing the short-term ‘pulse’ and reducing the long-term ‘press’ of
163 future warming, the abruptness of thermal exposure for 51% of species still exceeds a null
164 model expectation for abruptness in which grid cell exposure events occur independently
165 over time (Fig. 3j). Thus, neither the pulse nor the rapid press of future climate change is
166 sufficient to explain abrupt expansions in the area of species’ existing geographic ranges
167 projected to be at risk of thermal exposure over the coming decades.

168 Instead, we found that the underlying driver of abrupt thermal exposure is the
169 ubiquitous skew in the distribution of temperatures across a species’ geographic range (Fig.
170 4, see Methods). Within a species’ geographic range, most grid cells have relatively narrow
171 warming tolerances, that is, they currently experience maximum monthly temperatures
172 close to the species’ rangewide upper realised thermal limit. On average, 65% of a species’
173 geographic range lies in the hottest half of the realised thermal niche, with 27% of the
174 geographic range concentrated within only 10% of the thermal niche. Similar levels of warm-
175 skewness are observed across the geographic ranges of both terrestrial and marine species
176 (Extended Data Fig. 4). This clustering and skew in grid cell warming tolerances means that
177 even when the climate warms gradually, multiple grid cells across a species geographic range
178 are projected to experience thermal exposure near synchronously. Artificially removing this
179 effect by simulating a scenario in which grid cell warming tolerances are evenly spaced

180 between the hottest and coldest conditions occupied by a species (Fig. 3d,h), leads to thermal
181 exposure across a species geographic range accumulating more gradually (Fig. 3i, mean
182 abruptness = $18\% \pm 9\%$ s.d.) and at a rate that is consistent with a null model of random
183 independent exposure across the majority (84%) of species (Fig. 3j).

184 The warm-skewed structure of species geographic ranges is evident for both
185 simulated climate and interpolated observed weather data (Extended Data Fig. 4), and
186 mirrors the warm-skewed distribution of air and sea-surface temperatures available
187 globally (Extended Data Fig. 5). Within most terrestrial regions, area declines with increasing
188 elevation from warm lowlands to cold highlands²⁸. Over larger spatial extents, the warm-
189 skewed distribution of air and sea-surface temperatures arises because latitudinal bands
190 cover a smaller area towards the poles and because of the relatively flat meridional
191 temperature gradient across the tropics, compared to the narrower isotherms at high
192 latitudes²⁹. The greater area available at the warm end of thermal gradients has long
193 provided a core explanation for latitudinal and elevational gradients in global
194 biodiversity^{29,30}. Our study suggests that this basic geometry of the planet also causes the
195 distribution of temperatures across species geographic ranges to be skewed towards hotter
196 conditions, making species vulnerable to abrupt thermal exposure even when the climate
197 warms gradually. Simulations using a spreading dye algorithm (see Methods) support this,
198 showing that when species sample grid cells at random across the land or seascape, species
199 geographic ranges are expected to be strongly warm-skewed, matching very closely the
200 pattern observed in the empirical data (Extended Data Fig. 6).

201

202 **Abrupt exposure risks under increased global warming**

203 Because different GHG emission scenarios lead to similarly high rates of warming over the
204 next two decades, thermal exposure expands abruptly (Fig. 2a) and with similar timing
205 (Fig. 2b) irrespective of the future emission pathway (Supplementary Figure 4). The major
206 effect of GHG emissions—and thus the magnitude of 21st century global warming—is to
207 drastically change the magnitude (that is, the area of species' existing ranges at risk) of
208 thermal exposure (Fig. 2c). Under intermediate (SSP2-4.5) and high (SSP5-8.5) emission
209 scenarios, global temperatures increase throughout the century, driving a high magnitude

210 of exposure that continues to accumulate for many decades (Extended Data Fig. 3). In
211 contrast, under SSP1-2.6, warming plateaus by the middle of the century. This shorter
212 duration of warming under SSP1-2.6 constrains thermal exposure to occur relatively more
213 abruptly than in higher emissions scenarios as only those grid cells with a narrow warming
214 tolerance are projected to become exposed, but the total area of any species' existing range
215 at risk of these abrupt exposure events is reduced.

216 For any given GHG emission scenario, species with early, abrupt and widespread
217 thermal exposure could be expected to be especially at risk. The species-level approach
218 presented here that integrates abruptness, timing and magnitude of exposure could
219 increase the saliency of climate change risk information for assessing threats to species,
220 such as for the IUCN Red List, that often require information on both the extent and near-
221 term timing of a threat¹⁵. Indeed, our analysis suggests that the area at risk of thermal
222 exposure will expand abruptly for species assessed by the IUCN as threatened by extreme
223 temperatures (Fig. 5).

224 Comparing the dynamics of exposure across all combinations of climate models and
225 GHG emissions pathways, reveals that the number of species at risk of thermal exposure
226 events of both high magnitude and abruptness increases rapidly with the level of global
227 warming (Fig. 5a). For instance, at 1.5°C of warming, 15% of species are at risk of
228 experiencing exposure across at least 30% of their existing geographic range in a single
229 decade, but this doubles to 30% of species at 2.5°C of warming. This increase in risk is
230 continuous, so that every fraction of a degree of warming that can be avoided reduces the
231 number of species passing thermal thresholds leading to abrupt and widespread exposure.
232 These results provide evidence that failure to achieve the Paris Agreement climate goals of
233 limiting global warming "well below" 2°C, will substantially increase the risk of sudden
234 biodiversity losses.

235 Our model assumes that exposure occurs when temperatures consistently exceed
236 the hottest conditions across a species' geographic range over recent history. However, for
237 organisms where populations are adapted to local thermal regimes, such as some reef
238 building corals³¹, the departure from the bounds of local climate variability may be a more
239 appropriate metric of exposure than those based on species range-wide thermal limits.

240 Modifying our model to allow strong local adaptation across space (but not over time),
241 results in a dramatically steeper increase in the number of species at risk of widespread
242 and abrupt thermal exposure (Fig. 5a, Methods). Even at current levels of global warming
243 (~1.1°C), this model predicts that locally adapted species are at immediate risk of sudden
244 and widespread thermal exposure, consistent with the mass bleaching and mortality of
245 corals already occurring over wide geographic areas¹⁷ and the ubiquitous long-term
246 degradation of coral reefs projected to occur by 2°C global warming in the absence of
247 strong thermal adaptation over time³².

248 While strong local adaptation in space greatly increases risks, other factors could lead
249 to risks from thermal exposure being overestimated in our models. In particular, many
250 species will be limited by environmental²³ or biotic³³ factors other than temperature and
251 have fundamental thermal tolerances that exceed their upper realised limit^{4,34}. Species can
252 also be buffered against warming (at least temporarily) by behaviours to exploit cooler
253 microclimates³⁵, changes in phenology^{36,37}, the evolution of higher thermal tolerance^{13,32}, or
254 the contraction of populations into thermal refugia³⁸, such as higher elevations on land or
255 greater depths in the ocean. Thus, while the abruptness of projected thermal exposure is a
256 ubiquitous phenomenon, occurring across all terrestrial and marine organisms we studied,
257 our simple temperature based model of exposure will not be equally useful in understanding
258 climate risks for all species³⁹. However, uncertainty in thermal tolerances and heterogeneity
259 in responses to thermal exposure is unlikely to alter our conclusion that thermal risks will
260 expand abruptly across species existing geographic ranges under future warming. Repeating
261 our analysis using only those terrestrial ($n = 240$) and marine ($n = 866$) species in our sample
262 assessed by the IUCN as threatened by extreme temperatures (see Methods), leads to a
263 similar estimate of the acceleration in the risk of abrupt thermal exposure under future
264 warming (Fig. 5b-c). For these species at least, we can be more confident that increasing
265 thermal exposure will adversely impact existing populations, and our analysis suggests that
266 these risks will expand abruptly over the coming decades.

267

268 **Discussion**

269 **A new expectation for abrupt climate risks to biodiversity**

270 With continued global warming, the risk of passing tipping points leading to major and
271 irreparable disruption to key elements of the Earth system will increase⁴⁰. These tipping
272 points are characterised by positive feedback loops that can translate relatively gradual
273 changes in forcing conditions into a nonlinear and sometimes rapid shift in the state of the
274 system. Such amplifying feedbacks also characterise ecological tipping points, including the
275 collapse of populations (e.g. fisheries) and switching of ecosystems between alternative
276 stable states (e.g. Amazon forest dieback)⁴¹.

277 Our results on the dynamics of thermal exposure for thousands of species provide an
278 additional mechanism for a nonlinear increase in the magnitude of ecological disruption with
279 future warming—one that does not require amplifying feedbacks. While one might expect
280 that, in the absence of ecological or evolutionary dynamics, a linear rate of warming would
281 result in a linear increase in the area of a species' geographic range at risk of thermal
282 exposure, we show that this expectation may be incorrect. Instead, the warm-skewed
283 structure of species geographic ranges, means that as the climate warms, large numbers of
284 localities which currently share similar thermal conditions will exceed the thermal tolerance
285 of a species at similar times in the future, resulting in an abrupt expansion in the area that is
286 thermally exposed, even when temperatures rise at a constant rate. This result may be
287 informative not only for predicting threats from ongoing and future climate warming but
288 also for understanding the causes of abrupt collapses of populations in response to past
289 environmental change⁴².

290 Our models focus on the area of species' existing geographic ranges exposed over
291 time, and do not consider spatial variation in abundance⁴³ which could either reduce or
292 magnify risks of thermal exposure. If abundance is also skewed towards species' upper
293 thermal limits⁴⁴, these populations may be more resilient to exposure. Alternatively, such
294 skewed abundance could mean that climate risks to species—in terms of the total number
295 of individuals exposed—will increase even more abruptly than expected based on species
296 presence alone.

297 Variation in the steepness of thermal gradients across space is understood to be an
298 important factor determining the velocity of climate change, that is, the rate at which species
299 must disperse to track changing climates⁴⁵. For a given magnitude of warming, regions with

300 shallow thermal gradients across space require faster rates of dispersal than those where
301 spatial thermal gradients are steep. However, metrics of climate change velocity do not
302 indicate when thermal limits are likely to be exceeded or how the risks of thermal exposure
303 spread across a species' geographic range over time, and in particular whether this will occur
304 at a constant rate or in sudden pulses. Our results show that thermal exposure is expected
305 to expand in sudden pulses across species geographic ranges.

306 Here we do not attempt to project where species may potentially disperse to in the
307 future. While expansion at cold-range margins is critical to understanding range shifts⁵ and
308 risks of global extinction for a species¹², the climate driven decline or loss of local populations
309 arising from thermal exposure will cause disruption to the integrity and stability of
310 ecosystems regardless of the species' ability to disperse elsewhere. Many species also face
311 dispersal constraints and stand to lose more than they gain in range size from climate
312 change⁴⁶, such that abrupt thermal exposure that is widespread across species existing
313 geographic ranges will increase the risk of their global extinction. Sudden and widespread
314 thermal exposure could also impede expansion of species to cooler environments if
315 collapsing populations further limit the capacity for dispersal and evolutionary rescue^{42,47}.

316 The ecological interactions⁴⁸, demographic lags⁴⁹ and evolutionary processes^{36,50} not
317 considered in our models, could variously either delay, dampen or amplify the risk of abrupt
318 collapse in ways that will likely vary across species depending on both their ecology and life
319 history. Thus, rather than providing predictions of the timing and dynamics of local
320 extinction or geographic range loss, our models are best regarded as projections of how
321 climate risks to species existing geographic ranges will expand over space and time. Our
322 findings show that with continued warming, risks of exposure to dangerous thermal
323 conditions are set to expand abruptly across the geographic ranges of thousands of species,
324 highlighting the imperative of pursuing ambitious emission reduction targets to limit global
325 warming well below 2°C. They also highlight the critical need for advanced threat
326 assessments that utilise more refined estimates of species niche limits and finer temporal
327 resolution climate information, to identify both where and when dangerous thresholds for
328 warming will be exceeded for different species and ecosystems.

329 **Methods**

330 **Biodiversity data.** To model the dynamics of thermal exposure across species existing
331 geographic ranges, we combined expert verified geographic range maps for $n = 35,863$
332 species, from both terrestrial ($n = 31790$) and marine ($n = 4073$) environments (Extended
333 Data table 1), with climate model projections. Expert range maps provide the most
334 comprehensive information available on species global geographic distributions⁵¹, but are
335 available for only some well-studied organism groups. Our sample includes birds
336 (<http://www.birdlife.org>), reptiles⁵², amphibians, mammals, marine fish, benthic marine
337 invertebrates, habitat-forming corals and seagrasses (<https://www.iucnredlist.org>), krill⁵³
338 and cephalopods⁵⁴ (Extended Data table 1). We included only native breeding geographic
339 distributions for terrestrial taxa and excluded marine species that are restricted to depths
340 greater than 200 m (the lower limit of the epipelagic zone), as these species are less likely to
341 respond to changes in sea surface temperature. Range maps were converted to 96km
342 resolution equal-area grid cells (i.e. grid cells), the finest resolution justifiable for these data
343 globally without incurring false presences⁵⁵ and approximately matching the native
344 resolution ($\sim 1^\circ$) of simulated climate data.

345
346 **Climate model projections.** We used simulated monthly temperature projections from five
347 General Circulation and Earth System Models (hereafter GCMs) developed for CMIP6
348 (Extended Data table 2). For each model, we downloaded a single projection for near-surface
349 air (TAS) and sea surface temperature (TOS) (both in K and converted to Celsius) for the
350 historical run (1850–2014), as well as SSP1-2.6, SSP2-4.5 and SSP5-8.5 scenarios for the
351 years 2015–2100. Model output was downloaded from [https://esgf-](https://esgf-node.llnl.gov/projects/esgf-llnl/)
352 [node.llnl.gov/projects/esgf-llnl/](https://esgf-node.llnl.gov/projects/esgf-llnl/) (accessed 16th December 2021). Climate model data was
353 regridded to a 96km resolution grid using an area-weighted mean interpolation. Because the
354 adverse effects of thermal exposure are often associated with short-term temperature
355 anomalies rather than long term climate averages^{24,32}, we model the dynamics of exposure
356 according to the temperature of the hottest month each year, hereafter ‘maximum monthly
357 temperature’ (MMT).

358 GCMs provide climate projections at a relatively coarse spatial resolution. An
359 important consideration is the extent to which our conclusions are affected by the spatial
360 grain size of the modelled climate data we use. To address this, we repeated our analysis for
361 a subset of $n = 10,356$ terrestrial species using a Regional Climate Model for South America
362 obtained from the Coordinated Regional Downscaling Experiment (CORDEX)
363 <https://cordex.org>). This model generates dynamically downscaled climate projections at a
364 spatial resolution of 20km, compared to the 100km of GCMs. While the use of different
365 spatial grains and climate models inevitably leads to differences in the timing, magnitude
366 and abruptness of exposure, the overall dynamics were very similar (Supplementary Figure
367 1). For example, under an intermediate GHG emission scenario (SSP5-4.5), the median
368 abruptness of exposure for the species considered in this comparison is 63% and 73% at a
369 100km and 20km resolution respectively (Supplementary Figure 1). Thus, the abruptness of
370 projected thermal exposure that we report is unlikely to be an artefact of the spatial grain at
371 which climates are modelled, at least over the range of grain sizes explored here.

372

373 **Defining species thermal limits and the timing of exposure.** We define thermal exposure
374 as the year after which conditions in a grid cell consistently exceed the upper realised
375 thermal limit of a species. The realised niche describes the range of conditions, over both
376 space and time, under which a species exists. Beyond the realised niche, evidence for the
377 ability of the species to persist in the wild is lacking, leading to, at best, a sizable increase in
378 the uncertainty of species survival and, at worst, an increase in the likelihood the species will
379 be committed to local extinction¹⁰. For each species i , we estimated the upper realised
380 thermal limit $SpeciesMaxMMT_i$ using the MMT projections from the historical run of each
381 climate model (1850–2014) which includes variability due to observed changes in radiative
382 forcing from natural factors (e.g. volcanic eruptions), as well as anthropogenic emissions and
383 land use changes⁵⁶. Specifically, we calculated $SpeciesMaxMMT_i$ by taking the maximum
384 temperature historically experienced at each occupied grid cell j $SiteMaxMMT_j$ and then the
385 maximum of these values across the species' geographic range. To prevent estimates of
386 species thermal limits being inflated by outliers in either the temperature time series or from
387 the overestimation of species geographic ranges⁵⁵, we excluded values more than three

388 standard deviations above the mean value when calculating $SiteMaxMMT_j$ and the
389 maximum $SiteMaxMMT_j$ across the species geographic range. Sensitivity analyses show that
390 the precise way that $SiteMaxMMT_j$ is calculated, including the length of the historical time
391 window or whether outlier temperature values are included, has little effect on the projected
392 dynamics of thermal exposure (Supplementary Figure 2).

393 For each species i , we calculate the timing of thermal exposure of each grid cell j as
394 the year $Year_{ij}$ after which the MMT_j is projected to exceed the $SpeciesMaxMMT_i$ for at least
395 five consecutive years¹⁰. Because of the long-term warming trend under the future SSP
396 scenarios we used, an exposure period of five consecutive years equates to essentially
397 permanent exposure this century. Thus, using longer exposure periods (e.g. a run of 20
398 years) has been shown to have little influence on the timing of thermal exposure¹⁰. We note
399 that using an alternative definition of thermal exposure, based on the first decade where any
400 five years exceed $SpeciesMaxMMT_i$, resulted in very similar projected dynamics
401 (Supplementary Figure 3).

402 We calculated $Year_{ij}$ using individual climate simulations, as opposed to ensembles
403 or multi-model averages, because individual simulation runs include variance in climatic
404 time series due to internal climate variability such as the timing of El Niño–Southern
405 Oscillation events⁵⁷. This internal variability is a key component of the uncertainty in the
406 timing of exposure, and is smoothed out if using multi-model averages as input into the
407 analysis. By calculating $Year_{ij}$ using individual model simulation runs and then summarising
408 across models, we capture the uncertainty in the timing of exposure due to both internal
409 climate variability and climate model uncertainty (i.e., uncertainty about climate physics
410 across models), in line with ‘time of emergence’ analyses from climate science⁵⁸, which
411 identify when in the future local climate departs from the envelope of historical variability.

412

413 **Predicting the timing of thermal exposure within species geographic ranges.** To
414 understand the causes of variation in the timing of exposure across grid cells within a
415 species geographic range, for each species i we fit a linear model predicting $Year_{ij}$ as a
416 function of both the magnitude of 21st century warming at grid cell j

417

418

419

$$420 \quad \Delta MMT_j = \overline{MMT}_{2005-2014_j} - \overline{MMT}_{2090-2100_j}$$

421 and the warming tolerance (WT) at grid cell j ,

422

$$423 \quad WT_{ij} = SpeciesMaxMMT_i - \overline{MMT}_{2005-2014_j}$$

424

425 Here, the WT of a grid cell represents the difference between the current temperature at
426 that grid cell and the species' maximum realised thermal limit, analogous to the warming
427 tolerance calculated for an individual organism based on the difference between the
428 temperature of the organisms habitat and their critical thermal maxima (CT_{max})⁵⁹. We
429 jointly estimated the slope for each of these terms (Extended Data Fig. 2). We excluded grid
430 cells that were not exposed by 2100 and restricted our analysis to species where at least
431 ten grid cells were exposed in order to reliably estimate slopes (Extended Data table 3).

432

433 **Metrics of thermal exposure dynamics.** We summarised the dynamics of thermal
434 exposure using three independent metrics that capture different dimensions of climate
435 risk¹⁰. First, the magnitude of exposure is calculated as the percent of grid cells across the
436 species geographic range exposed by the end of the 21st century (Extended Data Fig. 1).
437 Second, we calculated the timing of exposure for each species in two ways, as (i) the year of
438 the first grid cell exposure time (i.e. onset) and (ii) the median grid cell exposure time
439 (Extended Data Fig. 1). Grid cells not exposed before the end of the 21st century were
440 excluded when calculating the median exposure year. Third, we used a moving window of
441 ten years duration, advancing in annual increments, to quantify the abruptness of exposure
442 as the percent of all grid cell exposure times that occur in the decade of maximum exposure
443 (Extended Data Fig. 1)¹⁰. For a given magnitude of exposure, a higher abruptness score
444 indicates that most of the exposure that takes place is concentrated in a relatively narrow
445 window of time. For each of these exposure metrics we report the median value across the
446 five climate models for a given GHG emission scenario (Extended Data Fig. 3).

447 Metrics of abruptness become less informative when few grid cells are exposed. For
448 example, a species exposed at a single grid cell must necessarily have an abruptness score
449 of 100%, while for a species exposed at two grid cells, abruptness must be 50% or 100%.
450 Using these values would artificially inflate the apparent abruptness of thermal exposure
451 (Extended Data Fig. 7). Sensitivity analysis shows that this effect is negligible when more
452 than ~10 grid cells are exposed and so we used this as a cut-off, only including abruptness
453 scores for species and GCM combinations where exposure occurs across at least 10 grid
454 cells ($n = 14,403$ species under SSP2-4.5, see Extended Data table 3 for sample sizes under
455 different SSP scenarios). Using such an area threshold reduces the number of analysed
456 species, particularly on land where species geographic range sizes are smaller, and under
457 low GHG emission scenarios where the magnitude of exposure is lower (Extended Data
458 table 3). However, we found that the overall distribution of abruptness scores was highly
459 consistent regardless of the cut-off used (from $n = 10$ to 250 exposed grid cells) (Extended
460 Data Fig. 7, Extended Data table 3).

461
462 **Null model of abruptness.** Even if the thermal exposure of grid cells occurred as
463 independent random events, some level of clustering in the timing of exposure events within
464 species would be expected simply by chance. To understand how abruptly thermal exposure
465 would be expected to occur by chance (that is, if exposure events occurred randomly over
466 time), we conducted the following randomization procedure: For each species we randomly
467 sampled, with replacement, years between the first (2015) and final year (2100 or 2500, see
468 below) of the future climate simulation run, keeping the number of grid cells that are
469 exposed fixed at the value projected for that species and GCM combination. We performed
470 200 replicate simulations and calculated the 95% quantile in projected abruptness (i.e. 1-
471 tailed test).

472
473 **Partitioning the cause of abrupt thermal exposure.** To test the factors driving the
474 abruptness of projected thermal exposure we conducted a computational experiment, in
475 which we systematically eliminated each potential cause by manipulating the future
476 warming trend (Fig. 3). First, for each grid cell we removed short-term temperature

477 fluctuations (i.e. inter-annual and decadal) to generate a constant, monotonic trend of
478 increasing temperatures over the 21st century (Fig. 3b). To do this, we assumed a linear
479 increase in temperature between the mean of the first (2004-2014) and final decade (2090-
480 2100) of the century. Second, we downgraded this smoothed future warming trend by a
481 factor of five, so that the level of warming projected to occur by the end of the century (2090-
482 2100, ~2.5°C under SSP2-4.5) is instead not reached until the middle of the millennium
483 (2490-2500) (Fig. 3c). This choice of time period is arbitrary but equates to a slow future
484 rate of warming of ~0.3°C per century (compared to ~1°C of warming since ~1970). Third,
485 in addition to smoothing and downgrading the temperature time series, we eliminated the
486 skewed distribution of grid cell warming tolerances for each species by making the current
487 temperatures $MMT_{2005-2014}$ across grid cells within a species geographic range uniformly
488 distributed between the species' lower and upper realised thermal limit (Fig. 3d). After each
489 of these three steps we recalculated the timing of grid cell thermal exposure events and the
490 projected abruptness of thermal exposure across each species' geographic range (Fig. 3e-i).

491
492 **Skew in grid cell warming tolerances.** For each species, we calculated a number of metrics
493 to describe the uneven distribution of occupied grid cells across the species' realised thermal
494 niche. First, we calculated the proportion of grid cells that are warmer than the midpoint of
495 the realised thermal niche. Second, we divided the species' realised thermal niche into ten
496 equally spaced temperature intervals (ordered from the warmest [interval = 1] to the coldest
497 [interval = 10]) and identified the temperature interval covering the largest area (i.e. number
498 of grid cells) (Fig 4a). When two or more temperature intervals were tied we took the mean
499 interval position and then calculated the median interval position for each species across
500 GCMs. Third, we calculated the skew in grid cell warming tolerances across each species'
501 geographic range, where positive values indicate most grid cells have a narrow warming
502 tolerance and are thus have temperatures close to the species' upper realised thermal limit
503 (Fig 4b). Finally, to illustrate how the density of occupied grid cells varies across the realised
504 thermal niche, for each species we standardised MMT values between 0 (warm edge) and 1
505 (cold edge) and used kernel density estimation accounting for boundary effects⁶⁰
506 implemented in the R⁶¹ package bde⁶² (Fig 4b).

507 To ensure these patterns were not an artefact of using simulated climate data we
508 repeated our analysis using observed weather data on the mean daily maximum air
509 temperature (1970-2000⁶³) and mean sea-surface temperature of the warmest month
510 (2000-2014⁶⁴), both available at 1km resolution (Extended Data Fig. 4). To match the scale
511 of the simulated climate data, we extracted the average air or sea-surface temperature within
512 ~100km grid cells.

513

514 **Geographical constraints on species thermal occupancy.** To describe the background
515 availability of thermal conditions, we calculated the probability density of air and sea-surface
516 temperatures globally at 100km grid cell resolution (Extended Data Fig. 5). We repeated this
517 for both simulated and observed climate data obtaining highly consistent results (Extended
518 Data Fig. 5). For the observed weather data, we also calculated the probability density of
519 temperatures averaged at different spatial grains, from the original 1km resolution up to
520 768km grid cells, obtaining very similar patterns (Extended Data Fig. 5). Thus, the warm-
521 skewed distribution of temperatures globally is not an artefact of the particular spatial
522 resolution employed.

523 To test if the warm-skewed structure of species geographic ranges is consistent with
524 that expected due to the background availability of thermal conditions, we implemented a
525 null model based on a spreading dye algorithm⁶⁵ (Extended Data Fig. 6). This approach has
526 been applied in studies examining the distribution of species richness⁶⁶ and geographic
527 ranges^{23,67} expected in the absence of environmental gradients. Starting from a single
528 randomly selected grid cell within the observed species geographic range, subsequent grid
529 cells are sequentially added until the observed range size is reached. Grid cells are selected
530 at random, but we enforce geographic range cohesion by sampling from those grid cells that
531 are adjacent, in any of the four cardinal directions, to those already selected. We simulate
532 terrestrial and marine species separately, sampling grid cells from their respective domains.
533 For those species distributed across multiple isolated regions (e.g. different continents,
534 ocean basins), each fragment of the species geographic range was simulated separately. For
535 each species we performed 20 replicate simulations. Our simulations thus maintain the
536 observed size, cohesion and approximate position of each species geographic range, but

537 assume that the occupation of grid cells is entirely random⁶⁷. As a result, the distribution of
538 temperatures across a species' geographic range in this model is dependent only on the
539 availability of thermal conditions.

540

541 **Global warming levels and risks of abrupt thermal exposure.** To understand how the
542 risk of abrupt and widespread thermal exposure increases with the magnitude of climate
543 warming, for each combination of GCM and GHG emission scenario ($n = 15$ combinations),
544 we calculated the projected increase in global mean surface temperature (GST) between the
545 pre-industrial (1850-1900) and end of the century (2080-2100), by averaging air
546 temperatures across the land and sea-surface temperatures across the oceans¹⁰. We then fit
547 a generalised additive model to estimate how the percentage of species where at least 30%
548 of their existing geographic range is exposed in a single decade varies as a function of GST
549 (Fig. 5). This 30% threshold is arbitrary, but we note that similar qualitative patterns were
550 obtained when using alternative thresholds (20 - 60%, Supplementary Figure 5). We fixed
551 the % of species passing this threshold to equal zero at 0.84°C, the average GST across
552 climate models at the end of the historical climate run (2006-2014). This model thus
553 assumes that risks of abrupt and widespread thermal exposure only began this century. This
554 is a conservative assumption, given that many species started to experience the adverse
555 effects of warming earlier than this.

556

557 **Species realised thermal limits and the consequences of thermal exposure.** The extent
558 to which $SpeciesMaxMMT_i$ reflects fundamental limits to species persistence—and thus the
559 risk of adverse consequences from thermal exposure—will vary across species. For species
560 where thermal tolerance exceeds the range of conditions previously experienced^{4,34}, thermal
561 exposure (as defined here) may occur without adverse consequences for local populations.
562 For species that had already experienced adverse impacts of warming (e.g. mass
563 mortality^{32,68}, population declines³, local extinctions^{1,2}, range contractions⁴⁻⁶) prior to the
564 year 2014 (that is, the end of the historical climate model run), our estimates of
565 $SpeciesMaxMMT_i$ may overestimate thermal tolerance and thus underestimate risks from
566 thermal exposure.

567 It is beyond the scope of our analysis to determine the number of species where
568 future thermal exposure is more likely to have adverse impacts on populations. However, for
569 the many species where extreme temperatures have already been identified as a threat, we
570 can at least evaluate for these species, how risks from thermal exposure are projected to
571 spread over time. To do this we repeated our analysis using a subset of species where
572 extreme temperatures have been identified as an ongoing or future threat (Fig. 5b,c). The
573 IUCN Red List of threatened species is the most comprehensive index of global species
574 extinction risks⁶⁹. Although the assessment of risk from climate change is recognized as
575 incomplete and biased towards particular groups, for those species where climate change is
576 listed we can be more confident that future climate warming will represent an increasing
577 threat to the long-term survival of populations and the species^{14,15}. Of the species assessed
578 by the IUCN, we extracted those where the IUCN Red List identifies climate change as a threat
579 (level-1 threat classification = 11), regardless of the species' current Red List category ($n =$
580 2485). We restricted our analysis to those species specifically identified as threatened by
581 thermal extremes (level-2 threat classification = 11.3) rather than any other aspect of climate
582 change. We also excluded species where thermal extremes were listed as a 'past threat' that
583 is 'unlikely to return'. In total, $n = 1106$ species in our analysis have thermal extremes listed
584 as a threat. For the majority of these species, thermal extremes are listed as an 'ongoing'
585 threat ($n = 1042$), with a smaller number listed as 'unknown' ($n = 8$), 'future' ($n = 51$) or a
586 'past threat, likely to return' ($n = 5$). We note that for most of these species, the 'severity' (n
587 = 857) and 'scope' ($n = 844$) of the threat posed by thermal extremes, indicating the pace of
588 population decline (severity) and the proportion of the population affected (scope), are not
589 evaluated.

590

591 **Local adaptation and risks of thermal exposure.**

592 Using $SpeciesMaxMMT_i$ assumes that thermal exposure is governed by a single species
593 range-wide thermal limit. However, populations may be locally adapted in space, potentially
594 leading to higher risks of thermal exposure⁷⁰. To consider this possibility, we estimate the
595 risk of abrupt and widespread thermal exposure assuming that populations at each grid cell
596 are perfectly adapted to the local thermal regime (Fig. 5a). In this case, the thermal limit of

597 species i at grid cell j is defined by the maximum MMT experienced at that grid cell
598 $SiteMaxMMT_j$ and $Year_{ij}$ is equivalent to the 'timing of local climate emergence'⁷¹. We
599 aggregated $Year_{ij}$ values across the grid cells occupied by a species to calculate the
600 magnitude and abruptness of exposure across the geographic range. Species are likely to
601 vary in the strength and scale of local adaptation but information required to parameterize
602 this variation is not widely available. Thus, simulations using either $SpeciesMaxMMT_i$ or
603 $SiteMaxMMT_j$ to calculate $Year_{ij}$ provide a best and worst case scenario respectively for
604 risks of thermal exposure based on realised distributions.
605

606 **Data availability**

607 Climate and biodiversity data are freely available for download or on request from the
608 original sources. Data generated for this project is available at DOI:
609 <https://doi.org/10.6084/m9.figshare.19825798>.

610

611 **Code availability**

612 Code to conduct the analysis is available at DOI:
613 <https://doi.org/10.6084/m9.figshare.19825798>.

614

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624

625 **Author Contributions**

626 A.L.P designed and conducted the analyses and wrote the first draft of the article. C.H.T,
627 C.M. and A.W contributed to design, analysis and writing the article.

628

629 **Competing interests**

630 The authors declare no competing financial interests.

631

632 **Figure Legends**

633

634 **Fig. 1. The spatiotemporal dynamics of thermal exposure across species geographic**
635 **ranges.** Contour maps shows the projected timing (i.e. year) of thermal exposure of grid cells
636 across four exemplar terrestrial (**a-b**) and marine (**c-d**) species for a single run of the Whole
637 Atmosphere Community Climate Model (CESM2-WACCM) under an intermediate
638 greenhouse-gas-emissions scenario (SSP2-4.5). For visualisation, spatial patterns of
639 exposure are smoothed across 100km grid cells. Colors indicate the timing of thermal
640 exposure binned into decadal windows, with grey indicating grid cells not exposed by the
641 end of the century. Below each map, 'Horizon profiles'¹⁰ show the cumulative % of grid cells
642 exposed over time within each species' range. The dashed line indicates the pattern expected
643 under a constant rate of exposure. Species shown are (**a**) *Pristimantis malkini*, (**b**) *Telescopus*
644 *beetzi*, (**c**) *Pectinia pygmaeus* and (**d**) *Abudefduf declivifrons*.

645

646 **Fig. 2. The abruptness, timing and magnitude of thermal exposure across species**
647 **geographic ranges.** The distribution of thermal exposure metrics is shown across $n =$
648 35,863 land and ocean species for three global warming scenarios. (**a**) Abruptness is the
649 maximum percentage of grid cell thermal exposure events occurring in any single decadal
650 window during the 21st century. (**b**) Timing is the onset (green) or median (brown) year of
651 grid cell exposure across each species geographic range. (**c**) Magnitude is the % of grid cells
652 across a species' geographic range exposed by the end of the century. For each metric, the
653 median species scores across GCMs are shown for a low (SSP1-2.6), intermediate (SSP2-4.5)
654 and high (SSP5-8.5) greenhouse gas (GHG) emission scenario. To avoid biased estimates of
655 abruptness, in (**a**) only species where at least 10 grid cells are exposed this century are
656 plotted ($n = 14,403$) (see Methods).

657

658 **Fig. 3. Partitioning the causes of abrupt thermal exposure.** (**a-d**) Computational
659 experiments in which (**a**) projected future climate warming trends for each grid cell within
660 a species' geographic range are artificially manipulated to be; (**b**) smoother than projected,
661 (**c**) smoother and more gradual than projected, (**d**) smoother, more gradual, and with grid

662 cell warming tolerances evenly distributed across the species' realised thermal niche. Data
663 used in **a-d**, is for illustration only, showing hypothetical warming trends for six exemplar
664 grid cells. In **(a)** the upper realised thermal limit for a hypothetical species (dashed line) is
665 indicated. Points in **(a-d)** show when in the future each grid cell is thermally exposed **(e-h)**
666 Horizon profiles show the cumulative % of grid cells exposed over time in each experiment
667 for this hypothetical scenario. **(i)** Density curves show the distribution of projected
668 abruptness (%) scores across real species (median across climate models) under an
669 intermediate greenhouse gas emission scenario SSP2-4.5 (grey) and for each experiment.
670 Abruptness is the maximum percentage of grid cell thermal exposure events occurring in any
671 single decadal window during the 21st century. Abruptness is only calculated for species and
672 climate models where at least 10 grid cells are exposed this century ($n = 14,403$ species). **(j)**
673 The % of species in each experiment where abruptness exceeds that expected under a null
674 model in which grid cell exposure events occur independently over time (5%, 1-tailed).

675 **Fig. 4. The warm-skewed structure of species geographic ranges.** **(a)** The top
676 histogram shows the interval (10%) of the realised thermal niche with the highest density
677 of grid cells for each species ($n = 18,714$ species). Only species occurring in at least 30 grid
678 cells are included. Values are the multi-model mean under an intermediate greenhouse-
679 gas-emissions scenario (SSP2-4.5). **(b)** The density distribution of grid cells within species
680 realised thermal niches are shown for a random sample of 2500 species for a single climate
681 model (CESM2-WACCM), coloured according to skew. Species in Fig. 1a-d are highlighted.

682

683 **Fig. 5. Increasing risks of abrupt thermal exposure with the magnitude of global**
684 **warming.** **(a)** The % of species projected to experience abrupt and widespread thermal
685 exposure (i.e. $\geq 30\%$ of their existing geographic range exposed in a single decade) for
686 different levels of global warming ($n = 35,863$ species). Risk is estimated assuming a single
687 range-wide upper thermal limit for a species (solid) or a separate upper thermal limit for
688 each grid cell within the geographic range (dashed), thus assuming that populations are
689 locally adapted to the conditions in each grid cell. Points show the risk across $n = 15$
690 climate model and greenhouse gas emission scenario combinations. Risk for **(b)** terrestrial

691 and (c) marine species separately, and for the species in each realm assessed under the
692 IUCN as threatened by thermal extremes.

693

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