nature climate change

LETTERS

PUBLISHED ONLINE: 19 FEBRUARY 2012 | DOI: 10.1038/NCLIMATE1415

Climate-induced range contraction drives genetic erosion in an alpine mammal

Emily M. Rubidge[1,2*†], James L. Patton[1,3], Marisa Lim[1], A. Cole Burton[2,4], Justin S. Brashares[2] and Craig Moritz[1,3]

Increasing documentation of changes in the distribution of species provides evidence of climate change impacts[1], yet surprisingly little empirical work has endeavoured to quantify how such recent and rapid changes impact genetic diversity[2]. Here we compare modern and historical specimens spanning a century to quantify the population genetic effects of a climate-driven elevational range contraction in the alpine chipmunk, *Tamias alpinus*, in Yosemite National Park, USA. Previous work showed that *T. alpinus* responded to warming in the park by retracting its lower elevational limit upslope by more than 500 m, whereas the closely related chipmunk *T. speciosus* remained stable[3,4]. Consistent with a reduced and more fragmented range, we found a decline in overall genetic diversity and increased genetic subdivision in *T. alpinus*. In contrast, there were no significant genetic changes in *T. speciosus* over the same time period. This study demonstrates genetic erosion accompanying a climate-induced range reduction and points to decreasing size and increasing fragmentation of montane populations as a result of global warming.

Biologists have ample evidence that climate change is among the greatest threats facing biodiversity[5], yet there remains much uncertainty regarding our ability to understand, predict and mitigate the responses of species to a changing climate. Mammals are one of the best known taxonomic groups[6] and several studies have investigated the influence of geologic-scale climate change on morphology[7], genetic diversity[7] and community assembly[8]. Others have examined the effects of contemporary climate change (that is, over recent decades) on mammalian body size[9], phenology[10] and distribution[3]. In contrast to the extensive literature on phylogeographic responses to millennial scale climate change[11], few studies have directly tested for genetic consequences of a recent (twentieth century) climate-induced range contraction, despite the importance of such diversity to population persistence[12].

The spatial genetic structure of natural populations has important consequences for ecological and evolutionary processes over both contemporary and geologic timescales. Evidence indicates that climate change can alter genetic connectivity among populations[13] and predictive models for montane taxa indicate that warming-induced fragmentation will reduce genetic diversity over time[2,14]. Here, we test this prediction by comparing changes in genetic diversity for populations of two species of small mammal that differ in responses to twentieth-century climate warming in and around Yosemite National Park (YNP), USA.

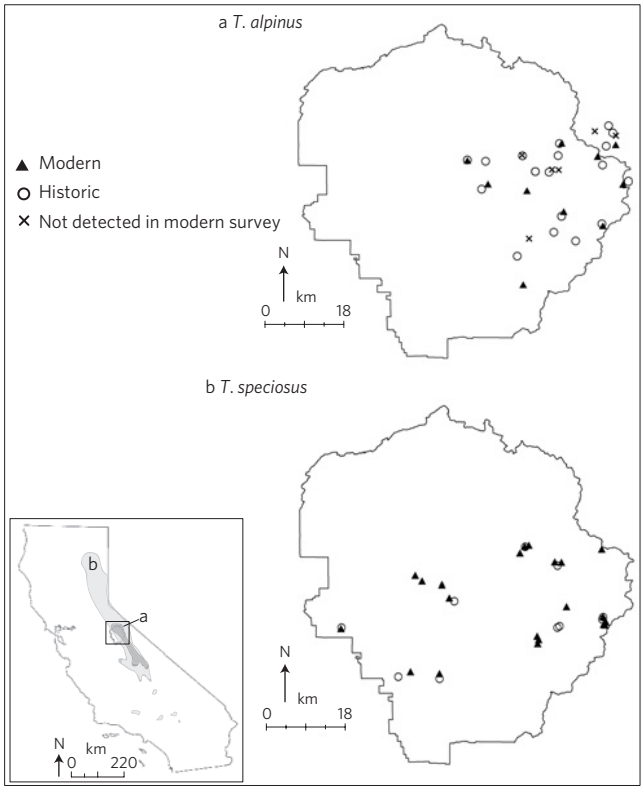

Figure 1 | Study area and sampling localities. Historical sampling localities (1915–1916) are shown in open circles and modern in filled black triangles (2003–2008) for *T. alpinus* and *T. speciosus*. Black crosses show sites that were sampled repeatedly in the present era but the species was not detected (probability of false absence at these sites is <10%; see refs 3,4 for more details). Inset shows the state of California with the distribution of *T. alpinus* (labelled a) and *T. specious* (labelled b) and the outline of YNP.

The alpine chipmunk *T. alpinus* is endemic to the high Sierra Nevada of California and has retracted its elevational range upwards as a result of a ~3 °C temperature increase in YNP over the past century. By contrast, the closely related and ecologically similar lodgepole chipmunk *T. speciosus* maintained a stable elevational range in YNP over the same period[3,4]. We used genetic samples from historical (1915–1916) and modern (2003–2008) specimens

[1]Museum of Vertebrate Zoology, 3101 Valley Life Sciences Building University of California, Berkeley, California 94720-3160, USA, [2]Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94720-3114, USA, [3]Department of Integrative Biology, University of California, Berkeley, California 94720-3160, USA, [4]Alberta Biodiversity Monitoring Institute, CW 405 Biological Sciences Building, University of Alberta, Edmonton, Alberta T6G 2E9, Canada. †Present address: 10434 135 Street NW Edmonton, Alberta T5N 2C6, Canada.
*e-mail: erubidge@gmail.com.

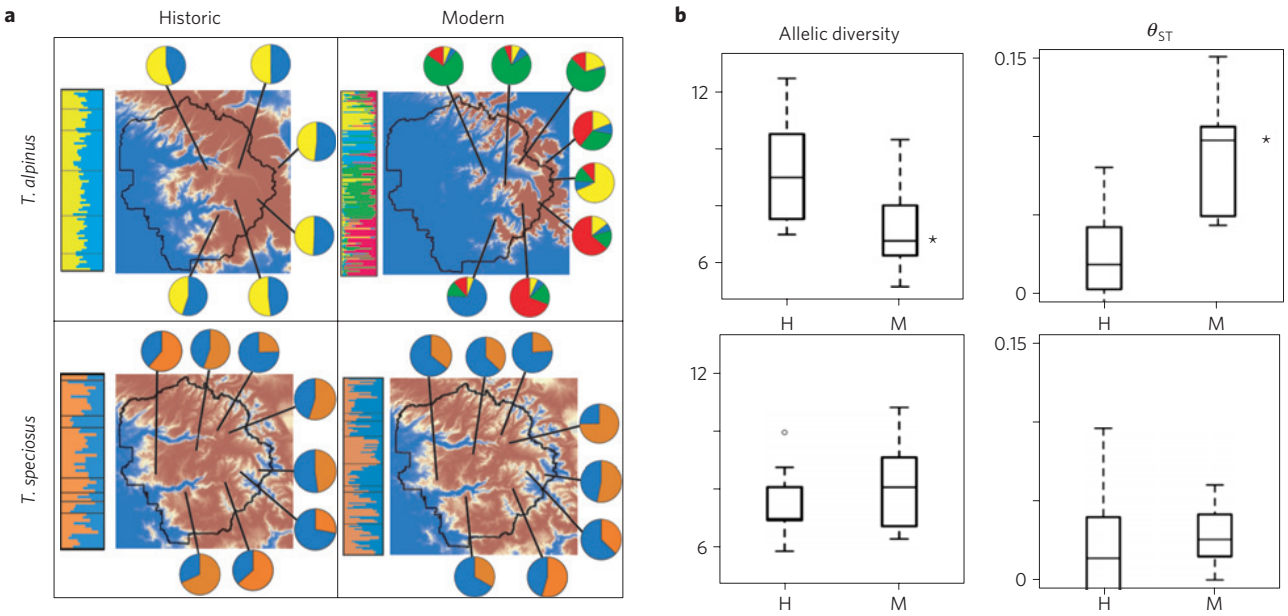

Figure 2 | Changes in genetic population structure and diversity. a, Maps show black outline of YNP and the probability of occupancy based on elevation for each era (see ref. 3 for details of occupancy models); historic (left) and modern (right). Red indicates areas of high probability of occupancy and blue shows a probability of occupancy of zero. Upper maps show the range contraction of *T. alpinus* from past to present whereas lower maps show the relative stability of occupancy of *T. speciosus* over time. Horizontal bar plots show the results of the program STRUCTURE for historic *T. alpinus* populations ($K = 2$, upper left), modern *T. alpinus* populations ($K = 4$, upper right), historic *T. speciosus* ($K = 2$; lower left) and modern *T. speciosus* ($K = 2$, lower right) based on seven microsatellite markers. Each individual is represented by a thin horizontal line in the bar graphs to the left of the maps, which are partitioned into coloured segments that indicate the individuals' cluster membership. Pie charts represent the sum of all individuals' membership in each cluster at each locality on the map, shown with black lines. **b**, Box plots showing changes in allelic richness and overall θ_{ST} from past to present in *T. alpinus* (upper) and *T. speciosus* (lower) populations over time (H, historic era; M, modern era). Asterisk indicates significant changes in mean values with $P < 0.05$.

and tissues from the same areas (Fig. 1) to test the predictions that: first, the range contraction in *T. alpinus* has reduced overall genetic diversity (measured by seven microsatellite loci) as lower elevation populations became extinct over time; second, the loss of local *T. alpinus* populations has increased genetic fragmentation as populations are increasingly confined to high-elevation montane isolates; and third, the relative stability of *T. speciosus* resulted in no significant changes in genetic diversity or population structure from the past to the present.

Our results are consistent with the predicted loss of overall genetic diversity of *T. alpinus*: we observed a significant decline in average allelic richness ($t = 1.919$, d.f. $= 11.5$, $P = 0.040$; Fig. 2b), though there was no statistically significant reduction in gene diversity between the two time periods (historical *T. alpinus* $H_S = 0.75$, s.e. $= 0.023$; modern *T. alpinus* $H_S = 0.71$, s.e. $= 0.023$, $W = 35$, $P = 0.21$; Supplementary Table S1). Six of the seven microsatellite loci used to measure diversity lost at least one allele from the past to the present (Supplementary Fig. S1). Consistent with our second prediction, we found that the range contraction observed in *T. alpinus* has resulted in increased genetic subdivision over the past century. Historical *T. alpinus* specimens represented an essentially panmictic population ($\theta_{ST} = 0.026$, 95% confidence interval: 0.000–0.044), whereas modern *T. alpinus* samples showed a significant increase in among-population diversity over time ($W = 5$, $P = 0.01$), with a global $\theta_{ST} = 0.086$ (95% confidence interval: $0.060 - 0.112$). Results of Bayesian cluster analyses were also consistent with an increase in *T. alpinus* population subdivision over time (estimated number of parental populations, K, was 2 for the historical samples and 4 for the modern data set; Fig. 2a). Finally, only the modern *T. alpinus* population showed significant isolation by distance ($Z = -40.37$, $r = 0.42$, $P = 0.03$).

Contrasting with results for *T. alpinus* and consistent with expectations, no significant changes in overall gene diversity, allelic richness or population structure were observed in the comparison of historical and modern *T. speciosus* populations (Fig. 2 and Supplementary Table S1). Although the modern *T. speciosus* population showed some minor structure that was not observed in the historical specimens (modern $\theta_{ST} = 0.029$, 95% confidence interval: $0.013 - 0.045$; historical $\theta_{ST} = 0.0185$, 95% confidence interval: $-0.007 - 0.049$), the small increase over time was not statistically significant ($W = 19$, $P = 0.535$). Furthermore, the same number of genetic populations was estimated by Bayesian cluster analyses for both historical and modern *T. speciosus* data sets ($K = 2$; Fig. 2).

These results strongly support our hypothesis that a climate-driven range contraction has decreased genetic diversity and increased local isolation for alpine chipmunk populations in YNP. This study provides clear evidence of a relationship between climate-driven habitat loss and fragmentation and loss of genetic diversity and gene flow in a terrestrial mammal. The elevational contraction and associated decline in abundance (signalled by the loss of genetic diversity) in *T. alpinus* are not restricted to our study area, but have also been observed in the southern Sierra Nevada (J. L. Patton *et al.*, unpublished data). Other montane mammals in the Sierra Nevada and elsewhere have undergone declines[3,13] and these populations may exhibit loss and restructuring of genetic diversity similar to that observed in the alpine chipmunk. As the climate continues to warm, this montane species is likely to further retract its elevational range, experiencing yet further genetic erosion and population fragmentation, and thus becoming more vulnerable to extinction throughout its distribution.

Maintenance of genetic diversity is important for mitigating climate change impacts[15]. Erosion of genetic diversity may be both a signal of demographic collapse and an indication of reduced fitness (for example, lowered adaptive potential, greater inbreeding

depression)[16]. With continued warming predicted for the Sierra Nevada[17], the distribution of this montane species, which is endemic to the region, is likely to contract and fragment further and could possibly lead to extinction. Climate change is implicated as the cause of elevational and latitudinal shifts observed across diverse taxa[1,5], and for montane taxa, such distributional shifts could result in increasingly fragmented populations. Such taxa are more vulnerable to extinction owing to stochastic effects such as genetic drift, demographic fluctuations and deterministic factors such as disease or habitat loss[18,19].

Although signatures of climate change are evident in many ecological processes, examples of climate-induced alteration of genetic or microevolutionary processes are still relatively rare[20,21]. We recognize that this study represents neutral genetic change associated with a climate-induced distributional shift, which does not necessarily predict evolutionary response to selection. However, it does provide clear evidence that twentieth-century climate change has affected the size and connectivity of populations of this species. This study also highlights the value of natural history collections in providing historical baselines and the importance of long-term monitoring or resurveys in documenting the responses of species to global change. Although further work is needed to examine changes in other taxa and ecosystems, our study provides empirical evidence of climate-induced diversity loss below the species level and highlights this powerful and often overlooked impact of climate change on biodiversity.

Methods

Museum skins used in this study are from the original specimens collected by Joseph Grinnell and colleagues from 1915 to 1916 and housed in the mammal collection in the Museum of Vertebrate Zoology, University of California, Berkeley. A square piece of skin measuring approximately 3 mm × 3 mm was removed from 88 *T. alpinus* and 59 *T. speciosus* museum specimens collected from several areas across YNP between 1915 and 1916 (Fig. 1 and Supplementary Table S2a,b). For the modern data set, resurvey teams live-trapped animals at original sites between 2003 and 2008. Modern data sets included a total of 146 *T. alpinus* and 115 *T. speciosus* samples.

All DNA extractions and polymerase chain reaction (PCR) set-up on historical samples were conducted in a separate laboratory devoted to ancient DNA research. We followed the museum protocol for the extraction of skin DNA[22] (see Supplementary Information). After numerous tests and PCR optimization trials, only seven microsatellites that gave reliable and repeatable signal in the museum skins were selected for the final analyses. PCR protocols and primer sequences are provided in Supplementary Table S3.

We tested for linkage disequilibrium and deviations from Hardy–Weinberg equilibrium in each population using the heterozygosity deficit test implemented in Genepop 4.0 (ref. 23). Bonferroni corrections were applied separately for each species and time period. Owing to significant deviations from the Hardy–Weinberg equilibrium at certain loci in historical populations (see Supplementary Information) we used the program FreeNa (ref. 24) to estimate the frequency of null alleles and to generate a data set corrected for null alleles that was used to examine their influence on estimates of genetic differentiation. The FreeNA-corrected data set yielded similar levels of pairwise genetic differentiation and overall θ_{ST} as the original data set, indicating that the data are robust to genotyping errors. Nevertheless, to err on the conservative side, we used the FreeNA-corrected values for both historical data sets. No linkage disequilibrium was detected between any loci in any of the data sets.

To examine changes in genetic diversity over time we pooled samples park-wide into a historical and modern data set for each species. We estimated Nei's measure of gene diversity (H_S; ref. 25) using the program FSTAT. To calculate allelic richness at each locus we used the hierarchical rarefaction approach implemented in HP-RARE to correct for differences in sample size between eras[26]. To statistically compare mean diversity measures between the historical and modern data sets, we used either a Welch two-sample t-test when data fit assumptions of normality or a Wilcoxon rank sum test when they did not. All comparative diversity statistical analyses were run in the program R (R Core Development Team, 2010).

The program FSTAT was used to estimate genetic differentiation among populations (F_{ST} analogue θ_{ST}; ref. 27) and tested for significance by bootstrapping across loci to generate 95% confidence intervals for overall θ_{ST}. Furthermore, to examine population structure without a priori definitions of populations and to avoid issues of uneven sampling between populations on pairwise θ_{ST} measures, we applied the Bayesian approach implemented in the software Structure 2.3.3 (ref. 28) to identify clusters of randomly mating individuals with minimum Hardy–Weinberg deviations and linkage disequilibrium (see Supplementary Information for model parameters and run details). To provide the most accurate estimation of K, we used the statistic ΔK introduced by Evanno *et al.*[29] (Supplementary Fig. S2a,b). Finally, we used the program Isolation by Distance Web Service[30] to conduct a Mantel test to test for patterns of spatially limited gene flow in both species using log(genetic distance) and log(geographic distance) with 5,000 randomizations. FreeNA-corrected pairwise F_{ST} and Euclidian distances were used.

Received 6 September 2011; accepted 18 January 2012; published online 19 February 2012

References

1. Parmesan, C. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37,** 637–669 (2006).
2. Bálint, M. *et al.* Cryptic biodiversity loss linked to global climate change. *Nature Clim. Change* **1,** 313–318 (2011).
3. Moritz, C. *et al.* Impact of a century of climate change on small mammal communities in Yosemite National Park, USA. *Science* **322,** 261–264 (2008).
4. Rubidge, E. M., Monahan, W. B., Parra, J. L., Cameron, S. E. & Brashares, J. S. The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. *Glob. Change Biol.* **17,** 696–708 (2011).
5. Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421,** 57–60 (2003).
6. Schipper, J. *et al.* The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* **322,** 225–230 (2008).
7. Blois, J. J. & Hadly, E. A. Mammalias response to Cenozoic climate change. *Annu. Rev. Earth Planet. Sci.* **37,** 181–208 (2009).
8. Blois, J. L., Mcguire, J. L. & Hadly, E. A. Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature* **465,** 771–775 (2010).
9. Ozgul, A. *et al.* Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466,** 482–485 (2010).
10. Réale, D., McAdam, A. G., Boutin, S. & Berteaux, D. Genetic and plastic responses of a northern mammal to climate change. *Proc. R. Soc. Lond. B* **270,** 591–596 (2003).
11. Hewitt, G. M. Genetic consequences of climatic oscillations in the Quaternery. *Phil. Trans. R. Soc. Lond. B* **359,** 183–195 (2004).
12. Soulé, M. E. in *Conservation Biology: An Evolutionary-Ecological Perspective* (eds Soulé, M. E. & Wilcox, B. A.) 151–169 (Sinauer, 1980).
13. Epps, C. W., Palsboll, P. J., Wehausen, J. D., Roderick, G. K. & McCullough, D. R. Elevation and connectivity define genetic refugia for mountain sheep as climate warms. *Mol. Ecol.* **15,** 4295–4302 (2006).
14. Ditto, A. & Frey, J. Effects of ecogeographic variables on genetic variation in montane mammals: Implications for conservation in a global warming scenario. *J. Biogeogr.* **34,** 1136–1149 (2007).
15. Hoffmann, A. A. & Sgro, C. M. Climate change and evolutionary adaptation. *Nature* **470,** 479–485 (2011).
16. Spielman, D., Brook, B. W. & Frankham, R. Most species are not driven to extinction before genetic factors impact them. *Proc. Natl Acad. Sci. USA* **101,** 15261–15264 (2004).
17. Cayan, D. R., Maurer, E. P., Dettinger, M. D., Tyree, M. & Hayhoe, K. Climate change scenarios for the California region. *Climatic Change* **87,** S21–S42 (2008).
18. Sih, A., Jonsson, B. G. & Luikart, G. Habitat loss: ecological, evolutionary and genetic consequences. *Trends Ecol. Evol.* **15,** 132–134 (2000).
19. McCallum, H. & Dobson, A. Disease, habitat fragmentation and conservation. *Proc. R. Soc. Lond. B* **269,** 2041–2049 (2002).
20. Hoffmann, A. A. & Willi, Y. Detecting genetic responses to environmental change. *Nature Rev. Genet.* **19,** 421–432 (2008).
21. Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A. & Merila, J. Climate change and evolution: Disentangling environmental and genetic responses. *Mol. Ecol.* **17,** 167–178 (2008).
22. Mullen, L. M., Hoekstra, H. E. & Feder, J. Natural selection along an environmental gradient: A classic cline in mouse pigmentation. *Evolution* **62,** 1555–1570 (2009).
23. Raymond, M. & Rousset, F. GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. *J. Heredity* **86,** 248–249 (1995).
24. Chapuis, M. P. & Estoup, A. Microsatellite null alleles and estimation of population differentiation. *Mol. Biol. Evol.* **24,** 621–631 (2007).
25. Nei, M. & Kumar, S. *Molecular Evolution and Phylogenetics* (Oxford Univ. Press, 2000).
26. Kalinowski, S.T. HP-RARE 1.0: A computer program for performing rarefaction on measures of allelic richness. *Mol. Ecol. Notes* **5,** 187–189 (2005).
27. Weir, B. S. & Cockerham, C. C. Estimating F-statistics for the analysis of population structure. *Evolution* **38,** 1358–1370 (1984).
28. Pritchard, J. K., Stephens, M. & Donnelly, P. Inference of population structure using multilocus genotype data. *Genetics* **155,** 945–959 (2000).

29. Evanno, G., Regnaut, S. & Goudet, J. Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Mol. Ecol.* **14,** 2611–2620 (2005).
30. Jensen, J. L., Bohonak, A. J. & Kelley, S. T. *Isolation by Distance Web Service* BMC Genetics 6: 13. v.3.16 http://ibdws.sdsu.edu/ (2005).

Acknowledgements

We are grateful to C. Conroy, the YNP resurvey field team, C. Patton and L. Chow for their role in collecting the modern field data and P. Elsen for his assistance in the lab. E.M.R. was supported by a National Science & Engineering Research Council PGS-D award, the Museum of Vertebrate Zoology and the Environmental Science, Policy and Management Department at the University of California, Berkeley, during this research. The project was financially supported by the Museum of Vertebrate Zoology at the University of California, Berkeley, the Yosemite Fund, the National Geographic Society and the National Science Foundation.

Author contributions

E.M.R., J.L.P. and C.M. designed the study; E.M.R., J.L.P. and M.L. collected data; E.M.R. analysed and interpreted data; E.M.R., C.M., A.C.B. and J.S.B. wrote the paper. All authors discussed the results and commented on the manuscript.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.M.R.