

Identifying drivers of historical genetic decline in an endemic Patagonian rodent, the colonial tuco-tuco, *Ctenomys sociabilis* (Rodentia: Ctenomyidae)

MAURO N. TAMMONE^{1,2*}, ULYSES F. J. PARDIÑAS¹ and EILEEN A. LACEY³

¹Instituto de Diversidad y Evolución Austral (IDEAus-CONICET), 9120 Puerto Madryn, Chubut, Argentina

²Programa de Estudios Aplicados a la Conservación del Parque Nacional Nahuel Huapi (CENAC-PNNH, CONICET), 8400 Bariloche, Río Negro, Argentina

³Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA

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Understanding the causes of pronounced losses of genetic diversity in natural populations may provide important insights into the evolutionary significance of these events. However, such analyses are typically based on post-reduction levels and patterns of variability in modern populations, which often lead to results that are biased towards more recent demographic events. In this context, population data recovered from the fossil record provide a powerful resource for studying historical processes of genetic decline. Using radiocarbon dating, stratigraphic analyses and DNA sequencing, we compared genetic variation and relative abundances of fossil specimens from the mid-Holocene to today to evaluate potential explanations for the marked historical loss of genetic diversity in the colonial tuco-tuco (*Ctenomys sociabilis*), a subterranean rodent that is endemic to Patagonia. We conclude that a general pattern of climatic change during the mid-Holocene, particularly changes in precipitation, led to changes in abundance of suitable habitats for this species. Loss of suitable habitat combined with the unusual demographic structure of this species may have facilitated the decline of populations of *C. sociabilis* by decreasing gene flow and increasing the potential for fixation of haplotypes due to genetic drift. Our analyses of temporal changes in abundance and genetic diversity in ctenomyids have implications for understanding more widespread patterns of Holocene change in the mammalian fauna of Patagonia.

ADDITIONAL KEYWORDS: competition – demographic history – environmental change – natural catastrophes – population decrease – tuco-tucos.

INTRODUCTION

Pronounced losses of genetic diversity within natural populations have important implications for both evolutionary and conservation biology (e.g. Lande, 1993; Lessa & Fariña, 1996; Brook *et al.*, 2008). For example, loss of genetic diversity may increase extinction risk (Lande & Shannon, 1996; Willi & Hoffmann, 2009), presumably due to the reduced genotypic variability available to respond to changes in environmental conditions (Bradshaw & Holzapfel, 2006; Chevin *et al.*, 2010). Loss

of genetic diversity may also impact the evolutionary trajectory of a population by altering the combination of genotypes present in future generations of individuals. In both contexts, the consequences of reduced genetic variability will be influenced by the nature and severity of the loss, each of which affects the post-reduction variability remaining in a population (Frankham & Kingslover, 2004). Accordingly, efforts to understand the causes of pronounced reductions in genetic variability in natural populations may provide important insights into the evolutionary significance of these events.

Identifying the factors contributing to reductions in genetic diversity can be challenging, particularly for historical declines or for those not associated with anthropogenic activities (Hofreiter, 2007). Under these

*Corresponding author. Current address: CENAC, Fagnano 244, 8400 SC de Bariloche, Argentina. E-mail: mtammone@gmail.com

conditions, inferences regarding the reasons for loss of genetic variation are typically based on post-reduction levels and patterns of variability (e.g. Collins *et al.*, 2014). The strength of these inferences is improved by direct comparisons of pre- and post-decline data, as exemplified by studies that contrast historical and modern genetic variability in taxa known to have experienced significant population declines (Campos *et al.*, 2010; de Bruyn *et al.*, 2011). When combined with information regarding changes in environmental conditions over the same time periods, such analyses can substantially enhance understanding of the reasons for pronounced declines in genetic variability.

Studies of the colonial tuco-tuco (*Ctenomys sociabilis*) provide an important opportunity to explore the factors contributing to a significant, naturally occurring decline in genetic variation. *Ctenomys sociabilis* is a group-living subterranean rodent whose current geographical distribution is restricted to a c. 700-km² area within Nahuel Huapi National Park, Neuquén Province, Argentina. While extant populations of this species are characterized by very limited genetic diversity (Chan *et al.*, 2005; Lacey, 2001), analyses of fossil specimens from three archaeological sites indicate that historical genetic diversity in this species was considerably greater (Chan *et al.*, 2005; Tammone *et al.*, 2017). Stratigraphic data from one of these sites suggest that loss of genetic diversity occurred 850–3300 years before the present (hereafter ybp; Chan *et al.*, 2005, 2006) and was associated with a marked decline in the relative abundance of *C. sociabilis* compared to its solitary congener *C. haigi* (Chan & Hadly, 2011; Tammone *et al.*, 2017). Previously proposed explanations for this decline and the concordant loss of genetic diversity include (1) eruption of the nearby Puyehue-Cordón Caulle (PCC) volcanic chain, (2) competitive exclusion by *C. haigi* and (3) broad-scale changes in the dynamic ecotonal environment in which *C. sociabilis* occurs (Chan *et al.*, 2005).

These scenarios generate distinct predictions regarding the spatial and temporal patterns of decline in genetic variability in *C. sociabilis*, suggesting that analyses of multiple archaeological sites located throughout the geographical distribution of this species can be used to elucidate the reasons for the historical loss of variability in these animals. Specifically, while a major volcanic eruption should have led to the simultaneous loss of genetic diversity throughout the geographical range of this species, both interspecific competition and broad-scale changes in environmental conditions are expected to have been more gradual and, potentially, more spatially heterogeneous. Competitive interactions, in turn, could only have occurred at a limited number of locations where the distributions of *C. sociabilis* and *C. haigi* are thought

to have overlapped; in contrast, more widespread changes in environmental conditions would probably have impacted all populations of *C. sociabilis*.

Using stratigraphic information, radiocarbon dating, and analyses of fossil and modern genetic diversity at multiple archaeological sites, we characterize the spatial and temporal patterns of loss of genetic diversity in *C. sociabilis*. In addition, we evaluate the ability of each hypothesis to explain the decline in genetic variability reported previously for this species (Chan *et al.*, 2005; Tammone *et al.*, 2017). To explore the effects of reported Holocene climatic changes (e.g. Markgraf *et al.*, 2002; Iglesias *et al.*, 2017) on the study species, we use ecological niche models generated from extant localities for *C. sociabilis* and *C. haigi* to predict the distributions of these animals under historical climate scenarios. In addition to characterizing the genetic history of *C. sociabilis* in greater detail, our results generate important new insights into how environmental conditions, ecology and demography interact to promote loss of genetic diversity in natural populations of vertebrates.

MATERIAL AND METHODS

STUDY SITES AND SAMPLE COLLECTION

Data were obtained from fossil specimens of small mammals recovered at three archaeological sites located in the Limay Valley region of south-western Argentina: Arroyo Corral (ACo), Cueva del Caballo (CdC) and Cueva Trafal (CTI; Fig. 1). Small mammal remains at these sites were deposited primarily by barn owls (*Tyto alba*); analyses of owl pellets are a powerful and relatively standard method for inferring changes in faunal assemblages across time periods (see Andrews, 1990; Terry, 2010). Stratigraphic and carbon dating analyses of associated excavations indicated that the fossil mammal materials recovered ranged in age from c. 12 000 ybp to the present (Tammone *et al.*, 2017). Detailed characterization of each site as well as complete descriptions of the procedures used to collect samples and to identify fossil specimens of *Ctenomys* to species are provided elsewhere (Hajduk *et al.*, 2007; Chan & Hadly, 2011; Tammone *et al.*, 2014, 2017).

Each archaeological site was paired with a modern locality from which tissue samples were obtained from extant populations of *Ctenomys*. The extant localities sampled were La Lonja (LL; paired with ACo) and Valle Encantado (VE; paired with CdC); because CTI occurs at the apparent intersection of the historical distributions of the two study species, the nearest extant localities of each species were paired with this site (*C. sociabilis*: Cerro Monte Redondo, CMR; *C. haigi*: Rio Trafal, RT; Fig. 1). Animals in extant

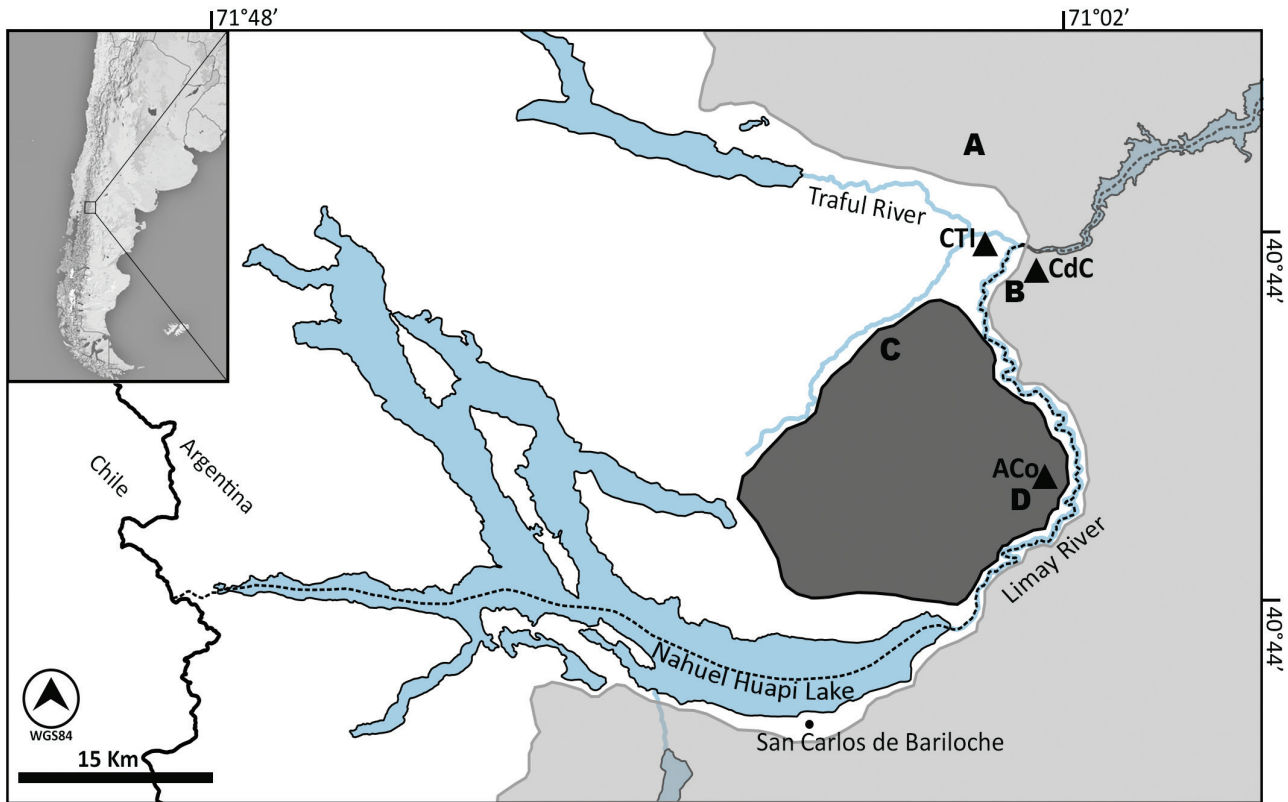


Figure 1. Map of the study area. The current geographical range of *Ctenomys sociabilis* is shown in dark grey while that of *Ctenomys haigi* is shown in light grey. Triangles denote the locations of the cave sites examined: Arroyo Corral (ACo), Cueva del Caballo (CdC) and Cueva Trafal I (CTI). Fossil specimens of *C. sociabilis* were present at all three sites, while fossil specimens of *C. haigi* were present only at CdC and CTI. Letters indicate the locations of the extant populations of tuco-tuco samples: (A) Río Trafal, (B) Valle Encantado, (C) Cerro Monte Redondo and (D) La Lonja. Data for CTI were obtained from Chan *et al.* (2005, 2011).

populations were identified to species based on a number of ecological, behavioural and pelage features that distinguish *C. sociabilis* and *C. haigi* (Tammone *et al.*, 2016b). Individuals in these populations were live-trapped and non-destructive tissue samples were obtained following the methods of Lacey (2001) and Cutrera *et al.* (2005), after which the animals were released at the point of capture. Genetic analyses of tissue samples (see below) were used to confirm species identifications made in the field.

STRATIGRAPHY AND DATING OF SAMPLES

To generate data regarding the ages of the stratigraphic levels present at ACo and CdC, 11 of the fossil specimens included in our analyses of genetic variation (see below) were subjected to radiocarbon dating at the AMS Laboratory at the University of Arizona. A total of 28 radiocarbon values – the 11 ctenomyid samples plus 17 reference samples of charcoal or bones from other mammalian taxa

(Supporting Information, Appendix S1) – were generated; these data encompassed the full stratigraphic range of each fossil site. The stratigraphic profile for each site was constructed using age–depth chronological models, as implemented in the R package Clam 2.2 (Blaauw, 2010). Additional details regarding radiocarbon dating of fossil materials from the study sites, calibration of these dates and age–depth modelling are provided in Tammone *et al.*, (2017). Radiocarbon dates for the CTI site were obtained from Chan & Hadly (2011). Radiocarbon-validated dates are reported as 95.4% confidence-calibrated ages in years bp (before present = AD 1950). These values incorporate the standard deviations associated with each radiocarbon estimate of sample age as well as standard calibrations applied to radiocarbon estimates (Bronk Ramsey, 2009). To facilitate comparisons across study sites, we used the midpoint of the probability distribution of each calibrated sample as the estimated age of that sample.

MITOCHONDRIAL DNA SEQUENCING OF SPECIMENS

Genetic variation in fossil and modern samples was assessed based on a 136-bp segment of the mitochondrial cytochrome *b* (*cyt b*) locus. The *cyt b* haplotypes analysed were obtained from Chan & Hadly (2011) and Tammone *et al.*, (2017) and included 114 fossil samples (ACo: $N = 12$; CdC: $N = 37$; CTI: $N = 65$) as well as 36 modern samples (LL: $N = 9$, RT: $N = 10$; VE: $N = 8$; CMR: $N = 9$). The *cyt b* sequences for fossil samples were generated following strict extraction and PCR protocols for ancient DNA as described in Cooper & Poinar (2000) and Chan *et al.* (2005). These included physical isolation of lab areas, multiple independent amplifications of ancient DNA extracts, and use of extraction and PCR-negative controls (Tammone *et al.*, 2017). Amplicons were sequenced by Elim BioPharmaceuticals (Hayward, CA, USA). All amplicons were sequenced in both directions to minimize the potential for erroneous reads (Hofreiter *et al.*, 2001). Sequence editing and alignment were performed using Sequencher (v.3.1.1, Gene Code Corporation, Ann Arbor, MI, USA). The resulting ancient sequences were identified as either *C. sociabilis* ($N = 60$) or *C. haigi* ($N = 54$) via (1) comparisons with complete *cyt b* sequences for these species available in GenBank and (2) neighbor joining analyses of modern and fossil haplotypes (Tammone *et al.*, 2017). In all cases, ancient sequences were unambiguously assigned to one of the two focal species. Modern *cyt b* sequences were generated as described by Tammone *et al.* (2017); all modern sequences unambiguously confirmed the species identifications made at the time that animals were captured in the field (*C. sociabilis* at LL and CMR; *C. haigi* at RT and VE).

HAPLOTYPE VARIATION AND RELATIVE SPECIES ABUNDANCE

For each fossil site, the number of *cyt b* haplotypes recovered per stratigraphic level and the relative frequency of each variant were calculated using the R script TempNet v.1.4 (Prost & Anderson, 2011). For each stratigraphic level, we estimated the relative abundance of *C. sociabilis* and *C. haigi* in two ways. First, we determined the per-level percentage of all ctenomyid specimens ($N =$ the minimum number of individuals – MNI; Grayson, 1984; Lyman, 2008) consisting of *C. sociabilis* or *C. haigi* based on the proportion of samples sequenced for that level that were assigned to each species. Second, we used the same sequence identities to estimate the per-level percentage of all small mammal remains ($N =$ MNI for all fossils recovered) assigned to each focal species. The first of these methods provides information regarding changes in the abundances of the *Ctenomys* species relative to

each other while the second captures changes in the abundance of *Ctenomys* relative to all small mammals recovered in our fossil deposits. Additional information regarding these analyses is provided in Tammone *et al.* (2017).

ECOLOGICAL NICHE MODELS

To explore how environmental changes from the mid-Holocene to the present may have affected the geographical distributions of *C. sociabilis* and *C. haigi*, we constructed ecological niche models (ENMs) for each species based on modern and projected historical conditions in the Limay Valley. Modern models were based on 19 climatic variables downloaded from the WorldClim database (<http://www.worldclim.org/>; Hijmans *et al.*, 2005) at a resolution of 30 arc-seconds (~1 km). For mid-Holocene (c. 6000 ybp) climate projections, we used the general circulation models (GCMs) contained in MIROC-ESM 2010 (Watanabe *et al.*, 2011) to estimate values for the 19 WorldClim variables relative to current climate conditions in the study region.

Species occurrence data were obtained from our field studies and from records contained in the GBIF database (www.gbif.org); these sources resulted in 80 records for *C. sociabilis* and 110 records for *C. haigi*. ENMs were generated in MaxEnt (3.3.3k) (Phillips *et al.*, 2006), which has been shown to perform as well as or better than other modelling strategies when using presence-only records of species occurrence (Elith *et al.*, 2006; Hernandez *et al.*, 2006). To reduce over-fitting and the complexity of our models, for each species and time period we performed a variable reduction step (jackknife analysis using MaxEnt default settings) that resulted in the removal of any climatic variables contributing < 1% to the overall model output. Final models were run using MaxEnt default settings with the following exceptions: we set the regularization multiplier to 2 and the feature classes to linear, quadratic and hinge to produce simpler, smoother and more realistic model outputs (Radosavljevic *et al.*, 2014; Shcheglovitova & Anderson, 2013). Ten replicate models were run for each species and time period; for each run, species occurrence records were resampled via bootstrapping, with 75% of records used as a model-training dataset and the remaining 25% used to test the resulting model. For each set of ten models, we generated a habitat suitability score (value = 0 to 1) using the average of the logistic output score for each model. To assess overall model performance, we calculated the mean for the area under the receiver operating characteristic curve (AUC) obtained for each replicate model (Phillips & Dudík, 2008).

RESULTS AND DISCUSSION

HOLOCENE CHANGES IN GENETIC DIVERSITY AND RELATIVE ABUNDANCE

Consistent with previous analyses of the study species (Chan *et al.*, 2005; Tammone *et al.*, 2017), we detected a pronounced loss of haplotype diversity in *C. sociabilis* at each of the three archaeological sites examined. In contrast, no comparable loss was detected for *C. haigi* at the two sites (CdC, CTI) at which this species occurred (see Tammone *et al.*, 2017). This difference in pattern of genetic change over time was associated with a marked decline in the relative abundance of *C. sociabilis* at all of the fossil sites examined. In contrast, *C. haigi* experienced an increase in relative abundance at CdC and CTI; no fossil samples of this species were detected at ACo (Fig. 2).

HYPOTHESIS 1: VOLCANIC ERUPTION

The Nahuel Huapi region of northern Patagonia – which includes the Limay Valley – has experienced a long history of volcanic activity, as revealed by

predominantly andisol soils resulting from the deposition of volcanic ash (Villarosa *et al.*, 2006; Corbella & Lara, 2008; Daga *et al.*, 2010). Most of these deposits – particularly those occurring north of Lago Nahuel Huapi – have been attributed to the PCC volcanic complex in eastern Chile. This complex has erupted multiple times since the Last Glacial Maximum in Patagonia (18–20 ka bp), most recently in 2011 (Gerlach *et al.*, 1988; Collini *et al.*, 2013). Ash from these eruptions has repeatedly covered the geographical distribution of *C. sociabilis* and parts of the distribution of *C. haigi* (Fig. 3).

One prominent layer of ash in this region is the pebble-sized Nahuel Huapi Tephra (NHT; Auer, 1960; Laya, 1977; Crivelli Montero & Silveira, 1983). Isopach analyses identify the PCC complex as the source of this layer, with an estimated ash fall of 0.2 m at CTI (Crivelli Montero *et al.*, 1993; Villarosa *et al.*, 2006; Fig. 3). Radiocarbon dating indicates that the NHT was deposited *c.* 2050–2350 cal ybp (Villarosa *et al.*, 2006), which is roughly concordant with the loss of genetic variability reported for *C. sociabilis* at CTI (*c.* 2600 ybp; Chan *et al.*, 2006). This similarity in dates

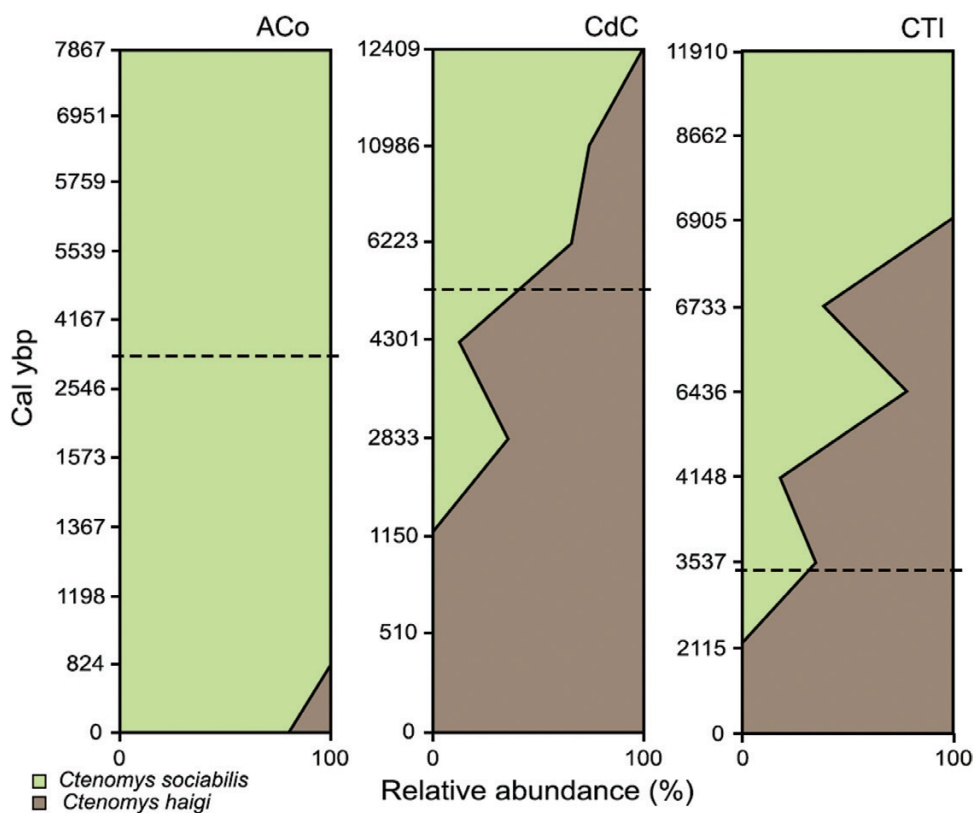


Figure 2. Relative abundances of *Ctenomys sociabilis* (green) and *Ctenomys haigi* (brown) at each study site (ACo, CdC, CTI). The proportion of each species was determined from fossil specimens for which *cyt b* sequences were generated; the total number of individuals sampled was determined via MNI analyses. Dashed lines denote the estimated timing of loss of haplotype diversity in *C. sociabilis* at each site.

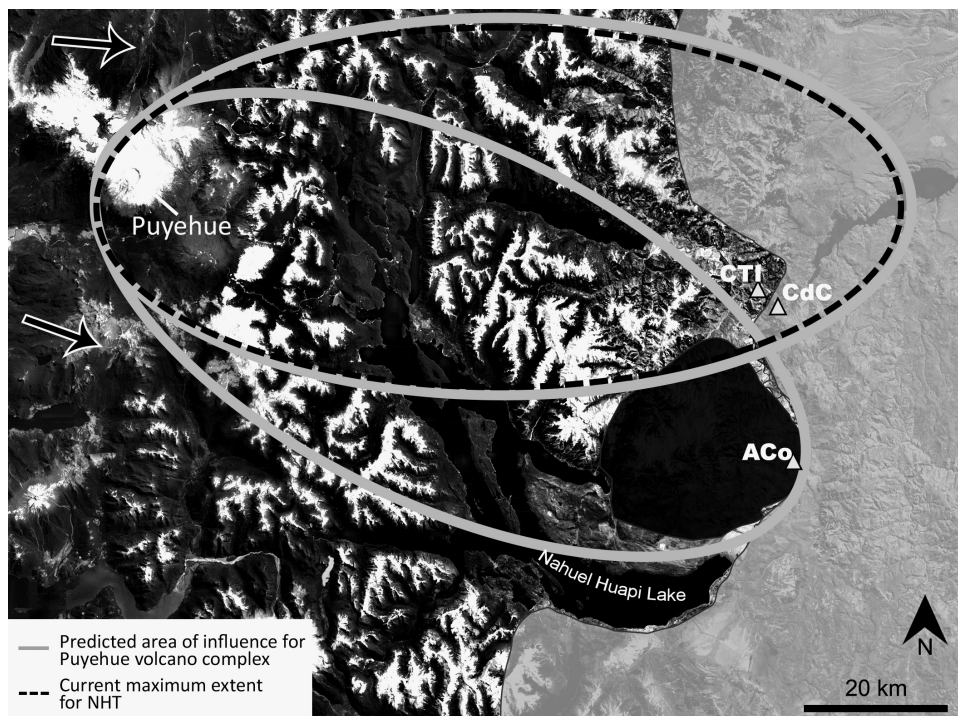


Figure 3. Predicted zone of ash fall for the Puyehue-Cordón Caulle volcanic complex relative to the distributions of the two study species; the distribution for *Ctenomys sociabilis* is shown in dark grey and that for *Ctenomys haigi* in light grey. The estimated ash fall from the eruption that produced the Nahuel Huapi Tephra (NHT) layer (*c.* 2600 ybp; dashed line) is shown relative to the locations of the three sampling sites. Arrows denote dominant westerly winds (figure adapted from Villarosa *et al.*, 2006).

and the documented impacts of volcanic eruptions on other species of *Ctenomys* (Pearson, 1994; Gallardo *et al.*, 1996) led Chan *et al.* (2005) to suggest that eruption of the PCC complex may have triggered the loss of genetic diversity detected for *C. sociabilis* at CTI.

If this hypothesis represents a general explanation for loss of diversity in *C. sociabilis*, then the abrupt and geographically widespread effects of this eruption should have resulted in concordant declines in genetic diversity in this species at all sites examined. In particular, given the projected distribution of ash from the NHT event (Fig. 3), the close proximity of sites CTI and CdC in the area of greatest tephra deposition suggests that genetic declines should have occurred simultaneously at these sites. To test this prediction, haplotype diversity in *C. sociabilis* was examined relative to the estimated radiocarbon date for each specimen sequenced (Fig. 4; Appendix S2). These analyses indicated that the timing of changes in genetic diversity differed between study sites. Specifically, loss of genetic diversity at CdC (4301–6223 cal ybp) preceded that at either ACo (2546–4167 cal ybp) or CTI (< 3537 cal ybp) (Fig. 4). Although these data do not preclude the possibility that changes in genetic diversity occurred concurrently at ACo and CTI, the loss of haplotypes at CdC was clearly temporally distinct

from the other sites and pre-dated the eruption that produced the NHT (Fig. 4; Appendix S3). Thus, our data do not support the hypothesis that the loss of genetic diversity in *C. sociabilis* was associated with a single, catastrophic volcanic event such as deposition of the NHT.

HYPOTHESIS 2: COMPETITION WITH OTHER CTENOMYIDS

Sympatry among different species of tuco-tucos is thought to be rare, presumably due in part to competition among animals that share numerous ecological and life history traits (Reig *et al.*, 1990; Kubiak *et al.*, 2015). With regard to our study species, several aspects of the biology of *C. sociabilis* – notably the more limited geographical distribution, greater habitat specialization and comparatively limited movement of individuals among populations (Lacey & Wieczorek, 2003, 2004; Tammone *et al.*, 2012) – suggest that this species would be more likely than *C. haigi* to experience range contractions or local extinctions as a result of competition between these taxa. Such reductions in distribution and local abundance may, in turn, lead to loss of genetic diversity due to decreased effective population sizes and decreased migration (Lande, 1999). These expectations, in conjunction with the local extinction and

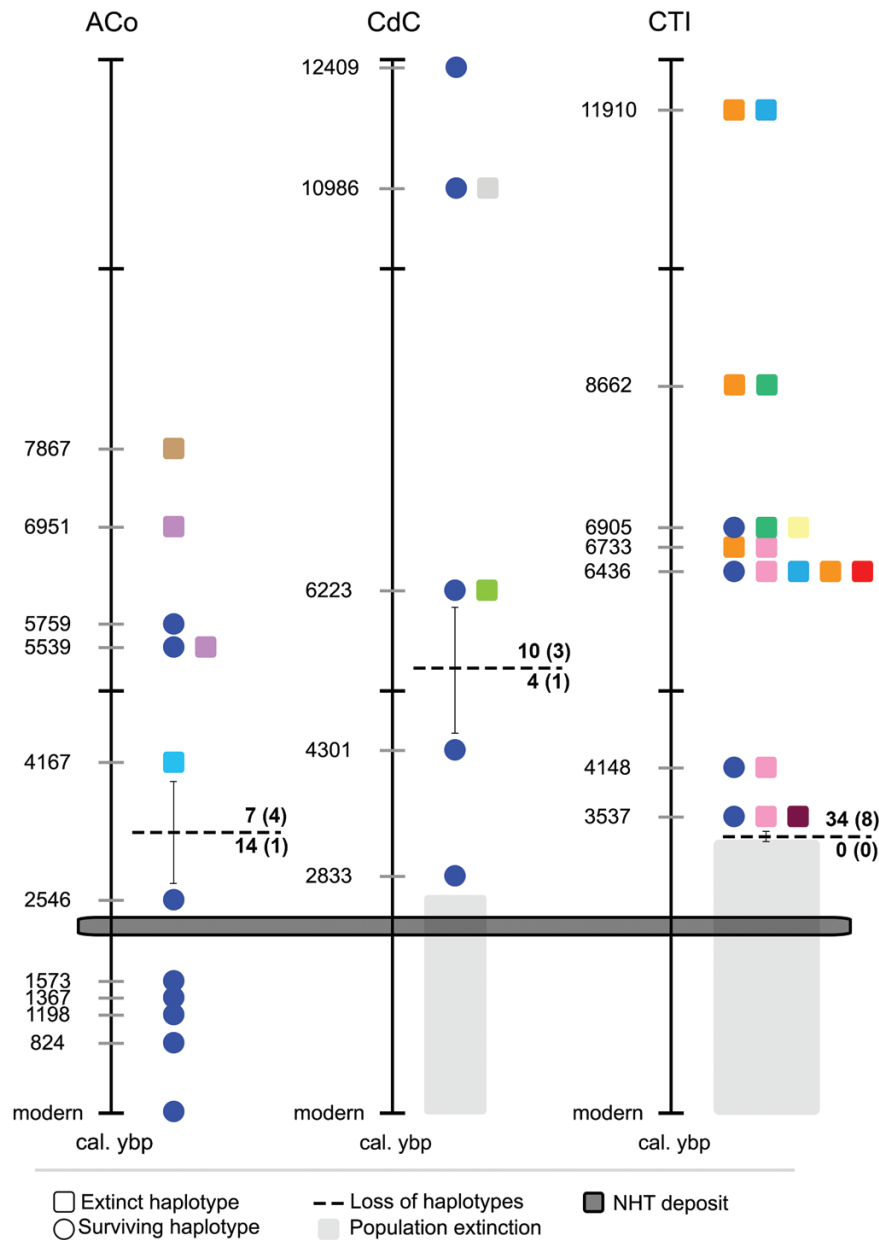


Figure 4. Timelines for declines in genetic variability in *Ctenomys sociabilis* at ACo, CdC and CTI. Each *cyt b* haplotype identified is depicted with a different colour. The number of distinct haplotypes detected at each stratigraphic level is indicated; radiocarbon dates for these levels are shown to the left of the timeline for each cave site. The timing of the deposition of the Nahuel Huapi Tephra (NHT) layer is indicated (dark grey horizontal rectangle), as is the apparent timing of the loss of haplotype diversity (dashed line) and local extinction (light grey rectangle) of *C. sociabilis* at each site. Numbers shown immediately above and below the dashed lines indicate the total number of specimens sequenced; the number of haplotypes detected in each sample is given in parentheses.

loss of genetic diversity in *C. sociabilis* at CTI, led Chan *et al.* (2005, 2006) to suggest that competition between *C. sociabilis* and *C. haigi* may also have contributed to the loss of genetic diversity in the former species.

If this hypothesis is correct, then declines in relative abundance and genetic diversity in *C. sociabilis* should

be evident only at localities at which this species co-occurred with *C. haigi*. Based on genetic identifications of ctenomyid remains (see also Chan & Hadly, 2011; Tammone *et al.*, 2017), both species were present historically at CTI and CdC (Fig. 2). In contrast, only *C. sociabilis* was detected in the fossil record recovered

from ACo. At both CTI and CdC, the relative abundance of *C. sociabilis* declined over the sampling period (Fig. 2), providing potential support for the proposed replacement of this species by *C. haigi*. Despite the historical absence of *C. haigi* at ACo, however, the same decrease in genetic diversity in *C. sociabilis* recorded at CTI and CdC was detected at this location (Fig. 4). Thus, the hypothesis that declines in genetic variation in *C. sociabilis* were driven by competitive interactions with *C. haigi* is not supported by our data.

HYPOTHESIS 3: ENVIRONMENTAL CHANGE

The ecotonal environment that characterizes much of the Nahuel Huapi region is complex and dynamic (e.g. Markgraf, 1983; Kitzberger, 2012). The study area sits at the interface between temperate cordilleran forest to the west and arid Patagonian steppe to the east, resulting in a mosaic of patches of each habitat type. This area is located within the rain shadow of the Andes and the resulting west to east rainfall gradient (–35 mm/km) contributes to pronounced changes in habitat over short distances (Markgraf, 1983; Ezcurra & Brion, 2005; Mermoz *et al.*, 2009; Bianchi & Ariztegui, 2011). In this setting, even relatively subtle changes in environmental conditions (e.g. precipitation, temperature) can have marked effects on the distributions of flora and fauna (Markgraf, 1983; Pearson, 1987; Monjeau, 1989; Pardiñas, 1999; Premoli, Kitzberger & Veblen, 2000; Heusser, 2003; Pardiñas & Teta, 2013; Iglesias *et al.*, 2014; Tammone *et al.*, 2014). These changes, in turn, may have produced direct (e.g. loss of suitable habitat) as well as more indirect (e.g. changes in predator regimes) effects on the study species, in particular the more ecologically specialized *C. sociabilis*, which is endemic to patchily distributed areas of open, more mesic grassland in these ecotonal habitats (Lacey & Wieczorek, 2003; Tammone *et al.*, 2012). The dynamic nature of this region combined with the documented ecological differences between the study species led Chan *et al.* (2005) to propose that gradual, broad-scale changes in environmental conditions during the Holocene may have more severely impacted *C. sociabilis*, contributing to the decline in genetic diversity in this species.

If this hypothesis is correct, then the gradual nature of the proposed environmental changes in conjunction with the mosaic distribution of habitat types suggests that declines in relative abundance and genetic diversity in *C. sociabilis* would probably have varied temporally among cave sites but would not have been limited to locations at which the two study species co-occurred. As indicated above, the timing of these declines differed among sites, with loss of genetic diversity occurring first at CdC, probably followed by ACo and then CTI (Fig. 5; Appendix S3). Relative to these declines, the timing of local extinctions of *C. sociabilis* at CdC

and CTI also differed, with a considerably greater lag between loss of diversity and local extinction at CdC (~ 3000 years) compared to CTI (~ 1500 years), potentially due to differences in effective population sizes between sites. In contrast, despite the decline in genetic diversity at ACo, local extinction of *C. sociabilis* did not occur at this site (Fig. 5). Thus, of the three hypotheses proposed by Chan *et al.* (2005), our data on loss of genetic diversity in this species are most consistent with the temporal and spatial heterogeneity predicted by response to gradual environmental changes.

HOLOCENE ENVIRONMENTS IN THE LIMAY VALLEY

If gradual changes in environmental conditions were the primary factors underlying the observed declines in relative abundance and genetic diversity in *C. sociabilis*, then it should be possible to identify more specific environmental parameters that have differentially impacted the study species. Among the most obvious targets for investigation are changes in precipitation. Currently, *C. haigi* is widely distributed in the Nahuel Huapi region, occurring in both arid and mesic habitat patches (Lacey & Wieczorek, 2003). In contrast, *C. sociabilis* is restricted primarily to patches of mesic grassland habitat (Lacey & Wieczorek, 2003; Tammone *et al.*, 2012), suggesting that mid-Holocene changes in precipitation would have been more likely to impact the occurrence of this species.

To explore this prediction, we compared the estimated dates for declines in relative abundance and losses of genetic diversity in *C. sociabilis* to a reconstruction of summer precipitation during the Holocene (Markgraf *et al.*, 2002). Based on this reconstruction, mean summer precipitation increased markedly between 6000 and 8000 ybp, with wetter summer conditions continuing until at least 2000 ybp (Fig. 5). Pollen records obtained from multiple sites in Patagonia located between 41°S and 43°S indicate that this increase in summer precipitation was associated with pronounced changes in the interface between forest and grassland habitats, resulting in expansion of *Nothofagus* and *Austrocedrus* forests and contraction of more open Poacea- and Asteracea-dominated grasslands (Markgraf, 1983; Markgraf *et al.*, 2002; Bianchi & Ariztegui, 2011; Iglesias *et al.*, 2014). Thus, perhaps somewhat counterintuitively, increased precipitation during the mid-Holocene probably reduced the availability of grassland habitat suitable for *C. sociabilis*, particularly west of the Rio Limay where expansion of forested habitat should have been most extensive. In comparison, the impacts of this change on *C. haigi* may have been less pronounced due to both the greater habitat generality of this species and its extensive distribution to the east of the Nahuel Huapi region, both

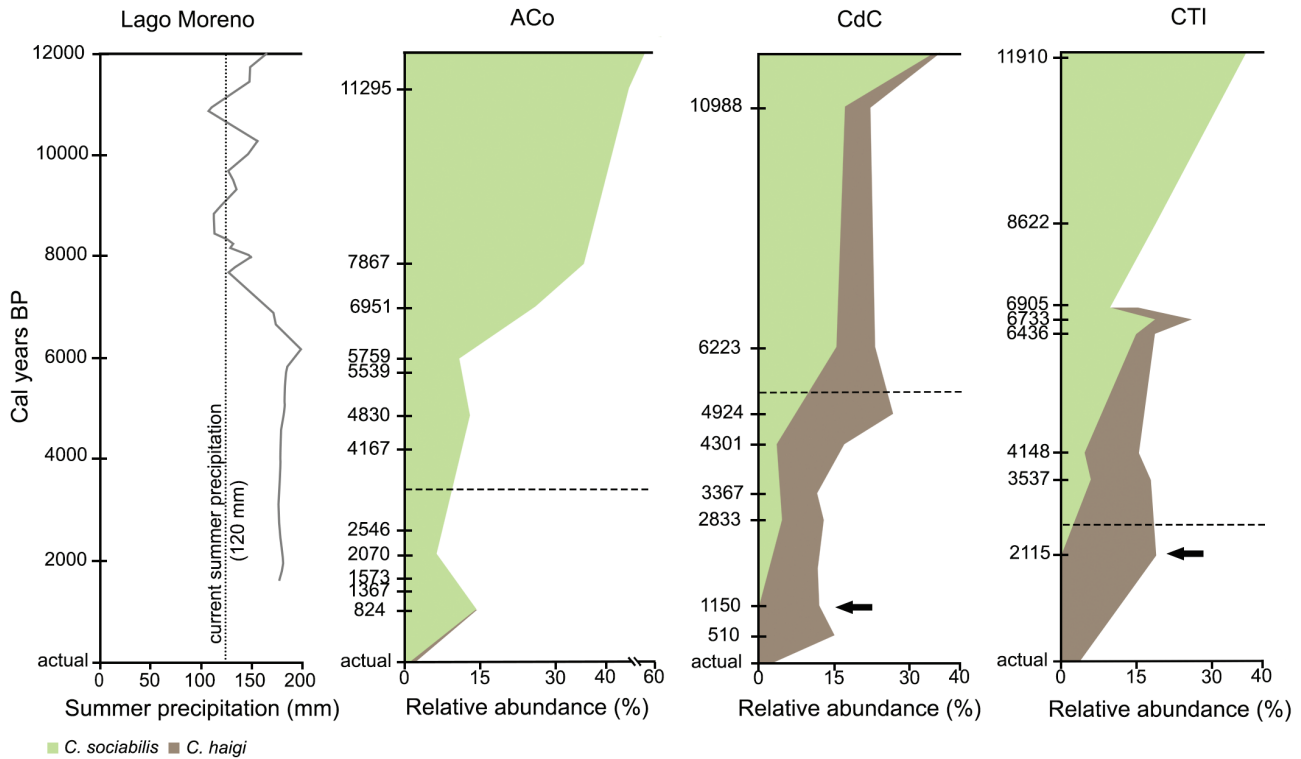


Figure 5. Changes in the abundances of the study species relative to mean summer precipitation in northern Patagonia; the reconstruction of historical precipitation levels is adapted from Markgraf *et al.* (2002). Relative abundances of *Ctenomys sociabilis* and *Ctenomys haigi* at each study site (ACo, CdC, CTI) were determined based on fossil specimens for which *cyt b* sequence data were obtained; these data were used to estimate the abundance of each study species among all small mammal remains recovered at each site. Dashed lines denote the timing of loss of haplotype diversity in *C. sociabilis* at each site; arrows indicate the estimated dates of extinction for this species at CdC and CTI.

of which would probably have contributed to the preservation of larger and more connected populations of *C. haigi* relative to *C. sociabilis*.

NICHE MODELS: IMPACTS OF HOLOCENE CHANGES ON CTENOMYID DISTRIBUTIONS

To assess more directly the impacts of climatic variables – particularly precipitation – on the distribution of *C. sociabilis*, we compared ENMs generated for *C. sociabilis* and *C. haigi*. The final list of environmental variables included in these models and their relative contributions to habitat suitability scores are provided in Appendix S4. For all final models, performance AUC values were greater than 0.9 for both training and test data sets. These models revealed that for modern environments, precipitation during the coldest quarter of the year was the greatest single predictor of the expected distributions of both study species (Fig. 6; Appendix S4). Overall, precipitation variables accounted for a greater percentage of the predicted distribution of *C. sociabilis* (66.9%) than of *C. haigi* (57.0%). The importance of precipitation variables in mid-Holocene environments

was greater for both study species (*C. sociabilis*: 78.1%; *C. haigi*: 64.6%). Although the single greatest predictor for each species differed in mid-Holocene models, in both cases the most important variable was a measure of precipitation (Appendix S4).

Comparing the distributions of the study species revealed that for both modern and mid-Holocene models, more suitable habitat was available for *C. haigi* (Fig. 6). Across time periods, suitable habitat – areas with suitability scores > 0.5 – was less abundant for *C. sociabilis* during the mid-Holocene than today. The time period encompassed by our historical models (~ 6000 ybp) corresponds roughly to the start of the interval during which changes in relative abundance and genetic diversity occurred in *C. sociabilis*. Thus, the results of our ENM analyses are consistent with the hypotheses that (1) precipitation-related changes in habitat availability contributed to the declines in relative abundance and genetic diversity detected for *C. sociabilis*, and (2) the greater specialization of this species for mesic habitat patches contributed to the apparent interspecific differences in response to these environmental changes.

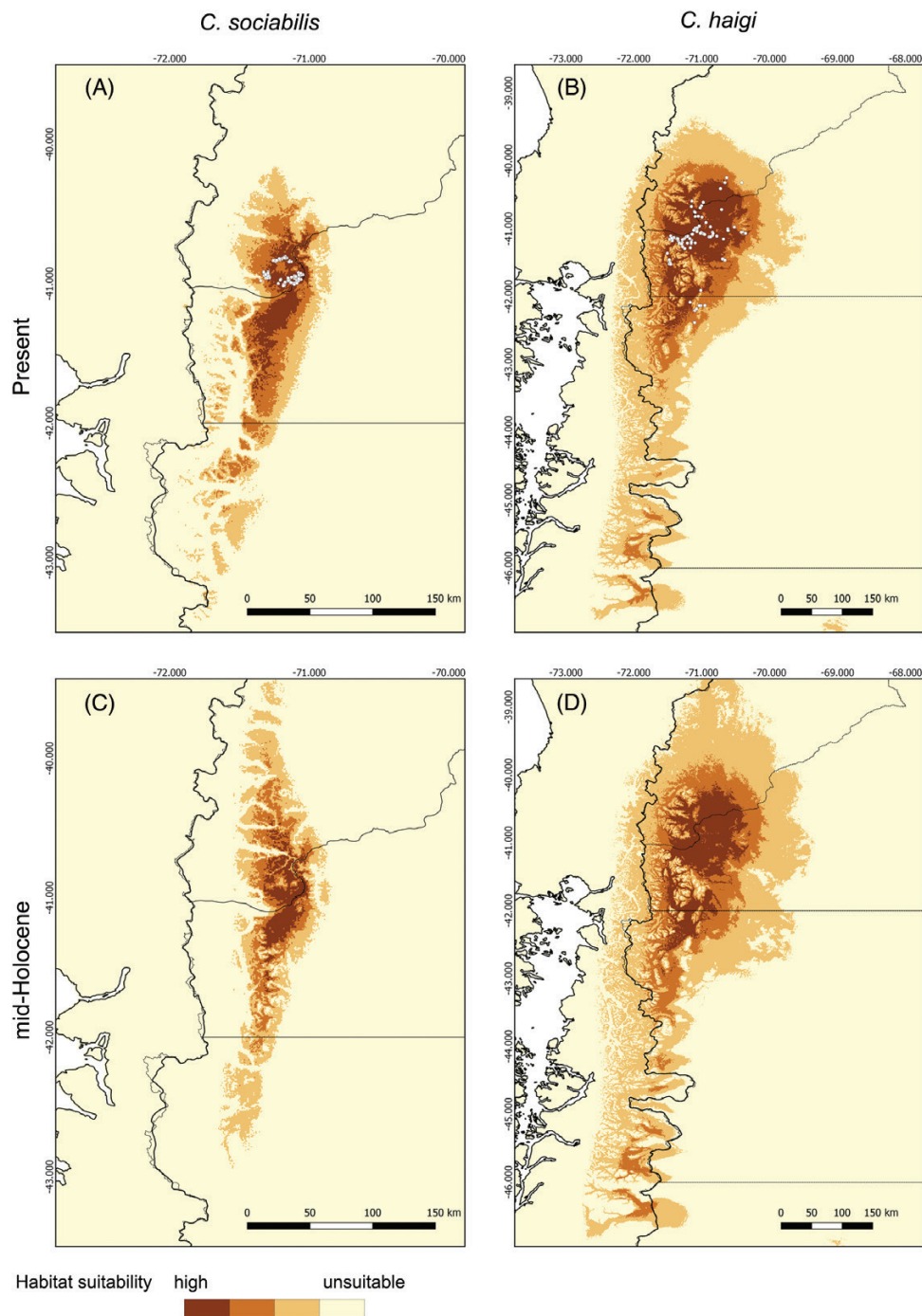


Figure 6. Results of ecological niche models constructed for *Ctenomys sociabilis* and *Ctenomys haigi*. Models were constructed in MaxEnt using modern occurrence data (white dots) for each species. Data on modern environmental conditions (A, B) were obtained from WorldClim (Hijmans *et al.*, 2005). Historical environmental conditions (C, D) were estimated following the procedure of Watanabe *et al.* (2011). Darker colours represent areas with a higher probability of species occurrence during each time period.

IMPACTS OF ENVIRONMENTAL CHANGES ON GENETIC DIVERSITY

The patchy distribution of the mesic grassland areas in which *C. sociabilis* occurs (Lacey & Wieczorek,

2003) suggests that as environmental conditions in the Nahuel Huapi region changed during the mid-Holocene, local populations of this species became more spatially restricted and isolated. Both changes are

expected to have facilitated loss of genetic diversity in this species by decreasing gene flow and thus increasing the potential for fixation of haplotypes due to genetic drift (Felsenstein, 1974; Frankham & Kingslover, 2004), processes that may have been reinforced by changes in geographical barriers (e.g. expansion of rivers during periods of increased precipitation), as has been reported for other subterranean rodents (e.g. Faulkes *et al.*, 2004; Visser *et al.*, 2014). These effects of greater habitat specialization may have been compounded by the demographic structure of *C. sociabilis*. Unlike most species of ctenomyids, *C. sociabilis* is group-living (Lacey *et al.*, 1997, 2000); social groups arise due to natal philopatry by females, with apparently limited migration of individuals between populations (Lacey & Wiczorek, 2004). In comparison, *C. haigi* is solitary (Lacey *et al.*, 1998); juveniles of both sexes disperse from their natal burrows and apparent rates of migration are higher than those for *C. sociabilis* (E. A. Lacey, unpublished data). These differences in demography and social structure are expected to increase further the potential for genetic drift and local fixation of haplotypes in *C. sociabilis* compared to *C. haigi*, thereby enhancing the predicted interspecific differences in response to changes in habitat availability. In sum, behavioural, demographic and ecological differences between the study species probably interacted with patterns of environmental change to produce the observed temporal patterns of change in relative abundance and genetic diversity. Future studies employing a landscape genetic framework (e.g. Mapelli *et al.*, 2012) should help to further clarify relationships among habitat use, demography and genetic diversity in the study species.

One puzzling aspect of the decline in genetic diversity in *C. sociabilis* is the presence of only a single *cyt b* haplotype in modern populations of this species. While historical populations of this species at CTI, CdC and ACo are characterized by multiple haplotypes – including private haplotypes not shared among localities (Fig. 4) – all extant populations of *C. sociabilis* contain only the same single haplotype (Chan *et al.*, 2005). Although increased opportunities for drift may have contributed to the loss of genetic variation in local populations of this species, this process should have led to the local fixation of different mitochondrial haplotypes (Kimura, 1983). While it is possible that the short fragment of *cyt b* examined here resulted in underestimation of genetic diversity in our historical samples, characterization of modern variation in *C. sociabilis* based on complete *cyt b* sequences also reveals only a single haplotype in all populations examined (Chan *et al.*, 2005; Tammone *et al.*, 2017). Alternative explanations for the retention of only a single haplotype in modern populations of this species include selection

on the *cyt b* locus (Da Silva *et al.*, 2009). Although this possibility has not been examined quantitatively, gradual changes in environmental conditions can substantially lower genetic diversity as populations adapt to novel habitat conditions (Jump *et al.*, 2006; Hoffmann & Sgro, 2011; Pauls *et al.*, 2013). If this scenario applies to *C. sociabilis* then the retention of multiple modern *cyt b* haplotypes in *C. haigi* suggests that despite their relatively close phylogenetic relationship and despite sharing the same general suite of habitats, the two study species have experienced different historical selective pressures. Clearly, further research is required to assess the potential role of selection or other evolutionary processes in the retention of only a single modern haplotype in *C. sociabilis*.

QUATERNARY EXTINCTIONS IN PATAGONIA

Our analyses of temporal changes in abundance and genetic diversity in ctenomyids from the Nahuel Huapi region have implications for understanding more widespread patterns of Holocene change in the mammalian fauna of Patagonia. Analyses of fossil deposits indicate that, in general, the second half of this epoch has been characterized by significant changes in the small mammal communities of this region, with a peak around the latest Holocene (e.g. Pearson, 1987; Pearson & Pearson, 1993; Fernández *et al.*, 2012, 2016; Pardiñas *et al.*, 2012; Pardiñas & Teta, 2013; Teta *et al.*, 2014). This includes evidence of range contractions, regional extinctions and population declines for several species of small mammals, ranging from marsupials to cricetids and caviomorph rodents (e.g. *Lestodelphys halli*, Formoso *et al.*, 2015; *Tympanoctomys kirchnerorum*, *Loxodontomys micropus* and *Notiomys edwardsii*, Pardiñas *et al.*, 2012; *Euneomys chinchilloides* and *E. mordax*, Pardiñas & Teta, 2013; Tammone *et al.*, 2016b; *C. sociabilis*, Tammone *et al.*, 2016a), but increases in the distributions and abundances of others (e.g. *Calomys musculinus*, *Eligmodontia* sp. and *Oligoryzomys longicaudatus*, Pardiñas *et al.*, 2000; de Tommaso *et al.*, 2014). In conjunction with faunal surveys conducted during the late 19th and early 20th centuries (e.g. Allen, 1903; Hatcher, 1903; Osgood, 1943) as well as recent field surveys of Patagonian small mammals (e.g. Pardiñas *et al.*, 2003, 2011; Formoso, 2013), these studies suggest that changes in local mammalian faunas – including local extinctions and species replacements – have been frequent (e.g. Pardiñas *et al.*, 2012; Teta *et al.*, 2014). The reasons for species-specific patterns of change are unknown and thus our analyses represent an important first step towards understanding the causal bases for temporal changes in ctenomyids and other rodent taxa. In particular, studies that combine analyses of fossil abundances

and ancient DNA variability with use of ecological and demographic niche modelling procedures (Hornsby & Matocq, 2012; Prost *et al.*, 2013) should prove useful for elucidating how environmental conditions intersect with species-specific ecological and demographic attributes to generate patterns of temporal change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

- Appendix S1.** Radiocarbon dates generated for the two cave sites characterized in this study.
- Appendix S2.** Fossil specimens of *Ctenomys sociabilis* examined.
- Appendix S3:** Estimated timing of loss of genetic diversity in *Ctenomys sociabilis*.
- Appendix S4.** Climatic variables included in final niche models for each study species.