

OPINION

Climate change and geothermal ecosystems: natural laboratories, sentinel systems, and future refugia

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Abstract

Understanding and predicting how global warming affects the structure and functioning of natural ecosystems is a key challenge of the 21st century. Isolated laboratory and field experiments testing global change hypotheses have been criticized for being too small-scale and overly simplistic, whereas surveys are inferential and often confound temperature with other drivers. Research that utilizes natural thermal gradients offers a more promising approach and geothermal ecosystems in particular, which span a range of temperatures within a single biogeographic area, allow us to take the laboratory into nature rather than *vice versa*. By isolating temperature from other drivers, its ecological effects can be quantified without any loss of realism, and transient and equilibrium responses can be measured in the same system across scales that are not feasible using other empirical methods. Embedding manipulative experiments within geothermal gradients is an especially powerful approach, informing us to what extent small-scale experiments can predict the future behaviour of real ecosystems. Geothermal areas also act as sentinel systems by tracking responses of ecological networks to warming and helping to maintain ecosystem functioning in a changing landscape by providing sources of organisms that are preadapted to different climatic conditions. Here, we highlight the emerging use of geothermal systems in climate change research, identify novel research avenues, and assess their roles for catalysing our understanding of ecological and evolutionary responses to global warming.

Keywords: aquatic, Arctic, complexity, global warming, natural experiment, spatial and temporal scale, terrestrial, whole-stream warming

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Introduction

Each of the past three decades has been successively warmer than any other since detailed records began, and most models predict a rise in global surface temperature of at least 1.5–2.0 °C by the end of this century (IPCC, 2013). Clear ecological responses to recent warming have already been observed, including species range shifts (Hickling *et al.*, 2006; Chen *et al.*, 2011), altered timing of life-cycle events (Menzel *et al.*, 2006; Wolkovich *et al.*, 2012), and reductions in the body size of many organisms (Daufresne *et al.*, 2009; Forster *et al.*, 2012). While these patterns are undeniable, we still lack

the mechanistic understanding required to predict ecological responses to warming accurately.

To achieve this, we need to understand physiological, ecological, and evolutionary responses to warming across multiple spatial and temporal scales (Shaver *et al.*, 2000). This knowledge will only be acquired through a combination of approaches, each with its own strengths and weaknesses. For instance, long-term monitoring of natural communities or space-for-time substitutions provide powerful insights into equilibrium responses to warming, but are inferential and/or confounded by latitude, altitude, or other physical-chemical variables (see Dunne *et al.*, 2004). Experimental studies are essential for detecting causal relationships (O'Gorman *et al.*, 2012), yet most are limited in spatial or temporal scope, often spanning less than a few square metres in extent and less

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than 1 year in duration (Stewart *et al.*, 2013; but see Sistla *et al.*, 2013). Laboratory microcosms provide key insight into mechanistic drivers (Newsham & Garstecki, 2007; Beveridge *et al.*, 2010), but they lack the complexity of natural systems and even large-scale field mesocosms (e.g. Grime *et al.*, 2000; Yvon-Durocher *et al.*, 2010) may be insufficient to fully address ecosystem-level responses. Long-term whole-ecosystem manipulations of temperature are critical, but such studies are rare because of the logistical and financial challenges of experimental warming at this scale (although see Hogg & Williams, 1996; Melillo *et al.*, 2011; Canhoto *et al.*, 2013). Systems in which all of these approaches can be leveraged could provide a linchpin in our struggle to predict complex ecological responses to warming.

Dunne *et al.* (2004) highlight a simple conceptual model to help address this goal. By embedding manipulative warming experiments within multiple sites along a natural thermal gradient, both short- and long-term responses to temperature change can be investigated. This framework was employed in a sub-alpine warming experiment, where ambient and heated plots were compared across four different elevations (see Dunne *et al.*, 2004). Flowering of plants in response to the timing of snow melt were consistent in both the short term (from experimental warming) and over longer timescales (along the altitudinal gradient), suggesting that phenological results were robust across multiple spatial and temporal scales (Dunne *et al.*, 2003). However, the relationship between soil organic carbon content and mean annual soil temperature differed between the altitudinal gradient and the experimental plots due to long-term changes in litter quality (Saleska *et al.*, 2002). These results underscore the importance of designing research programs that explicitly deal with temporal scale.

Here, we suggest an analogous approach that complements and advances the framework of Dunne *et al.* (2004) by constraining the spatial scale over which such natural gradients and manipulative experiments are combined, thus reducing the impact of confounding factors. Geothermally heated ecosystems present an excellent opportunity to achieve that goal within a global warming context. They typically occur where heated water accumulates beneath impermeable rock at high pressure, maintained by continuous circulation of heat, and fluid through recharge zones and discharge areas (Barbier, 2002). High-temperature fields are especially common around tectonic plate boundaries (Shapiro & Ritzwoller, 2004), although less extreme areas can be found throughout the globe (see Fig. 1). These geothermal systems provide a window

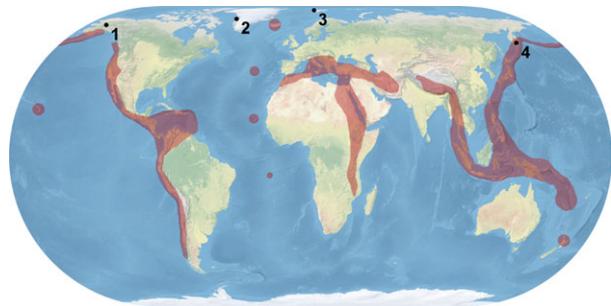


Fig. 1 Map of the hottest geothermal areas around the world (in red; underlying data adapted from the US Geological Survey). Numbered black points relate to four high-latitude ecosystems (1: Alaska; 2: Greenland; 3: Svalbard; 4: Kamchatka), recently identified as potential new natural laboratories for global warming experiments (see further details in Box 3).

into long-term ecological and evolutionary responses to warming because their biota has typically been exposed to elevated ambient temperature regimes for multiple generations, without the added complication of changes in altitude or latitude. They also offer a low-cost solution to manipulating temperature at shorter time scales, and can thus serve as natural laboratories for studying both immediate and transient responses to warming. In addition, they act as sentinel systems by highlighting early responses to warming, as well as providing 'future refugia' which hold organisms that are preadapted to different climatic conditions, thereby acting as a buffer to help safeguard against the impacts of environmental change. Thus, we argue that geothermal ecosystems provide an ideal platform for conducting multi-scaled research to help disentangle complex ecological responses to warming.

Combining natural and manipulative warming experiments

Geothermal gradients have been used to illustrate the biological effects of temperature in a range of terrestrial and aquatic environments, e.g. above-ground communities (Convey *et al.*, 2000), soil microbes (Norris *et al.*, 2002), forest ecosystems (Burns, 1997), and freshwater springs (Owen *et al.*, 2008; Miller *et al.*, 2009; Sayeh *et al.*, 2010). Often, the focus has been on understanding life in extreme environments rather than temperature per se, which is commonly confounded with gradients in soil or water chemistry, e.g. high acidity and mineral content (Burns, 1997; Sayeh *et al.*, 2010). For instance, much of the marine research conducted in geothermal systems remains focused on understanding the unusual biology of hydrothermal vent communities (see Tarasov

et al., 2005 for an overview). Similarly, research in iconic hotspots such as Yellowstone National Park has focused on understanding extremophile biology (Brock, 1978; Inskip *et al.*, 2013), with high concentrations of solutes like phosphorus and arsenic limiting our ability to isolate the effects of temperature from other drivers (Boylen & Brock, 1973; Stauffer *et al.*, 1980). Many unique plants and microbes may also be found in extreme geothermal areas, adapted to high temperatures and fluctuating thermal environments (Stout & Al-Niemi, 2002; Sayeh *et al.*, 2010; Ward *et al.*, 2012), making extrapolations to other systems of questionable value.

Nonetheless, many far more 'benign' geothermal systems (<40 °C) exist that are not confounded by soil or solute chemistry and which are ideal for isolating the effects of temperature on multiple scales and levels of biological organization in environments that are representative of Earth's major biomes. For example, an ongoing terrestrial study in Iceland highlights the potential for conducting natural soil-warming experiments (see Box 1). Other examples have appeared in recent years from moderate temperature gradients in standing and flowing freshwaters (Duggan *et al.*, 2007; O'Gorman *et al.*, 2012; Starke *et al.*, 2013). A catchment of geothermal streams in Iceland has revealed the effects of temperature on population abundances, community composition, food web structure, and ecosystem functioning (Friberg *et al.*, 2009; Woodward *et al.*, 2010; Demars *et al.*, 2011; O'Gorman *et al.*, 2012; Hannesdóttir *et al.*, 2013). Some of these findings have challenged current ecological thinking, such as revealing important exceptions to the supposed ubiquity of temperature-size rules (O'Gorman *et al.*, 2012; Adams *et al.*, 2013) based on meta-analyses of surveys (Daufresne *et al.*, 2009) and laboratory experiments (Forster *et al.*, 2012). Such discrepancies between theory and observation could, however, simply reflect short-term (transient) vs. long-term (equilibrium) responses to warming, which can be relatively easily disentangled in geothermal systems, e.g. via reciprocal translocation and temperature change experiments (Perkins *et al.*, 2012).

Given that anthropogenic warming is occurring on a relatively short timescale, transient biological responses are likely in the initial stages, whereby many members of the biota will be unable to keep pace either by adaptation or migration. Thus, embedding controlled experiments within geothermal systems multiplies the strength of the overall approach by also tackling these short-term responses. *In situ* microcosms and mesocosms can be used to manipulate a subset of organisms across a temperature gradient (e.g. Lamberti & Resh, 1983), while still exposing them to the complexity and variation represented in natural ecosystems (see

Stewart *et al.*, 2013). Comparisons with experiments carried out under uniform, controlled laboratory conditions will help to corroborate how well lab-based findings can be extrapolated to (and identify mechanistic explanations for) field-based observations (e.g. Norris *et al.*, 2002). Transient responses can also be studied by taking advantage of large-scale natural shifts in warming regimes (see Box 1), via direct translocation of biota (e.g. Perkins *et al.*, 2012), or by experimental use of local heat sources (see Box 2).

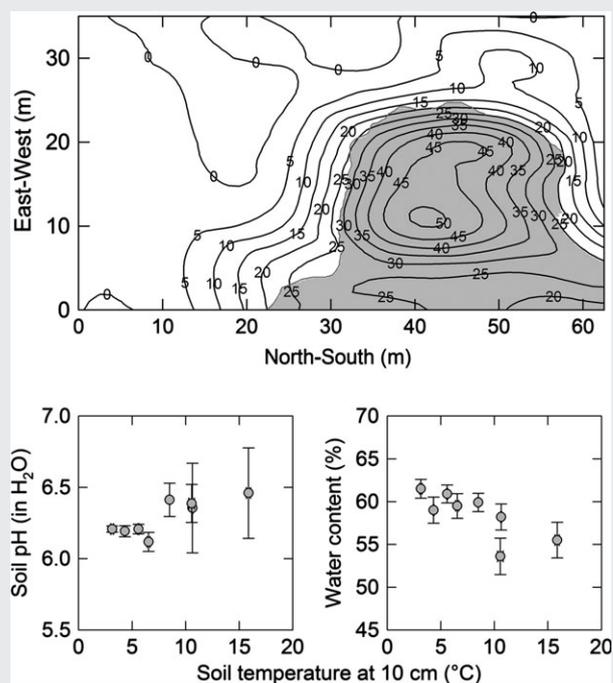
To illustrate the point, we provide examples of studies carried out along spatial and temporal gradients of temperature that might have benefited from being carried out within a geothermal system. Jacobsen *et al.* (1997) found that cold stream communities from high altitudes in Ecuador were taxonomically more similar to those in lowland Denmark than they were to warmer, low altitude Ecuadorian systems. By comparing streams in the same locale but exposed to differential geothermal heating (e.g. Woodward *et al.*, 2010), the same question could be addressed without the confounding effects of biogeography, dispersal constraints, or atmospheric conditions. Translocation of fauna between streams of different temperature, or direct warming/cooling of reaches within a stream, could also mechanistically demonstrate the impact of temperature on faunal composition because streams in geothermal areas are open to colonization from higher to lower temperatures – something that is rarely possible in altitudinal or latitudinal studies. Oechel *et al.* (2000) examined decadal trends in CO₂ flux from Arctic soils in response to rising temperatures and found that long-term adaptation to warming could influence periods of the year when the soil was a net CO₂ sink. Long-term investigations of carbon sequestration are also possible in geothermally heated soils, but with the added benefit of comparing patterns across multiple starting temperatures within the same biogeographical area. There is greater potential to determine the context-dependency of starting conditions and the possibility of nonlinear trends by examining long-term carbon flux trajectories across a thermal gradient. This can be examined at both transient and equilibrium scales, depending on the duration of soil warming (see Box 1), increasing the predictability of future impacts.

Careful integration of natural and experimental techniques within geothermal areas can therefore help to tease apart responses to warming across a wide spectrum of space, time, and biological complexity, and to confront theory with data collected at scales and organizational levels that are relevant to the real world. Coupling field and laboratory measurements of ecosystem respiration, for instance, has revealed

Box 1

Integrating transient and equilibrated responses to geothermal heating: a terrestrial case study

Using geothermal gradients as proxies for warming in natural communities is often tempered by the long-term adaptation of constituent organisms to a given thermal regime (which could potentially span several millennia). Given that climate change is occurring on a much more rapid timescale (i.e. years or decades), many longer lived organisms (e.g. trees) will be unable to adapt *in situ*. However, geothermal activity sometimes creates new hotspots after major tectonic events, exposing previously ambient ecosystems to warmer temperatures and so generating opportunities for research into transient responses to rapid warming. For example, an earthquake in the south of Iceland in 2008, measuring 6.3 on the Richter scale (Halldorsson & Sigbjörnsson, 2009), led to warming of soils at Reykir (64.008°N, 21.178°W) by up to 50 °C within a previously cool four hectare area (see Box 1 Figure). The FORHOT project (www.forhot.is) has revealed subsequently stable levels of soil warming, with similar seasonal fluctuations to unheated soils and no chemically confounded geothermal water in the root zone. Key soil chemistry characteristics (such as pH and water content) do not change substantially along the soil temperature gradient (see Box 1 Figure). Study sites have since been established within two locally typical ecosystems, natural grasslands (see Figure S1a) and 45 year old Sitka spruce plantations, with monitoring of community structure, nutrient cycling, and carbon dynamics. Warming impacts are particularly clear at the forest site, with dramatic die-off of Sitka spruce trees (see Box 1 Figure). Monitoring of a natural grassland site less than 2.5 km away, which has been exposed to longer term geothermal heating (see Figure S1b), has facilitated comparisons of transient and equilibrated responses to temperature. Such coupling of short- and long-term exposure of natural ecosystems to temperature gradients makes geothermal areas an important tool for understanding responses to warming across a range of temporal scales.



Top panel: schematic diagram showing the spatial distribution of geothermal soil warming at the FORHOT forest site in Reykir, Iceland. Isolines show differences in soil temperature (°C) at 10 cm depth between unaffected and warmed areas. The grey area indicates >98% Sitka spruce mortality 5 years after the initiation of the warming. The bottom panels show the narrow ranges of soil pH (~0.5 units) and water content (~10%) along the first 20 °C of soil warming. Note that both parameters are at levels that are unlikely to adversely affect biotic composition.

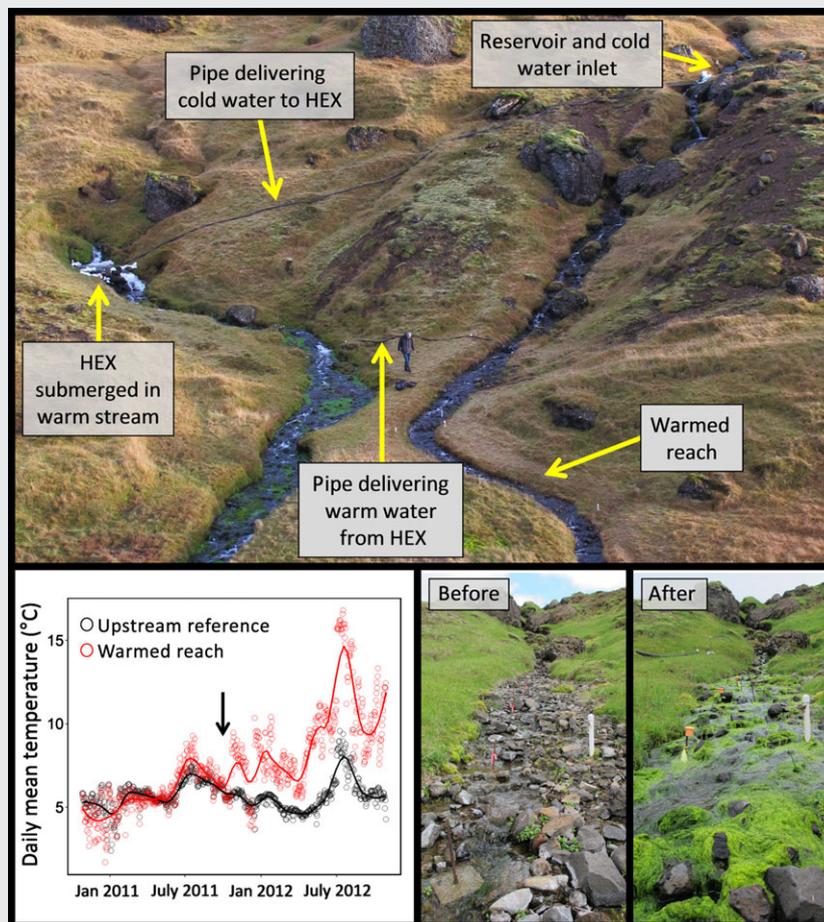
remarkably consistent temperature dependency, despite huge species turnover and disparities in spatiotemporal scales (Yvon-Durocher *et al.*, 2010; Demars *et al.*, 2011; Perkins *et al.*, 2012). This suggests that eco-

system processes are far more predictable than community-level responses, and that small-scale transient responses may also reflect those at larger scale, equilibrated conditions.

Box 2

Optimizing the geothermal laboratory: direct temperature manipulations

Two field studies at Hengill in Iceland have recently demonstrated the feasibility of manipulative warming experiments in geothermal areas by using heat exchangers to warm cooler water. The first experiment, started in October 2011, uses a single, large heat exchanger (13 m²) to warm a 35 m stream reach by an average of 3 °C above ambient (see Box 2 Figure and Figure S2a). Ongoing research is examining community- and ecosystem-level responses to long-term warming at this relatively large spatial scale, providing an important bridge between the initial transient phase of warming and the eventual new equilibrium state. The second experiment, conducted in the summer of 2013 near a different stream, uses smaller heat exchangers (0.4 m²) to mix warmed and cool source water, providing three replicated experimental channels at each of five different temperatures (see Figure S2b). This provides the platform for a more highly controlled and replicated investigation of specific transient responses to warming (e.g. community structure, herbivory, or nutrient cycling) at smaller, but easy to manipulate temporal and spatial scales. While the design of these systems is not trivial, their construction and operation is straightforward and relatively inexpensive: both set-ups were built from stainless steel tubing and home plumbing supplies, while each is gravity-fed and low-maintenance. There are site-level constraints to the use of heat exchangers, however, as they must be close to a cool water source and to an effective heat source of adequate temperature and flow rate. Where these conditions are met, geothermal heat exchangers can fill a key gap in climate change research, which would be extremely difficult to overcome using conventional methods.



Top panel: gravity-fed geothermal heat exchange (HEX) system used for a whole-stream warming experiment in the Hengill catchment, western Iceland (see Figure S2a for a close-up of the HEX design). Bottom left panel: daily mean water temperature in the experimental stream above and below the warm water outlet. The experimental warming commenced in October 2011 (indicated by the arrow). Bottom right panels: experimental stream reach in July 2011 (before warming) and July 2013 (after warming). Note the large increase in biomass of the green alga *Ulva*.

Sentinel systems and future refugia: monitoring responses to and buffering against the impacts of rapid warming

Climate change will be patchy over space and time in the coming decades, with the Arctic experiencing especially rapid warming (IPCC, 2013). Given this mosaic of change, some geothermal systems may play important roles not just as field laboratories, but also as 'sentinel systems' for generating critical baseline data to track responses to rapid warming (Woodward *et al.*, 2010). Identifying ecological observatories that combine long-term monitoring with natural warming experiments offers a way to develop more realistic projections of

future change (O'Gorman & Woodward, 2013). For instance, the scope for convergence of community or ecosystem properties at ambient sites with those of their contemporaneous geothermally heated counterparts can be assessed and tracked as the climate warms, enabling the refinement, and iterative retesting of forecasting models over time. To highlight this potential, we conducted a cursory survey that has identified dozens of candidate sites spanning the Arctic Circle and Boreal Zone, which could be used to monitor, manipulate, and model responses of multispecies systems *in situ* (see Box 3).

In addition to acting as observatories for tracking biotic responses to climate change, geothermal systems are

Box 3

The ubiquity of geothermal systems: examples of replicated stream catchments from across the Arctic Circle and Boreal Zone

A cursory survey of high-latitude geothermal stream catchments undertaken during summer 2013 revealed that multiple sites could be found in suitable areas in Kamchatka (mean summer stream temperature 5–27 °C), Alaska (5–28 °C), Greenland (1–15 °C), and Svalbard (1–25 °C). These four geothermal systems span a latitudinal gradient from 52 to 79°N, with the coolest streams at each site acting as a reference point for ambient water temperatures. All four systems are groundwater-fed and hence hydrologically stable, with no confounding effects of water chemistry across the temperature gradient (see Box 3 Figure). The systems vary with regard to isolation, land-mass size, and regional biodiversity, making them ideally suited to test linkages between temperature and biogeographical or spatial-scale controls. Additionally, the cold streams provide a long-term benchmark for the effects of regional warming on community structure and ecosystem processes in 'sentinel' high-latitude systems. They may also be the final refugia for cold stenotherms in a warming climate, given the insulating effect of soil and rock in mitigating the impacts of climate in groundwater systems (Davis *et al.*, 2013).

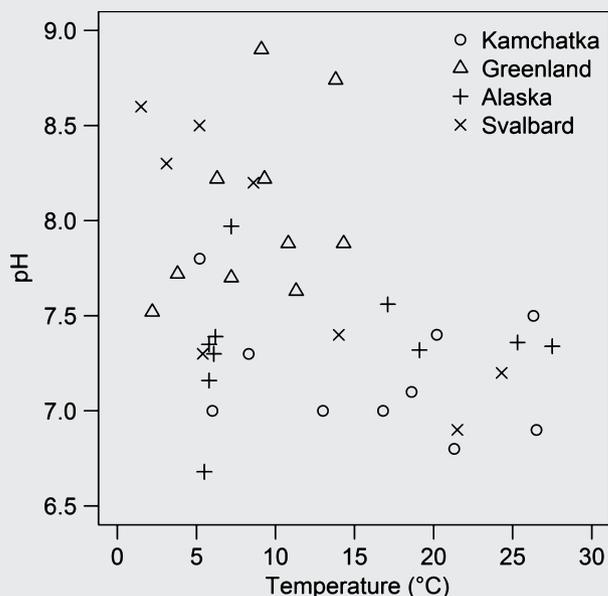


Figure highlighting the moderate gradients in pH (6.5–9.0) and temperature (0–30 °C) at four recently identified geothermal stream systems: central Alaska in the USA, Disko Island off Greenland, Jotunn and Troll springs in Svalbard, and Kamchatka in Russia (see locations in Fig. 1).

also likely to play a far more active role in maintaining regional biodiversity, by providing pockets of potential propagules to seed the future communities that will emerge as the climate changes. This may be considered analogous to the survival and evolution of biota in glacial refugia during and after the Pleistocene glaciations (Provan & Bennett, 2008), but rather than simply acting as safe havens from warming (Keppel *et al.*, 2012; Davis *et al.*, 2013), they may be sources of species or communities adapted to a gradient of different climatic conditions. Geothermal systems possess multiple local environments that have already advanced to different points along the trajectory of predicted regional change. With so many geothermal hotspots around the world (see Fig. 1), there is huge potential for their preadapted organisms to leap-frog into nearby nongeothermal habitats as ambient temperatures increase. These colonists will likely have a head start, by short-circuiting the slower polewards invasions from lower latitudes that will follow in their wake. Rapid colonization of range margins may then be feasible from these hotspots, which could provide 'future refugia' for preserving ecosystem functioning through a mechanism similar to that described for glacial refugia (Pearson, 2006).

In addition to colonization dynamics and dispersal constraints, the persistence of populations exposed to rapid environmental change depends on resistant types (e.g. those with higher thermal optima) that are already present, or which can quickly adapt, being able to restore population growth (Orr & Unckless, 2008). This 'evolutionary rescue' provides a mechanism by which population decline following a perturbation is halted and then followed by exponential increases in adapted types (Bell & Gonzalez, 2009). The threat of extinction from rapid warming in the coming century may therefore be mitigated by the presence of geothermal refugia that could accelerate evolutionary rescue in species for which it might otherwise be unfeasible, due to small population size, long generation times, or limited genetic variability in the surrounding landscape (Vander Wal *et al.*, 2013). This mechanism has been demonstrated in laboratory microcosms (Bell & Gonzalez, 2011), where populations exposed to historical environmental change were more likely to experience evolutionary rescue after perturbations if they were embedded within connected metapopulations in more stable environments. Geothermal systems would be ideal models for testing these ideas in the field.

Conclusion

Most bioclimatic envelope models ignore the respective roles of species interactions, refugia, and evolutionary

mechanisms, and these shortcomings can be addressed by studying geothermal areas. These natural laboratories, sentinel systems, and providers of future refugia could therefore prove to be key to understanding and predicting global warming impacts in multispecies systems, as well as buffering against the future effects of climate change. The global distribution of geothermal sites makes such exercises feasible, given enough vision and international collaboration. Establishing ecological observatories in these systems could become as important for understanding the impacts of climate change on biodiversity across all its organizational levels as the Mauna Loa and other CO₂ observatory data have been for understanding the chemistry and physics of climate science.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Schematic diagram showing the spatial distribution of geothermal soil warming at the FORHOT grassland sites in Reykir, Iceland (see Box 1). Isolines show differences in soil temperature ($^{\circ}\text{C}$) at 10 cm depth between unaffected and warmed areas. (a) Grassland site which has only been exposed to geothermal warming since an earthquake in 2008; (b) Grassland site that has been geothermally heated for a much longer time period.

Figure S2. (a) Heat exchangers used in the geothermal Hengill region of Iceland. The left panel shows a large heat exchanger (13 m^2 surface area) used for the whole-stream warming experiment described in Box 2. This system successfully warmed a 35 m reach of the experimental stream to $\sim 3.5\text{ }^{\circ}\text{C}$ above ambient. The panels on the right show smaller heat exchangers used in the streamside channel experiments described in Box 2. (b) Experimental stream warming array and resulting temperature data across treatments. The channel array on the left provides a platform for replicated studies conducted along a temperature gradient at small temporal and spatial scales. A system of three small heat exchangers, shown in (a), warms water from a cool source to four controlled, higher temperatures (up to a maximum of $\sim 25\text{ }^{\circ}\text{C}$), allowing three replicated experimental channels at each of five temperatures. The figure on the right shows average temperatures and box plot quantiles for an 8 week experiment in summer 2013.