



Using the palaeontological record of *Microtus* to test species distribution models and reveal responses to climate change

Jenny L. McGuire^{1*} and Edward Byrd Davis²

¹School of Environmental and Forest Science, University of Washington, Seattle, WA, 98195, USA, ²Museum of Natural and Cultural History and Department of Geological Sciences, University of Oregon, Eugene, OR, 97403, USA

ABSTRACT

Aim We used newly identified fossil specimens to reconstruct the Quaternary distributions of five *Microtus* species (Rodentia: Arvicolinae) from the Pacific coast of the United States. We used these distributions to test the hypothesis that when projected onto past, alternative climate surfaces, species distribution models (SDMs) created using only climate variables are concordant with the empirical data of fossil *Microtus* species occurrences.

Location Specimens from 11 fossil localities in California, Oregon and Nevada were identified and evaluated.

Methods Geometric morphometrics and discriminant analyses were used to identify fossil *Microtus* specimens. Using a maximum-entropy modelling approach, the best model for all five species was selected using the Akaike information criterion. Nineteen bioclimate variables were used to create SDMs for the five *Microtus* species using both Community Climate System Model (CCSM) and Model for Interdisciplinary Research on Climate (MIROC) models.

Results We confidently identified 144 *Microtus* fossils, including the first fossil specimens of *Microtus oregoni* and *Microtus townsendii*. SDMs reconstructed approximately half the extralimital fossil occurrences (i.e. those found outside the present-day range). Those species with extralimital occurrences not reconstructed have niche models primarily influenced by precipitation variables. The two species whose extralimitals were well predicted occupy indistinguishable climatic niches.

Main conclusions The ranges of Pacific coast *Microtus* species have undergone substantial regional contractions since the Last Glacial Maximum (LGM; 21 ka). Inconsistencies between LGM SDMs and Quaternary fossil ranges indicate potential problems with LGM precipitation reconstructions, although interspecific interactions are also likely to contribute to these differences. Overall, the study highlights the need for further, detailed, species-level palaeodistributions to put recent observations in a broader temporal context and examine the effectiveness of SDMs coupled with climate models for predicting range dynamics under scenarios of climate change.

Keywords

Arvicolinae, ecological niche, MaxEnt, *Microtus*, palaeontology, Quaternary, range, rodent, species distribution model, western USA.

*Correspondence: Jenny L. McGuire, School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA.
E-mail: jennymcg@u.washington.edu

INTRODUCTION

The greatest challenge in conservation biology is to protect biodiversity in the context of future environmental change.

Monitoring efforts and predictive modelling provide us with data about how species are currently reacting to climate change and how we expect them to react in the future. Both for conservation purposes and to understand the interplay of

climate change with ecology and evolution (e.g. Peterson *et al.*, 2002; Parmesan, 2006; Moritz *et al.*, 2008), it is illuminating to supplement natural history data with palaeontological data (Hadly & Barnosky, 2009). Fossil data put short-term observations into a deeper-time perspective, allowing an additional test of the effectiveness of predictive models for individual species. For example, as temperatures have risen in recent times, species distributions have been shifting polewards and upwards in elevation (Parmesan, 2006; Moritz *et al.*, 2008). Several Quaternary studies (2.58 Ma–present) have indicated that these range shifts may be part of a long-term trend, initiated around the end of the Pleistocene (Graham *et al.*, 1996; Grayson, 2005; Guralnick, 2007; McGuire, 2011). McGuire (2011) found that upward elevational shifts in species distributions over the last 100 years may be occurring an order of magnitude more rapidly than parallel shifts over the previous 10 ka. Thus, the intensity of 20th-century change is brought into sharp relief when illuminated by the fossil record. These palaeontological studies highlight the necessity of combining detailed, species-level palaeontological data with increasingly sophisticated analytical methods to place climate change biology in a deeper temporal context, revealing nuances in biological responses to changing environments.

A current trend in modern ecological studies is to construct species distribution models (SDMs) that predict how organisms will respond to changing climate. The abundant availability of environmental data, as well as recent methodological advancements, have facilitated rapid expansion in the use of SDMs over the last decade (Svenning *et al.*, 2011). The most common SDMs use modern environmental variables to hypothesize the distribution of a species on an alternative climate landscape, frequently generated by future climate projections. These methods have also been applied to the palaeontological record in two ways (Svenning *et al.*, 2011; Varela *et al.*, 2011): (1) using modern data as a training set to hindcast distributions, habitats, ecosystems or biodiversity on a palaeoclimate layer (e.g. Hilbert *et al.*, 2007; Waltari *et al.*, 2007; Rodríguez-Sánchez & Arroyo, 2008); or (2) during a discrete historical time period where a species' distribution is geographically undersampled, using the known fossils and palaeoclimate data or proxies to predict the full species distribution (e.g. Stigall Rode & Lieberman, 2005; Nogués-Bravo *et al.*, 2008; Rodríguez-Sánchez & Arroyo, 2008; Maguire & Stigall, 2009). In the end, all of these methods predict where species distributions would occur under alternative climate landscapes.

Herein, we take a different approach to palaeontological SDMs in that we hindcast SDMs with the explicit goal of testing the resultant distributional hypotheses using empirical fossil data under alternative climate landscapes. In cases where the Quaternary palaeontological record provides ample empirically derived palaeogeographical distributions under truly novel climate landscapes, such as during glacial–interglacial cycles, the data are available to provide these critical methodological tests. Palaeoclimate reconstructions have recently become available for North America during the

most recent glacial cycle, the Last Glacial Maximum (LGM; 21 ka) (Braconnot *et al.*, 2007; <http://pmip2.lsce.ipsl.fr/>). Using fossil data in conjunction with these palaeoclimate reconstructions, we can begin to test the distribution hypotheses created by SDMs.

There are two main steps in creating a SDM. The first step is to construct the actual model by sampling the range of environmental variables where the species is found, and the second step is to geographically project those ranges of environmental variables onto a climate landscape, constructing a distribution hypothesis. Here, we projected the model onto palaeoclimate surfaces from the LGM to create hindcasts about what distributions five species would have occupied under this alternative climate landscape. We used modern times and the LGM as endpoints of the Quaternary climate spectrum. The LGM represents a relatively cool, moist period, and the present day represents a relatively hot, dry period in California (Davis, 1999). Fossil specimens and localities are from time periods with climates that are intermediate between these two climates. Because SDMs use climate to reconstruct species' distributions, the actual ranges of the species at intermediate climate periods should therefore be intermediate between the predictions that SDMs would reconstruct for these two climatic extremes. Once we had constructed LGM SDMs, we then examined how the empirically derived fossil distributions compare with those predicted by the SDMs.

We face a taxonomic challenge in incorporating palaeontological data into research on climate change. Many palaeoecological studies are performed at the genus level (e.g. Hadly *et al.*, 2009; Blois *et al.*, 2010), whereas most present-day monitoring and predictive studies are performed at the species level (e.g. Parmesan, 2006; Moritz *et al.*, 2008). This difference in preferred taxonomic scale arises because fossil specimens are often fragmentary and not diagnostic to species, allowing only genus-level determination; we have, however, been able to implement a novel geometric morphometrics approach (McGuire, 2011) to ensure high-quality species-level identifications in our study.

Here, we examine five species of *Microtus* (Rodentia: Arvicolinae) from the west coast of the United States: *Microtus californicus* (Peale, 1848), *Microtus longicaudus* (Merriam, 1888), *Microtus montanus* (Peale, 1848), *Microtus oregoni* (Bachman, 1839) and *Microtus townsendii* (Bachman, 1839). Western *Microtus* species are abundant in both present-day and Pleistocene ecosystems, are well represented in the fossil record, and are sensitive to climate (McGuire, 2010a). As their abundance indicates, they play an important role in many ecosystems, influencing the structure of plant communities (Borchert & Jain, 1978) and falling prey to many small to medium-sized predators (Huntly, 1991). Additionally, researchers have demonstrated strong interspecific competition between *Microtus* species, documenting the process that drives the species to have little distributional overlap (Findley, 1954; Koplín & Hoffmann, 1968; Conley, 1976). However, as indicated earlier, the main challenge to using

Microtus for palaeoecological research has been the difficulty in confidently identifying Quaternary *Microtus* fossils to the species level. Recent investigations (Wallace, 2006; McGuire, 2011) developed methods for identifying *Microtus* species in the fossil record. We utilized these methods to reconstruct the geographical distributions of the fossil specimens of the five *Microtus* species living in California today, examine how those ranges have changed since the LGM, and compare those distributions with LGM distribution hypotheses generated using SDMs.

MATERIALS AND METHODS

Specimen sampling

Fossil specimen identification

Microtus specimens were identified using geometric morphometric and discriminant analyses. Identifications were based upon the position of *Microtus* first lower molars (m1) in morphological shape space, as determined by the digitization and analysis of 21 two-dimensional landmarks (described in McGuire, 2011) using TPSDIG2.10 (Rohlf, 2006) and COORDGEN 6 H (Sheets, 2000). The modern training set consisted of 251 specimens of known identity (50 specimens of *M. californicus*, 50 of *M. longicaudus*, 50 of *M. montanus*, 50 of *M. oregoni* and 51 of *M. townsendii*). Modern specimens were correctly identified 95% of the time and 83% when jackknifed (McGuire, 2011). Here, this discriminant analysis was applied to *Microtus* m1s of fossil specimens from 11 fossil localities from California, Oregon and Nevada (Table 1, Fig. 1f).

Two potential problems could occur from identifying fossil specimens using a discriminant analysis built with present-day specimens. First, if the tooth shape of a species has changed through time, previously looking more similar to another species in the analysis, the shape of that specimen would appear intermediate between two species. In this case, the reported confidence for identification of that specimen represents the probability that the specimen belonged to each of the two potential species based on the training set, for example, 0.5 if it were exactly half-way between. Second, if a specimen does not belong to any of the species included in the training set, it may have a high identification confidence (because it looks most like one particular species), but its shape may fall far outside the range of shapes displayed by that species. To deal with these two problems, we adopted two criteria. First, for a specimen to be considered confidently identified, only specimens with ≥ 0.95 identification confidence were used. Second, the Mahalanobis distance of the specimen had to fall within two standard deviations of the mean shape for the species.

Fossil localities

The examined fossil localities are distributed throughout California, southern Oregon and east-central Nevada (Fig. 1f,

Table 1 Fossil localities in the western USA, the species of *Microtus* identified at each, and the ages of each. Late Pleistocene localities are designated as the Rancholabrean North American Land Mammal Age (NALMA). Asterisks (*) next to species indicate extralimital fossils at each locality.

Locality	Species	Specimen ages
(1) Carpinteria, CA CIT 139	<i>M. californicus</i>	c. 40,000–10,000 years old (biostratigraphic) ¹
(2) Emery Borrow, CA LACM 7053 LACM 6689	<i>M. californicus</i>	late Pleistocene (biostratigraphic) ³
(3) Montezuma, CA V-71001 V-6312	<i>M. californicus</i> * <i>M. longicaudus</i>	late Pleistocene (biostratigraphic) ²
(4) McKittrick Brea, CA CIT 138	<i>M. californicus</i>	37,011–0 cal. yr BP ¹
(5) Pacheco 2, CA V-78027	<i>M. californicus</i> * <i>M. longicaudus</i>	late Pleistocene (biostratigraphic) ²
(6) Paisley Caves, OR 35LK3400	<i>M. longicaudus</i> <i>M. montanus</i> * <i>M. oregoni</i> * <i>M. townsendii</i>	c. 11,000–1300 cal. yr BP ⁴ c. 10,500–500 cal. yr BP ⁴ 13,011–12,151 cal. yr BP ⁴ c. 9400 cal. yr BP ⁴
(7) Palos Verdes, CA LACM 3877	<i>M. californicus</i> * <i>M. longicaudus</i>	late Pleistocene (biostratigraphic) ³
(8) Prune Avenue, CA V-5301	<i>M. californicus</i> * <i>M. longicaudus</i>	4283–836 cal. yr BP ⁶
(9) Samwell Cave, CA V-65217	<i>M. californicus</i> <i>M. longicaudus</i> * <i>M. townsendii</i>	8275–0 cal. yr BP ⁵ 7523–6520 cal. yr BP ⁵ 1505–0 cal. yr BP ⁵
(10) Smith Creek, NV LACM 251	<i>M. longicaudus</i> <i>M. montanus</i>	29,959–0 cal. yr BP ¹
(11) Woodburn, OR UO-3859 UO-3038 UO-3867	* <i>M. californicus</i> <i>M. longicaudus</i> * <i>M. montanus</i> <i>M. oregoni</i> <i>M. townsendii</i>	11,842–11,278 cal. yr BP ⁷

¹From NEOMAP Database;

²from UCMP Database;

³from LACM Database;

⁴pers. comm. D. L. Jenkins, 2010;

⁵Blois *et al.* (2010);

⁶McGuire (2011);

⁷Campbell & Stenger (2002).

Table 1). All sites but four were dated biostratigraphically from the databases at their respective museum holdings (Table 1) or from NEOMAP (<http://www.ucmp.berkeley.edu/neomap/>, accessed July 2010), a database of Quaternary fossil mammals compiled from the literature. Fossil bone specimens from Prune Avenue and Samwell Cave in California were radiocarbon dated at the Lawrence Livermore National Laboratory CAMS facility (Blois *et al.*, 2010; McGuire, 2011). Radiocarbon dates for the Woodburn locality in northern Oregon and the Paisley Caves in south-central Oregon are taken from the literature (Campbell & Stenger, 2002; Jenkins *et al.*, 2012). The radiocarbon dates were calibrated with OxCal 4.1.56 (Bronk Ramsey *et al.*, 2009), using the IntCal09 calibration curve (Reimer *et al.*, 2009).

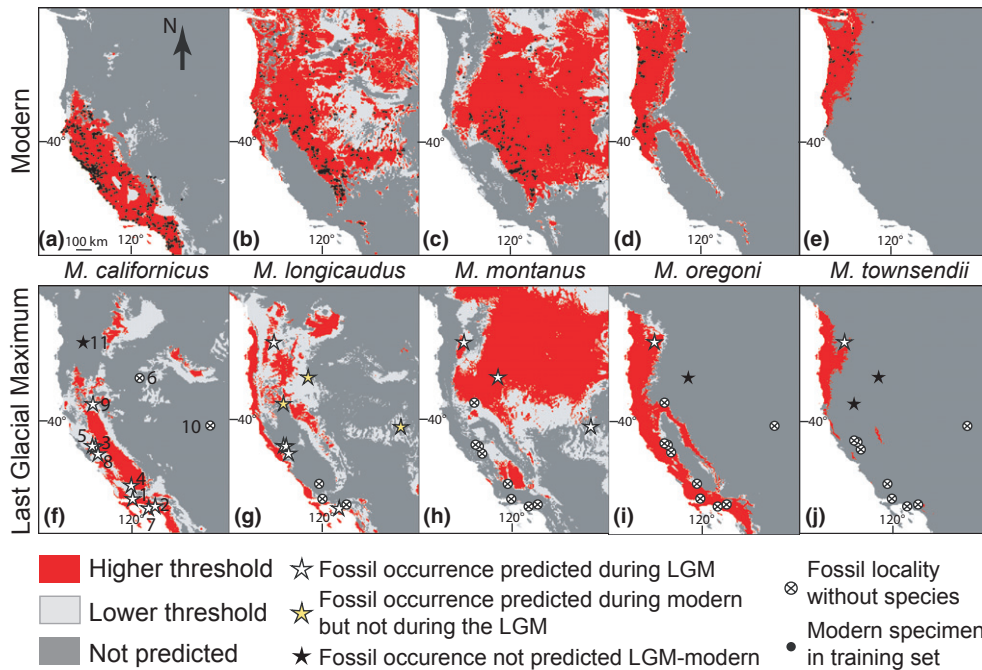


Figure 1 Regional snapshots of the western portions of species distribution models for five species of *Microtus* in the western USA for the present (a–e) and the Last Glacial Maximum (f–j) based on all 19 MIROC bioclimate layers. Red indicates a higher, equal training sensitivity and specificity, threshold. Light grey represents a lower, maximum training sensitivity plus specificity, threshold. Each species was modelled throughout its entire distribution; these maps are zoomed in to the area of interest where fossil occurrences are located. Numbers in (f) correspond to fossil locality names in Table 1. Area under the receiver operating characteristic curve (AUC) values for the test data of each model are as follows: (a) 0.978; (b) 0.936; (c) 0.965; (d) 0.993; (e) 0.997. These AUC values are consistent with values of models commonly considered acceptable in the literature (Phillips *et al.*, 2006).

Present-day specimens and ranges

Occurrence data are from the Arctos database (<http://arctos.database.museum/>, accessed July 2010), which includes natural history records from the University of Alaska Museum of the North, the Museum of Southwestern Biology and the Museum of Vertebrate Zoology at the University of California, Berkeley. Duplicate specimens of species from any locality were removed. Presence-only data were used, because absence data were not readily available for the species of interest. Each species was sampled from throughout its entire modern distribution.

Climate data

All climate layers were downloaded from the WorldClim data set (Hijmans *et al.*, 2005; <http://www.worldclim.org/>, accessed July 2010–September 2012). WorldClim bioclimatic variables were used for all analyses. These variables are derived from 30-arc-second resolution monthly temperature and precipitation values and are selected to represent biologically meaningful variables including climatic annual trends, seasonality and extremes (Hijmans *et al.*, 2005). LGM climate data available through WorldClim are calibrated and statistically downscaled from the PMIP2 LGM data set (Brannon *et al.*, 2007; <http://pmip2.lsce.ipsl.fr/>). These LGM

data are derived from two general circulation models – the Community Climate System Model (CCSM; Collins *et al.*, 2006) and the Model for Interdisciplinary Research on Climate (MIROC, version 3.2; Hasumi & Emori, 2004).

Model reconstructions of LGM ranges

SDMs were built for the present-day data and then projected back in time to the LGM, approximately 21 ka. Although few of the fossil localities are as old as the LGM, this time period represents one extreme in Quaternary climate (cool and moist in this region) with the present day representing the opposite extreme (hot and dry). Therefore, if the SDMs adequately describe the climate tolerances of species, fossil occurrences of each species should only be found in localities intermediate between the LGM predictions and present-day predicted distributions. Fossil occurrences are compared both to the hindcast SDMs and the modern SDMs to establish whether they fall outside of the habitats predicted by this full climatic range. However, we note that the Holocene climatic optimum, approximately 9000–5000 years ago, is reconstructed as warmer than today in some parts of the globe. Four species occurrences may fall within this time period: *M. longicaudus* and *M. montanus* from Paisley Caves, OR, and *M. californicus* and *M. longicaudus* from Samwell Cave, CA (Table 1). However, none of these species occurrences

are extralimital, and their presences do not affect the interpretations of the study.

Distribution modelling

MAXENT 3.3.2 (Phillips & Dudík, 2008) was used to construct SDMs of present-day and LGM species distributions using presence-only occurrence data. Although several programs are available to produce niche models, MAXENT has been demonstrated to be among the most accurate of the programs that use presence-only (rather than presence-absence) data (Phillips *et al.*, 2004; Elith *et al.*, 2006; Phillips, 2008). The program creates distribution models by contrasting presence records with pseudo-absence data resampled from the background study area.

Phillips & Dudík (2008) have programmed the most recent versions of MAXENT with default parameters that maximize results under a wide variety of circumstances. The default parameters were used with the exception that 25% of localities were reserved for model testing. MAXENT provides a probability surface with grids on a logarithmic scale, ranging in value from essentially 0 to 1. This surface indicates the relative similarity of an area to the present-day niche of the species. Clamping was performed to determine whether any of the modelled regions were outside the values of the bioclimatic variables encountered during training (Hijmans & Graham, 2006), but these areas were not excluded from our SDMs. One purpose of this study is to determine how well these models perform in alternative climate landscapes, so it was preferable that some modelled climates were beyond those encountered by modern-day training sets. SDMs based on present-day climate were then projected onto LGM climates derived from the CCSM and the MIROC (described above).

We used ENMTOOLS to select the best of several models for each species using the Akaike information criterion (AIC), AIC corrected for small sample size (AIC_c) and Bayesian information criterion (BIC) (Warren *et al.*, 2010; Warren & Seifert, 2011). The models examined included: (1) the full set of 19 current (1950–2000) bioclimatic variables (see Appendix S3 in Supporting Information); (2) the seven bioclimatic variables that are minimally correlated in California (Appendix S3; as determined by Rissler *et al.*, 2006); (3) temperature-only bioclimate variables; (4) precipitation-only bioclimate variables; (5) temperature bioclimate variables plus the subset of precipitation variables that are minimally correlated in California; and (6) precipitation bioclimate variables plus the subset of temperature variables that are minimally correlated in California. We also used ENMTOOLS to examine whether the five species of interest have statistically distinguishable niche identities (Warren *et al.*, 2008).

Comparing fossil ranges and LGM modelled ranges

Fossil localities were plotted on LGM palaeogeographical distribution models. Extralimital fossil specimens, those fossils found outside the present-day range of the species (asterisked

Table 2 The higher (equal training sensitivity and specificity) and lower (maximum training sensitivity plus specificity) thresholds used for five species of *Microtus* from the western USA.

Species	Higher	Lower
<i>M. californicus</i>	0.401	0.118
<i>M. longicaudus</i>	0.315	0.184
<i>M. montanus</i>	0.235	0.098
<i>M. oregoni</i>	0.114	0.065
<i>M. townsendii</i>	0.107	0.106

species occurrences in Table 1), were then plotted on the maps of each model using ARCGIS 9.3 (ESRI, Redlands, CA, USA), and the probability value for each extralimital specimen on each LGM model was determined. Those values were then compared to thresholds with maximum training sensitivity plus specificity (Manel *et al.*, 2001; Hernandez *et al.*, 2006) (Fig. 1, Table 2) – the most geographically inclusive of several standard thresholds for converting the continuous probability surface to a presence-absence surface. This threshold is referred to herein as the lower threshold. Equal training sensitivity and specificity thresholds (Fielding & Bell, 1997) are herein described as higher thresholds (Fig. 1, Table 2).

RESULTS

Of the 220 *Microtus* fossils, 144 specimens were confidently identified, 68 were rejected for low identification confidence, 6 were rejected for large Mahalanobis distances, and 2 were rejected for both reasons. The fossils identified herein (see Table 1 and Appendix S1) constitute the first positively identified fossil specimens of these *Microtus* species. Although some tentative extralimital fossil specimens have previously been reported for *M. longicaudus* and *M. montanus* east of the Rocky Mountains (Hoffman & Jones, 1970; Turner, 1974; Stewart, 1978; Wallace, 2001), these are the first extralimital fossil specimens confidently identified and reported for these species from the western portion of their distributions (Table 1) (McGuire, 2011). For *M. oregoni* and *M. townsendii*, these are the first extralimital fossil specimens reported (Table 1). All five of the *Microtus* species, with the possible exception of *M. montanus* (Appendix S2), exhibited regional geographical range contractions between the LGM and today (as indicated by the presence of past extralimital specimens; Table 1, Fig. 1): the eastern range limits of *M. oregoni* and *M. townsendii* have contracted, the southern and eastern range limits of *M. longicaudus* have contracted, the western range limit of *M. montanus* has possibly contracted (but see Appendix S2), and the northern range limit of *M. californicus* has contracted.

Extralimital fossils predicted by LGM modelled ranges

AIC, AIC_c and BIC did not differ in their model rankings. Each species had a different model identified as the strongest

for that species. The models including all 19 bioclimatic variables were used for all analyses, as this model received the best score of all models given weighted sums across species. Using these models, the niche identity test in ENMTOOLS (Warren *et al.*, 2008) found that *M. montanus* and *M. longicaudus* have statistically indistinguishable climate niches ($P > 0.05$), whereas the climatic niches of all other species pairs are more different than would be expected by chance ($P < 0.01$).

SDMs were unable to predict the presence of fossils at several localities under any modelling scenarios. Clamping revealed no palaeoclimate ranges outside of the training range under either MIROC or CCSM models. MIROC models generally predicted larger ranges for species during or since the LGM, and are therefore more conservative. These models are shown in Fig. 1f–j. Full maps of the MIROC and CCSM models can be found in Appendix S3, together with MIROC and CCSM models that use the set of seven bioclimate variables that are minimally correlated.

Microtus californicus

Microtus californicus was identified in nine of the eleven fossil localities (Fig. 1f, Table 1). The only extralimital fossil specimen is from Woodburn in northern Oregon. The fossils from the Woodburn locality are dated to 11,842–11,278 cal. yr BP. When compared to the lower thresholds (Table 2), the model probability values for the extralimital *M. californicus* specimens at Woodburn (MIROC = CCSM = 0.029) indicate that the habitat would not have been suitable for this species during or since the LGM (Fig. 1f).

Microtus longicaudus

Microtus longicaudus was identified in eight of the eleven localities (Fig. 1g, Table 1). Specimens at four Californian localities were extralimital relative to the current distribution: Montezuma, Pacheco 2, Prune Avenue and Palos Verdes. The first three of these are in the San Francisco Bay area (SF Bay). The Prune Avenue specimens were dated to 836–4283 cal. yr BP. Montezuma and Pacheco 2 are both from the late Pleistocene (c. 11–45 ka). Palos Verdes is from the Los Angeles region and is known only to be Rancholabrean in age (c. 11–240 ka) according to the Los Angeles County Museum (LACM) collection information (Table 1). When compared to the lower thresholds (Table 2), the model probability values for the extralimital *M. longicaudus* specimens at Montezuma (MIROC = CCSM = 0.217), Pacheco 2 (MIROC = CCSM = 0.217), Prune Avenue (MIROC = CCSM = 0.217) and Palos Verdes (MIROC = CCSM = 0.301) all indicate that those habitats would have been suitable for the species during or since the LGM (Fig. 1g).

Microtus montanus

Microtus montanus was identified in three of the eleven localities (Fig. 1h, Table 1). The only extralimital fossil specimens

are found in Woodburn in northern Oregon (11,842–11,278 cal. yr BP). However, when we examined present-day specimen data, we observed that Woodburn lies within a sparsely surveyed region between two areas that do contain *M. montanus* (Appendix S2). Additionally, the present-day SDM for *M. montanus* predicts that Woodburn represents marginally suitable habitat for this species. Thus, it is uncertain whether *M. montanus* currently occupies this locality or not. When compared to the lower thresholds (Table 2), the model probability values for the extralimital *M. montanus* specimens at Woodburn (MIROC = CCSM = 0.244) indicate that those habitats would have been suitable for the species during or since the LGM (Fig. 1h).

Microtus oregoni

The first known fossil specimens of *M. oregoni* were identified at two of the eleven localities (Fig. 1i; Table 1). The only extralimital fossil specimen is found in Paisley Caves in south-central Oregon and is dated to 12,581 ± 430 cal. yr BP (Jenkins *et al.*, 2012). When compared to the lower thresholds (Table 2), the model probability values for the extralimital *M. oregoni* specimens at Paisley Caves (MIROC = 0.0002; CCSM = 0.0001) indicate that the habitat would not have been suitable for this species during or since the LGM (Fig. 1i).

Microtus townsendii

The first known fossil specimens of *M. townsendii* were identified at three of the eleven localities (Fig. 1j, Table 1). Extralimital fossil specimens are from Paisley Caves in south-central Oregon and Samwell Cave in northern California. The *M. townsendii* specimen from Paisley Caves is dated at approximately 9000 cal. yr BP, and the specimen from Samwell Cave is dated at 0–1505 cal. yr BP. When compared to the lower thresholds (Table 2), the model probability values for the extralimital *M. oregoni* specimens at Paisley Caves (MIROC = CCSM = 0.002) and Samwell Cave (MIROC = 0.048; CCSM = 0.0043) indicate that the habitats would not have been suitable for this species during or since the LGM (Fig. 1j).

DISCUSSION

Fossil ranges and LGM modelled ranges

The LGM SDMs do not predict the presence of several of the extralimital fossil occurrences – notably *M. californicus*, *M. oregoni* and *M. townsendii* (Fig. 1f,i,j). The most conservative LGM SDMs (i.e. those SDMs that hindcast the most extralimitals: MIROC and CCSM) only captured five of the nine extralimital fossil occurrences. The four missed occurrences are shown as black stars in Fig. 1f,i,j. In the event that some fossil specimens have been misidentified, these results would require revision, but we think this unlikely (McGuire,

2011). Other instances of discordance between LGM SDMs and fossil distributions have previously been reported, indicating that SDMs which use modern climate variables and project niche models into the past often have difficulty in reconstructing the prehistoric distributions of species (e.g. Varela *et al.*, 2009; Guralnick & Pearman, 2010).

It is of equal interest to find that two of the species – *M. longicaudus* and *M. montanus* – have extralimital fossil occurrences that are accurately hindcast by the LGM SDMs. This is particularly notable in the case of *M. longicaudus*, which has several fossil occurrences well outside the present-day range and at considerably lower elevations. Additionally, this model has the lowest AUC values (Fig. 1), indicating that it performs the least well of the five models under modern conditions. Nonetheless, the LGM coastal range of this species is hindcast precisely where we find the fossil specimens.

What fossils reveal about SDMs

Three potential sources of error could account for discrepancies between SDM distribution hypotheses and species' true ranges under alternative climate regimes: (1) inaccurate climate models; (2) the evolution of climate tolerances; and (3) the fundamental niches modelled do not reflect species' realized niches (Jackson & Overpeck, 2000; Phillips, 2008; Guralnick & Pearman, 2010). The palaeontological record is an excellent resource for examining these potential sources of error and determining how to improve SDMs in the process, because it provides an empirical set of data with which to test each scenario. Additionally, niche analyses inherent to SDMs can tell us a lot about species evolution and ecological changes since the LGM.

Because climate is a key variable in SDMs, any climatic error can affect the accuracy of these models. Inaccuracies in LGM climate models have been previously suggested (Jackson *et al.*, 2000), and Pausata *et al.* (2009) demonstrated that seasonal and spatial variability in atmospheric pressure can lead to the misinterpretation of proxy signals in the development of past climate models. The fact that the two species whose fossil distributions were accurately hindcast – *M. longicaudus* and *M. montanus* – also have statistically indistinguishable climate niche space is suggestive that some climate niches may be more accurately modelled than others. This could result if LGM climate models more accurately predict some climate variables than others.

To examine this possibility in more detail, we looked to the analysis of variable contributions, which gives a heuristic estimate of the relative contribution of each environmental variable to the present-day SDM of each species (Phillips & Dudík, 2008). In both the full model and the model that uses only the seven least-correlated bioclimate variables, we find that different components of climate contribute to the different species niche reconstructions. These findings are also consistent with the ENMTOOLS AIC tests, which demonstrate which models were the strongest for each species. In

both the ANOVA and the ENMTOOLS AIC tests, we found that *M. californicus*, *M. oregoni* and *M. townsendii* all have niche reconstructions that are most strongly influenced by precipitation variables, whereas *M. longicaudus* and *M. montanus* both have niche reconstructions that are most strongly influenced by temperature variables. Interestingly, the three species whose extralimital palaeodistributions were not predicted by the SDMs all have models that are most strongly affected by precipitation variables, suggesting potential problems with the precipitation landscapes reconstructed by the circulation models used to create the LGM climate layers. Future studies that include a greater breadth of species should perform robust analyses of variable importance to determine whether there is a consistent pattern in those species not being accurately hindcast.

Modern climate error could also contribute to SDM error. As is typical for many SDM studies (e.g. Pineda & Lobo, 2009; Waltari & Guralnick, 2009), the occurrence data set we used to train our SDMs was compiled from natural history collections and observations made over the course of the 20th century. Error created by 20th-century climate change could artificially inflate the apparent niche breadth of the species, widening the range of predicted distributions and decreasing accuracy. In this case, this larger hypothesized distribution is conservative with regard to the hypotheses being examined.

A second potentially important source of error arises from change in the niche through time through evolution or phenotypic plasticity. When this occurs, SDMs will not accurately predict that species' distribution under an alternative climate landscape. The fact that we find that these congeners, which are relatively recently diverged, have different niches from one another indicates that these species are likely to evolve quickly. In fact, McGuire's (2010b) preliminary analysis of *M. californicus* indicates that over the last 10 kyr, some populations of this species that were adapted to cooler, moister temperatures have been extirpated. Such rapid niche shifts with respect to climate could very well account for the mismatches between the SDM hindcast hypotheses and the empirical fossil data. The rapidity of current climate change, pushing organisms to the limits of their phenotypic plasticity, and widespread extirpations (if not extinctions) are both also likely to affect future predictions for species distributions.

Another possible explanation for why SDM hindcasts are not in agreement with palaeodistributions is that interspecific interactions make the realized niches of species smaller than their fundamental niches (Hutchinson, 1957). If non-climatic factors play an important role in determining the distribution of a species or if a dispersal barrier is present, the current realized niche space would be much smaller than the fundamental niche space for a species; therefore, any climate-projected species distributions are likely to be smaller than the observed ranges (Guisan & Thuiller, 2005). The same type of mismatch can occur if regions of the fundamental niche are more or less optimal for the species, and

the realized niche of that species becomes suboptimal during stressful times. Both competition and predation have been demonstrated to have strong effects on members of the genus *Microtus*, indicating that these species' realized niches may be considerably smaller than their fundamental niches (Findley, 1954; Koplin & Hoffmann, 1968; Conley, 1976; Huntly, 1991; Norrdahl & Korpimäki, 1993). Competition experiments in *Microtus* species have repeatedly shown that these species demonstrate strong avoidance behaviour and are negatively affected by congeners in close proximity (Findley, 1954; Koplin & Hoffmann, 1968; Conley, 1976). Additionally, predators play an important role in the population cycles of *Microtus* (Huntly, 1991), and have been demonstrated to preferentially take certain species over others, resulting in apparent competition (Norrdahl & Korpimäki, 1993). Given that competition plays such an important role in *Microtus* population size, congener presence, predator presence and possibly even predator density may be necessary parameters for accurate predictive distribution models.

Many recent iterations of SDMs have begun to try to incorporate many more diverse input variables for predicting distributional shifts, including interspecific interactions (e.g. Zurell *et al.*, 2009; Kissling *et al.*, 2012), dispersal considerations (e.g. De Marco *et al.*, 2008) and physiological limitations (e.g. Kearney & Porter, 2009; Buckley *et al.*, 2010; Bykova *et al.*, 2012). To determine how to most effectively improve these models, however, it will be valuable to use the approach described herein to determine the common variables among species whose fossil occurrences disagree with SDM hindcasts. The suite of hypotheses to explain LGM data–model mismatches can only be evaluated in the context of a large number of detailed species-level reconstructions of palaeodistributions, highlighting any consistencies in the causes of discrepancies, and allowing the systematic improvement of SDM methods. Perhaps most importantly, the pattern of deviation between SDM reconstructions and fossil distributions has the potential to resolve the relative importance of biotic and abiotic factors in individual species distributions.

CONCLUSIONS

This study highlights the utility of integrating species-level palaeontological analyses with recent ecological monitoring and SDMs to investigate the species-specific mechanisms governing range shifts in response to climate change. LGM SDMs did not correctly reconstruct the presences of several extralimital fossil specimens. This mismatch could result from issues with precipitation reconstructions in LGM climate models, biotic and anthropogenic effects (including 20th-century climate change) on present-day realized niches, species evolution or phenotypic plasticity. Similar comparisons across many more species would more definitively pinpoint the source of error in these models, and robust species identification metrics such as those employed herein (McGuire, 2011) must be used to ensure the accuracy of the fossil species occurrences. Our findings emphasize that the addi-

tion of deep-time data to a study can only enhance the understanding of species reactions to climate change, putting it in a broader context.

ACKNOWLEDGEMENTS

We thank Tony Barnosky, Steve Beissinger, Craig Moritz, Kevin Padian, Kaitlin Maguire, Simon Sponberg, Rob Guralnick, Sara Varela and two anonymous referees for their comments on earlier drafts. We thank Lawrence Livermore National Lab's Center for Accelerator Mass Spectrometry, notably Paula Zermino and Tom Guilderson, for radiocarbon dating instruction and use of lab facilities. Thanks to the UCMP, LACM, MNCH, MVZ and their staff, particularly Dennis Jenkins and Chris Conroy, for specimen access and assistance. The ESRI Conservation Program allowed the use of ArcGIS. We acknowledge the international modelling groups for providing their data for analysis and the Laboratoire des Sciences du Climat et de l'Environnement (LSCE) for collecting and archiving the model data. The PMIP2/MOTIF Data Archive is supported by CEA, CNRS, the EU project MOTIF (EVK2-CT-2002-00153) and the Programme National d'Étude de la Dynamique du Climat (PNEDC). We also acknowledge data provided by NatureServe. Funding for this project was provided by the BNHM NSF GK-12 Program, Junea W. Kelly Research Fellowship, National Sigma Xi Grant, UCMP Welles Fund Grant, and National Evolutionary Synthesis Center (NSF Grant no. EF-0905606).

REFERENCES

- Blois, J.L., McGuire, J.L. & Hadly, E.A. (2010) Small mammal diversity loss in response to late-Pleistocene climatic change. *Nature*, **465**, 771–774.
- Borchert, M.I. & Jain, S.K. (1978) The effect of rodent seed predation on four species of California annual grasses. *Oecologia*, **33**, 101–113.
- Braconnot, P., Otto-Bliesner, B., Harrison, S., Joussaume, S., Peterschmitt, J.-Y., Abe-Ouchi, A., Crucifix, M., Driesschaert, E., Fichefet, T., Hewitt, C.D., Kageyama, M., Kitoh, A., Loutre, M.-F., Marti, O., Merkel, U., Ramstein, G., Valdes, P., Weber, L., Yu, Y. & Zhao, Y. (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 2: feedbacks with emphasis on the location of the ITCZ and mid- and high latitudes heat budget. *Climate of the Past*, **3**, 279–296.
- Bronk Ramsey, C., Higham, T.F.G., Brock, F., Baker, D. & Ditchfield, P. (2009) Radiocarbon dates from the Oxford AMS system: *Archaeometry* datelist 33. *Archaeometry*, **51**, 323–349.
- Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.-A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2131–2138.

- Bykova, O., Chuine, I., Morin, X. & Higgins, S.I. (2012) Temperature dependence of the reproduction niche and its relevance for plant species distributions. *Journal of Biogeography*, **39**, 2191–2200.
- Campbell, K.E. & Stenger, A.T. (2002) A new teratorn (Aves; Teratornithidae) from the Upper Pleistocene of Oregon, USA. *Proceedings of the 5th Symposium of the Society of Avian Paleontology and Evolution, Beijing, 1–4 June 2000* (ed. by Z. Zhou and F. Zhang), pp. 1–11. Science Press, Beijing.
- Collins, W.D., Bitz, C.M., Blackmon, M.L., Bonan, G.B., Bretherton, C.S., Carton, J.A., Chang, P., Doney, S.C., Hack, J.J., Henderson, T.B., Kiehl, J.T., Large, W.G., McKenna, D.S., Santer, B.D. & Smith, R.D. (2006) The Community Climate System Model version 3 (CCSM3). *Journal of Climate*, **19**, 2122–2143.
- Conley, W. (1976) Competition between *Microtus*: a behavioral hypothesis. *Ecology*, **57**, 224–237.
- Davis, O.K. (1999) Pollen analysis of a late-glacial and Holocene sediment core from Mono Lake, Mono County, California. *Quaternary Research*, **52**, 243–249.
- De Marco, P., Jr, Diniz-Filho, J.A.F. & Bini, L.M. (2008) Spatial analysis improves species distribution modelling during range expansion. *Biology Letters*, **4**, 577–580.
- Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Findley, J.S. (1954) Competition as a possible limiting factor in the distribution of *Microtus*. *Ecology*, **35**, 418–420.
- Graham, R.W., Lundelius, E.L., Graham, M.A., Schroeder, E.K., Toomey, R.S., III, Anderson, E., Barnosky, A.D., Burns, J.A., Churcher, C.S., Grayson, D.K., Guthrie, R.D., Harington, C.R., Jefferson, G.T., Martin, L.D., McDonald, H.G., Morlan, R.E., Semken, H.A., Jr, Webb, S.D., Werdelin, L. & Wilson, M.C. (1996) Spatial response of mammals to late Quaternary environmental fluctuations. *Science*, **272**, 1601–1606.
- Grayson, D.K. (2005) A brief history of Great Basin pikas. *Journal of Biogeography*, **32**, 2103–2111.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.
- Guralnick, R. (2007) Differential effects of past climate warming on mountain and flatland species' distributions: a multispecies North American mammal assessment. *Global Ecology and Biogeography*, **16**, 14–23.
- Guralnick, R. & Pearnan, P.B. (2010) Using species occurrence databases to determine niche dynamics of montane and lowland species since the Last Glacial Maximum. *Data mining for global trends in mountain biodiversity* (ed. by E.M. Spehn and C. Körner), pp. 125–135. CRC Press, Boca Raton, FL.
- Hadly, E.A. & Barnosky, A.D. (2009) Vertebrate fossils and the future of conservation biology. *Conservation paleobiology: using the past to manage for the future* (ed. by G.P. Dietl and K.W. Flessa), pp. 39–59. Yale University Press, New Haven, CT.
- Hadly, E.A., Spaeth, P.A. & Li, C. (2009) Niche conservatism above the species level. *Proceedings of the National Academy of Sciences, USA*, **106**, 19707–19714.
- Hasumi, H. & Emori, S. (eds) (2004) *K-1 coupled GCM (MIROC) description*. Center for Climate System Research, University of Tokyo, Tokyo.
- Hernandez, P.A., Graham, C.H., Master, L.L. & Albert, D.L. (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, **29**, 773–785.
- Hijmans, R.J. & Graham, C.H. (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hilbert, D.W., Graham, A. & Hopkins, M.S. (2007) Glacial and interglacial refugia within a long-term rainforest refugium: the Wet Tropics Bioregion of NE Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **251**, 104–118.
- Hoffman, R.S. & Jones, J.K., Jr (1970) Influence of late-glacial and post-glacial events on the distribution of the Recent mammals of the Northern Great Plains. *Pleistocene and Recent environments of the central Great Plains* (ed. by W. Dort Jr and J.K. Jones Jr), pp. 355–394. University Press of Kansas, Lawrence, KS.
- Huntly, N. (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*, **22**, 477–504.
- Hutchinson, G.E. (1957) Concluding remarks. *Population studies: animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Jackson, S.T. & Overpeck, J.T. (2000) Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, **26**, 194–220.
- Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb, T., III, Williams, J.W. & Hansen, B.C.S. (2000) Vegetation and environment in Eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 489–508.
- Jenkins, D.L., Davis, L.G., Stafford, T.W., Jr, Campos, P.F., Hockett, B., Jones, G.T., Cummings, L.S., Yost, C., Connolly, T.J., Yohe, R.M., II, Gibbons, S.C., Raghavan, M., Rasmussen, M., Paijmans, J.L.A., Hofreiter, M., Kemp, B.M., Barta, J.L., Monroe, C., Gilbert, M.T.P. & Willerslev, E. (2012) Clovis Age Western Stemmed projectile points and human coprolites at the Paisley Caves. *Science*, **337**, 223–228.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modeling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Kissling, W.D., Dormann, C.F., Groeneveld, J., Hickler, T., Kühn, I., McNerny, G.J., Montoya, J.M., Römermann, C.,

- Schiffers, K., Schurr, F.M., Singer, A., Svenning, J.-C., Zimmermann, N.E. & O'Hara, R.B. (2012) Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography*, **39**, 2163–2178.
- Koplin, J.R. & Hoffmann, R.S. (1968) Habitat overlap and competitive exclusion in voles (*Microtus*). *American Midland Naturalist*, **80**, 494–507.
- Maguire, K.C. & Stigall, A.L. (2009) Using ecological niche modeling for quantitative biogeographic analysis: a case study of Miocene and Pliocene Equinae in the Great Plains. *Paleobiology*, **35**, 587–611.
- Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology*, **38**, 921–931.
- McGuire, J.L. (2010a) Geometric morphometrics of vole (*Microtus californicus*) dentition as a new paleoclimate proxy: shape change along geographic and climatic clines. *Quaternary International*, **212**, 198–205.
- McGuire, J.L. (2010b) *The effects of Quaternary environmental changes on Microtus distribution and morphology*. PhD Thesis, University of California, Berkeley, CA.
- McGuire, J.L. (2011) Identifying California *Microtus* species using geometric morphometrics documents Quaternary geographic range contractions. *Journal of Mammalogy*, **92**, 1383–1394.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.
- Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. & Araújo, M.B. (2008) Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biology*, **6**, e79.
- Norrdaahl, K. & Korpimäki, E. (1993) Predation and interspecific competition in two *Microtus* voles. *Oikos*, **67**, 149–158.
- Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.
- Pausata, F.S.R., Li, C., Wettstein, J.J., Nisancioglu, K.H. & Battisti, D.S. (2009) Changes in atmospheric variability in a glacial climate and the impacts on proxy data: a model intercomparison. *Climate of the Past*, **5**, 489–502.
- Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sánchez-Cordero, V., Soberón, J., Buddemeier, R.H. & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Phillips, S.J. (2008) Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson *et al.* *Ecography*, **31**, 272–278.
- Phillips, S.J. & Dudík, M. (2008) Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.
- Phillips, S.J., Dudík, M. & Schapire, R.E. (2004) A maximum entropy approach to species distribution modeling. *Proceedings of the 21st International Conference on Machine Learning, Banff, Canada, 2004* (ed. by C.E. Brodley), pp. 655–662, ACM Press, New York.
- Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.
- Pineda, E. & Lobo, J.M. (2009) Assessing the accuracy of species distribution models to predict amphibian species richness patterns. *Journal of Animal Ecology*, **78**, 182–190.
- Reimer, P.J., Baillie, M.G.L., Bard, E. *et al.* (2009) Intcal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal bp. *Radiocarbon*, **51**, 1111–1150.
- Rissler, L.J., Hijmans, R.J., Graham, C.H., Moritz, C. & Wake, D.B. (2006) Phylogeographic lineages and species comparisons in conservation analyses: a case study of California herpetofauna. *The American Naturalist*, **167**, 655–666.
- Rodríguez-Sánchez, F. & Arroyo, J. (2008) Reconstructing the demise of Tethyan plants: climate-driven range dynamics of *Laurus* since the Pliocene. *Global Ecology and Biogeography*, **17**, 685–695.
- Rohlf, F.J. (2006) *tpsDig*. State University of New York at Stony Brook, NY.
- Sheets, H.D. (2000) *Coordinate Generator*. Canisius College, Buffalo, NY.
- Stewart, J.D. (1978) Mammals of the Trapshoot local fauna, late Pleistocene, of Rooks County, Kansas. *Proceedings of the Nebraska Academy of Science*, **1978**, 45–46.
- Stigall Rode, A.L. & Lieberman, B.S. (2005) Paleobiogeographic patterns in the Middle and Late Devonian emphasizing Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **222**, 272–284.
- Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nogués-Bravo, D. & Normand, S. (2011) Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews*, **30**, 2930–2947.
- Turner, R.W. (1974) Mammals of the Black Hills of South Dakota and Wyoming. *Miscellaneous Publications of the Museum of Natural History, University of Kansas*, **60**, 1–178.
- Varela, S., Rodríguez, J. & Lobo, J.M. (2009) Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. *Journal of Biogeography*, **36**, 1645–1655.
- Varela, S., Lobo, J.M. & Hortal, J. (2011) Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **310**, 451–463.
- Wallace, S.C. (2001) Confirmations of *Microtus montanus* (mountain vole) from the late-Wisconsinan Jones Local Fauna, Meade Co., Kansas. *Current Research in the Pleistocene*, **18**, 117–119.
- Wallace, S.C. (2006) Differentiating *Microtus xanthognathus* and *Microtus pennsylvanicus* lower first molars using discriminant analysis of landmark data. *Journal of Mammalogy*, **87**, 1261–1269.
- Waltari, E. & Guralnick, R.P. (2009) Ecological niche modeling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. *Journal of Biogeography*, **36**, 148–161.

- Waltari, E., Hijmans, R.J., Peterson, Á.T., Nyári, A.S., Perkins, S.L. & Guralnick, R.P. (2007) Locating Pleistocene refugia: comparing phylogeographic and ecological niche model predictions. *PLoS ONE*, **2**, e563.
- Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications*, **21**, 335–342.
- Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, **62**, 2868–2883.
- Warren, D.L., Glor, R.E. & Turelli, M. (2010) ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, **33**, 607–611.
- Zurell, D., Jeltsch, F., Dormann, C.F. & Schröder, B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography*, **32**, 733–744.

SUPPORTING INFORMATION

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

Appendix S1 Table of fossil identifications.

Appendix S2 Modern sampling of *M. montanus* specimens near Woodburn, OR.

Appendix S3 Full species distribution models for the present and LGM.

BIOSKETCHES

Jenny L. McGuire is a postdoctoral researcher at the University of Washington. She researches how organisms in the past have reacted to climate change, and how we can use an understanding of this to predict how organisms will evolve, shift their ranges, or go extinct given impending climate change. Exploring mammalian reactions to changing climates on several spatial and temporal scales, she examines how environmental changes not only alter species' ranges, but also can elicit evolutionary responses in phenotype and alter variation within populations.

Edward Byrd Davis is Fossil Collections Manager for the UO Museum of Natural and Cultural History, a position he has held since 2008. His research spans several themes within palaeomammalogy, ranging from palaeomacroecology, to the evolution of development of cranial appendages in ruminant artiodactyls, to the functional morphology of mammalian postcrania.

Editor: Brett Riddle