Occupation of environmental and morphological space: climatic niche and skull shape in *Neotoma* woodrats

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ABSTRACT

Background: Theoretical and empirical studies suggest that in some circumstances niche evolution may be very slow – a phenomenon called 'niche conservatism'. Evidence for niche conservatism comes mainly from studies of niches whose axes are climatic variables with broad ranges of spatial covariance (coarse-grained niche variables). The geographic area inside the physiologically viable climatic extreme values (i.e. climate tolerances) is usually large and may expose populations to a wide range of finer-grained selective pressures.

Hypothesis: Coarse-grained niche variables lead to different evolutionary patterns than do finer-grained niche variables.

Data: Skulls from museum specimens of rats of the genus *Neotoma* provided data on lateral, ventral, dorsal, and mandibular aspects. Climate data were assembled for each place where a specimen had been caught.

Key assumption: Rats of the genus *Neotoma* respond to selective pressures that are coarse-grained in space, whereas their cranial dimensions respond to fine-grained selective pressures. The volume of a minimally enclosing ellipsoid in the principal component (PCA) space of either climatic or morphological variables is a surrogate for the species' breadth of occupation of climatic and morphological spaces.

Methods: We measured and analysed overall variance in climatic variables and morphology using geometric morphometry methods. We analysed ellipsoid volumes, together with summaries of skull shape and climatic tolerances, as to the influence of phylogeny on patterns of variation. And we also searched for contrasting patterns of morphological and climatic features.

Conclusions: Patterns in climatic and morphological variables were different. Climatic PC axes were mostly uncorrelated with morphological PC axes. Ellipsoid volumes of the climatic variables were significantly smaller than those of the morphological variables. Blomberg's *K* did show that the evolution of most of the PC axes (four morphological and three climatic) cannot be distinguished from Brownian motion. However the evolution of two PCs – the PC dominated by dryness and the one dominated by ventral view of the skull – have been restricted by phylogeny.

Keywords: fundamental niche, geometric morphometry, *Neotoma*, niche conservatism, North America, realized niche, skull.

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INTRODUCTION

Since the early 1990s, the idea of niche conservatism, *sensu lato*, has been a popular topic of research (Huntley *et al.*, 1989; Harvey and Pagel, 1991; Holt and Gomulkiewicz, 1997; Peterson *et al.*, 1999, 2011; Ackerly, 2003; Wiens, 2004; Wiens and Graham, 2005), with 300 papers identified using 'niche conservatism' as a search criterion in the Web of Science. The original application of the term niche (Harvey and Pagel, 1991; Harvey and Purvis, 1991) was as having a role in a community (i.e. aquatic vs. terrestrial species), essentially that phylogenetically close species should share similar roles. However, as it happens so often in ecology, the term was later applied to a substantially different problem: Holt and Gomulkiewicz (1997) examined the feasibility of adapting outside a population's 'fundamental niche', meaning not the role of the species, but its range of tolerance to environmental conditions in the absence of competitors. They found that it was unlikely that a population could adapt to a severe environmental change that would place it outside its fundamental niche, mostly because the time to extinction for such a population would be almost always shorter than the time needed to adapt. For these authors, 'niche conservatism' meant difficulty to adapt to conditions outside a range of tolerances. This theoretical argument was tested indirectly by Peterson *et al.* (1999), who presented evidence to show that related species tend to share similar environmental requirements, arguing that niche conservatism in environmental preferences is manifested by little change in these preferences in sister lineages over the period of evolution since the time of speciation; later reanalysis by Warren *et al.* (2008) confirmed these results.

Reviews of niche evolution for the most part have not distinguished explicitly between niche as a role and niche as a set of tolerances. Wiens and Graham (2005) defined the term niche conservatism as: 'the tendency of species to retain aspects of their fundamental niche over time'. Pearman *et al.* (2007) provided two definitions: (1) 'the tendency of a species niche to remain unchanged over time', and (2) 'the tendency for related species to have similar fundamental and/or realized niches'. Thus, the term 'conservatism' has been applied both to niches as ecological roles and niches as environmental preferences, and sometimes to fundamental niches and sometimes realized niches, although since the classic paper by Hutchinson (1957), it has been shown that substantial differences exist between the two (Colwell and Futuyma, 1971). Perhaps only Holt and Gomulkiewicz (1997) have presented quantitative, formal definitions of niche conservatism and the fact remains that 'niche' is a vague and poorly defined term (Real and Levin, 1991; Chase and Leibold, 2003; Peterson *et al.*, 2011), such that to analyse its evolution requires considerable caution.

Among the many issues that require clarification, an important one is what types of variables comprise the niche space in question. In an almost forgotten chapter, Hutchinson (1978) proposed we distinguish between so-called scenopoetic variables (those that are not coupled to changes in population sizes of the species in question) and bionomic variables (those that are affected dynamically by changes in population size of the species in question). This distinction must be taken as a first approximation, but it nevertheless is useful for several reasons. First, the spatio-temporal structure of selective pressures in the two types of variables is likely to be radically different (Peterson *et al.*, 2011), as illustrated in Fig. 1. This texture in the selective environment is probably key in determining whether a species exhibits niche conservatism in some dimension (Holt and Gomulkiewicz, 1997) because, for example, variables with wide ranges of spatial covariance (e.g. climatic variables) create very different adaptive landscapes than those with narrower ranges (e.g. biotic interactions). Second, scenopoetic variables can easily be represented by sets, whereas bionomic variables
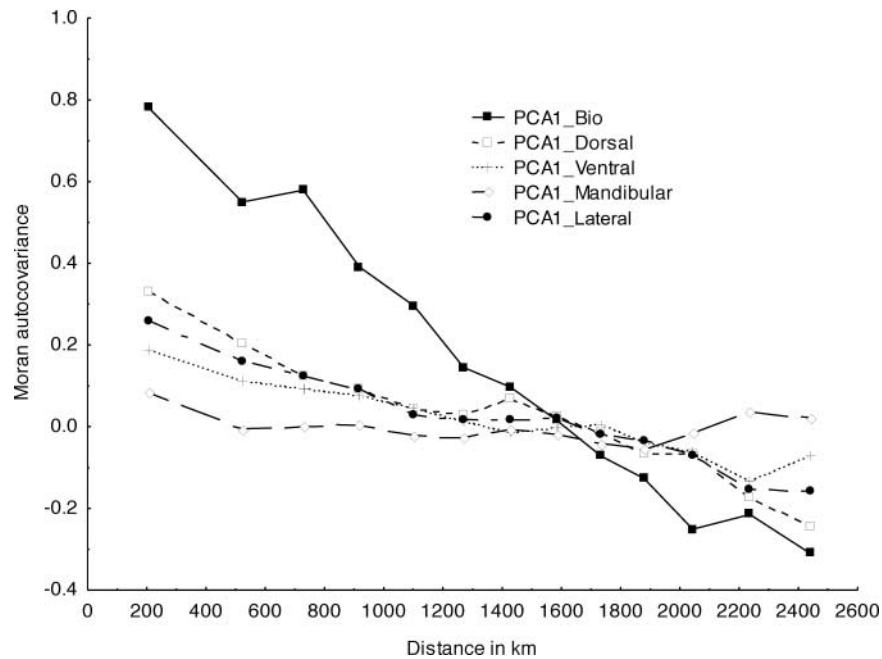
Fig. 1. Spatial autocovariance indices (Moran's *I*) for the first principal component axes of the environmental (Bio) and morphometric (dorsal, lateral, mandibular, ventral) variables. The figure illustrates the fact that morphological variables have much shorter spatial covariances than climatic variables.

often require functions to be described (Chase and Leibold, 2003). Finally, although this issue is mostly practical in nature, large databases of scenopoetic variables exist that can be applied when measuring niches, whereas bionomic variables mostly need to be measured specifically in each case.

In view of the above, and as discussed in detail elsewhere (Soberón, 2007; Peterson *et al.*, 2011), two extreme classes of niches (Grinnellian and Eltonian) can be defined based on whether the multidimensional space of ecological variables is composed of scenopoetic variables or of bionomic functions. Most evidence in favour of conservatism was obtained using niches defined by climate, which comprise the archetypical scenopoetic variables; however, since the spatial structure (grain and extent) of selective pressures may differ in scenopoetic variables versus bionomic variables, one would expect different evolutionary dynamics in characters responding to each (Soberón, 2007).

Another fundamental confusion exists regarding whether it is the fundamental or the realized niche that is evolving. Since the classic paper by Hutchinson (1957), we know that substantial differences exist between fundamental and realized niches (Colwell and Futuyma, 1971), so 'conservatism' must mean very different things in each case. Specifically, a realized niche is a reduction of the fundamental niche as a result of interactions, limitations in movements, and change in available environments with time, mostly ecological factors that can distort, obscure or cover up real evolutionary changes or stasis. Unfortunately, studying fundamental niches is complicated, since they can be rigorously defined for scenopoetic conditions only by means of physiological experiments or from first principles

of biophysics (Buckley, 2008; Kearney and Porter, 2009). For Eltonian niches, defining a fundamental niche requires specification of models of resource exploitation and interaction with competitors (Chase and Leibold, 2003), which are very seldom obtainable under field conditions. In this case, distinguishing between fundamental and realized niches may be more a matter of theoretical rigour than of practicality.

In this paper, we explore differences in the pattern of evolution of differently defined 'niches' by studying phenotypes expressed as shapes in two multivariate spaces. Specifically, we examine the volumes occupied in climatic and morphological space by a monophyletic rodent clade. The climatic space is defined using 'bioclimatic' variables (Hijmans *et al.*, 2005) measured at sites of known occurrence for each of the species, which has recently been equated to the scenopoetic niche. We assume that shapes in morphological space, particularly for resource-relevant dimensions, such as cranial form, can be used as surrogates of non-scenopoetic niches. Mandibular and cranial morphology are indeed related to trophic niches (Ruber and Adams, 2001; Sibbing and Nagelkerke, 2001; Böhning-Gaese *et al.*, 2003; Christiansen, 2008; Moncayo-Estrada *et al.*, 2010); however, equating morphological measures with trophic position or other ecological measures of performance must be done on a case by case basis. Here, we define morphospace by geometric morphometrics techniques and analyse the shape of the skull of *Neotoma* rats from four different perspectives. Essentially, we compare what parts of environmental and morphological space species of the rodent clade occupy, and hypothesize that their evolutionary dynamics should be different.

METHODS

The genus *Neotoma* (Say and Ord, 1825) is a group of species of medium-sized rodents that occupy diverse ecological conditions from southern Mexico to northern Canada, making it a good group to study climatic and morphological variables. We measured the crania and mandibles of 596 individuals from 14 *Neotoma* species, as follows: *N. floridana* ($n = 117$), *N. magister* ($n = 20$), *N. albigula* ($n = 29$), *N. goldmani* ($n = 11$), *N. leucodon* ($n = 63$), *N. micropus* ($n = 47$), *N. isthmica* ($n = 17$), *N. picta* ($n = 19$), *N. mexicana* ($n = 80$), *N. stephensi* ($n = 23$), *N. lepida* ($n = 38$), *N. macrotis* ($n = 32$), *N. fuscipes* ($n = 29$), and *N. cinerea* ($n = 71$). We focused on taxa represented in the phylogenetic analyses of Matocq *et al.* (2007), which included 14 of the 24 described species (see Appendix 1). Only adults were included (based on presence of a third molar), and males and females were pooled for analysis because there were no statistically significant differences between them. To include the full spectrum of morphometric and environmental variation, we selected individuals from across the known distribution of each species (Hall, 1981). Specimens were obtained from the collections of the University of Kansas Natural History Museum and the US National Museum of Natural History.

Using a Canon EOS 500D camera equipped with a 100 mm Flat Field macro lens and tripod, we photographed each cranium from the dorsal, ventral, and lateral views, as well as the ramus of the mandible. We sampled shape based on homologous landmarks: we used 9, 15, 7, and 9 landmarks for the dorsal view, ventral view, lateral view, and mandible, respectively (see Appendix 2 for anatomical descriptions), plus 8 semi-landmarks (points along a curving shape) in the lateral view (Zelditch *et al.*, 2004). An arbitrary grid drawn with MakeFan (Sheets, 2001) was used to define semi-landmarks (Appendix 2). The landmarks and semi-landmarks in a total of 2384 pictures were digitized using tpsDig 2.16 (Rohlf and Slice, 1990).

Morphometric analyses were performed using the Integrated Morphometric Package (IMP Sheets 2001). A Procrustes Superimposition was carried out to eliminate non-shape information related to differences in size, position, and rotation (Rohlf and Slice, 1990; Webster and Sheets, 2010). Next, alignment coordinates were projected into Euclidian space to produce a set of partial warp (PW) scores (Bookstein, 1991). Size disengaged from shape (Bookstein, 1991) was obtained for each view and averaged across the four views of each individual for comparative analysis (see below). The PW scores were centred and standardized and then subject to principal components analysis for further comparison with environmental niche variables (Böhning-Gaese et al., 2003).

The environmental space was characterized by means of eight environmental variables at a resolution of 0.01° (~1.2 km^2) downloaded from WorldClim (Hijmans et al., 2005). These variables are thin-plate smoothing splines fitted to daily data from nearly 3000 climate stations (Hijmans et al., 2005). The original data included monthly maximum, minimum, and mean temperatures, which were then converted to 19 'bioclimatic' variables in the WorldClim database (Hijmans et al., 2005). The dimensionality in the climatic database was reduced by principal components analysis on the centred and standardized matrix. *Neotoma* presence records were assigned the corresponding values of the PCA-transformed environmental space, corresponding to their spatial positions.

To check for phylogenetic signature, we used Blomberg's *K* statistic (Blomberg et al., 2003), which compares a quantitative character distribution at the tips of a phylogenetic tree to a theoretical expectation based only on the tree structure (topology and branch lengths) and on the assumption of Brownian motion character evolution. *K*-values close to 1 indicate distributions of characters indistinguishable from a Brownian change process along tree branches, whereas values >1 and <1 imply more or less influence of phylogeny in trait values, respectively.

To compare structures in both morphological and environmental space, we estimated robust minimum volume ellipsoids (MVEs, R package MASS) in three dimensions. MVEs minimally enclose the points in environmental and morphological space. Since morphometric and environmental space were scaled similarly, the volumes of the ellipsoids in the two spaces reflect the total amount of three-dimensional space occupied in the same units, and can be compared robustly. The ellipsoids are defined by a centroid and by a covariance matrix that determine the direction and size of the semi-axes (Legendre and Legendre, 1998). We used canonical correlation analysis (Manly, 2005) to test for relationships between environmental and morphological space. Finally, we tested for differences in variances in the PC axes among different characters using Kruskal-Wallis rank-based one-way analyses of variance (Quinn and Keough, 2002), with individual as the unit of replication. These analyses were performed in Statistica 9.

RESULTS

The first three PCs of the morphological covariance matrices accounted for 44% of variance in dorsal measures, 32.5% of variance in ventral measures, 50% of variance in mandibular measures, and 53% of variance in lateral measures. Overall, in morphological space, 12 components were necessary to summarize 70% of the variance. A visual inspection of PC plots (not shown) revealed differences in disparity [phenotypic variety (Zelditch et al., 2004)] among *Neotoma* subclades: the *mexicana* and *micropus* groups tended to cluster more tightly, while the other groups were more broadly spread.
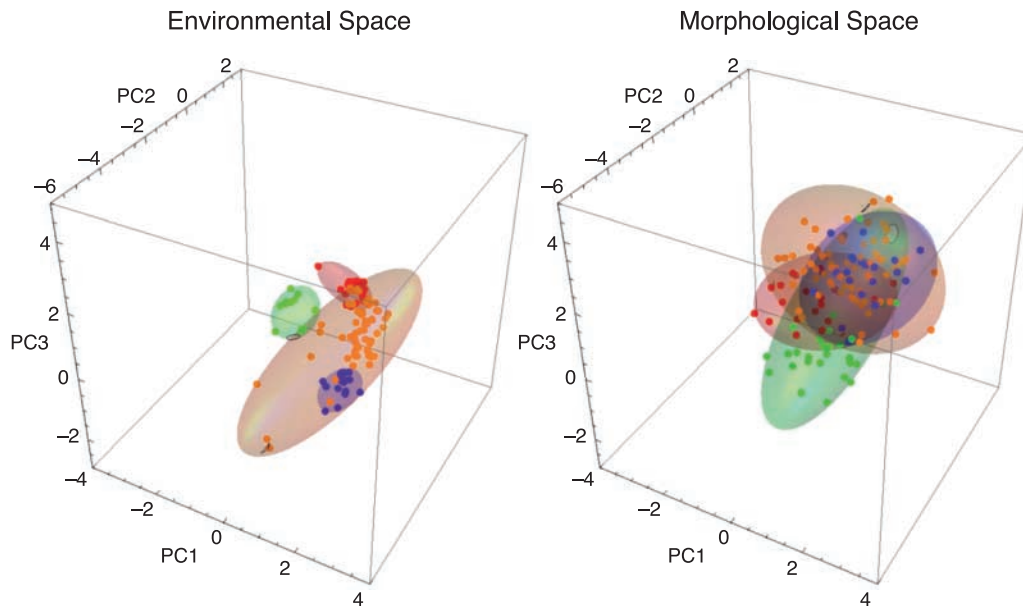
Fig. 2. Occupation of environmental and morphological space by four species. The axes are the first three principal components based on centred and standardized environmental and morphological variables. Four species were chosen to illustrate the idea of modelling niche occupation with ellipsoids. The ellipsoids are minimum volumes enclosing 95% of available points. The scale is the same for both graphs. The species are: orange, *Neotoma cinerea*; green, *N. fuscipes*; red, *N. stephensi*; and blue, *N. magister*.

The first three bioclimatic PCs explain 81.4% of variance. PC1 was most influenced by minimum temperature of the coldest month, mean temperature of the coldest quarter, and diurnal temperature range. PC2 was most influenced by annual precipitation and precipitation of the driest quarter. Finally, PC3 was highly influenced by mean temperature of the warmest quarter.

As an illustration, in Fig. 2 we display the MVE of four species in environmental and morphological space (using mandible measures). The centroids are located in different regions of space, which is not surprising, but the ellipsoids also show contrasting orientations and volumes.

We tested for phylogenetic effects on volume using Blomberg's K statistic (Blomberg *et al.*, 2003). The K statistic showed a dominant influence of phylogeny only in one of three climatic and one of four morphological axes. Most did not depart from Brownian models (Table 1). The two exceptions were environmental PC3 (dominated by dryness) and morphological PC4 (mostly a ventral view). These two spaces presented less variation than expected under a Brownian model, suggesting strong phylogenetic restrictions.

A weak relationship existed between patterns of environmental and morphological diversification. Canonical correlation values between the first five PCAs in morphology and the corresponding environmental axes were always positive, but significant at $P \leq 0.01$ only in 12 of 40 cases. A Bonferroni correction reduces this number to 3 out of 40. The H_0 of a slope $= 0$ was rejected consistently only for *N. floridana* (every morphological variable), *N. micropus* (dorsal and lateral views), *N. cinerea* (lateral and mandibular views), and

Table 1. Blomberg's *K*-values together with *P*-values for the first principal components (PCs), with corresponding eigenvalues

	K	*P*	Variance (%)
Shape and size			
PC1	0.745	0.054	18
PC2	0.814	0.195	10
PC3	0.648	0.924	8
PC4 ventral	1.280	0.032*	9
Size	0.746	0.351	—
Volume (average)	0.711	0.457	—
Environment			
PC1	0.902	0.074	47
PC2	0.709	0.595	32
PC3	1.233	0.028*	16
Volume (average)	0.675	0.588	—

*PCs significantly different from a Brownian evolution model.
Volume values are averaged over all species.

Table 2. Canonical correlations and *P*-values between the first five morphological and environmental principal components, for all the species with enough data points for analysis

		Dorsal		Lateral		Mandibular		Ventral	
Species	Area (km²)	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
N. cinerea	3,598,453	0.512	0.236	**0.633**	**0.010**	**0.647**	**0.002**	**0.674**	**0.000**
N. fuscipes	171,378	0.789	0.025	0.738	0.284	0.766	0.030	0.798	0.052
N. macrotis	154,714	0.771	0.065	0.750	0.209	0.543	0.720	0.711	0.025
N. lepida	1,010,122	0.673	0.038	**0.838**	**0.002**	0.703	0.025	0.724	0.046
N. stephensi	226,750	0.835	0.065	0.712	0.508	0.876	0.062	0.655	0.771
N. mexicana	1,787,163	0.536	0.016	0.515	0.016	0.384	0.500	**0.632**	**0.002**
N. micropus	1,064,626	**0.752**	**0.003**	**0.691**	**0.001**	0.582	0.227	0.604	0.085
N. leucodon	959,261	0.515	0.221	0.500	0.111	0.533	0.385	**0.656**	**0.000**
N. albigula	834,924	0.725	0.077	0.679	0.171	0.661	0.718	0.685	0.147
N. floridana	1,848,589	**0.530**	**0.001**	**0.622**	**0.000**	**0.730**	**0.000**	**0.662**	**0.000**

Note: Significant values in **bold**. The area of occupancy appears in the first column (Natureserve: www.natureserve.org/getData/mammalMass.isp).

N. lepida (lateral view) (Table 2). This result suggests that the evolution of environmental preferences and morphological variables may have been mostly independent of each other, and that phylogeny is generally a good explanation for morphological diversity in the genus *Neotoma*.

The volumes of the MVEs (Fig. 3) were smaller in general for environmental space than for morphological space. This pattern was tested using a rank-based ANOVA on the variances of principal component measures. This showed that the first and third principal
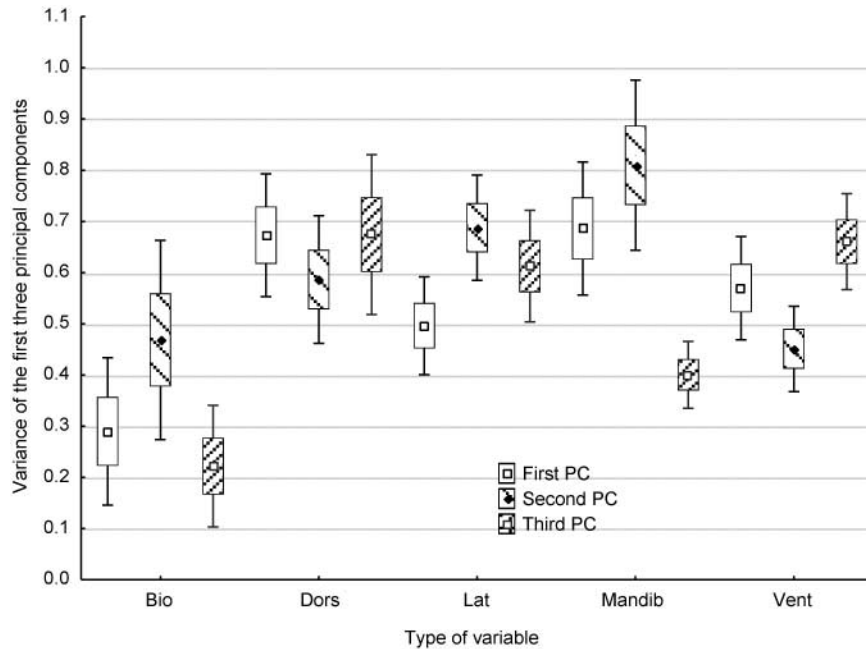
Fig. 3. Box plots of variances of the first three principal components in environmental (Bio), dorsal (Dors), lateral (Lat), mandibular (Mand), and ventral (Vent) spaces. Marker is mean value, box is standard error, and whiskers are 95% confidence intervals. The variances in environmental PC are smaller in general than those in morphological space.

components in environmental space indeed differed from the corresponding components in morphological space (PC2: $\chi^2 = 19.52$, d.f. = 4, $P = 0.0006$; PC3: $\chi^2 = 30.725$, d.f. = 4, $P < 0.0001$). In general, the volumes of niches in environmental space were smaller than the corresponding volumes in morphological space (Fig. 4).

DISCUSSION

This paper has explored the pattern of differences in environmental and morphological variables within species of the *Neotoma* clade. Characterizing size and shape in multivariate spaces is not a simple task. We chose to use minimum volume ellipsoids for mathematical simplicity. Van Valen (1974) highlighted the risks of using ellipsoids, namely, if variance on a single dimension is low or zero, the entire volume may diminish drastically, and choosing the number of dimensions is an arbitrary decision. In view of this, we used only the first three axes in each space, and analysed variances separately. Variation in accumulated environmental space increased faster with number of dimensions than that in morphological space; however, for the same number of dimensions, the volume remains an independent measure of occupied space. The main advantage of using volumes is that they represent an overall measure of niche-variable space that can be compared among different types of variables.

Following the suggestion of Holt and Gomulkiewicz (1997), Soberón (2007) proposed that characters related to climatic niches may have a different pattern of conservatism than those
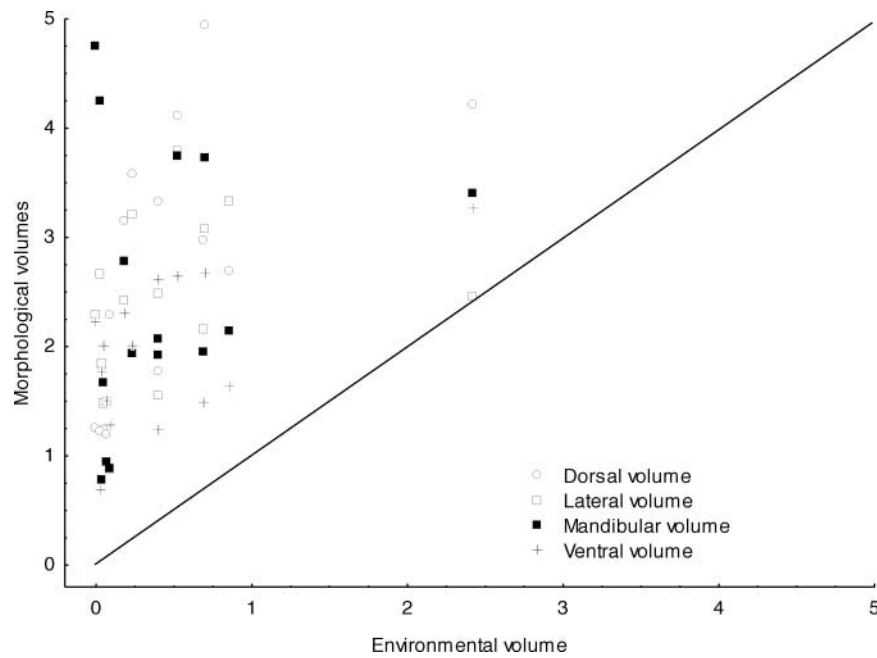
Fig. 4. Occupied volumes in morphological space (y-axis) versus environmental space (x-axis). Volume occupied in morphological space was always larger than that occupied in environmental space. A line of slope 1, passing through the origin, is provided as reference.

associated with bionomic variables, mostly due to the wider range in spatial covariance of selective pressures. While much evidence argues in favour of climatic conservatism (Peterson *et al.*, 1999; Peterson, 2011), conservatism in niches defined with non-scenopoetic variables remains an open question, not least because climatic niches have been widely modelled in recent years and conservatism can be defined operationally, whereas niches defined using other types of variables are more difficult to analyse.

For example, in scenopoetic niches some key distinctions are easy to define operationally. Niche conservatism should be applied to fundamental niches, but most often one measures realized niches. Peterson *et al.* (2011) proposed a basic inequality for scenopoetic niches:

$$N_R \subseteq N_F^* = N_F \cap E \subseteq N_F \tag{1}$$

N_F is the fundamental niche, in principle obtained from physiological experiments (Hooper *et al.*, 2008) or biophysical first principles (Kearney and Porter, 2009), and it represents the physiological tolerances of the species. This niche should be intersected with the climates that actually exist and which the populations of the species may experience (E), to give the existing niche – originally called the potential niche (Jackson and Overpeck, 2000). Finally, this niche is reduced by biological interactions to the realized climatic niche N_R, which can be estimated by presence data using niche modelling techniques.

Therefore, evolution in the shape of the fundamental niche may be masked by variation in E, in the dispersal capacities of the species relative to the presence of barriers and time available, and in biotic interactions. Evolutionary interpretations of changes in a scenopoetic N_R should always be made in light of these complicating factors. More specifically, invariance in N_R is compatible with the possibility of no change in N_F,

but change in N_R does not imply change in N_F (Dormann *et al.*, 2010). We found evidence of slower-than-random niche change only in one climatic variable (Table 1), which would be the only one compatible with a hypothesis of niche conservatism in the fundamental niche.

On the other hand, we do not have an inequality like (1) for non-scenopoetic niche spaces. In morphometric space, we found that MVEs related to cranial morphology in *Neotoma* were phylogenetically conservative in just one case (Table 1). The Muridae is a diverse family containing 24% of all known mammals (Wilson and Reeder, 2005); however, they display low levels of morphological diversity, or disparity (Hautier *et al.*, 2011). The notable loss of eight homeobox genes in this lineage compared with other groups of mammals may provide part of the explanation (Zhong and Holland, 2011). A complementary argument suggests that selection favouring small body size in this group (Gardezi and da Silva, 1999) will also impose limits on morphological evolution.

The results of shape and size in *Neotoma* were compatible with historical limitations on evolution imposed by phylogeny and, to a lesser extent, with process-imposing limits to disparity. In a similar study of the genus *Rattus*, Rowe *et al.* (2011) found less variation than expected under a Brownian model in morphological measures; furthermore, they reported only limited ecological innovation. In a study of Australian murids, Geffen *et al.* (2011) found that most life-history traits do not represent adaptations to new environmental conditions, but rather exhibit retention of ancestral states. Álvarez *et al.* (2011), using a geometric morphometric approach, did not find departures from Brownian model expectations in mandibles of three superfamilies of South American rodents, even though they differ notably in their ecology. We suggest that if this constrained evolution is a common pattern in Murids, then episodes of adaptive radiation would be uncommon. Rather, random or slower-than-random niche change in both the scenopoetic and morphological dimensions would be the norm in this section of the mammal phylogeny.

Our results showed positive but mostly non-significant associations between environmental niche and morphology. Colangelo *et al.* (2009) reported significant associations between environmental variables and morphology at the species level in three species of African rodents. Other studies with *Neotoma* also have concluded that evolution of niche-related features is related to trophic variables (Sorensen *et al.*, 2004). Positive associations between these variables might exist, but further study and more data are needed to document them.

The area of distribution of a species may be constrained from expanding by several factors, including gene flow that prevents marginal populations from adapting to environments different from those in the core of its distribution (Haldane, 1956; Mayr, 1963), lack of genetic variation, inbreeding load, and others (Kawecki, 2008). In the short term, by being restricted to a given area, a species is also constrained to remain inside a certain climatic niche envelope; this latter idea has gained support recently in mathematical treatments (García-Ramos and Kirkpatrick, 1997; Kirkpatrick and Barton, 1997). On the other hand, evolution as related to selective pressures other than climatic ones, but within the range set by the climatic niche envelope, would not be so restricted. Thus different aspects of niches should show contrasting patterns (Soberón, 2007). We found a consistent signature of broader spread in morphological space than in climatic space. In essence, we suggest that most axes of climatic niches, although presenting the same or less variation than expected under null models (Cooper *et al.*, 2010), are more constrained in their occupation of environmental space, whereas axes related to morphological features are again mostly consistent with random change, but occupy more space.

In this paper, we present some evidence of random change and some niche conservatism in *Neotoma* in two contrasting groups of variables. However, we also found some marked differences between the two groups. The most important one is that niches defined using environmental variables are consistently narrower than those defined using morphology. Although morphological change may be constrained by a number of genetic and mechanical factors, in terms of units of variance, morphological variables take up more niche space than climate-related variables. This is in line with the theoretical predictions of Holt and Gomulkiewicz (1997) and Soberón (2007), although much work remains to be done to explore these predictions. An important corollary of our results is that the term 'niche conservatism' is too broad. To quantify the phenomenon and to better understand its evolutionary dynamics, it is necessary to provide a detailed disaggregation of niche variables, and to develop methods that allow for comparisons among very different types of niche variables. Otherwise one is simply playing with words.

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APPENDIX 1

Maximum parsimony phylogeny depicting the relationships among species of *Neotoma*. Numbers above branches are bootstrap values, whereas numbers below branches are decay indices. The phylogeny was based on four nuclear and four mitochondrial markers (Matocq *et al.*, 2007). Different methods of phylogenetic reconstruction produced similar results;

however, some discrepancy exists in the position of *N. cinerea* and *N. stephensi*, which requires future investigation.
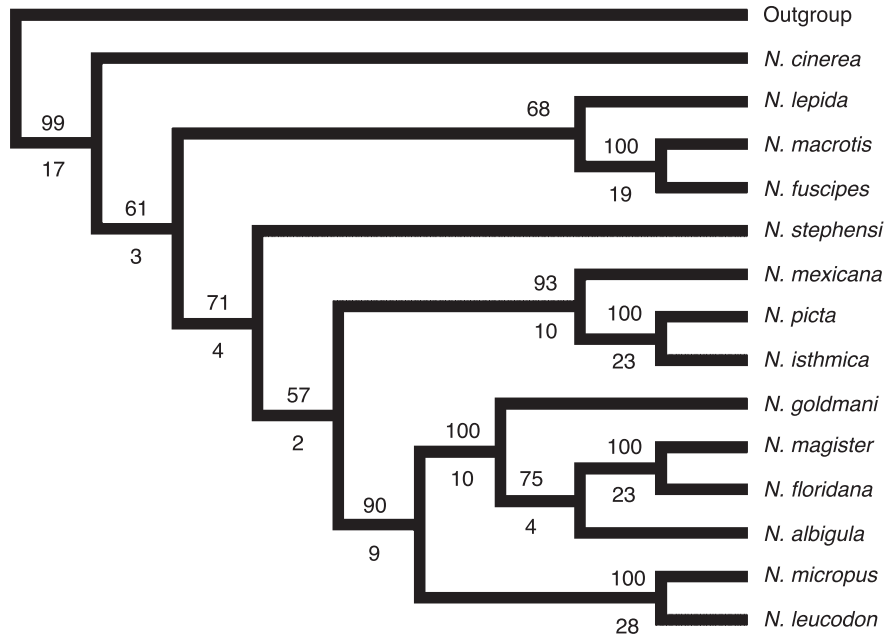
APPENDIX 2

Skull and mandible of *N. stephensi* showing the locations of landmarks (after an unpublished original by R. Hall, 1981).
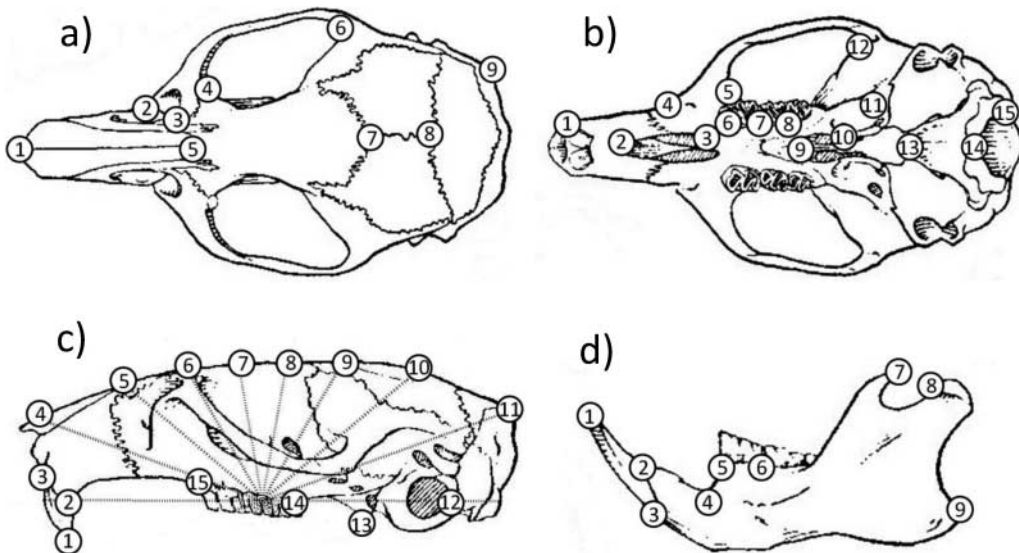
Description of landmarks

Dorsal (a): 1 = anterior extreme of rostrum; 2 = corner formed between interorbital fossa and interorbital foramen; 3 = intersection among premaxilla, maxilla, and frontal; 4 = intersection between lacrimal and frontal; 5 = suture between nasals and frontals; 6 = interior corner of posterior zygomatic arch; 7 = suture between parietals and frontals; 8 = suture between parietal and interparietal; and 9 = posterior lateral of occipital.

Ventral (b): 1 = lateral point of incisive alveolus; 2 = anterior extreme of incisive foramen; 3 = posterior extreme of incisive foramen; 4 = lateral union between maxilla and posterior rostrum; 5 = extreme anterior point of interior corner of zygomatic arch; 6 = lingual anterior edge of M1; 7 = central contact point between M1 and M2; 8 = contact between M2 and M3; 9 = anteriormost point of mesopterygoid fossa; 10 = lateral union between presphenoid and basisphenoid; 11 = centre of foramen ovale; 12 = interior corner of the posterior zygomatic arch; 13 = midpoint of suture between basisphenoid and basioccipital; 14 = midpoint of posterior basioccipital suture; and 15 = interior corner of basioccipital condyle.

Lateral (c): 1 = tip of incisor; 2 = union between interior face of incisor and premaxillary; 3 = union between external face of incisor and premaxillary; 12 = intersection between basioccipital and auditory bulla; 13 = tip of pterygoid process; 14 = anterior junction of maxillary and molars; and 15 = posterior junction of maxillary and molars. Eight semi-landmarks were sampled as follows. A radius circle was drawn using MakeFan6 (IMP series) between landmarks 2 and 12. Landmarks were set at the intersection of the radius and the shape's limit; landmarks 4, 5, 6, and 7 cover the rostrum, and 8, 9, 10, and 11 the basicranium.

Ramus (d): 1 = tip of incisor; 2 = interior point between incisor and alveolus; 3 = exterior limit between incisor and alveolus; 4 = mental foramen; 5 = anterior margin of first molar; 6 = posterior margin of first molar; 7 = tip of coronoid process; 8 = interior corner of condyle; and 9 = tip of angular process.