Extinction risk from climate change

Chris D. Thomas[1], Alison Cameron[1], Rhys E. Green[2], Michel Bakkenes[3], Linda J. Beaumont[4], Yvonne C. Collingham[5], Barend F. N. Erasmus[6], Marinez Ferreira de Siqueira[7], Alan Grainger[8], Lee Hannah[9], Lesley Hughes[4], Brian Huntley[5], Albert S. van Jaarsveld[10], Guy F. Midgley[11], Lera Miles[8]*, Miguel A. Ortega-Huerta[12], A. Townsend Peterson[13], Oliver L. Phillips[8] & Stephen E. Williams[14]

[1]*Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, UK*
[2]*Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK, and Conservation Biology Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK*
[3]*National Institute of Public Health and Environment, P.O. Box 1, 3720 BA Bilthoven, The Netherlands*
[4]*Department of Biological Sciences, Macquarie University, North Ryde, 2109, NSW, Australia*
[5]*University of Durham, School of Biological and Biomedical Sciences, South Road, Durham DH1 3LE, UK*
[6]*Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, South Africa*
[7]*Centro de Referência em Informação Ambiental, Av. Romeu Tórtima 228, Barão Geraldo, CEP:13083-885, Campinas, SP, Brazil*
[8]*School of Geography, University of Leeds, Leeds LS2 9JT, UK*
[9]*Center for Applied Biodiversity Science, Conservation International, 1919 M Street NW, Washington, DC 20036, USA*
[10]*Department of Zoology, University of Stellenbosch, Private Bag X1, Stellenbosch 7602, South Africa*
[11]*Climate Change Research Group, Kirstenbosch Research Centre, National Botanical Institute, Private Bag x7, Claremont 7735, Cape Town, South Africa*
[12]*Unidad Occidente, Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F. 04510 México*
[13]*Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas 66045 USA*
[14]*Cooperative Research Centre for Tropical Rainforest Ecology, School of Tropical Biology, James Cook University, Townsville, QLD 4811, Australia*

* Present address: UNEP World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge CB3 0DL, UK

Climate change over the past ~30 years has produced numerous shifts in the distributions and abundances of species[1,2] and has been implicated in one species-level extinction[3]. Using projections of species' distributions for future climate scenarios, we assess extinction risks for sample regions that cover some 20% of the Earth's terrestrial surface. Exploring three approaches in which the estimated probability of extinction shows a power-law relationship with geographical range size, we predict, on the basis of mid-range climate-warming scenarios for 2050, that 15–37% of species in our sample of regions and taxa will be 'committed to extinction'. When the average of the three methods and two dispersal scenarios is taken, minimal climate-warming scenarios produce lower projections of species committed to extinction (~18%) than mid-range (~24%) and maximum-change (~35%) scenarios. These estimates show the importance of rapid implementation of technologies to decrease greenhouse gas emissions and strategies for carbon sequestration.

The responsiveness of species to recent[1–3] and past[4,5] climate change raises the possibility that anthropogenic climate change could act as a major cause of extinctions in the near future, with the Earth set to become warmer than at any period in the past 1–40 Myr (ref. 6). Here we use projections of the future distributions of 1,103 animal and plant species to provide 'first-pass' estimates of extinction probabilities associated with climate change scenarios for 2050.

For each species we use the modelled association between current climates (such as temperature, precipitation and seasonality) and present-day distributions to estimate current distributional areas[7–12]. This 'climate envelope' represents the conditions under which populations of a species currently persist in the face of competitors and natural enemies. Future distributions are estimated by assuming that current envelopes are retained and can be projected for future climate scenarios[7–12]. We assume that a species either has no limits to dispersal such that its future distribution becomes the entire area projected by the climate envelope model or that it is incapable of dispersal, in which case the new distribution is the overlap between current and future potential distributions (for example, species with little dispersal or that inhabit fragmented landscapes)[11]. Reality for most species is likely to fall between these extremes.

We explore three methods to estimate extinction, based on the species–area relationship, which is a well-established empirical power-law relationship describing how the number of species relates to area ($S = cA^z$, where S is the number of species, A is area, and c and z are constants)[13]. This relationship predicts adequately the numbers of species that become extinct or threatened when the area available to them is reduced by habitat destruction[14,15]. Extinctions arising from area reductions should apply regardless of whether the cause of distribution loss is habitat destruction or climatic unsuitability.

Because climate change can affect the distributional area of each species independently, classical community-level approaches need to be modified (see Methods). In method 1 we use changes in the summed distribution areas of all species. This is consistent with the traditional species–area approach: on average, the destruction of half of a habitat results in the loss of half of the distribution area summed across all species restricted to that habitat. However, this analysis tends to be weighted towards species with large distributional areas. To address this, in method 2 we use the average proportional loss of the distribution area of each species to estimate the fraction of species predicted to become extinct. This approach is faithful to the species–area relationship because halving the habitat area leads on average to the proportional loss of half the distribution of each species. Method 3 considers the extinction risk of each species in turn. In classical applications of the species–area approach, the fraction of species predicted to become extinct is equivalent to the mean probability of extinction per species. Thus, in method 3 we estimate the extinction risk of each species separately by substituting its area loss in the species–area relationship, before averaging across species (see Methods). Our conclusions are not dependent on which of these methods is used. We use $z = 0.25$ in the species–area relationship throughout, given its previous success in predicting proportions of threatened species[14,15], but our qualitative conclusions are not dependent on choice of z (Supplementary Information). As there are gaps in the data (not all dispersal/climate scenarios were available for each region), a logit–linear model is fitted to the extinction risk data to produce estimates for missing values in the extinction risk table (Table 1). Balanced estimates of extinction risk, averaged across all data sets, can then be calculated for each scenario.

For projections of maximum expected climate change, we estimate species-level extinction across species included in the study to be 21–32% (range of the three methods) with universal dispersal, and 38–52% for no dispersal (Table 1). For projections of mid-range climate change, estimates are 15–20% with dispersal and 26–37% without dispersal (Table 1). Estimates for minimum expected climate change are 9–13% extinction with dispersal and 22–31% without dispersal. Projected extinction varies between parts of the world and between taxonomic groups (Table 1), so our estimates are affected by the data available. The species–area methods differ from one another by up to 1.41-fold (method 1 versus method 3) in estimated extinction, whereas the two dispersal scenarios produce a 1.98-fold difference, and the three climate scenarios generate 2.05-fold variation.

©2004 Nature Publishing Group

Given its role in conservation planning, we also use a different approach to estimate extinction, modified from the IUCN Red Data Book listing procedure[16]: this is semi-numerical and includes components of expert judgement. Species are assigned to different threat categories based on distribution sizes and declines, with each category carrying a specified probability of extinction[16] (see Methods and Supplementary Information). For scenarios of maximum expected climate change, 33% (with dispersal) and 58% (without dispersal) of species are expected to become extinct (Table 1). For mid-range climate change scenarios, 19% or 45% (with or without dispersal) of species are expected to become extinct, and for minimum expected climate change 11% or 34% (with or without dispersal) of species are projected to become extinct.

We can compare these values with the proportions of species projected to become extinct as the result of global habitat losses, currently the most widely recognized extinction threat. We apply the species–area relationship to changes in global land use that have taken place since human land conversion began[17]. Estimates of extinction range from 1% to 29%, depending on the biome (considering only species restricted to single biomes; Table 2). Given that a high proportion of the world's species reside in tropical forests (extinction estimate 4%; Table 2), global extinction related to habitat loss would be expected to be in the lower half of the range, and thus lower than the rate projected for scenarios of mid-range climate change (24%; average of area methods). Projected conversion of humid tropical forest at an annual rate of 0.43% (ref. 18) from 1990 to 2050 predicts a further 6.3% of species committed to extinction.

Regional differences are expected, so we also compare the relative risks during 2000–2050 associated with land use and climate change (using area approaches) for the three region–taxon combinations that correspond most closely to single habitat or biome types. First, for montane Queensland forests[12], extinction risk is dominated by climate change (7–13% and 43–58% predicted extinction for minimum and maximum climate scenarios, respectively; 0% predicted on the basis of further habitat destruction, given its legal protection). Second, for cerrado vegetation in Brazil, high rates of habitat destruction[19] make it possible that only current reserves will survive. Making this pessimistic assumption, an estimated additional 34% of all original species will be committed to extinction due to habitat destruction during 2000–2050, a value lower than the 48–56% of woody plant species projected to be committed to extinction for mid-range climate warming (38–45% for minimum warming). Last, for South African Proteaceae, 27% of all original species are projected to become extinct as a result of land use

Table 1 **Projected percentage extinctions for different taxa and regions**

Taxon	Region	With dispersal			No dispersal		
		Minimum expected climate change	Mid-range climate change	Maximum expected climate change	Minimum expected climate change	Mid-range climate change	Maximum expected climate change
Mammals	Mexico	2, 4, 5	2, 5, 7	–	9, 14, 18	10, 15, 20	–
	$n = 96$	**5**	**8**		**24**	**26**	
	Queensland	10, 13, 15	–	48, 54, 80	–	–	–
	$n = 11$	**16**		**77**			
	South Africa	–	24, 32, 46	–	–	28, 36, 59	–
	$n = 5$		**0**			**69**	
Birds	Mexico	2, 2, 3	3, 3,4	–	5, 7, 8	5, 7, 8	–
	$n = 186$	**4**	**5**		**9**	**8**	
	Europe	–	–	4, 6, 6	–	–	13, 25, 38
	$n = 34$			**7**			**48**
	Queensland	7, 9, 10	–	49, 54, 72	–	–	–
	$n = 13$	**12**		**85**			
	South Africa	–	28, 29, 32	–	–	33, 35, 40	–
	$n = 5$		**0**			**51**	
Frogs	Queensland	8, 12, 18	–	38, 47, 67	–	–	–
	$n = 23$	**13**		**68**			
Reptiles	Queensland	7, 11, 14	–	43, 49, 64	–	–	–
	$n = 18$	**9**		**76**			
	South Africa	–	21, 22, 27	–	–	33, 36, 45	–
	$n = 26$		**0**			**59**	
Butterflies	Mexico	1, 3, 4	3, 4, 5	–	6, 9, 11	9, 12, 15	–
	$n = 41$	**7**	**7**		**13**	**19**	
	South Africa	–	13, 7, 8	–	–	35, 45, 70	–
	$n = 4$		**0**			**78**	
	Australia	5, 7, 7	13, 15, 16	21, 22, 26	9, 11, 12	18, 21, 23	29, 32, 36
	$n = 24$	**7**	**23**	**33**	**16**	**35**	**54**
Other invertebrates	South Africa	–	18, 15, 24	–	–	28, 46, 80	–
	$n = 10$		**0**			**85**	
Plants	Amazonia	–	–	44, 36, 79	–	–	100, 100, 99
	$n = 9$			**69**			**87**
	Europe	3, 4, 5	3, 5, 6	4, 5, 6	9, 11, 14	10, 13, 16	13, 17, 21
	$n = 192$	**6**	**7**	**8**	**18**	**22**	**29**
	Cerrado	–	–	–	38, 39, 45	48, 48, 57	–
	$n = 163$				**66**	**75**	
	South Africa Proteaceae	–	24, 21, 27	–	–	32, 30, 40	–
	$n = 243$		**38**			**52**	
All species		9, 10, 13	15, 15, 20	21, 23, 32	22, 25, 31	26, 29, 37	38, 42, 52
		11	**19**	**33**	**34**	**45**	**58**
		$n = 604$	$n = 832$	$n = 324$	$n = 702$	$n = 995$	$n = 259$

Projected percentage extinction values are given, based on species–area (for $z = 0.25$) and Red Data Book (bold) approaches. The three species–area estimates are ordered in each cell with method 1 given first, followed by method 2, then method 3. Values for 'All species' are based on both these raw values and estimates interpolated for the empty (–) cells (see Methods). In each instance, n is the number of species assessed directly.

©2004 Nature Publishing Group

Table 2 **Estimated eventual extinction based on habitat loss**

Biome	Percentage of world surface area (from ref. 17)			Percentage of species expected to go extinct by the species–area approach ($z = 0.25$)
	Undisturbed	1990	Area lost	
Cropland	0.0	10.9	0.0	0.0
Pasture	0.0	23.1	0.0	0.0
Ice	1.7	1.7	0.0	0.0
Tundra	4.8	4.6	0.2	1.0
Wooded tundra	2.0	1.9	0.1	1.1
Boreal forest	13.0	12.5	0.5	0.9
Cool conifer forest	2.7	2.1	0.6	6.1
Temperate mixed forest	5.2	2.2	3.0	19.2
Temperate deciduous forest	4.5	1.5	3.0	24.2
Warm mixed forest	4.7	1.9	2.8	20.3
Grassland/steppe	13.7	6.9	6.8	15.7
Hot desert	14.9	11.8	3.1	5.6
Scrubland	7.3	1.9	5.4	28.9
Savannah	11.9	6.2	5.7	15.1
Tropical woodland	6.1	4.4	1.7	8.0
Tropical forest	7.6	6.4	1.1	4.0

changes during 2000–2050 (for a pessimistic linear extrapolation of land use scenarios after 2020)[20], falling between the 30–40% (without dispersal) and 21–27% (with ubiquitous dispersal, which is unlikely for these plants) projected extinction for mid-range climate scenarios.

Many unknowns remain in projecting extinctions, and the values provided here should not be taken as precise predictions. Analyses need to be repeated for larger samples of regions and taxa, and the selection of climate change scenarios need to be standardized. Some of the most important uncertainties follow (see also Supplementary Information). We estimate proportions of species committed to future extinction as a consequence of climate change over the next 50 years, not the number of species that will become extinct during this period. Information is not currently available on time lags between climate change and species-level extinctions, but decades might elapse between area reduction (from habitat loss) and extinction[14]. Land use should also be incorporated into analyses: extinction risks might be higher than we project if future locations of suitable climate do not coincide with other essential resources (such as soil type or food resources). There is also uncertainty over which species will inhabit parts of the world projected to have climates for which no current analogue exists[6]. Equally importantly, all parts of the world will have historically unprecedented CO_2 levels[6], which will affect plant species and ecosystems[21,22] and herbivores[23], resulting in novel species assemblages and interactions.

Despite these uncertainties, we believe that the consistent overall conclusions across analyses establish that anthropogenic climate warming at least ranks alongside other recognized threats to global biodiversity. Contrary to previous projections[24], it is likely to be the greatest threat in many if not most regions. Furthermore, many of the most severe impacts of climate-change are likely to stem from interactions between threats, factors not taken into account in our calculations, rather than from climate acting in isolation. The ability of species to reach new climatically suitable areas will be hampered by habitat loss and fragmentation, and their ability to persist in appropriate climates is likely to be affected by new invasive species.

Minimum expected (that is, inevitable) climate-change scenarios for 2050 produce fewer projected 'committed extinctions' (18%; average of the three area methods and the two dispersal scenarios) than mid-range projections (24%), and about half of those predicted under maximum expected climate change (35%). These scenarios would diverge even more by 2100. In other words, minimizing greenhouse gas emissions and sequestering carbon[25] to realize minimum, rather than mid-range or maximum, expected climate warming could save a substantial percentage of terrestrial species from extinction. Returning to near pre-industrial global temperatures as quickly as possible could prevent much of the projected, but slower-acting, climate-related extinction from being realized. □

Methods

Climate-envelope modelling

The statistical match between climate variables and the boundaries of a species' distribution (climate envelope) represents conditions in which a species (normally) shows a positive demographic balance (rarely the absolute physical limits of a species, but the set of conditions under which it survives in at least some multi-species communities). The statistical approach is generic, but specific methods vary between studies (Supplementary Information). The approach has been validated by successfully predicting distributions of invading species when they arrive in new continents and by predicting distributional changes in response to glacial climate changes; its scope has been discussed widely (see, for example, refs 12, 26–29). Dispersal is assumed to be universal or zero (main text), except for the Mexican study in which 'universal dispersal' is movement through contiguous habitats[11].

Climate scenarios

Climate projections for 2050 were divided into three categories: minimum expected change resulting in a mean increase in global temperature of 0.8–1.7 °C and in CO_2 of 500 p.p.m. by volume (p.p.m.v.); mid-range scenarios with temperature increases of 1.8–2.0 °C and CO_2 increases of 500–550 p.p.m.v.; and maximum expected scenarios with temperature increases of >2.0 °C and CO_2 increases >550 p.p.m.v. (ref. 30). Projections for the year 2100 were allocated to 2050 scenarios according to their end temperatures and CO_2 levels (Supplementary Information).

Species

Within each region we use only data for endemic species (near-endemic in two cases). Near-endemics are defined as >90% of the distribution area known to occur (European birds) or thought to occur (cerrado plants, given incomplete data) within the region modelled. For European birds, near-endemics are included only if their extra-European distribution is similar to climate space within Europe. The focus on endemics permits us to model all range boundaries of each species (Supplementary Information).

Species–area approaches

Method 1 analyses overall changes in distribution areas, summed across species. The proportion of species in a region going extinct (E_1) is estimated as

$$E_1 = 1 - (\Sigma A_{\text{new}}/\Sigma A_{\text{original}})^z$$

where A_{original} is the area initially occupied by a species, and A_{new} is the future area projected for the same species, with summation carried out across species.

Method 2 is based on the average proportional change in distribution area, averaged across species. Regional extinction risk (E_2) is

$$E_2 = 1 - \{(1/n)[\Sigma(A_{\text{new}}/A_{\text{original}})]\}^z$$

where n is the number of species and $A_{\text{new}}/A_{\text{original}}$ is the proportional distribution change for each species in turn.

Method 3 estimates the extinction risk of each species in turn, averaging across species to derive regional estimates of extinction (E_3):

$$E_3 = (1/n)\Sigma[1 - (A_{\text{new}}/A_{\text{original}})^z]$$

Species for which $A_{\text{new}} > A_{\text{original}}$ were analysed as though $A_{\text{new}} = A_{\text{original}}$; that is, zero extinction would be returned by each equation if every species was projected to

©2004 Nature Publishing Group

expand (Supplementary Information). It is important to recognize that further work is required to establish empirically how the absolute and proportional area losses of individual species (in other words, the type of data from climate envelope projections) are related to extinction risk. As yet, no agreed standard method exists for such calculations: assumptions and uncertainties inherent in the three methods will be considered in detail elsewhere.

Extinction probability estimates were not available for all scenarios in every region/taxon, so means of scenarios were calculated after using a least-squares analysis of variance model to impute missing values. Region/taxon mean probabilities of extinction for each scenario were logit-transformed and a three-way analysis of variance was fitted (region/taxon × climate scenario × dispersal scenario; weighted by $\sqrt{N_{\text{species}}}$ per region/taxon study). The fitted model was used to impute expected values of the probability of extinction for those region/taxon and scenario combinations for which direct estimates were not available. Scenario means were then calculated from the combined direct estimates and imputed values, using $\sqrt{N_{\text{species}}}$ for each region/taxon as weights.

Red Data Book criteria

Each species is assigned to a threat category[16], or classified 'Not Threatened' (0% risk), depending on the projected decline in area over 50 or 100 years (Supplementary Information) and the final distribution area. Existing areas were considered, so we present only the extra extinction attributable to climate change. Logit-transformed three-way analysis of variance was used to estimate extinction risks for empty cells, as with the species–area approaches.

Extinct: species with a projected future area of zero (100% of species assumed to be committed to eventual extinction).

Critically endangered: projected future distribution area $<10\,\text{km}^2$, or decline by $>80\%$ in 50 years (species assigned a 75% chance of extinction[16]).

Endangered: projected area 10–500 km^2, or 50–80% decline in 50 years (species assigned a 35% chance of extinction[16]).

Vulnerable: projected area 500–2,000 km^2, or $>50\%$ decline in 100 years on the basis of linear extrapolation of 50-year projection (species assigned a 15% chance of extinction[16]).

Received 10 September; accepted 13 October 2003; doi:10.1038/nature02121.

1. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37–42 (2003).
2. Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421,** 57–60 (2003).
3. Pounds, J. A., Fogden, M. L. P. & Campbell, J. H. Biological response to climate change on a tropical mountain. *Nature* **398,** 611–615 (1999).
4. Overpeck, J., Whitlock, C. & Huntley, B. in *Paleoclimate, Global Change and the Future* (eds Alverson, K., Bradley, R. & Pedersen, T.) 81–103 (Springer, Berlin, 2002).
5. Benton, M. J. & Twitchett, R. J. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol.* **18,** 358–365 (2003).
6. Houghton, J. T. *et al. Climate change 2001: the Scientific Basis. Contributions of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ. Press, 2001).
7. Bakkenes, M., Alkemade, J. R. M., Ihle, F., Leemans, R. & Latour, J. B. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biol.* **8,** 390–407 (2002).
8. Beaumont, L. J. & Hughes, L. Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change. *Global Change Biol.* **8,** 954–971 (2002).
9. Erasmus, B. F. N., van Jaarsveld, A. S., Chown, S. L., Kshatriya, M. & Wessels, K. Vulnerability of South African animal taxa to climate change. *Global Change Biol.* **8,** 679–693 (2002).
10. Midgley, G. F., Hannah, L., Rutherford, M. C. & Powrie, L. W. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecol. Biogeogr.* **11,** 445–451 (2002).
11. Peterson, A. T. *et al.* Future projections for Mexican faunas under global climate change scenarios. *Nature* **416,** 626–629 (2002).
12. Williams, S. E., Bolitho, E. E. & Fox, S. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proc. R. Soc. Lond. B* **270,** 1887–1892 (2003).
13. Rosenzweig, M. L. *Species Diversity in Space and Time* (Cambridge Univ. Press, 1995).
14. Brooks, T. M., Pimm, S. L. & Oyugi, J. O. Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* **13,** 1140–1150 (1999).
15. Brooks, T. M., Pimm, S. L. & Collar, N. J. Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conserv. Biol.* **11,** 382–394 (1997).
16. *IUCN Red List Categories and Criteria*, version 3.1. (IUCN Species Survival Commission, Gland, Switzerland, 2001).
17. Gaston, K. J., Blackburn, T. M. & Goldewijk, K. K. Habitat conversion and global avian biodiversity loss. *Proc. R. Soc. Lond. B* **270,** 1293–1300 (2003).
18. Achard, F. *et al.* Determination of deforestation rates of the world's humid tropical forests. *Science* **297,** 999–1002 (2002).
19. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403,** 853–858 (2000).
20. Roget, M., Richardson, D. M., Cowling, R. M., Lloyd, J. W. & Lombard, A. T. Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biol. Conserv.* **112,** 63–85 (2003).
21. Woodward, F. I. Potential impacts of global elevated CO_2 concentrations on plants. *Curr. Opin. Plant Biol.* **5,** 207–211 (2002).
22. Bond, W. J., Midgley, G. F. & Woodward, F. I. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biol.* **9,** 973–982 (2003).
23. Whittaker, J. B. Impacts and responses at population level of herbivorous insects to elevated CO_2. *Eur. J. Entomol.* **96,** 149–156 (1999).
24. Sala, O. E. *et al.* Biodiversity—global biodiversity scenarios for the year 2100. *Science* **287,** 1770–1774 (2000).
25. Lackner, K. S. A guide to CO_2 sequestration. *Science* **300,** 1677–1678 (2003).
26. Beerling, D. J. The impact of temperature on the northern distribution limits of the introduced species *Fallopia japonica* and *Impatiens glandulifera* in north-west Europe. *J. Biogeog.* **20,** 45–53 (1993).
27. Baker, R. H. A. *et al.* The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agric. Ecosyst. Environ.* **82,** 57–71 (2000).
28. Peterson, A. T. & Vieglais, D. A. Predicting species invasions using ecological niche modeling. *BioScience* **51,** 363–371 (2001).
29. Pearson, R. G. & Dawson, T. P. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeog.* **12,** 361–371 (2003).
30. Intergovernmental Panel on Climate Change. *Climate Change 2001: The Scientific Basis.* http://www.grida.no/climate/ipcc_tar/wg1/figts-22.htm (2001).

Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank the following for many contributions: E. Bolitho, V. Perez Canhos, D. A. L. Canhos, S. Carver, S. L. Chown, S. Fox, M. Kshatriya, D. Millar, A. G. Navarro-Sigüenza, R. S. Pereira, B. Reyers, E. Martínez-Meyer, V. Sánchez-Cordero, J. Soberón, D. R. B. Stockwell, W. Thuiller, D. A. Vieglais and K. J. Wessels, researchers involved in the Projeto de Cooperação Técnica Conservação e Manejo da Biodiversidade do Bioma Cerrado, EMBRAPA Cerrados, UnB, Ibama/DFID e RBGE/Reino Unido, and the European Bird Census Council. We thank G. Mace, J. Malcolm and C. Parmesan for valuable discussions, many funding agencies for support, and B. Orlando and others at IUCN for bringing together many of the coauthors at workshops. Comments from J. A. Pounds and S. Pimm greatly improved the manuscript.

Authors' contributions The fourth and subsequent authors are alphabetically arranged and contributed equally.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to C.D.T. (c.d.thomas@leeds.ac.uk).

Derivation of embryonic germ cells and male gametes from embryonic stem cells

Niels Geijsen[1,2], Melissa Horoschak[1,3], Kitai Kim[1,3], Joost Gribnau[1], Kevin Eggan[4] & George Q. Daley[1,3]

[1]*Whitehead Institute for Biomedical Research, 9 Cambridge Center, Cambridge, Massachusetts 02142, USA*
[2]*Center for Regenerative Medicine and Technology, Massachusetts General Hospital, Boston, Massachusetts 02114, USA*
[3]*Department of Biological Chemistry and Molecular Pharmacology, Harvard Medical School, and Division of Pediatric Hematology/Oncology, The Children's Hospital and Dana Farber Cancer Institute, Boston, Massachusetts 02115, USA*
[4]*Department of Molecular and Cellular Biology, Harvard University, 7 Divinity Avenue, Cambridge, Massachusetts 02138, USA*

Egg and sperm cells (gametes) of the mouse are derived from a founder population of primordial germ cells that are set aside early in embryogenesis. Primordial germ cells arise from the proximal epiblast, a region of the early mouse embryo that also contributes to the first blood lineages of the embryonic yolk sac[1]. Embryonic stem cells differentiate *in vitro* into cystic structures called embryoid bodies consisting of tissue lineages typical of the early mouse embryo[2,3]. Because embryoid bodies sustain blood development, we reasoned that they might also support primordial germ cell formation. Here we isolate primordial germ cells from embryoid bodies, and derive continuously growing lines of embryonic germ cells. Embryonic germ cells show erasure of the

©2004 Nature Publishing Group

Copyright of Nature is the property of Nature Publishing Group and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.