

Meetings

Climate refugia: from the Last Glacial Maximum to the twenty-first century

Workshop on Climate Refugia: Joint Inference from Fossils, Genetics, and Models, in Eugene, Oregon, USA, August 2012

The history of Earth is a history of recurrent climate change. Today's global biodiversity demonstrates that many species have been able to cope with climate shifts in the past. Yet great concern exists that modern climate change is likely to overstrain the capacity of many species to track suitable climate spaces, potentially leading to widespread extinctions through the coming decades. This view is further promoted by a large number of species distribution modeling (SDM) forecasts. It remains, however, relatively little appreciated that the deeply troubling picture stands in contrast to empirical records of species responses to past climatic changes (Botkin *et al.*, 2007). Fossil data indicate that extensive range dynamics and massive community reshuffling occurred during past periods of rapid climate transitions. But, at least for plants, there is little evidence that past major warming events were accompanied by increased global-scale extinction rates (Willis & MacDonald, 2011). One possible explanation for this apparent contradiction is that climate refugia – areas where local populations of a species can persist through periods of unfavorable regional climate – could have been much more common and widespread than previously thought. Such areas would have helped sustain regional biodiversity through periods of adverse climate or major climatic transitions, and served as sources for the subsequent re-expansion of confined populations. The existence and identification of refugia during the Last Glacial Maximum (*c.* 19–26 kyr BP; Clark *et al.*, 2009) has been a topic of active research for decades. Recent evidence indicates that many temperate and boreal species have maintained populations at considerably higher latitudes than previously assumed (Hu *et al.*, 2009; Mosblech *et al.*, 2011). Such locations are commonly referred to as 'cryptic refugia', a term that nicely conveys the difficulties in inferring the past existence of these small and scattered refugial populations. The crucial role of climate refugia for the long-term maintenance of regional to global biodiversity, and the growing awareness that refugia may be similarly relevant as 'safe havens' under future climate warming, have sparked great interest in their identification and functioning (e.g. Médail & Diadema, 2009; Stewart *et al.*, 2010; Keppel *et al.*, 2012).

Joining research perspectives and approaches

Where and how did populations persist through abrupt climate changes? What can we learn from this history to gauge extinction risks from ongoing climate change? Information from distinctly different research fields can help elucidate these questions. Paleocological records, genetic or genomic surveys, and the modeling of past climates and species distributions each provide relevant insights into the complex histories of populations and species. The emerging body of evidence regarding historical climate refugia expands our knowledge on ecological resilience, improves estimates of species migration rates in response to shifting climates, and contributes to explain disjunct ranges on the modern landscape. It can thus significantly enhance our understanding of how populations may react to future climate changes and help identify possible refugia for species of concern. The workshop 'Climate Refugia: Joint Inference from Fossils, Genetics, and Models' was held on 1–3 August 2012 in Eugene, Oregon, USA. The meeting convened 33 researchers from 10 countries with backgrounds in paleoecology, population genetics, evolutionary biology, landscape ecology, climatology, and species distribution modeling. The aim of the workshop was to reach a better understanding of how populations persist in some geographical areas through major climate changes and to promote interdisciplinary approaches for investigating the location and environmental settings of these areas as well as their conservation implications. This was, to our knowledge, the first international workshop dedicated specifically to climate refugia.

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The meeting revealed that different research communities have developed notably distinct notions of refugia (see Table 1 for some examples) and that a common framework and terminology will be required for communication between fields. Three issues that deserve particular attention are the spatio-temporal scale of interest, the level of biotic organization, and the relationship of refugia with the core distribution range. Additionally, it proved to be valuable to assemble researchers working on past (that is, glacial) as well as present-day and putative future (that is, interglacial) climate refugia. One insight with wide-ranging implications is that glacial

Table 1 Some recent definitions of climate refugia that vary in their emphasis on the spatio-temporal scale of interest, the level of biotic organization involved, and the relationship with the core distribution range

Reference	Definition
Médail & Diadema (2009)	An area where distinct genetic lineages have persisted through a series of Tertiary or Quaternary climate fluctuations owing to special, buffering environmental characteristics.
Stewart <i>et al.</i> (2010)	The geographical region or regions that a species inhabits during the period of a glacial/interglacial cycle that represents the species' maximum contraction in geographical range.
Dobrowski (2011)	Areas that support locally favorable climates, in which populations of species can survive outside their main distribution, protected from regionally limiting climatic factors.
Keppel <i>et al.</i> (2012)	Habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions.

refugia no longer exist and can hence only be inferred by indirect means, whereas interglacial refugia can be directly observed and studied. Accordingly, investigations on each refugium type have largely focused their efforts on different core questions.

Inferring refugia: a richer view from interdisciplinary approaches

A primary concern raised at this workshop was to improve our ability to identify glacial refugia using independent sources of information (Hu *et al.*, 2009). For instance, fossils can offer the clearest evidence for the presence of a species in a given locale, but they are often too scarce and for many taxa they are completely lacking. Even pollen records of trees with abundant wind-dispersed pollen have been found to be unreliable at detecting small populations. By contrast, phylogeographic analyses excel at revealing cryptic refugia and past population expansions (though rarely below the scale of large landscapes), but they are unable to detect extinctions or to conclusively inform about the timing of past events. These and other limitations, together with the traditional focus of both disciplines on the inhabitants of refugia, and not their environmental settings, have been hindering a detailed understanding of what distinguishes a climate refugium. Other insights are being gained by using SDM, which are increasingly applied to hindcast potential distributions of species in the past (Varela *et al.*, 2011). However, SDM depend on fossil or phylogeographical data to confirm that putative refugia were actually occupied by a species (and that model predictions are not spurious due to unrealistic assumptions). A further important limitation is that the spatial resolution of available climate data is too coarse to detect spatially restricted refugia.

Despite the complementary nature of the described research approaches, few studies have to date integrated input from more than two fields at a time. However, ongoing conceptual and

technical developments promise to advance interdisciplinary thinking and the development of research approaches that systematically embrace the different data sources available (e.g. Espíndola *et al.*, 2012). For example, novel genomic techniques are poised to rapidly accelerate the progress of phylogeographic studies, providing abundant data that can be used to test fossil and/or SDM-based specific hypotheses about the history of a species. Ultimately, the goal has to be the development of a quantitative framework that explicitly considers the strengths and weaknesses of each approach for rigorous assessment of past refugia and migration patterns.

Understanding refugia: from mechanisms to forecasts

In contrast to glacial refugia, extant interglacial refugia can be directly studied *in situ* using a range of methods from climatology, biogeography, evolutionary biology, as well as population, functional, and community ecology (Hampe & Jump, 2011). Climate refugia, by definition, are unique climatically and biologically within their regional contexts (Table 1, see also Fig. 1). As such, an understanding of the physical and biotic processes that allow for their persistence is important to understand how biota may respond to ongoing climate changes. Efforts are being made to elucidate the local climatic, hydrologic, and physiographic characteristics of sites that are acting as interglacial refugia. It remains challenging to characterize 'refugial climates' at scales that are relevant to biota. However, recent attempts combining dense networks of climate sensors with new generations of regional climate simulations to achieve a realistic downscaling over complex terrain (Dobrowski, 2011) represent a promising approach. Such efforts will eventually provide a much-needed mechanistic understanding of how refugia operate. They are moreover key for improving our forecasts of climate change impacts on species distributions. In turn, these high-resolution topoclimatic data could be incorporated with SDM approaches integrating dynamic demographic and dispersal processes (e.g. Pagel & Schurr, 2012) in order to assess whether



Fig. 1 Landscape features that help decouple local climate trends from those occurring at regional scale (such as canyons, water bodies or steep aspects), are ideal locations for supporting climate refugia. Shown here is a canyon containing a perennial spring that supports a community of mesic-adapted plant species within a semi-arid landscape in central Oregon, USA. Courtesy of Daniel Gavin.

species can actually colonize sites whose environmental conditions qualify them as potential refugia in the future.

Overall, the discussion during the meeting led to the conclusion that we need a considerably more quantitative and mechanistic understanding of what makes and maintains climate refugia. Some major emerging questions were: Can we infer species' ability to persist in refugia from their life history or functional traits? Which climatic drivers are most relevant for population performance? Which specific landscape features promote the maintenance of suitable microclimates under a deteriorating regional climate? Can we predict the location of refugia based on species traits and landscape features? Can we anticipate the evolution of refugia under continued climate shifts? These questions highlight the need for further study of the processes that underlie refugial dynamics and the conservation of biodiversity in a warming world.

Acknowledgements

The authors thank the PAGES project of the International Geosphere-Biosphere Program (IGBP) and the University of Oregon for supporting the workshop.

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References

- Botkin DB, Saxe H, Araújo MB, Betts R, Bradshaw RHW, Cedhagen T, Chesson P, Dawson TP, Etterson JR, Faith DP *et al.* 2007. Forecasting the effects of global warming on biodiversity. *BioScience* 57: 227–236.
- Clark PU, Dyke AS, Shakun JD, Carlson AE, Clark J, Wohlfarth B, Mitrovica JX, Hostetler SW, McCabe AM. 2009. The Last Glacial Maximum. *Science* 325: 710–714.
- Dobrowski SZ. 2011. A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology* 17: 1022–1035.
- Espíndola A, Pellissier L, Maiorano L, Hordijk W, Guisan A, Alvarez N. 2012. Predicting present and future intra-specific genetic structure through niche hindcasting across 24 millennia. *Ecology Letters* 15: 649–657.
- Hampe A, Jump AS. 2011. Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics* 42: 313–333.
- Hu FS, Hampe A, Petit RJ. 2009. Paleoecology meets genetics: deciphering past vegetational dynamics. *Frontiers in Ecology and the Environment* 7: 371–379.
- Keppel G, Van Niel KP, Wardell-Johnson GW, Yates CJ, Byrne M, Mucina L, Schut AGT, Hopper SD, Franklin SE. 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography* 21: 393–404.
- Médail F, Diadema K. 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *Journal of Biogeography* 36: 1333–1345.
- Mosblech NAS, Bush MB, van Woesik R. 2011. On metapopulations and microrefugia: palaeoecological insights. *Journal of Biogeography* 38: 419–429.
- Pagel J, Schurr FM. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography* 21: 293–304.
- Stewart JR, Lister AM, Barnes I, Dalén L. 2010. Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B, Biological Sciences* 277: 661–671.
- Varela S, Lobo JM, Hortal J. 2011. Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeography, Palaeoclimatology, Palaeoecology* 310: 451–463.
- Willis KJ, MacDonald KM. 2011. Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annual Review of Ecology, Evolution and Systematics* 42: 267–287.

Key words: climate change, glacial refugia, global warming, Last Glacial Maximum, paleobiogeography, species distribution modeling (SDM).