

Thomas *et al.* reply — We reconsider our estimates of climate-related extinction¹ in the light of three questions raised by Thuiller *et al.*², Buckley and Roughgarden³ and Harte *et al.*⁴. We are able to confirm our original conclusion that climate change represents a major threat to terrestrial species¹.

First, how much do estimates of extinction depend on the specific approach used to model current and future species distributions? From Table 1 in Thuiller *et al.*², we calculate that distribution model choice produces 1.33-fold variation, on average, in projected extinction in pairwise comparisons of methods. This is important, but smaller than both the twofold variation due to contrasting dispersal assumptions and the twofold variation due to the different climate-change scenarios that we reported¹. The number of environmental variables used during modelling could also affect conclusions, but we found no correlation between these and our estimates of extinction risk in global samples ($r^2 = 0.001$; not significant; each study: 1 d.f.).

Results consistent with our original estimates can be derived from simple population projections without the need for formal distribution models. An index of total population sizes for 12 endemic bird species in Queensland, Australia, has been derived by measuring population density in elevation bands and multiplying by the habitat area in each band (S.E.W. and Luke P. Shoo, manuscript in preparation). Population change was projected directly using the relationship

between elevation and temperature (Australian Meteorological Bureau data). The resulting rate of decline in population size was very similar to the rate of decline in distribution area projected using BIOCLIM (S.E.W. and Luke P. Shoo, manuscript in preparation), which is a distribution modelling method we used to project extinctions¹.

Overall estimates of area loss and extinction risk do not seem to be particularly sensitive to model details when averaging over many species, as we did¹. By contrast, the details can be critical when considering the prognosis for an individual species (for example, when explaining why some species survive in small areas² but others die out). We fully agree that the relative merits of different approaches need further assessment.

Second, can modified species–area relationship methods (SAR) be used to translate average range–area losses into estimates of extinction^{2–4}? We do not accept Buckley and Roughgarden’s assertion that our analysis is circular³. As they note, summed area (ΣA) is correlated with the number of species: $\Sigma A = SR$ where S is the number of species and R is the mean range–area of species, either before (R_{original}) or after (R_{new}) some environmental change. We can substitute SR_{new} and SR_{original} in place of ΣA_{new} and $\Sigma A_{\text{original}}$ in our original method (1), such that S cancels out (species with new range sizes of zero are included) and the number of species does not enter into the calculation (for E , the proportion of species projected to become extinct, $E = 1 - [R_{\text{new}}/R_{\text{original}}]^z$). Only mean range change per species matters.

As 50% destruction of a given habitat generates a mean of 50% decline in range area per species, mean area loss per original species (the method that we use) and habitat area loss (as in traditional SAR applications to habitat destruction) on average return the same estimate of expected extinction. None of our three methods is affected by this criticism. Because mean values are used, there is no “double counting” of range areas.

For one vegetation type (the Fynbos floral kingdom in South Africa), we can compare a traditional habitat-based SAR estimate of extinction risk with estimates based on our species-averaging methods. Proteaceae-containing Fynbos vegetation should decline in area by 65% with climate change (climate scenario HadCM2n = Gga [IS92a], for 2050)⁵. The resultant estimate of extinction is 23% (traditional SAR, $z = 0.25$), which is close to our corresponding estimate of 24% of Proteaceae species at risk (mean of three SAR methods, $z = 0.25$, full dispersal, modelled using the same climate scenario and environmental variables)¹. This ‘full dispersal’ comparison is appropriate because traditional SAR applies to habitat area and does not consider additional extinctions caused by range dislocations, when a habitat moves as well as contracts. A third of Fynbos Proteaceae have been predicted to show no overlap between current and future ranges⁵, in line with our estimate of 34% extinction (no dispersal mean of SAR estimates).

Our general conclusions do not even rely on using SAR methods. Harte *et al.*⁴ suggest estimating how many species will lose all of

Table 1 Loss of climatically suitable areas for different species by 2050

Taxon	Region	With dispersal			No dispersal		
		Minimum	Mid-range	Maximum	Minimum	Mid-range	Maximum
Mammals	Mexico (n=96)	0% 0% 10%	0% 4% 15%		3% 6% 39%	3% 10% 37%	
	Queensland (n=11)	0% 9% 36%		64% 73% 100%			
	South Africa (n=5)		20% 40% 80%			40% 60% 100%	
Birds	Mexico (n=186)	0% 0% 4%	0% 1% 8%		0% 0% 11%	1% 1% 8%	
	Europe (n=34)			0% 0% 9%			18% 29% 76%
	Queensland (n=13)	0% 0% 23%		38% 77% 100%			
	South Africa (n=5)		0% 40% 100%			0% 40% 100%	
Frogs	Queensland (n=23)	4% 9% 30%		39% 61% 100%			
Reptiles	Queensland (n=18)	0% 6% 33%		33% 56% 100%			
	South Africa (n=26)		4% 12% 77%			11% 38% 100%	
Butterflies	Mexico (n=41)	0% 2% 17%	0% 5% 34%		0% 2% 7%	2% 2% 12%	
	South Africa (n=4)		0% 0% 25%			50% 75% 100%	
	Australia (n=24)	0% 0% 8%	0% 4% 42%	0% 8% 83%	0% 0% 25%	0% 4% 75%	4% 21% 100%
Other invertebrates	South Africa (n=10)		10% 10% 50%			70% 80% 100%	
Plants	Amazonia (n=9)			78% 78% 78%			100% 100% 100%
	Europe (n=192)	1% 1% 7%	1% 1% 10%	1% 1% 14%	3% 3% 26%	3% 3% 36%	4% 8% 51%
	Cerrado (n=163)				4% 50% 99%	10% 74% 100%	
	South Africa						
	Proteaceae (n=243)		1% 17% 72%			7% 35% 100%	
All species		4% 9% 38%	4% 14% 47%	13% 32% 68%	8% 21% 60%	12% 30% 66%	19% 47% 87%
	(n=604)		(n=832)	(n=324)	(n=702)	(n=995)	(n=259)

Estimated percentages of species projected¹ to lose 100% (first number in each cell), >90% (second number) and >50% (third number) of climatically suitable areas by 2050 (see ref. 1 for climate scenarios). “No dispersal” assumes species survive only in areas of overlap between current and projected future ranges. “With dispersal” assumes species track changing climate distributions perfectly. n , Numbers of species in each category. “All species” values are based on the modelled means (weighted by square-root of number of species in each category, using interpolated values for missing taxa/regions): 100% projected loss implies that surviving populations will be living in climatic zones no longer suitable for their long-term persistence. They are predicted to be “committed to extinction” if 2050 conditions persist indefinitely. Extinctions may be caused by physical aspects of the climate or by biotic interactions that are affected by climate.

their range area. We projected that 5%, 8% and 16% (mean of dispersal scenarios) of the species considered would have lost 100% of their climatically suitable area by 2050, for minimum, mid-range and maximum climate warming, respectively (Table 1). Some 15%, 22% and 40% (mean of dispersal scenarios) of species are projected to have lost more than 90% of their climatically suitable areas by 2050 for minimum, mid-range and maximum warming, respectively (Table 1). A comparable increase in temperature is expected between 2050 and 2100 as between now and 2050 (ref. 6), so distribution changes will continue unabated after 2050. We previously assigned species losing 90% of their climatically suitable area by 2050 a 44% chance of eventual extinction using the method (3) that provided the highest estimate of extinction¹. This was modest, considering that most species projected to lose 90% of their suitable range by 2050 will subsequently lose the remainder as a result of continuing climate change.

Third, how will local adaptations affect the ability of species to respond to climate change, and why will species not be able to evolve adaptations to new conditions, rather than become extinct? Harte *et al.*⁴ are correct

in their assertion that distribution models implicitly assume that locally-adapted regional populations are capable of evolving up to, but not beyond, the set of conditions inhabited by the species as a whole, and they may not always achieve this^{7–9}. Evolving to exploit conditions outside those currently used by the entire species may be difficult because asymmetric gene-flow from distribution cores to margins and/or lack of appropriate variation in marginal populations can prevent the establishment of adaptations that would allow them to colonize ever more extreme environments¹⁰. Why, otherwise, are range sizes for most taxa very small¹¹? In practice, the Quaternary record shows that species have typically responded to past climate changes by shifting range, rather than by evolving *in situ*. Evolutionary responses provide additional uncertainty^{7,12}. If Harte *et al.*⁴ are correct about limitations imposed by ecotypic variation, our estimates of extinction risk will be conservative.

Although further investigation is needed into each of these areas, it is unlikely to result in substantially reduced estimates of extinction. Anthropogenic climate change seems set to generate very large numbers of species-level extinctions.

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1. Thomas, C. D. *et al.* *Nature* **427**, 145–148 (2004).
2. Thuiller, W. *et al.* *Nature* doi:10.1038/nature02716 (2004).
3. Buckley, L. B. & Roughgarden, J. *Nature* doi:10.1038/nature02717 (2004).
4. Harte, J., Ostling, A., Green, J. L. & Kinzig, A. *Nature* doi:10.1038/nature02718 (2004).
5. Midgley, G. F., Hannah, L., Millar, D., Rutherford, M. C. & Powrie, L. W. *Global Ecol. Biogeog.* **11**, 445–451 (2002).
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, Cambridge, 2001).
7. Davis, M. B. & Shaw, R. G. *Science* **292**, 673–679 (2001).
8. Pimm, S. L. *Nature* **411**, 531–532 (2001).
9. Thomas, C. D. *et al.* *Nature* **411**, 577–581 (2001).
10. Kirkpatrick, M. & Barton, N. H. *Am. Nat.* **150**, 1–23 (1997).
11. Gaston, K. J. *The Structure and Dynamics of Geographic Ranges* (Oxford Univ. Press, Oxford, 2003).
12. Holt, R. D. *Evol. Ecol. Res.* **5**, 159–178 (2003).