



0 Biotic responses of canids to the terminal Pleistocene megafauna extinction 53

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Trophic downgrading is a major concern for conservation scientists. The largest consumers in many ecosystems have become either rare or extirpated, leading to worry over the loss of their ecosystem function. However, trophic downgrading is not a uniquely modern phenomenon. The extinction of 34 genera of megafauna from North America ~13 000 yr ago must have led to widespread changes in terrestrial ecosystem function. Studies that have examined the event address impacts on vegetative structure, small mammal communities, nutrient cycling, and fire regimes. Relatively little attention has been paid to community changes at the top of the food chain. Here, we examine the response of carnivores in North America to the Pleistocene extinction. We employ fossil data to model the climatic niche of endemic canids, including the extinct dire wolf *Canis dirus*, over the last 20 000 yr. Quantifying the abiotic niche allows us to account for expected changes due to climate fluctuations over the late Quaternary; deviations from expected responses likely reveal influences of competition and/or resource availability. We quantify the degree of niche conservatism and interspecific overlap to assess species and community responses among canids. We also include in our analyses a novel introduced predator, the domestic dog *Canis lupus familiaris*, which accompanied humans into the New World. We find that endemic canid species display low fidelity to their climatic niche through time. We find that survivors increasingly partition their climatic niche throughout the Holocene and, surprisingly, do not expand into niche space presumably vacated by the extinction of very large carnivores. These results suggest that loss of megaherbivores and competition with humans likely outweighed advantages conferred from the loss of very large predators. We also find that wolves and dogs decrease their niche overlap throughout the Holocene, suggesting a distinctive relationship between dogs and man. 65
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30 Late Pleistocene ecosystems in North America were vastly different from today. Tens of millions of large-bodied mammals, including species such as mammoths, mastodons, camels, horses, giant ground sloths, cheetahs, lions and massive carnivorous bears were widespread across the landscape. Their loss, around 13 ka, during a time transgressive extinction that occurred on multiple continents, resulted in an ecologically depauperate world (Martin and Szuter 1999, Hadly and Barnosky 2009). 85

35 The Pleistocene extinction has long captivated scientists and the public alike because it has all the characteristics of a classic ‘Who done it?’ murder mystery. In North America alone, some 34 genera and ~75 species of megafauna went extinct; similar numbers were lost in South America (Lyons et al. 2004). The event was highly size selective; indeed, the average mass of mammals that went extinct in the Americas was ~900 kg (Smith et al. 2003b, Lyons et al. 2004), Fig. 1). Attribution has been a subject of heated debate, and has largely settled on two competing causes: humans (Martin 1984, Martin and Szuter 1999, Alroy 2001, Lyons et al. 2004, Surovell et al. 2005, Sandom et al. 2014) or climate (Guthrie 1984, Graham et al. 1996, Grayson 2001, 2007, Grayson and Meltzer 2002). While both factors undoubtedly contributed to ecological changes at the end of 40
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52 the Pleistocene, humans appear to be especially culpable in North America (Koch and Barnosky 2006).
Paleoecology has the potential to provide temporal and spatial insights into modern ecological studies. However, most analyses of the terminal Pleistocene extinction have focused on the cause, not the consequences of the loss of tens of millions of large-bodied animals from the landscape. Understanding how North American ecosystems were altered is of more than historic interest; today, most large-bodied animals are imperiled. Yet, few bridges exist between paleontologists, who study the terminal Pleistocene extinction, and conservation biologists interested in the role of extant megafauna. 90
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105 Extant megaherbivores in Africa have a disproportionate impact on vegetation and trophic interactions (Owen-Smith 1987) and considerable effort is underway to understand the role of megafauna in contemporary ecosystems. As such, recent work has begun addressing the effect of the Pleistocene megaherbivore extinction on vegetation communities (Gill et al. 2009, 2012, Johnson 2009, Gill 2014), fire regimes (Burney et al. 2003, Robinson et al. 2005, Rule et al. 2012) and nutrient cycling (Doughty et al. 2013). Notably absent, however, from the research of the last decade are studies investigating the impacts at the top of the food chain in the

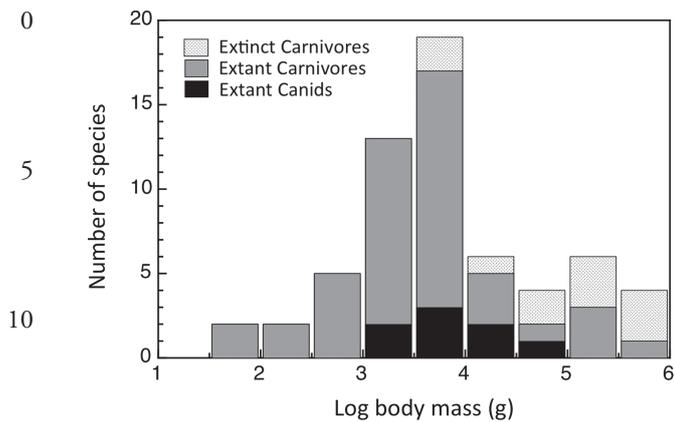


Figure 1. Body size distribution of North American carnivores. All extant carnivores are shown in grey; species that went extinct in the terminal Pleistocene are indicated by hatch marks, extant canids in black. Data from MOM ver. 5.0 (updated version of Smith et al. 2003b). Note the distinctive size signature of the extinction. Within each carnivore family, the largest species were extirpated (Lyons et al. 2004).

carnivore community. Yet, the loss of large consumers from ecological systems, particularly carnivores, is a significant and growing modern conservation concern across all ecosystem types (Estes et al. 2011).

The removal of large consumers, called trophic downgrading, occurred across all trophic levels during the Pleistocene extinction, including among carnivores. Indeed, most of the largest carnivores, including the short-faced bear (720 kg), American cave lion (433 kg), saber-tooth cat (400 kg), scimitar cat (190 kg), Florida spectacled bear (150 kg) and the dire wolf (65 kg) went extinct (Fig. 1), leaving only medium-sized predators, or ‘mesocarnivores’ (Smith et al. 2003b). With the exception of the surviving bears, modern terrestrial carnivores in North America all weigh less than 100 kg, and most considerably less (Smith et al. 2003b). Mesocarnivores do not fulfill the same ecological functions as larger species; they tend to be less carnivorous and less threatening to both prey and competitors (Gittleman 1985, Simberloff and Dayan 1991, Prugh et al. 2009, Roemer et al. 2009). Moreover, because hierarchies within the carnivore guild are largely structured by body size (Hairston et al. 1960, Koehler and Hornocker 1991, Ripple et al. 2001, Ripple and Beschta 2003, Van Valkenburgh et al. 2004), it is likely that trophic downgrading significantly alters intra-guild interactions. For example, in addition to mediating herbivory, large carnivores regulate smaller predators (Soulé et al. 1988). Such intra-guild predation imparts a disproportionately high benefit to the winner and cost to the loser (Ritchie and Johnson 2009). Without regulation by ‘top carnivores’, the increased abundance of smaller species can be ecologically devastating. Their loss can also lead to shortening of food chains, a reduction in the number of interspecific interactions, and ‘simpler’ ecosystems with less functional redundancy and resilience (Elmhagen et al. 2010, Letnic et al. 2012, Ritchie et al. 2012). Thus, the disappearance of top carnivores resulting from the late Pleistocene extinction may have had considerable impacts on ecosystems.

Here, we characterize how trophic downgrading at the end of the Pleistocene altered interactions and structure

within surviving Canidae, which includes species varying in size from 1.9–65 kg (Smith et al. 2003b). We selected this group for several reasons. Species from within this family have similar life histories, good representation as fossils, and exhibit high degrees of intrafamilial mortality and strong competitive interactions in modern ecosystems (Palomares and Caro 1999, Smith et al. 2003a, Berger and Gese 2007, Atwood and Gese 2008, 2010, Merkle et al. 2009). In addition to the five endemic North American canid species, we include in our analyses a new predator that invaded North American ecosystems in the terminal Pleistocene, the domestic dog. Dogs may represent a competitor in their own right, a proxy for competitive interactions with humans, or some combination of both; we cannot differentiate here between these alternatives.

Although the number of very large carnivores decreased at the end of the Pleistocene, the extinction of megaherbivores was proportionally greater: for species over 100 kg, 5 out of 12 carnivores survived (a reduction of 58%) but only 15 out of 61 herbivores avoided extinction (a reduction of about 75%) (Kurtén and Anderson 1980). The loss of very large competitors, on the one hand, could have opened up available niche space to surviving carnivores. On the other hand, massive losses of very large herbivores may have resulted in prey switching and increased competition between remaining large carnivores over reduced resources. Moreover, the colonization of the Americas by humans may have been especially problematic because they were accompanied by domestic dogs, an invasive mesocarnivore competitor, and hunted prey from a variety of size categories.

Our study aims to identify changes in the spatial distribution of canids in response to the Pleistocene extinction, within the context of Late Quaternary climate change. Specifically, we ask: 1) how well do canid species track their environmental niche over time? 2) How much niche separation occurs between canid species and is this related to their body size and trophic status? 3) Does the degree of niche separation change over time after the largest carnivore in the guild (*Canis dirus*) goes extinct? Finally, 4) how do domestic dogs fit into the broader context of interspecific interactions within the guild?

Methods

Project framework

Because climate also shifted at the terminal Pleistocene, we employ maximum entropy niche modeling (Maxent, Phillips and Dudík 2008) to model the changing abiotic niche over time. A niche modeling framework allows us to describe broad continent wide changes and develop predictions for where animals should occur based solely on abiotic factors. Deviations from the abiotic niche suggest the influence of biotic factors – most likely prey availability or competition. We quantify both the degree of niche conservatism for each canid species and the degree of interspecific overlap to assess community responses within the community, which we hypothesize will be size-related. To test for niche separation, we correlated observed spatial likelihoods between species within a time interval.

0 Study area and fossil species occurrences

Our study area encompasses much of the North American continent, excluding Mexico. A minimum convex polygon was constructed enclosing all fossil mammal localities to define the study area, and represents the maximum area in which effort has been made to collect fossil samples by previous investigators (FAUNMAP Working Group 1994; Fig. 2, gray polygon). Fossil occurrences for all carnivores were obtained from FAUNMAP (FAUNMAP Working Group 1994) using the Neotoma Paleobiological Database portal (<www.neotomadb.org>; Fig. 2). Data with non-specific or ambiguous species identifications were eliminated and subspecies, except for *C. lupus familiaris*, were grouped together at the species level. Records with poor temporal control (e.g. their age range exceeded 3000 yr) were eliminated. Each occurrence was binned into a temporal window: late Pleistocene (20–10 ka), Early–Middle Holocene (10–5 ka), and late Holocene (4–1 ka). The mean age of each occurrence was then associated with a paleoclimate simulation that was closest to its mean age. Finer temporal resolutions were not possible because many fossils were not more precisely dated.

25 Paleoclimate data

We employed 35 spatially downscaled paleoclimate variables derived from the National Center for Atmospheric Research Community Climate System Model ver. 3 (CCSM3) (Liu et al. 2009, Veloz et al. 2012; Supplementary material Appendix 1, Table A1). Climate reconstructions were at 1000 yr intervals, with 0.5×0.5 degree spatial resolution, from 1–20 ka. Environmental variables from each simulation were associated with species occurrences using a geographic information system. Each time interval contained several species occurrences of different ages and the associated environmental variables simulated for those ages. Therefore, each occurrence was given environmental data from a location-time coordinate (latitude, longitude, simulation age). Ice sheet surface data were obtained from the Paleoclimate Modelling Intercomparison Project Phase II

(PMIP 2) ICE-5G (ver. 1.2) datasets (Peltier 2004), and were used to mask areas where glaciers were present prior to niche modeling.

65 Ecological niche modeling (ENM) in Maxent

Models were trained and analyzed from data confined within the geographic extent of the study area. Species' niches were modeled using the maximum entropy method and projected for each time interval in Maxent (Phillips et al. 2004, 2006). Maxent is the most appropriate tool for our analyses because it is a presence-only method, and records from FAUNMAP are inherently presence-only data sets (Phillips et al. 2004, Phillips and Dudík 2008, Elith et al. 2011). The logistic output of this model, although not an explicit probability of occurrence, provides habitat suitability values, or likelihoods of occurrence given the environmental variables of the model.

Background data for each species model were taken from 10 000 random location-time coordinates within the time interval. To account for simulation ages where no fossils for a given species occurred, the environmental data for those ages were omitted from data used to populate the background dataset. The background data, therefore, provide an estimate of the environmental conditions a species could have potentially used over the duration of a time interval.

Niche models were produced using the logistic output in Maxent, using a bootstrap resampling method with 100 replicates and random starting points. We used 25% of occurrences for testing and 'auto features' for algorithm selection. Models were initially run with all 35 climatic variables to determine which variables contributed most to the model for each species at each time interval. We retained the top three contributing variables for each individual model as indicated from the Maxent output (Supplementary material Appendix 1, Table A2) and reran the models a second time to produce likelihoods of occurrence given this smaller subset of the climate variables. The average of the 100 replicates from these models were used for all further mapping, statistical, and spatial analyses.

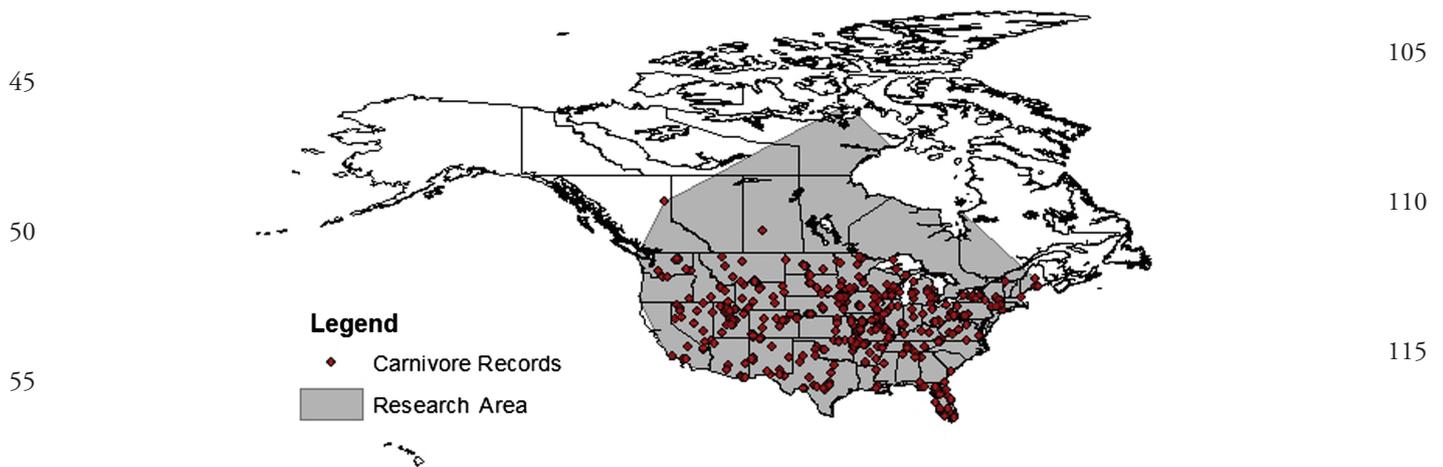


Figure 2. All FAUNMAP sites that contain carnivore records within the time period of this study. The gray area is the research area as defined by the minimum convex hull that contains all mammal records in FAUNMAP.

Two types of ecological niche models (ENM) were created for each species at each time interval. An observed ENM for a species was created using location and background data for the time interval in question (e.g. Pleistocene, Early–Middle Holocene or Late Holocene); this was projected onto a climatic reconstruction for that time interval (20 ka, 10 ka, or 4 ka, respectively). An expected ENM for a species was also created by projecting the ENM from the previous time interval forward in time onto the climatic template used for the observed ENM. This resulted in five potential ENMs for each species (Supplementary material Appendix 2): 1) an observed ENM for each species during the late Pleistocene, 2) an observed during the Early–Middle Holocene, 3) an expected for the Early–Middle Holocene that was projected from the Pleistocene model, 4) an observed for the Late Holocene, and 5) an expected for the Late Holocene that was projected from the Early–Middle Holocene model. For the purpose of statistical analyses outside of the Maxent environment, ENMs were rasterized to 0.5×0.5 degree grids within the research area.

Hypothesis testing

Intra-guild predation is prevalent among carnivores, especially canids (Polis et al. 1989, Palomares and Caro 1999, Fedriani et al. 2000). Thus, the extinction of large competitors may have increased available niche space. To test for niche conservation or expansion we correlated the observed likelihoods from a rasterized ecological niche model for a given time interval with the expected likelihoods derived from the previous time interval. If the niche is conserved, then we predict the expected niche and observed niche should be significantly positively correlated. If, however, the niche is not conserved, the expected should be a poor predictor for the observed niche.

To examine the extent of niche conservation following the extinction, we calculated the Pearson's coefficient of correlation between paired observed and expected likelihood values of each raster cell from ENMs for the Early–Middle Holocene and the Late Holocene. Rasters were of equal dimensionality and spatial extent and were constrained to the research area defined in training the model. Grid cells where both the observed and expected likelihood values were below 0.10 were omitted from these analyses. The correlation between observed and expected likelihood values were tested for statistical significance and we evaluated significant correlation changes between time periods by comparing 95% confidence intervals.

To evaluate the degree of observed niche separation, we calculated the Pearson's coefficient of correlation of gridded

observed likelihood values between pairs of species for each time interval. Rasters were of equal dimensionality and spatial extent and were constrained to the research area defined in training the model. Grid cells where both species were unlikely to occur (likelihood values below 0.10) were omitted from these analyses. A significant positive correlation indicates that the niche of two species overlaps, whereas a negative correlation indicates that the niches are partitioned. Zero correlation indicates no relationship. Interspecific overlap may also be influenced by abiotic factors; therefore, expected interspecific overlap was similarly calculated for each species pair using expected likelihood values. We then compared observed and expected interspecific correlations across time intervals.

If surviving canids moved into open niches, thereby increasing niche separation following the Pleistocene extinction, then observed interspecific correlation values will decrease more than expected between species through time. If biotic interactions increased niche overlap, then observed correlation values will increase more than expected through time. If biotic interactions remained constant, then the expected interaction should predict the observed.

Data available from the Dryad Digital Repository: [AQ1] <<http://dx.doi.org/10.5061/dryad.XXXXXX>> (Pardi and Smith 2015).

Results

Model evaluation

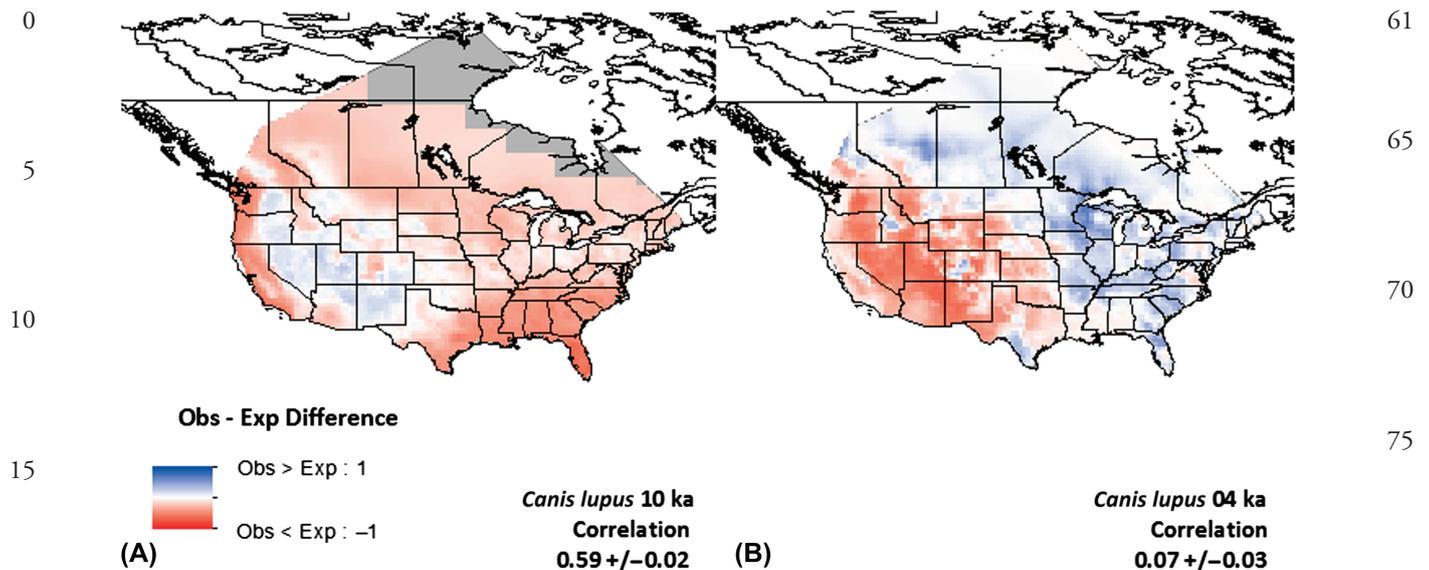
All of our niche models for all time intervals performed better than random. Table 1 provides the average area under the curve (AUC) for 100 model replicates calculated by Maxent to evaluate performance, as well as the number of randomly chosen training and testing samples used for each model. An AUC of 0.5 corresponds to a random model, while values over 0.75 are considered potentially useful (Phillips and Dudík 2008). For our study most of the models performed on average with AUC values greater than 0.8, however the 20 kyr BP model for *Canis lupus* had an average value of 0.773 ± 0.067 .

Ecological niche conservation

Across all models and species we find a mismatch between expected occurrences and observed patterns. We calculated differences between the expected (Supplementary material Appendix 2, Fig. A2 and Fig. A4) and observed (Supplementary material Appendix 2, Fig. A1, Fig. A3, and

Table 1. Average AUC values calculated from 100 model replicates. All models performed better than random, most averaged greater than 0.8. The 20 kyr BP model for *Canis lupus* performed worst, with an AUC of 0.773 ± 0.067 . The number of random points used to train and test the model are given in parentheses, respectively. No data is indicated by a dash.

	20 kyr BP	10 kyr BP	4 kyr BP
<i>Canus dirus</i>	0.828 \pm 0.058 (9, 3)	–	–
<i>Canis lupus</i>	0.7730 \pm 0.067 (7, 2)	0.857 \pm 0.039 (11, 3)	0.854 \pm 0.017 (52, 17)
<i>Canis lupus familiaris</i>	–	0.806 \pm 0.054 (6, 1)	0.931 \pm 0.010 (98, 32)
<i>Canis latrans</i>	0.820 \pm 0.073 (10, 3)	0.903 \pm 0.034 (15, 5)	0.869 \pm 0.015 (56, 18)
<i>Vulpes vulpes</i>	0.814 \pm 0.063 (6, 1)	0.810 \pm 0.058 (9, 3)	0.864 \pm 0.025 (30, 10)



20 Figure 3. Differences between expected and observed likelihood values for *Canis lupus*. (A) the Early–Middle Holocene (10 kyr BP) and (B) the Late Holocene (4 kyr BP). The expected model was subtracted from the observed: positive values, blue, indicate that the expected underpredicted the observed likelihoods (niche expansion), negative values, red, indicate that the expected overpredicted the observed likelihoods (niche contraction). Pearson correlation coefficients are given in each panel between the observed and the expected, with 95% confidence intervals.

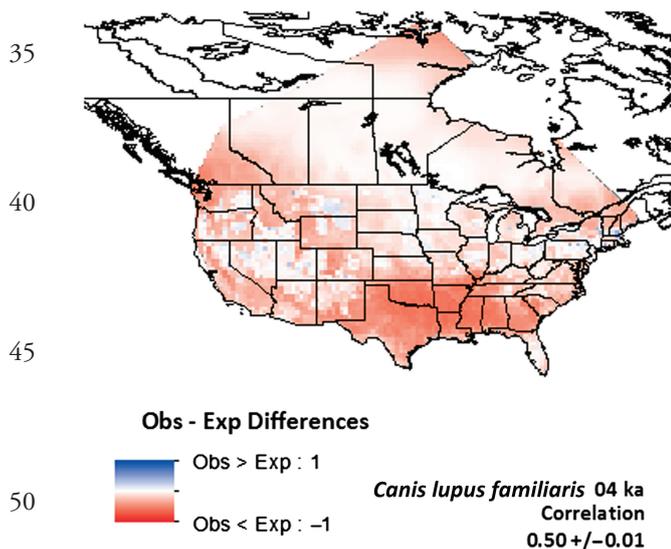
25 Fig A5) likelihoods of occurrence by subtracting the expected raster values from the observed (Fig. 3–6). We were able to calculate differences between the observed and expected for 10 ka and 4 ka for *Canis lupus* (Fig. 3), *C. latrans* (Fig. 5), and *Vulpes vulpes* (Fig. 6); however, data were only available to calculate a difference at 4 ka. for *Canis lupus familiaris* (Fig. 4). Positive values (blue shading) indicate areas where species had a high observed value, but a low likely

expectation. Negative values (in red) indicate areas where a species had a low observed value, yet was expected to occur. Light colors or white indicates regions where the expected and observed were in concordance. Across all species, differences between the observed and expected niche differ significantly throughout the Holocene.

We find a strong signal of a changing climatic niche for each species over time; correlations between expected and observed occupancy decrease through time for all endemic species in the Early–Middle Holocene (Fig. 3–6; Pearson correlation for the expected and observed models are given for each time period with 95% confidence intervals). The expected and observed models for *Canis lupus* and *Canis latrans* are moderately correlated in the Early–Middle Holocene (Fig. 3A, 0.59 +/- 0.02 and Fig. 5A, 0.58 +/- 0.02, respectively), but lowly correlated in the late Holocene (Fig. 3B, 0.07 +/- 0.03 and Fig. 5B, 0.29 +/- 0.03, respectively). Lastly, *Vulpes vulpes* is fairly well predicted in the Early–Middle Holocene (Fig. 6A, 0.79 +/- 0.01), but this relationship falls apart in the late Holocene (Fig. 6B, 0.33 +/- 0.02).

The difference between the observed versus the expected niche is qualitatively different throughout the guild. In the Early–Middle Holocene, the observed extent of the niche for *Vulpes vulpes* is somewhat larger than expected (Fig. 6A, blue regions), but the observed niches for *Canis lupus* and *Canis latrans* are smaller than expected (Fig. 3A and Fig. 5A, red regions). However, in the Late Holocene *Vulpes vulpes* has an observed niche that is much smaller than expected (Fig. 6B, red regions) and an observed niche that is poorly correlated with the expected (Fig. 6B, 0.33 +/- 0.02). *Canis lupus familiaris* had an observed niche that was more reduced than expected, resulting in an observed niche that was poorly correlated with the expected (Fig. 4, 0.50 +/- 0.01).

We conclude that the Canidae are not showing fidelity to their climatic niche through time. The observed niche in the late Holocene is less predictable than in the



55 Figure 4. Differences between expected and observed likelihood values for *Canis lupus familiaris* for the Late Holocene (4 kyr BP). The expected model was subtracted from the observed: positive values, blue, indicate that the expected underpredicted the observed likelihoods (niche expansion), negative values, red, indicate that the expected overpredicted the observed likelihoods (niche contraction). Pearson correlation coefficients are given in each panel between the observed and the expected, with 95% confidence intervals.

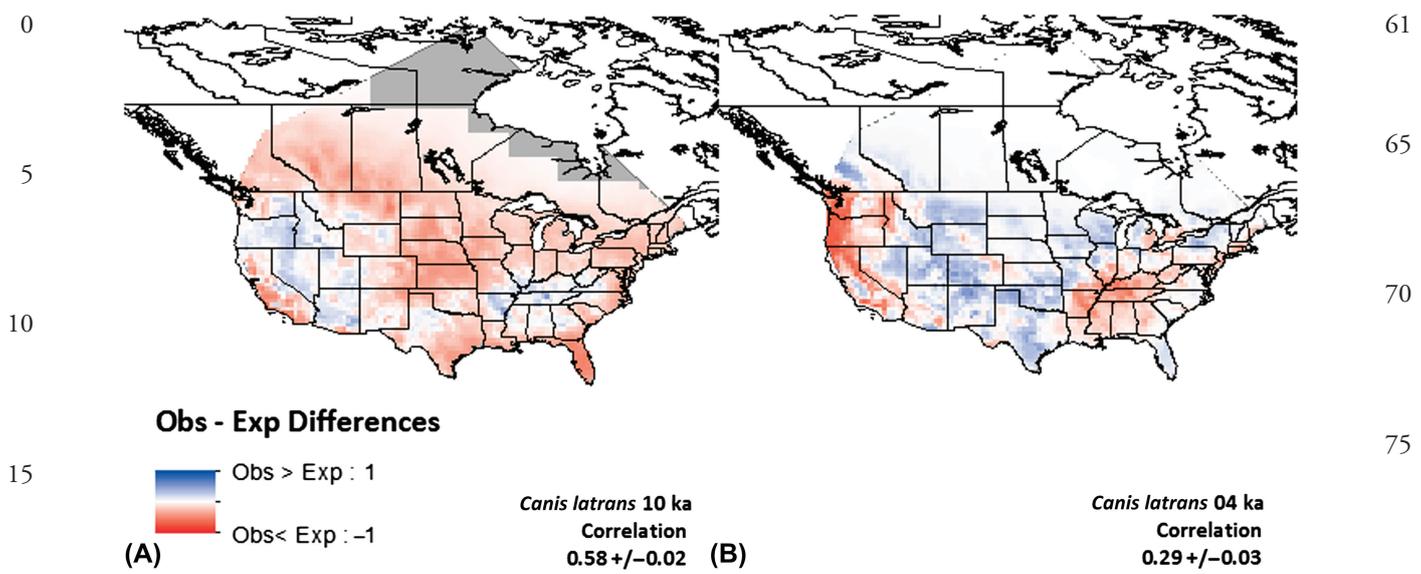


Figure 5. Differences between expected and observed likelihood values for *Canis latrans*. (A) the Early–Middle Holocene (10 kyr BP) and (B) the Late Holocene (4 kyr BP). The expected model was subtracted from the observed: positive values, blue, indicate that the expected underpredicted the observed likelihoods (niche expansion), negative values, red, indicate that the expected overpredicted the observed likelihoods (niche contraction). Pearson correlation coefficients are given in each panel between the observed and the expected, with 95% confidence intervals.

Early–Middle Holocene, for all species modeled. We find this pattern despite a relatively more stable climate throughout the Holocene than across the Pleistocene–Holocene boundary.

Interspecific correlations

Observed interspecific overlap decreases for species pairs throughout the Holocene, with a few exceptions. In several cases abiotic conditions alone would predict increased overlap, but the observed value trends in the opposite direction than expected. However, in the Early–Middle Holocene, the correlation between *Canis lupus* and *Vulpes vulpes* is expected at 0.63 +/- 0.02 and observed at 0.64 +/- 0.02 (Fig. 7, middle column). Likewise, during this same time, the correlation between *Canis latrans* and *Vulpes vulpes* is expected at 0.57 +/- 0.02 and is observed at 0.58 +/- 0.02. By the Late Holocene, all species pairs are observed at lower correlations than expected.

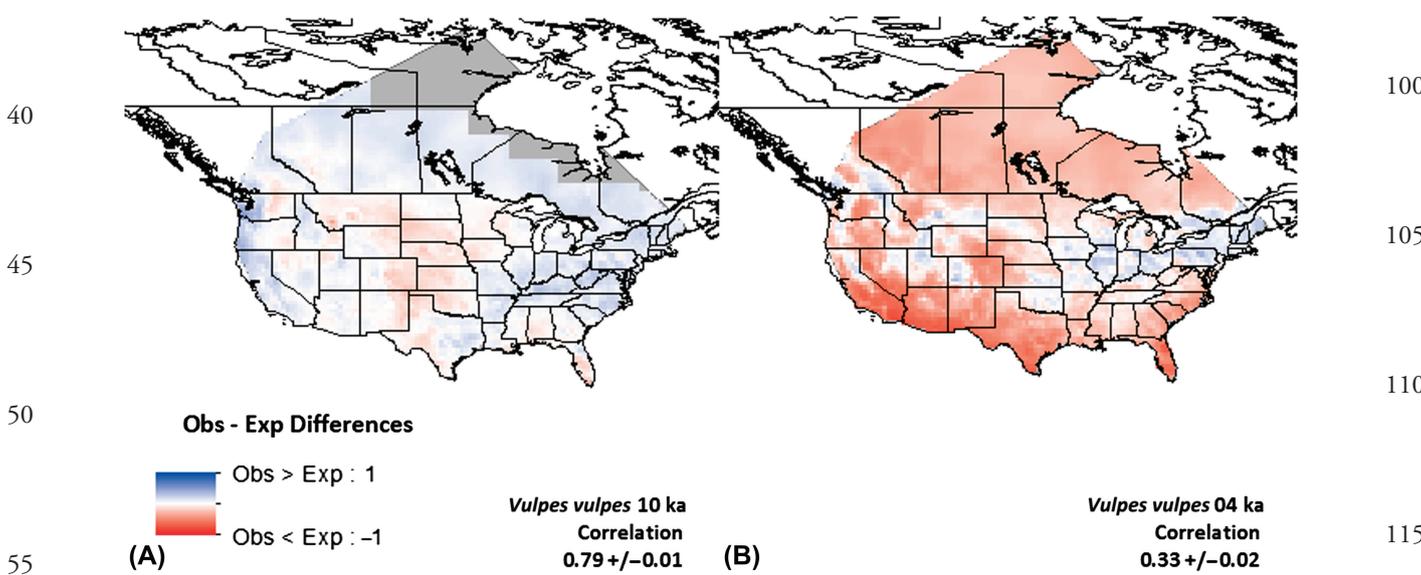


Figure 6. Differences between expected and observed likelihood values for *Vulpes vulpes*. (A) the Early–Middle Holocene (10 kyr BP) and (B) the Late Holocene (4 kyr BP). The expected model was subtracted from the observed: positive values, blue, indicate that the expected underpredicted the observed likelihoods (niche expansion), negative values, red, indicate that the expected overpredicted the observed likelihoods (niche contraction). Pearson correlation coefficients are given in each panel between the observed and the expected, with 95% confidence intervals.

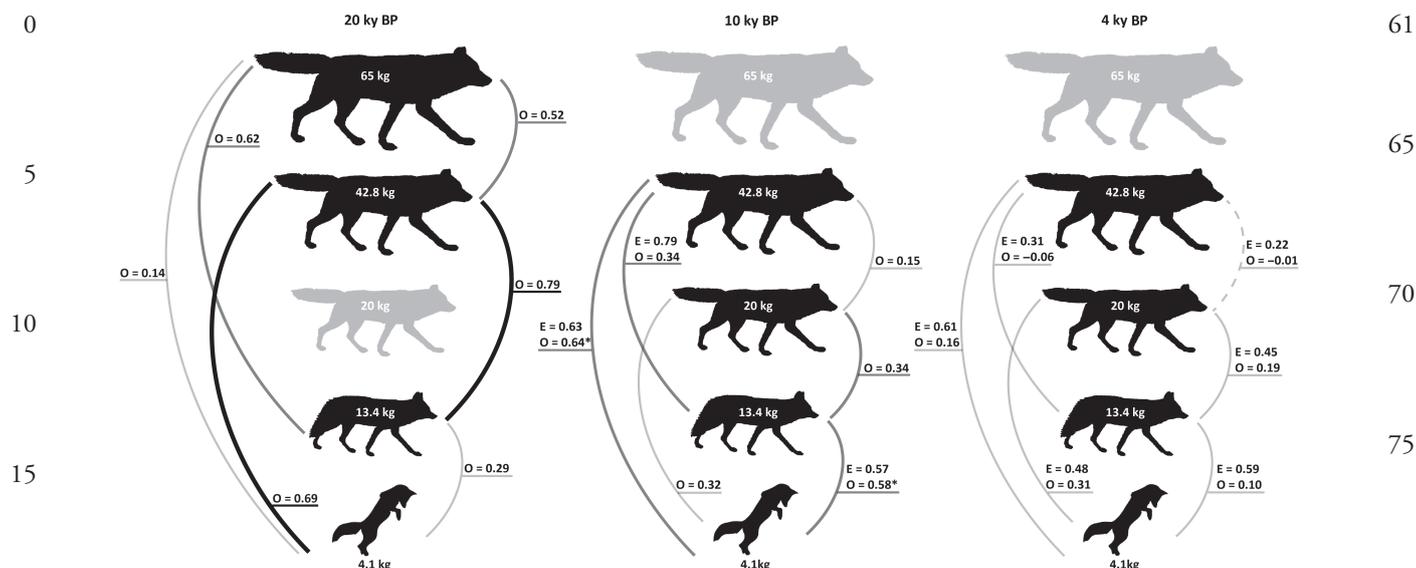


Figure 7. Interspecific correlations across study periods. Pearson correlation coefficients are given. For clarity, 95% confidence intervals are omitted but are included where referenced in the text. All correlation values are significant unless otherwise specified. Lines are shaded and bolded according to the strength of the observed correlation; observed values not statistically different from zero are dashed. * indicates that the observed and expected overlap are not statistically different. Body size estimates for endemic species come from Smith et al. 2003b. Estimates for domestic dog, averaged around 20 kg, are based on that of the dingo (Allen et al. 2013) and is included as a point of reference, not as a definitive assessment of size. Shaded figures indicate that a species was not present for a given analysis.

Discussion

Our findings indicate that interactions among survivors within the canid community dramatically changed after the end Pleistocene event. Overall, species changed their spatial distribution, but did not track climatic niche space (Fig. 3–6), which suggests a role for changing biotic interactions within the community. Additionally, we identify a net increase in niche partitioning among surviving canids after the Pleistocene that is independent of climate (Fig. 7), following the extirpation of their largest competitors.

Niche changes occurred individualistically across species, with the timing of changes varying across body size of endemics. The two larger species, *Canis lupus* and *Canis latrans*, decreased their observed niche in the Early–Middle Holocene (Fig. 3A and Fig. 5A, larger red area), where as *Vulpes vulpes* exhibited a niche that was somewhat larger than expected (Fig. 6A, larger blue area), suggesting the immediate effects of the extinction provided slight niche release for foxes. In the Late Holocene, *Canis lupus* and *Canis latrans* shifted their niches, but the overall extent of the observed was similar to the expected (Fig. 3B and 5B). *Vulpes vulpes*, on the other hand, dramatically reduced the extent of the observed niche by (Fig. 6B, red regions). The immediate effects of the End Pleistocene event appear to have greater impacts on larger species, but over the long term impacted smaller bodied species as well.

We are confident that the lack of niche conservatism we find across species is a real biological pattern and not a quirk of the climatic variables used in our niche models. The CCSM3 was also employed in the species distribution models constructed by Veloz et al. 2012; similar to our findings, they observed a lack of niche conservatism in several Late Quaternary North American plant genera. The

conclusions of their study were statistically robust to both the transient version of the CCSM3 (Liu et al. 2009) and the Hadley Center general circulation model (HadCM3) (Singarayer and Valdes 2010). Our results are, therefore, consistent with other niche models for species of differing taxonomic and trophic groups, as well as a broader scope of literature which has concluded carnivores may be more strongly impacted by biotic interactions than abiotic factors (McNab 1971, Geist 1987, Meachen and Samuels 2012, Veloz et al. 2012).

Our results may appear to be at odds with previous studies which have concluded that niches are stable over ecological time periods (Ricklefs and Latham 1992, Holt 1996, Holt and Gomulkiewicz 1997, Peterson et al. 1999, Martínez-Meyer et al. 2004, Huntley et al. 2010), however this is not the case. We have modeled a small subset of the entire vertebrate fauna: just the Canidae. Prior work attempting to test for niche conservation, likewise, has tested for conservatism in subsets of taxa. For example, Martínez-Meyer et al. 2004 concluded that niches were stable throughout the Late Quaternary via an analysis of 23 extant mammal species, with the following exceptions: *Ochotona princeps*, *Castor canadensis*, *Canis latrans*, *Ursus americanus*, and *Lynx rufus* (Martínez-Meyer et al. 2004). Three out of the five of these species are both 1 species with broad ranges and 2 carnivores. Furthermore, Martínez-Meyer et al. 2004 used a different metric for niche stability, but they too found a lack of conservation in *Canis latrans*. Unlike our study, they did not analyze *Canis lupus* or *Vulpes vulpes*. Our results are therefore not at odds with other studies, because we make no claim about the niche stability of species we did not analyze. However, our study is part of a growing body of research that suggests care should be taken in making assumptions of niche conservation, especially while making predictions

0 about the future distribution of species in the face of global
climate change (Davis et al. 1998, Veloz et al. 2012).

The differing biogeographic histories of the three largest
canids in our study system may help explain the patterns we
observe from our niche modeling approach. Unlike *Canis*
5 *dirus* and *Canis latrans*, which are long time endemics in
North America with a history of interaction, *Canis lupus*
was a relative newcomer to the scene in the Late Pleistocene
(Merriam 1912, Dundas 1999). *Canis lupus* occurred in low
densities relative to *C. dirus* during the Late Pleistocene,
10 and their numbers increase following the extinction of *C.*
dirus (Merriam 1912). *Canis latrans* was larger during the
Pleistocene and would have been similar in size to *C. lupus*
when it initially expanded into North America (Meachen
and Samuels 2012, Meachen et al. 2014), so these two spe-
15 cies may have initially been competing more directly for
resources. The increased abundance of a competitor with
a similar dietary niche may have promoted partitioning of
resources by *C. latrans* and induced a shift in its niche dur-
ing the Holocene. This hypothesis is consistent with other
20 studies that identify body size reduction and morphologi-
cal changes towards omnivory in coyotes in the Holocene
(Meachen and Samuels 2012, Meachen et al. 2014). These
are physical responses that might be expected in a species that
is drastically changing its niche and ecological function.

In this study we asked whether the niches of endemic
North American canids were conserved following the end
Pleistocene event. We find that niches were not conserved
for any of the species we analyzed. Correlation values
between the expected and observed likelihoods of occur-
30 rence decreased through time, indicating that the climatic
niche became less predictable through the Holocene. In par-
ticular, wolves dramatically changed their niche during the
Holocene and hence, the likelihood of occupancy became
highly unpredictable. There is a weak but significant nega-
35 tive correlation between where wolves are expected in the
Late Holocene and where they actually occur (Fig. 3B).
This differs significantly from the Early–Middle Holocene,
where the occurrence of wolves is more predictable despite
significant global climatic changes (Fig. 3A). The wolf niche
40 changed between the end of the Pleistocene and the Late
Holocene in a manner that is not explained by climate alone,
and this species had high likelihoods of occurrence in places
it was predicted to be rare or absent.

Overall guild structure changed over time after the largest
45 carnivore in our study, *Canis dirus*, went extinct, along with
the other megafauna. Interestingly, most endemic canids
were highly intercorrelated in the Pleistocene, except for the
relationship between *Canis dirus* and *Vulpes vulpes* (Fig. 7,
left column). These species may simply have been too eco-
50 logically dissimilar in resource use or body size to be inter-
acting significantly. Correlation values between all species
decreased in the Early–Middle Holocene. Linkages between
trophic levels disintegrated by the Late Holocene and overall
structure within the guild changed. These finding suggest an
55 overall restructuring of guild from the top down.

The relationship with domestic dogs was not uniform
across the canid community throughout the Holocene.
Niche correlations in the Early–Middle Holocene was low-
est between wolves and domestic dog. By the Late Holocene
60 both coyotes and red fox further separated their niches from
wolves, but niche overlap between foxes and domestic dogs
had not changed since the Early Holocene. The correlation
between wolves and dogs is not statistically different from
zero for the Late Holocene, which suggests that they were
not interacting. This is interesting considering domestic dogs
65 and wolves are, technically speaking, the same species.

Domestic dogs were likely very successful invaders of the
North American landscape. Despite being newcomers to the
carnivore community, they established a widespread niche
by the Early–Middle Holocene (Supplementary material
Appendix 2, Fig. A3). The complete lack of Late Holocene
70 interaction between wolves and dogs is distinct from the rela-
tionship between dogs and the other endemic canids (Fig. 7,
right column). This relationship developed over the course of
the Holocene. Interestingly, much like the rest of the endemic
75 canid species, dogs failed to have a Late Holocene observed
niche that was of the extent expected (Fig. 4). Despite favor-
able abiotic conditions and their relationship with humans,
they are also limited by biotic interactions.

The modeled distribution of *Canis lupus familiaris* may be
80 reflecting spatial patterns of human presence on the North
American landscape. Indeed, previous investigators have
utilized domestic dog fossils as a proxy for humans (Witt
et al. 2015). Observed likelihoods of *Canis lupus familiaris*
are greatest in the northeastern and northwestern regions of
85 the United States (Supplementary material Appendix 2,
Fig. A3). This pattern is qualitatively similar to the appar-
ent presence of humans; the greatest densities of archaeo-
logical radiocarbon dates also occur in greater abundance in
the northeastern and northwestern regions of the continent
90 (Peros et al. 2010). If this is indeed a true pattern, our analy-
ses indicate domestic dogs in a sense ‘defected’ from the wolf
niche in favor of what may be described as the human niche.
This may also explain why the observed and expected niche
of Late Holocene domestic dogs are not highly correlated.
95

The lack of association we find between wolves and
domestic dogs may speak to the intense competition between
humans and larger endemic carnivores. It may also reflect the
rapid rate in which dog domestication may have occurred, as
100 new research suggests there may have been multiple crosses
between dogs and wolves, as well as a possible second domes-
tication in North America (Witt et al. 2015). These observa-
tions are not at all surprising given that packs of wolves and
hunter gatherer societies obtain similar prey in a analogous
105 fashion, and similarity in group social structure may have
facilitated wolf domestication (Hall and Sharp 1978, Olsen
1985).

One of our most surprising outcomes from our analy-
ses was the relatively greater interconnectedness we found
within the late Pleistocene canid community relative to the
110 Holocene. This is, however, consistent with findings pre-
sented by other authors. Several carnivore species in the late
Pleistocene exhibit high frequencies of tooth breakage (Van
Valkenburgh and Hertel 1993, Binder and Van Valkenburgh
2010), implying a greater utilization of large prey, carcasses,
115 and bones. Such findings have been interpreted as evidence
for overall greater competition for food resources in the past.
Megaherbivore carcasses may have also been an important
source of food for smaller carnivores in Pleistocene com-
munities, facilitating scavenging by smaller carnivores and
120 promoting spatial overlap of multiple species (Pereira et al.

0	2014). Even in modern community ecology, the importance of scavenging is often overlooked and underappreciated (Selva et al. 2005, Wilson and Wolkovich 2011). Furthermore, the presence of megafauna, as in modern African communities, may have promoted the coexistence of a more diverse megacarnivore fauna (Sandom et al. 2013). The hunting of megafauna explains adaptive jaw structures and size in some Pleistocene carnivores (Van Valkenburgh and Koepfli 1993, Biknevicius and Van Valkenburgh 1996, Meachen-Samuels and Van Valkenburgh 2009, Meachen et al. 2014), and megaherbivore extinction explains the decrease we find in Early–Middle Holocene canid niche overlap.	61
5		65
10		70
15	Our models, like all niche models, only account for those aspects of the niche for which data are available. We have modeled only the abiotic aspect, but biotic interactions may be particularly important for defining the carnivore niche. They are no doubt responding to their own physiological tolerances, the location and availability of prey, as well as competition with other carnivores. The end of the Pleistocene caused major upheavals in both biotic and abiotic systems (Graham and Lundelius Jr 1984, Graham et al. 1996, Burney et al. 2003, Robinson et al. 2005, Gill et al. 2009, Rule et al. 2012, Doughty et al. 2013, Gill 2014). We do not, however, view this as a confounding issue for our study. Quantifying the environmental niche allows us to account for the expected changes due to climate fluctuations over the late Quaternary; deviations from expected responses likely reveal the influence of competition and/or resource availability. Where our models fail to predict a species' occurrence with only abiotic variables, we have identified potentially interesting changes with the biotic aspect of the niche.	75
20		80
25		85
30		90
	Conclusions	
35	Carnivores responded to both changes in climate and the megafauna extinction, but the biotic factors had a stronger net impact. Our modeling suggests that climatic change should have led to an increase in the overall area of suitable habitat, and potentially greater co occurrence of species if biotic interactions had remained constant. The removal of large carnivores should have reduced intraguild competition and also potentially led to range expansions. We find that the response was more complex and that shifts occurred across the canid guild, but the timing of the changes was species specific and probably related to body size or trophic level. Future stable isotope analyses of dietary niches could help resolve whether canids made these spatial shifts while maintaining their dietary habits, or if prey utilization changed. Stable isotopes would also reveal changing degrees of biotic overlap by quantifying interspecific resource use and overlap among sympatric carnivore species.	95
40		100
45		105
50		110
55	The end Pleistocene event changed both individual species' niches as well as interspecific relationships among species in the Canidae. Biotic changes likely played a large role in determining the geographic occurrences of these carnivores in the Holocene. This is supported by changes in the climatic niche of individual species. Greater niche separation during the Holocene changed overall guild connectivity between trophic levels, and likely altered ecological function in the carnivore community.	115
60		121
	The Holocene was characterized by the presence of introduced and novel competitors: humans and their domesticated dogs. The presence of humans on the landscape potentially impacted the realized niche and spatial distribution of endemic canid species. The apparent divergence between wolves and dogs occurred early on in the Holocene and intensified in the Late Holocene, during a time when the human population was rapidly increasing (Peros et al. 2010). Further study is needed to elucidate the nature of this relationship between man, dog, and wolf.	
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	Supplementary material (Appendix ECOG-01596 at < www.ecography.org/readers/appendix >). Appendix 1–2.		90
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