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Geographical limits to species-range shifts are suggested by climate velocity

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1 **Climate Velocity And Geographical Limits To Shifts In Species Distributions** 2 3 Michael T. Burrows^{1*}, David S. Schoeman², Anthony J. Richardson^{3,4}, Jorge García 4 Molinos¹, Ary Hoffmann⁵, Lauren B. Buckley⁶, Pippa Moore^{7,8}, Christopher J. Brown⁹, John 5 F. Bruno⁶, Carlos M. Duarte^{10,11,12}, Benjamin S. Halpern^{13,14}, Ove Hoegh Guldberg⁹, Carrie 6 V. Kappel¹³, Wolfgang Kiessling¹⁵, Mary I. O'Connor¹⁶, John M. Pandolfi¹⁷, Camille 7 Parmesan^{18,19}, William J. Sydeman²⁰, Simon Ferrier²¹, Kristen J. Williams²¹, Elvira S. 8 Poloczanska³ 9 10 11 The reorganisation of patterns of species diversity driven by anthropogenic climate 12 change, and the consequences for humans¹, are not yet fully understood or 13 appreciated^{2,3}. Nevertheless, changes in climate conditions are useful for predicting 14 shifts in species distributions at $global^4$ and local scales⁵. Here we use the velocity of 15 climate change^{6,7} to derive spatial trajectories for climatic niches from 1960 to 2009⁷ 16 17 and up to 2100, and use the properties of these trajectories to infer changes in species distributions. Coastlines act as barriers and locally cooler areas act as attractors for 18 trajectories, creating source and sink areas for local climatic conditions. Climate source 19 areas indicate where locally novel conditions are not connected to areas where similar 20 21 climates previously occurred, thereby inaccessible to climate migrants tracking isotherms: 16% of global surface area for 1960 to 2009, and 34% of ocean for the 22 RCP8.5 "business as usual" climate scenario⁸. Climate sink areas are where climate 23 conditions locally disappear, potentially blocking the movement of climate migrants, 24 1.0% of ocean area and 3.6% of land and prevalent on coasts and high ground. Using 25 26 this approach to infer shifts in species distributions gives global and regional maps of 27 the expected direction and rate of shifts of climate migrants, and suggests areas of 28 potential loss of species richness. By reorganizing natural systems², climate change is poised to be one of the greatest

By reorganizing natural systems², climate change is poised to be one of the greatest threats to biodiversity of this century³, compromising the integrity, goods and services of living systems¹. Increased understanding of how species distributions and persistence are likely to be affected can inform effective conservation under climate change, as part of a range of considerations⁹. Predictions from complex models may incorporate ecological

complexity but come with a high degree of uncertainty¹⁰. A simpler approach is to consider 34 35 the local speed and direction of shifting climate contours as an expectation of how species' distributions would have to shift to track the location of their thermal niches^{6,10}. This is the 36 velocity of climate change^{6,7}: the temporal trend divided by the spatial gradient in a climate 37 variable such as temperature⁶ or precipitation^{10,11}. Land and seascapes have different patterns 38 of climate velocity⁷ and consequential residence times of climate, giving different 39 implications for species' persistence and priorities for conservation¹². Patterns of shifts in 40 distributions of many taxa in the ocean already been shown to follow the velocity of climate⁵. 41

42 Here we use velocity-derived trajectories to indicate global regions susceptible to effects 43 of geographical limits to climate-driven distribution shifts. Climate trajectories are paths that 44 points on an isotherm will travel over specific periods (Fig. 1, see Methods for details), 45 integrating spatially variable speeds and directions of climate velocity along the way to show 46 effects that static velocity maps cannot. Geographical limits to trajectories, either barriers 47 such as coasts and mountains or lack of connections to cooler or warmer environments, suggest limits to climatic niche shifts and, by inference, local species persistence or 48 replacement from warmer environments (Figs 2-3). Velocity fields were derived for 1960-49 2009 for land and ocean surface temperatures⁷ on a 1° grid, allowing inference at a global 50 51 scale, but sacrificing small-scale detail such as thermal minima on mountain tops or sharp gradients associated with ocean fronts¹³. 52

53 We categorized types of trajectory behaviour using trajectory length and the percentages 54 of trajectories starting in, ending in and passing through cells (Fig. 1). Short trajectories 55 indicated non- or slow-moving thermal niches. Cells were classed as relative climate sinks if a 56 high proportion of trajectories terminated there. Absolute climate sinks were also 57 distinguished: *coastal climate sinks* where trajectories were blocked by coasts, and *internal* 58 *climate sinks* where velocities in neighbouring cells converged. Cells were classed as *climate* 59 sources if no trajectories ended there. Thereafter, cells with a high proportion of trajectories passing through were classed as *corridors*. *Divergence* cells were identified as those where 60 fewer trajectories ended than started in that cell, and *convergence* cells if the opposite were 61 62 true.

63 Uncertainty evaluated by bootstrap resampling of annual average temperature maps gave
64 a likely (>66% consistency) designation of types for 59% of ocean and 72% of land cells
65 (Fig. 2 and Extended Data Figs. 2 to 4). Consistency was <66% where spatial gradients and

temperature trends are most uncertain, such as where inter- and multidecadal climate
variability dominates as for the El Niño-Southern Oscillation in the tropical Pacific. Very
likely classification (>90%) was achieved for 40% of land and 26% of ocean cells, mainly
sources, coastal sinks and low velocity areas (Extended Data Fig. 4).

70 The proportions of land and sea areas classed as climate sources and sinks are similar at 71 a global scale (sources: land 17.4%, ocean 15.9%; sinks: land 3.6%, ocean 1.0%), but the latitudinal pattern differs (Fig. 2 and Extended Data Figs 5-9 for regional maps). For ocean 72 73 surface temperatures, climate sources are concentrated within 10° latitude of the Equator 74 (Figs. 2c,d), a pattern not evident on land (Fig. 2a,b). Topographic complexity on land 75 generates more local warm and cold source and sink areas compared to the ocean. 76 Importantly, 12.0% of land trajectories and 5.4% of ocean trajectories terminate in sinks, 77 representing 'lost' local conditions: 6.1% (5.0%) land (ocean) ending in coastal sinks, 5.9% (0.4%) in internal sinks). These losses are analogous to 'disappearing climates'¹⁴ but here 78 79 result from local connections to thermal minima rather than global loss of combinations of 80 climatic conditions.

81 In the ocean, coastal sources form where poleward trajectories depart from coastlines, as in North Africa, and coastal sinks where equatorward coastlines block trajectories, as in 82 83 southern France (Fig. 3a). The opposite occurs on land to a degree: sources on equatorward 84 coastlines and sinks along poleward coastlines. However, cooler, higher regions of 85 continents, such as mountain ranges in Europe, 'attract' trajectories towards the interior, 86 disrupting the otherwise-poleward flow, resulting in internal sinks at greater elevations (Fig. 87 3b). Elevated land is also more likely to comprise non- or slow-moving areas. Corridors are 88 evident in areas of convergent trajectories and high climate velocities, as in the northern 89 North Sea and in southern Germany (Fig. 3a,b).

90 Future climate trajectories for sea surface temperature using an example global climate 91 model (ACCESS1.0) for 2006-2100 produce similar patterns of shifting climates to those 92 seen globally for 1960-2009. Sources were indicated at thermal maxima around the equator (Fig. 4a, c). Greater warming in the RCP8.5 "business as usual" scenario⁸ run (2.95°C 93 94 increase in annual average SST for 2080-2099 over 1960-2009) results in longer trajectories 95 than the RCP4.5 scenario run (1.75°C increase) and a doubling in size of areas identified as 96 sources (RCP8.5, 34.1% of scenario cells as sources vs 19.8% for RCP4.5). Local-scale 97 patterns were also similar (Fig. 4b, d), since thermal gradients that determine trajectory

direction are reproduced in the climate models. No-analogue climate futures¹⁵ will emerge in
 source areas with novel climates¹⁴, especially around the equator, but not in sources that
 result from coastal barriers disconnected from similar climates elsewhere.

101 Each climate trajectory feature has different implications for the migration patterns of climate-sensitive species through climate connectivity (Extended Data Table 1). Species 102 103 richness in *climate source* areas may decline, because climate migrants leaving may not be 104 replaced: sources lack connection routes for new migrants. Converging temperature 105 isotherms in *relative climate sinks* may concentrate climate migrants, increasing local diversity, while absolute *climate sinks* represent climatic dead-ends where species cannot 106 107 spread along thermal gradients into cooler areas, creating potential for local extinction. Large 108 numbers of trajectories traversing a limited pathway suggest important *corridors* for climate 109 migrants.

110 Patterns of distribution shifts indicated by trajectory behaviour raise questions for ecology and conservation of climate-sensitive species¹², especially when considered 111 alongside the magnitude and latitude of change change¹⁶. Long 'climate residence times' in 112 areas of low velocity¹⁰ have been associated with high levels of historical endemism¹⁷ and 113 have led to such areas being proposed as genetic and evolutionary refugia¹⁸. The non-114 replacement of climate migrants in climate source areas may result in net loss of species 115 richness, and facilitate the establishment of new species into abandoned niches¹⁹, such as in 116 the eastern Mediterranean Sea via the Suez Canal²⁰. A larger number of inbound climate 117 118 migrants in convergent areas, corridors and sinks implies that local communities should face greater reshuffling of species and novel ecological interactions²¹, and compromised genetic 119 diversity through gene swamping²² but with increased adaptive gene flow²³. Climate migrants 120 121 face local extinction in climate sink areas, unless the species involved can adapt to changed conditions. 122

123 Climate velocity is emerging as a good predictor for range shifts in the ocean^{4,5}, whereas 124 the relationship is still to be investigated on land, although terrestrial species distribution 125 shifts have been related to latitudinal shifts in isotherms²⁴. The similarity in trajectory maps 126 of future projections with past reconstructions suggests that the ecological implications and 127 therefore the management actions for conserving biodiversity, as informed by current climate 128 trajectories, could remain effective into the future. Species losses from both source and sink 129 areas may accelerate with climate change, with greater warming resulting in areas of novel and lost climates, suggesting that impacts may be greatest in these areas. The approach
developed here offers a rapid global method to quantify and map patterns of shifting thermal
niches, and by implication those species tracking thermal conditions, and highlights those
areas of the globe that may be at risk from the effects of barriers to climate migrants.

134 Methods Summary

135 Velocity fields were derived for 1960-2009 land and ocean surface temperatures using Hadley Centre HadISST v1.1 and Climate Research Unit CRU TS3.17 datasets, and for 136 137 global climate model projections for 2006-2100 using example GCM model data from 138 CMIP5 experiments for RCP4.5 and RCP8.5 scenarios. Velocity was calculated by dividing 139 the 50-year temperature trend by the spatial gradient in 50-year means, taking the direction from the spatial gradient⁶. Trajectories of climate were obtained by calculating 140 displacements using local velocity. If trajectories hit a coastal barrier and a cooler or warmer 141 142 cell was found locally then the trajectory continued toward that cell, else the cell was 143 designated as a *coastal sink*.

144 The collective behaviour of trajectories was obtained from 0.1°-spaced trajectories projected over 50 years at 0.1-year intervals. Cells were classed (Fig. 1b) as: (1) slow or non-145 146 moving where 50-year trajectories were less than 100km; (2) coastal and internal sinks, where trajectories halted on coastlines or converged towards a central point; (3) five types 147 148 based on proportions of trajectories starting from, ending in, and flowing through cells: 149 sources, cells where no trajectories ended; sinks where many trajectories ended; corridors, 150 cells with a high proportion of trajectories passing through; and *divergence* and *convergence* 151 cells as those where fewer/more trajectories ended than started in that cell.

Uncertainty of classification into areas based on trajectory behaviour was estimated using bootstrap resampling (n=500) of the temperature datasets. Each bootstrap sample comprised a random selection with replacement of 50 annual mean temperatures from the original series, from which mapped temporal and spatial temperature trends, and thereby velocity, were calculated. 50-year trajectories based on these maps gave a bootstrap classification of trajectory areas. Consistency of types by grid cell was expressed as the percentage of cells in bootstrap maps that were the same type as the original classification.

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Author contributions

- 235 M.T.B., D.S., A.J.R. and E.S.P. conceived the research. M.T.B., J.G.M and D.S. analysed
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- 237 contributed equally to discussion of ideas and analyses, and commented on the manuscript.

238 Author information

- 239 Data used in analyses are available from the University of East Anglia Climate Research Unit
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- 243 declare no competing financial interests. Readers are welcome to comment on the online
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- 277 Figure Legends
- 278

279 Figure 1 | Climate-change features emerging from the properties of climate velocity 280 trajectories using Australia landmass as an example. (a) Trajectories show predicted 50-281 year (1960-2009) shifts based on isotherm velocity. Features described by trajectory 282 properties (colours), implications for climate migrants (symbols), typical locations and 283 physical characteristics (sinks, orange, red, brown; sources, dark blue; corridors, magenta; 284 convergence, yellow; divergence, blue; slow, light green; and non-moving areas, grey). (b) 285 Hierarchical sequential classification of climate change features based on length of trajectories (Step 1), geographical features (Step 2) and the relative abundance of trajectories 286 287 ending in, starting from and flowing through each cell (Step 3). 288 289 Figure 2 | Global patterns of climate trajectory classes on (a) land and (c) in the ocean, 290 and (**b**, **d**) proportional areas by latitude. Uncertainty in classification of areas is shown by 291 the cross hatching on (\mathbf{a}, \mathbf{c}) : <66% of 500 bootstrap class maps consistent with underlying 292 class map. Non-hatched areas have likely (>66% consistent) classification. Uncertainty 293 between convergence and divergence areas and slow and non-moving areas is not shown (see 294 Extended Data Fig. 2). 295 296 Figure 3 | Regional patterns of climate velocity trajectory classes for land and sea 297 surface temperatures. We show 50-year trajectories of climates (1960-2009) for Europe for 298 1° grid cells, overlaid on climate trajectory classes for (a) ocean and (b) land. 299 300 Figure 4 | Global and regional patterns of 50-year climate trajectory classes based on trends from ensembles of global climate models for 2006-2100. We present classes for 301 two CMIP5 scenarios: (**a**, **b**) the 4.5 Wm^{-2} (RCP4.5) scenario and (**c**, **d**) the 8.5 Wm^{-2} (RCP8.5) 302 303 scenario, derived from temperature trends and spatial patterns in temperature in data from the 304 ACCESS1.0 CMIP5 global climate model. 305

306 Methods

307 Data sets and calculation of velocity

308 Velocity fields were derived for the period 1960-2009 for the ocean using the Hadley 309 Centre sea surface temperature dataset HadISST v1.1 and for land with the Climate Research Unit CRU TS3.1⁷. Velocity was calculated for 1° grid cells by dividing the local 50-year 310 311 trend in temperature (from linear regression) in °C/yr by the spatial gradient in °C/km, and angles were derived from the direction of the spatial gradient⁶. We also calculated velocity 312 313 fields for sea surface temperature from global climate model projections for 2006-2100. We aimed to use ensemble-average data from CMIP5 experiments⁸ RCP4.5 and RCP8.5, 314 scenarios with approximate radiative forcing of 4.5 and 8.5Wm⁻², projected onto the same 1° 315 grid coordinates as the HadISST data (courtesy of Daithi Stone and William Skirving). 316 317 However, differences in grid resolution produced artefacts at coastal margins for ensemble 318 means, so model runs from a single model, the CSIRO ACCESS1.0 model, were used 319 instead. Long-term trends and averages for each 1° cell were calculated for the 95 years of 320 scenario data, and used to calculate velocity in the same way as for HadISST data.

321 Calculating trajectories

322 We produced trajectories of climate for 1960-2009, and for a 50-year period based on 323 trends and patterns from global climate models for the period from 2006 to 2100, by forward 324 iteration of climate locations through velocity fields with speed V and direction θ . 325 Displacement at each time step was determined from local grid-cell speed and direction to 326 give shifts in km in x- and y-directions ($\Delta x = V \sin(\theta)$ and $\Delta y = V \cos(\theta)$). The proposed new 327 grid location was then converted back to latitude and longitude (Longitude + 328 $\Delta x/111.325 \times \cos(\text{latitude})$, and Latitude + $\Delta y/111.325$). A short time interval (0.1 year) was 329 used to minimise the incidence of displacements spanning more than one grid cell. This 330 occurred only where velocity values exceeded 1000km/yr, affecting 50 of 16752 grid cells on 331 land (0.3%) and 451 of 42974 cells (1.04%) in the ocean, and in these cases displacements were limited to 1° latitude or longitude. If new locations fell on land or ocean, such that a 332 333 coastal barrier or pole was not encountered, then that location became the starting point for 334 the next calculation. If the proposed location were beyond a land- or sea-barrier, a search 335 began for the immediate non-diagonal neighbour cell in the same medium: with the lowest (highest) temperature if velocity was positive (negative). If a cooler or warmer cell was 336 337 found then the trajectory was moved along in the direction to that cell (φ) at a speed given by 338 $(V/\cos(\varphi - \theta))$, and limited to a maximum displacement of 1° of latitude or longitude. If the

339 search was not successful, such that the focal cell was the warmest or coolest in its local 340 neighborhood, or the trajectory went beyond either pole, then the trajectory was halted and 341 the cell was designated as a coastal sink. This approach allowed trajectories to flow

342 realistically along coastlines and around islands.

343 **Collective behaviour of trajectories**

363

344 The collective grid-scale behaviour of trajectories was investigated by starting 100 trajectories at 0.1° intervals in each grid cell across the globe, separately for the land and 345 346 ocean velocity fields, and projecting locations forwards for 50 years at 0.1-year intervals. Our 347 trajectory classification followed three hierarchical sequential steps (Fig. 1b):

348 1. Cells were first identified as slow or non-moving climate cells where the length of 349 velocity trajectories over a 50-year simulation period (L_t) spanned less than the approximate dimensions of a single cell ($L_t \le 100$ km). The boundary limit between non- and slow-moving 350 351 was set at $L_t < 20$ km (i.e. <4 km/decade).

352 2. The second stage involved the identification of coastal and internal sinks. Coastal sinks captured the potential cul-de-sac effect imposed by continental margins on climate 353 354 migrants where climate trajectories hit the land (or the ocean for terrestrial trajectories) and no cooler (warmer) neighbouring cells are available to move to under a warming (cooling) 355 356 climate. We defined internal climate sinks based on trajectory velocity angles as areas where 357 thermal gradients in neighbouring cells converge towards their central point of intersection.

358 3. The remaining cells were finally classified by reference to the total number of 359 trajectories per cell based on the proportions of three variables: the number of trajectories 360 starting from (N_{st}) , ending in (N_{end}) , and flowing through (N_{FT}) a cell during the period.

361 While the number of trajectories starting is constant for a given trajectory resolution (100

362 starting trajectories for a 0.1° resolution), its proportion changes in relation to the other two

variables and, together with that of trajectories ending in a cell, indicates the degree to which 364 an area releases (receives) climates shifting to (from) other areas. Similarly, the proportion of

365 trajectories flowing through a cell gives an index of the flux of climate conditions through

366 that cell. Based on the relative magnitude of these three variables, we subsequently described

367 collective trajectory cell behaviour by dividing the 'trajectory space' into five classes using a

368 ternary plot (Fig. 1b, Extended Data Fig. 1): climate sources where no trajectories ended in a

cell ($N_{end} = 0$), relative climate sinks when the relative number of trajectories ending in a 369

cell was high and the proportion of starting trajectories was low ($N_{end} > 45\%$, $N_{st} < 15\%$), 370

371 and corridors as cells with a high proportion of trajectories passing through ($N_{FT} > 70\%$, 372 $\%N_{end} > 0$). Finally, divergence and convergence cells were identified respectively as those 373 where fewer/more trajectories ended than started in that cell.

374 Evaluation of uncertainty in trajectory area classes

375 Uncertainty of classification into areas based on trajectory behaviour was estimated using bootstrap resampling of the 1960-2009 HadISST 1.1 and CRU TS 3.1 datasets. For 376 377 each bootstrap sample, 50 years were randomly selected with replacement from the period. 378 The corresponding yearly global maps of annual means were used to calculate bootstrap 379 maps of temporal and spatial trends in temperature, and thereby velocity. Classification of 50-year trajectories based on these maps therefore gave a bootstrap realisation based on 380 381 variability in temporal trends, and directions and magnitudes of the spatial gradients in temperature (Extended Data Fig. 2). The bootstrap process was repeated 500 times. 382 383 Consistency of area classifications was expressed as the percentage of cells in bootstrap maps 384 were the same as the original maps based on all the 1960-2009 data.

386 Extended Data Figure Legends

- Extended Data Figure 1 | Ternary plots containing the trajectory classes: based on the proportions of trajectories starting from (N_{st}) , ending in (N_{end}) , and flowing through (N_{ft}) a cell. In a ternary plot three-dimensional cell coordinates (adding up to a 100%) are projected in a two-dimensional space. The arrows by the axes indicate the direction in which each variable is projected into the trajectory space. Point clouds represent global 1° resolution cell coordinate projections into the trajectory space based on 50-year climate trajectory simulations for (a) sea and (b) land surface temperature (1960-2009), and 2006-2100 rcp45
- 394 (c) and (d) rcp85 climate scenarios for ocean temperatures.
- 395

396 Extended Data Figure 2 | Uncertainty associated with the proposed trajectory

- 397 **classification.** (a) Mean standard error of the trend, (b) standard deviation in magnitude and
- 398 (c) angular deviation of the spatial gradient associated to bootstrapped (n = 500) mean annual
- 399 surface temperature series. Bootstrap-derived uncertainty associated with (d) the proposed
- 400 trajectory classification and (e) after collapsing slow/non-moving and
- 401 convergence/divergence areas into a single category each.
- 402

403 Extended Data Figure 3 | Frequency distribution of the uncertainty associated with the

- 404 trajectory-based classification of land and ocean. (a) Frequency histogram of the
- 405 proportion of coincident categories between the proposed 1960-2009 trajectory classification
- 406 and classifications resulting from 500 bootstrapped surface temperature climate series (see
- 407 Methods for details). (b, c) Cumulative frequency plots of the mean distribution of
- 408 bootstrapped trajectory categories contained in each category of the proposed trajectory
- 409 classification for (b) land and (c) ocean regions.
- 410

411 Extended Data Figure 4 | Global patterns of climate-velocity trajectory classes for (a, c)

412 ocean and (b, d) land surface temperatures. Uncertainty in classification of areas is shown

413 by the cross hatching on very likely (a, b; <90% consistency) and likely (c, d; <66%

414 consistency) areas of original global patterns with 500 bootstrap class maps.

415

416 Extended Data Figure 5 | Regional maps for (a) the North and (b) South Atlantic

- 417 showing 50-year trajectories (1960-2009) overlaid on corresponding categories
- 418

419	Extended Data Figure 6 Regional maps for (a) the North and (b) South Pacific,	
420	showing 50-year trajectories (1960-2009) overlaid on corresponding categories	
421		
422	Extended Data Figure 7 Regional map for the Coral Triangle showing 50-year	
423	trajectories (1960-2009) overlaid on corresponding categories.	
424		
425	Extended Data Figure 8 Regional maps for (a) the Eurasia, (b) Africa and (c) South	
426	America showing 50-year trajectories (1960-2009) overlaid on corresponding trajectory	
427	categories.	
428		
429	Extended Data Figure 9 Regional maps for (a) the North and Central America and (b)	
430	South-East Asia and Oceania detailing 50-year trajectories (1960-2009) overlaid on	
431	corresponding categories	
432		
433	Extended Data Table 1 Summary of trajectory classes, with implications for species range	
434	shifts if species distributions track shifting climatic niches. Descriptions of climate sources	
435	and sinks and their effects are for warming regions. Minimum levels of consistency in cell	
436	classification are shown for each type [%], based on Extended Data Figure S4.	
437		













а

b

С

d

Standard Error trend (C yr ⁻¹)				
	0.00014 - 0.002			
	0.002 - 0.004			
	0.004 - 0.005			
	0.005 - 0.006			
	0.006 - 0.007			
	0.007 - 0.008			
	0.008 - 0.009			
	0.009 - 0.01			
	0.01 – 0.012			
	0.012 - 0.016			



0 - 0.0001
0.0001 - 0.00015
0.00015 - 0.0002
0.0002 - 0.00025
0.00025 - 0.0003
0.0003 - 0.0004
0.0004 - 0.0006
0.0006 - 0.0008
0.0008 - 0.0012
0.0012 - 0.0018



0 – 0.015
0.015 - 0.03
0.03 - 0.06
0.06 – 0.1
0.1 – 0.15
0.15 – 0.25
0.25 – 0.4
0.4 – 0.5
0.5 – 0.75
0.75 – 1.2



0 – 10
10 – 20
20 – 30
30 – 40
<u> </u>
50 - 60
60 – 70
70 – 80
80 – 90
90 - 100

Proportion coincident classes (%)

$\begin{array}{c} 0 - 10 \\ 10 - 20 \\ 20 - 30 \\ 30 - 40 \\ 40 - 50 \\ 50 - 60 \\ 60 - 70 \\ 70 - 80 \\ 80 - 90 \end{array}$
80 – 90
90 – 100











Trajectory category













Extended Data Table 1. Summary of trajectory classes, with implications for species range shifts if species distributions track shifting climatic niches. Descriptions of climate sources and sinks and their effects are for warming regions. Minimum levels of consistency in cell classification are shown for each type [%], based on Extended Data Figure S4.

Trajectory Class	Effects on populations and distributions	Effects on species richness	
Climate connectivity			
[% consistent]			
Climate Sources	Leading edges cannot invade High climate emigration, No climate immigration	Species richness declines as climate emigrants not replaced	
Disconnected from warmer locales			
[>80%]		Empty niches for invaders	
Climate Sinks	Species have no adjacent cooler place to	Local extinction possible, but lost species	
Disconnected from cooler locales	relocate	replaced	
[Coastal >60%	Trailing edges may disappear	Richness stable	
Internal >30%]	No climate emigration, high climate immigration		
	nigh chinate inningration		
Climate Corridors	Species arriving from geographically distinct locations	Richness stable or increased	
Pathways of strong/intense isotherm		Increased effects of species interactions on	
[> 60%]]	species	Torinoso	
[>00 /8]	High emigration and immigration		
Convergence / Divergence	Areas for rapid shifts	Richness change depends on balance of	
Areas where isotherms gather and slow, or speed up and disperse	Moderate emigration and immigration	migrants	
[>50%]			
Low-velocity areas	Little, or slow change in distributions	Little change	
Climate change does not propagate rapidly across the surface			
[>80%]			