

Differential effects of temperature change and human impact on European Late Quaternary mammalian extinctions

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Abstract

Species that inhabited Europe during the Late Quaternary were impacted by temperature changes and early humans, resulting in the disappearance of half of the European large mammals. However, quantifying the relative importance that each factor had in the extinction risk of species has been challenging, mostly due to the spatio-temporal biases of fossil records, which complicate the calibration of realistic and accurate ecological niche modeling. Here, we overcome this problem by using ecotypes, and not real species, to run our models. We created 40 ecotypes with different temperature requirements (mean temperature from -20°C to 25°C and temperature range from 10°C to 40°C) and used them to quantify the effect of climate change and human impact. Our results show that cold-adapted ecotypes would have been highly affected by past temperature changes in Europe, whereas temperate and warm-adapted ecotypes would have been positively affected by temperature change. Human impact affected all ecotypes negatively, and temperate ecotypes suffered the greatest impacts. Based on these results, the extinction of cold-adapted species like *Mammuthus primigenius* may be related to temperature change, while the extinction of temperate species, like *Crocota crocuta*, may be related to human impact. Our results suggest that temperature change and human impact affected different ecotypes in distinct ways, and that the interaction of both impacts may have shaped species extinctions in Europe.

Keywords: climate change, ecotypes, extinction, megafauna, Pleistocene, range shift

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Introduction

The fossil record indicates that around 30% of genera and 50% of mammal species that inhabited Europe during last 21 000 years went extinct as a result of the global changes that took place in that period (Barnosky *et al.*, 2004a,b). Charismatic species like the woolly mammoth, *Mammuthus primigenius*, and the woolly rhino, *Coelodonta antiquitatis*, large carnivores like the cave bear, *Ursus spelaea*, and large species of deer, like the Irish elk, *Megaloceros giganteus*, disappeared with at least nine other species of large mammals (>20 kg) (see Table 1). Most of these species became globally extinct, but others were able to survive in Africa, Asia, or North America (including the spotted hyena, *Crocota crocuta*; the Saiga antelope, *Saiga tatarica*; and the muskox, *Ovibos moschatus*).

The majority of the studies attempting to distinguish the effect of climate change from that of human impacts have analyzed extinctions at a continental scale and have focused on the temporal overlap between observed extinctions and climate change and/or early human arrivals (Barnosky *et al.*, 2004a,b; Lyons *et al.*, 2004; Lima-Ribeiro & Diniz-Filho, 2013). However, results from those studies are contradictory, mostly because the majority of the vertebrate fossil record lacks a fine temporal and spatial resolution (Field *et al.*, 2013). To overcome this problem, some researchers focus on species with an extensive fossil record, like the woolly mammoth (Mcneil *et al.*, 2005; Stuart, 2005; Stuart *et al.*, 2005; Nogues-Bravo *et al.*, 2008; Iwase *et al.*, 2012; Macdonald *et al.*, 2012; Mann *et al.*, 2013), the cave lion (Stuart & Lister, 2011), or the woolly rhinoceros (Stuart & Lister, 2012). These studies suggest that both global climate change and human impact played key roles in observed species extinctions. Climate warming could have led to the shrinkage of species' geographic ranges, and humans may have impacted the remaining,

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Table 1 List of large mammal species (>20 kg) that inhabited Europe at the end of the Pleistocene, from the Stage 3 Project (<http://www.esc.cam.ac.uk/research/research-groups/oistage3>), mean temperature and temperature range (°C) calculated from the occurrences of each species during the last glacial maximum, and predicted increase/decrease of their ranges (%) as a consequence of temperature change and human impact calculated using the ecotypes. Extinct = 1 means that the species is extinct, and extinct = 0 means that the species is not extinct

Species	Extinct	Mean temperature (°C)	Temperature range (°C)	Predicted % increment of range (by humans)	Predicted % increment of range (by temperature change)
<i>Panthera spelaea</i>	1	-0.51	15.1	-48	10
<i>Saiga tatarica</i>	1	-0.34	12.8	-48	10
<i>Crocota crocuta</i>	1	6.97	12.4	-51	99
<i>Megaloceros giganteus</i>	1	-0.89	17.5	-58	41
<i>Mammuthus primigenius</i>	1	-3.60	27.9	-57	-72
<i>Ovibos moschatus</i>	1	-5.53	0.2	-57	-72
<i>Panthera pardus</i>	1	-1.03	14	-48	10
<i>Coelodonta antiquitatis</i>	1	-5.02	10.8	-50	-43
<i>Equus hydruntinus</i>	1	7.41	2.8	-50	168
<i>S. hemitoechus</i>	1	8.20	2.2	-45	194
<i>Ursus spelaea</i>	1	2.54	17	-47	31
<i>Bison priscus</i>	1	4.11	14.6	-47	31
<i>Bos primigenius</i>	1	4.33	17.5	-50	168
<i>Ursus arctos</i>	0	-3.63	14.4	-43	-28
<i>Equus ferus</i>	0	4.17	17.5	-50	168
<i>Alces alces</i>	0	7.00	5.1	-50	168
<i>Rangifer tarandus</i>	0	1.29	20	-41	-12
<i>Cervus elaphus</i>	0	4.57	20.1	-43	12
<i>Capra pyrenaica</i>	0	8.60	0	-45	194
<i>Sus scrofa</i>	0	6.46	13.9	-47	31
<i>Capra ibex</i>	0	6.40	14.8	-47	31
<i>Canis lupus</i>	0	-0.32	18.3	-41	-12
<i>Rupicapra rupicapra</i>	0	6.12	14.8	-47	31
<i>Capreolus capreolus</i>	0	6.97	12.4	-51	99

reduced populations (Nogues-Bravo *et al.*, 2008; Lima-Ribeiro *et al.*, 2013).

Here, we propose a new approach to distinguish the effects of climate change from human impacts, based on the auspices of a virtual ecologist (Zurell *et al.*, 2010). We did not use fossil record because the strong spatial and temporal biases can lead to misestimations of the real effects of temperature change and early human impact (Varela *et al.*, 2011). Instead, we created virtual ecotypes based on different temperature requirements to mimic the living conditions of real extinct and extant European mammals. Temperature is one of the main climatic drivers of species distributions and species diversity across broad spatial and temporal scales (Šimová *et al.*, 2011; Gouveia *et al.*, 2014). Thus, we parsimoniously decided to create simple, but reliable, ecotypes using this single climatic dimension (temperature). We assumed that each ecotype has its particular Grinnellian niche (Grinnell, 1917) – in our case the set of temperature conditions (defined by a

temperature mean and a temperature range) in which the species that belongs to this ecotype can survive – and that each ecotype would respond differently to temperature change, depending on its requirements (Martinez-Meyer *et al.*, 2004). In addition, we assume that ecotypes that shared a large percentage of their ranges with early humans should be subject to greater anthropogenic pressures than ecotypes that shared small portions of their ranges with humans (Pushkina & Raia, 2008). We created 40 ecotypes with different temperature requirements, estimated their ranges in the last glacial maximum and quantified the effect that temperature change and early human impacts had on their potential distributions. We then related the predicted impacts to the extinct and extant European large mammals by linking real species with their virtual ecotypes (using species observed temperature mean and temperature range from the empirical fossil records). By doing this, we aimed to: (i) quantify the effects of past temperature change and early human impact

on different kinds of ecotypes; (ii) identify the ecotypes that were most affected by past temperature change and those affected by human impact; and (iii) link our theoretical results with the extinct and extant species distributions to understand the spatio-temporal pattern of extinctions in Europe.

Materials and methods

Virtual ecotypes

In continental Europe, the thermal niche of endothermic mammals varies from species adapted to arctic conditions to species adapted to desert and warm conditions (Porter & Kearney, 2009). To cover this range of observed thermal niches, we created 40 different ecotypes combining 10 mean temperatures (−20, −15, −10, −5, 0, 5, 10, 15, 20, and 25 °C) and 4 temperature ranges (5, 10, 15 and 20 °C), and defined a two-dimensional climatic envelope for each ecotype. Thus, we had four different ecotypes for each mean temperature, ranging from ecotypes with very narrow temperature range (5 °C from the mean) to ecotypes with a broad temperature range (20 °C from the mean) (see Table S1). This simple model (climatic envelope) can explore the role of temperature change in the context of Late Quaternary extinction. Future analyses could add complexity to these models to further explore the consequences of additional climatic dimensions of the species niche in relation to past climatic changes.

Climatic data

We mapped the potential geographic ranges of all ecotypes during the last glacial maximum (LGM; 21 000 years before present) and in the present. We used the mean annual temperature from the CCSM-Atmosphere-Ocean General Circulation Model (Shin *et al.*, 2003; Prange, 2008; Brandefelt & Otto-Bliesner, 2009) for the LGM cold scenario, and the mean annual temperature from WorldClim for the present warm scenario (Hijmans *et al.*, 2005). WorldClim variables are statistical interpolations of real data from weather stations, while the Community Climate System Model (CCSM) is a General Circulation Model that simulates the earth's climate system and that has been used to predict past, present, and future climate change. We selected the CCSM model because temperature estimates in Western Europe are concordant with paleoclimatic reconstructions from pollen records (Shin *et al.*, 2003). All variables were downloaded at 2.5 min resolution from the WorldClim web repository (<http://www.worldclim.org>).

Temperature change impact:

We projected the envelope of each ecotype onto the last glacial maximum and the current climatic scenarios using the R-package *raster* (Hijmans & Etten, 2013). We then cropped the raster files to the European range (longitude from 10°W to 50°E and

latitude from 30°N to 80°N) and mapped the potential distribution of each ecotype, assuming that ecotypes could track thermally suitable conditions through time. Then, because range fragmentation increases vulnerability, we quantified the core area of the potential distribution of the ecotypes in the LGM and the present using the function PatchStat of *SDM-Tools* (Vanderwal *et al.*, 2012). This function measures the area of the largest patch, ignoring smaller and fragmented patches of potentially suitable habitat. We then quantified the impact of the temperature change on the ecotypes by measuring the percentage of change in their core areas between the last glacial maximum and the present (size of the core areas in the last glacial maximum vs. size of the core areas in the present). Thus, our measure of the impact of temperature change for each ecotype summarizes both loss and fragmentation of the suitable range.

We used range size (area) to quantify extinction vulnerability because range size is correlated with extinction probability (Diniz-Filho *et al.*, 2005) and large mammals are particularly sensitive to range size decreases [extinction vulnerability sharply increases above a threshold body mass of 20 kg (Cardillo *et al.*, 2005)]. By including population dynamics and dispersal abilities, future analyses could explore a more complete suite of parameters from various metapopulation models to understand the role of species traits in the context of fragmentation related to climate change on observed extinction rates (Elmhagen & Angerbjorn, 2001).

Human impact

We used the archaeological database from the Stage 3 Project for identifying European areas with high human impact during the Late Quaternary (<http://www.esc.cam.ac.uk/research/research-groups/oistage3>). This database was built to study the extinction of the Neanderthals in Europe and compiles 347 fossil sites with reliable human records (stone tools and/or fossil remains) (Gamble *et al.*, 2004; Stewart, 2005). The identification of the species (*H. sapiens* or *H. neanderthalensis*) based on stone tools is controversial (D'errico *et al.*, 1998). However, the two species did not overlap in time for a long period and the last populations of Neanderthals went extinct in Southern Europe before the last glacial maximum (Finlayson *et al.*, 2006). Thus, we removed fossil sites older than the last glacial maximum to solve this potential taxonomical problem. We selected the fossil sites with human remains younger than 25 000 years to map human occurrences in Europe since that time (including Late Pleistocene and early Holocene fossil sites).

Archaeological record demonstrates that long-distance exchange networks in lithics, raw materials, and marine shells during the Upper Paleolithic (50 000–10 000 BP) reach the order of several hundred kilometers (Bar-Yosef, 2002). Therefore, we constructed a map of the areas potentially impacted by early humans using the simplest approach: we set an arbitrary buffer zone with the radius of 100 km around all human fossil sites. Finally, we measured human impact as the differences (percentage) between the size of the core areas of the ecotypes in the initial last glacial maximum scenario, and the

size of the core area of the ecotypes after removing the areas potentially impacted by humans.

European Late Quaternary mammals:

We used the palaeontological database from the Stage 3 Project (Stewart *et al.*, 2003) downloaded from <http://www.esc.cam.ac.uk/research/research-groups/oistage3>, with 273 georeferenced and dated fossil sites in Central and Southern Europe. We selected the fossil occurrences of each species ranging in age from 25 000 to 17 000 BP, overlapping the last glacial maximum (~21 000 BP). In general, past global climatic conditions for this temporal interval were cold and they did not vary significantly. We then we obtained the mean annual temperature for all occurrences of each species during the last glacial maximum extracting the local climatic data of each fossil locality from the CCSM BIO1 climate layer. Finally, we calculated the mean, maximum and minimum temperature for each species.

Finally, correlations between the mean temperature of the ecotypes, the temperature range of the ecotypes and the effects of the climatic and human impacts (increase/loss of suitable area as a consequence of climate change and human impacts) have been calculated using the function *cor.test* of the package *stats* (R Core Team, 2013). All R-scripts are available in the supplementary material and on the GitHub repository <https://github.com/SaraVarela/LateQuaternarySpecies>.

Results

A preliminary analysis of spatial patterns of temperature change shows that, although average temperature has increased 11.8 °C since the last glacial maximum, the spatial pattern of temperature change was not homogeneous across the continent (Fig. 1). The maximum temperature changes (33 °C) were predicted in Northern Europe, while temperature changes in Southern Europe were less extreme, increasing less than 5 °C in the Iberian Peninsula, Italy, and Greece (Fig. 1). Conversely, early human populations in Europe younger than 21 000 years were mainly located in Central and Southern Europe (data from the Stage 3 Project: <http://www.esc.cam.ac.uk/research/research-groups/oistage3>, Fig. 2). Thus, given that the spatial patterns of the two different impacts are not geographically correlated, we should be able to disentangle their individual effects.

Our results indicate that the effects of temperature change and early human impact were different for each ecotype (Table S1). On the one hand, Late Quaternary temperature change decreased the geographic range of cold-adapted ecotypes. Potential geographic ranges of all ecotypes with a temperature mean below zero decreased, and this decrease was greater than 50% for ecotypes with a temperature mean below -10 °C. At

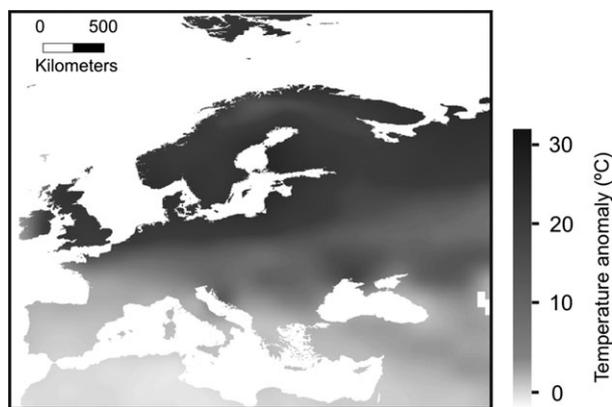


Fig. 1 Spatial pattern of the temperature change (temperature anomaly) from the last glacial maximum to the present (difference between mean annual temperature from CCSM last glacial maximum scenario and WorldClim current scenario). Northern Europe suffered the most extreme temperature change, with its annual mean temperature increasing by more than 20 °C. Southern Europe has remained climatically more stable, with an increment of less than 5 °C.

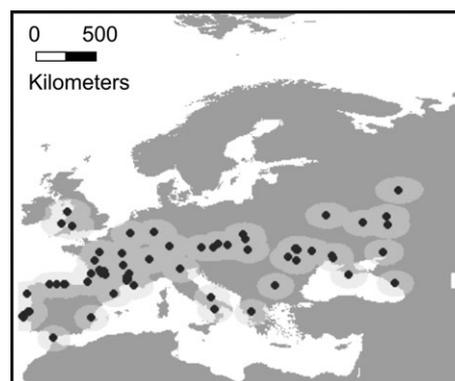


Fig. 2 Distribution of the early human fossil records in Europe with chronologies between 25 000 and 17 000 BP (from <http://www.esc.cam.ac.uk/research/research-groups/oistage3>). Dots represent fossil sites with records of *Homo sapiens* and gray circles delimit 100 km around the fossil sites (the areas potentially impacted by those populations).

the same time, potential distributions of temperate and warm-adapted ecotypes increased as a consequence of climatic warming. The geographic range of ecotypes with a temperature mean over 5 °C increased by more than 50% (Fig. 3a). On the other hand, the distribution of human populations mainly overlapped with temperate ecotypes (mean temperature from -10 °C to 10 °C). The geographic ranges of those ecotypes overlapped with the geographic range of early humans in more than 40% of their ranges (Fig. 3b). Cold and warm-adapted ecotypes were predicted to be impacted less by the distribution of the early human populations.

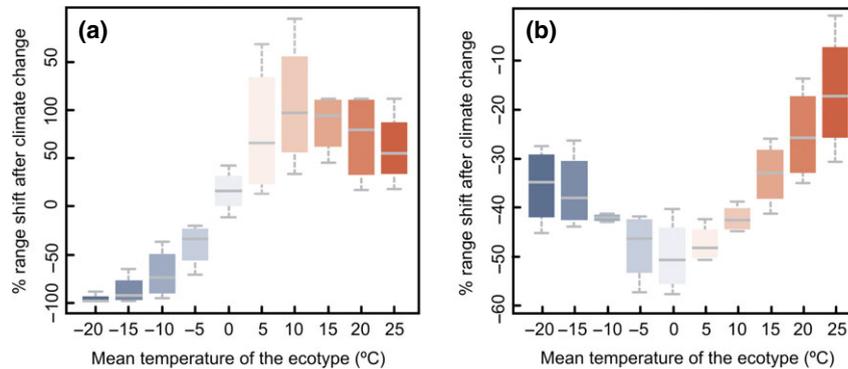


Fig. 3 Effects of temperature change (a) and early humans (b) on the potential distribution of the different ecotypes in Europe. Observed temperature change decreases the ranges of cold-adapted ecotypes and increases the ranges of temperate and warm-adapted ecotypes (a). On the other hand, early human populations decrease the range of all ecotypes, but temperate ecotypes (mean from -10 °C to 10 °C) show the largest range shift (b). Note that Y-axes present different scales.

The temperature mean of the ecotypes, a component of their thermal niche, clearly determined their extinction risk. The temperature mean of the ecotypes was highly correlated with the decrease in their geographic distributions as a result of climatic changes, ($\text{cor} = 0.80$, $t = 8.324$, $\text{df} = 38$, $P\text{-value} < 0.0001$) as well as with the decrease in their geographic distribution as a result of human impact ($\text{cor} = 0.46$, $t = 3.1931$, $\text{df} = 38$, $P\text{-value} = 0.0028$). Conversely, the temperature range of the ecotypes, the second component of their thermal niche, revealed no clear correlation with the predicted impacts. The temperature range of the ecotypes was not significantly correlated with the decrease of their geographic distributions as a consequence of climatic changes ($\text{cor} = -0.012$, $t = -0.0777$, $\text{df} = 38$, $P\text{-value} = 0.9384$), neither with the decrease of the distribution of ecotypes due to human impact ($\text{cor} = -0.192$, $t = -1.2085$, $\text{df} = 38$, $P\text{-value} = 0.2343$).

Calculated Late Quaternary temperature optima from the Stage 3 fossil record followed the expected adaptations of the species (Table 1). For instance, cold-adapted species (such as the woolly rhino *Coelodonta antiquitatis*) showed a temperature mean below zero, while warm-adapted species had temperature optima above zero (e.g. the Southern European rhino *Stephanorhinus hemitoechus*). Moreover, observed temperature range was broad for species with wide geographic ranges (e.g. *Mammuthus primigenius*) and narrow for restricted species (e.g. *Capra pyrenaica*). Our results indicate that only the distributions of cold-adapted species, like *M. primigenius*, *C. antiquitatis*, and *Ovibos moschatus*, would have decreased due to Late Quaternary temperature change, whereas the potential distributions of the rest of the species that inhabited Europe would have increased. On the other hand, early human populations were located in Central-Southern Europe (Fig. 2), such

that their distribution overlapped with all large mammal species that inhabited Europe. They potentially impacted at least 40% of all core areas of the species (Table 1). Our results thus suggest that all the Late Quaternary mammal species would have been exposed to human pressures.

Discussion

Our new approach based on virtual ecotypes enabled us to quantify the potential effect of past temperature change and early human impact on different kinds of species. Our findings indicate that temperature change results in a complex pattern of geographic range shifts depending on ecological requirements of different ecotypes. It is thus evident that climate warming could not have a uniformly negative impact on all species over the Late Quaternary. Rather, its effect might be polarized into groups of winners and losers. In the studies of Late Quaternary extinctions, species are not typically separated by their climatic requirements, and it is often assumed that all species were negatively impacted by past climatic changes (Barnosky, 2005). Our results suggest that averaging the effect of temperature change across species could mask its real impacts, and that mammal extinction events should be further studied by separating the species into groups according to their climatic requirements.

Different dimensions of the thermal niche showed distinct effects on the potential distribution of the ecotypes in Europe. The temperature mean of the ecotypes was much more important in determining extinction vulnerability than temperature range. Specifically, climate warming decreased the potential distribution of cold-adapted ecotypes, independent of their temperature range (Fig. 3). This result is supported by the

analyses of empirical Late Quaternary fossils in Europe and ancient DNA, which demonstrate that geographic ranges (hence populations) of real cold-adapted species like woolly mammoths and woolly rhinos shrank as a consequence of the Late Quaternary climatic warming (Prost *et al.*, 2010; Lorenzen *et al.*, 2011) in spite of their wide temperature range (see Table 1). Therefore, although our virtual ecotypes are described by a simple climatic envelope and defined only by two dimensions (temperature mean and temperature range), our findings were able to reproduce real patterns of observed extinctions.

To further explore the consequences of our general findings, we linked our virtual simplified ecotypes with Pleistocene species (by the species' observed temperature mean and range). According to our simple ecotype models, the geographic ranges of extinct cold-adapted species like *Mammuthus primigenius* and *Ovibos moschatus* may have decreased by at least 70% after the last glacial maximum as a consequence of climate warming (assuming that they were able to track changing climate). Conversely, temperate species, like *Megaloceros giganteus*, *Bos primigenius*, or *Crocota crocuta*, would have increased their geographic ranges, assuming they were able to track the temperature change. However, in spite of their predicted expansion, those species disappeared from Europe. Thus, our results indicate that not all the mammal extinctions in Europe can be directly linked to past global climatic changes (Varela *et al.*, 2010; Lima-Ribeiro *et al.*, 2013).

On the other hand, human impact affected all ecotypes (Fig. 3), and our results suggest that temperate species may have been especially vulnerable to the impact of early humans (Table 1 and Fig. 3). We hypothesize that many temperate species failed to track climate changes and expand their geographic ranges after the last glacial maximum as a consequence of the early human impacts. Similar patterns are observed today. Human populations largely affect temperate habitats, while warm and cold habitats are exposed to less human pressure (Kareiva *et al.*, 2007). And even the species that have coped with past global changes and survived, such as the American bison, *Bison bison*, have suffered from the historical anthropogenic impacts over the last 300 years, leading to recent population declines (Metcalf *et al.*, 2014).

Our ecotype-based results indicate that extant species suffered less potential impacts from early humans than extinct species (see Table 1; $t = 2.85$, $df = 21.998$, $P\text{-value} = 0.0093$). Therefore, human pressure may have played a key role in observed extinctions in Europe (see Sandom *et al.*, 2014). Indeed, species with the lowest proportion of range overlap with humans during the last glacial maximum (e.g. *Cervus elaphus*,

Rangifer tarandus, and *Canis lupus*) did not go extinct. That said, some species that were highly impacted by human populations also survived; for example small-sized species, like *Capreolus capreolus*, withstood these global impacts. Future analyses could therefore use more complex models comprising species size or meta-population dynamics to fully understand observed extinction patterns in Europe.

In summary, Late Quaternary extinction risk in Europe was strongly determined by the species temperature mean, but not by the species temperature range. Cold-adapted species were predicted to be highly impacted by temperature change, while early human populations primarily impacted temperate species. Concordantly, the large mammals that survived past global changes in Europe were those least affected by both temperature change and human impact. Our findings thus support the idea of a complementary effect of both stressors, since a single stressor would not produce similar extinction patterns (see also Barnosky *et al.*, 2004a,b). This conclusion can also apply to other continents, such as North America, where Late Quaternary climate change and early human impact show different spatial patterns. Future conservation efforts can benefit from considering the lessons learned from past extinctions, achieving greater success by understanding the effect of the combination of climate change and direct human pressure.

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Supporting Information

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

Table S1. Summary of the climatic requirements of the 40 different ecotypes created.