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Article

The endemic Patagonian vespertilionid assemblage is a depauperate ecomorphological vicariant of species-rich neotropical assemblages

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Abstract

Vespertilionidae is the most diverse chiropteran family, and its diversity is concentrated in warm regions of the World; however, due to physiological and behavioral adaptations, these bats also dominate bat faunas in temperate regions. Here we performed a comparative study of vespertilionid assemblages from two broad regions of the New World, the cold and harsh Patagonia, versus the remaining temperate-to-subtropical, extra-Patagonian eco-regions of the South American Southern Cone. We took an ecomorphological approach and analyzed the craniodental morphological structure of these assemblages within a phylogenetic framework. We measured 17 craniodental linear variables from 447 specimens of 22 currently recognized vespertilionid species of the study regions. We performed a multivariate analysis to define the morphofunctional space, and calculated the pattern and degree of species packing for each assemblage. We assessed the importance of phylogeny and biogeography, and their impact on depauperate (Patagonian) versus rich (extra-Patagonian) vespertilionid assemblages as determinants of morphospace structuring. We implemented a sensitivity analysis associated to small samples of rare species. The morphological patterns were determined chiefly by the evolutionary history of the family. The Patagonian assemblage can be described as a structurally similar but comparatively depauperate ecomorphological version of those assemblages from neighboring extra-Patagonian eco-regions. The Patagonian assemblage seems to have formed by successively adding populations from Northern regions that eventually speciated in the region, leaving corresponding sisters (vicariants) in extra-Patagonian eco-regions that continued to be characteristically richer. Despite being structurally akin, degree of species packing in Patagonia was comparatively very low, which may reflect the effect of limited dispersal success into a harsh region for bat survival.

Key words: Vespertilionidae, Patagonia, morphological space, biogeography, phylogeny.

With 47 genera (Hoofer and Van Den Bussche 2003; Simmons 2005) and some 407 species (Simmons 2005; Lack and Van Den Bussche 2010; Van Den Bussche and Lack 2013), Vespertilionidae is the most diverse chiropteran family (Hoofer and Van Den Bussche 2003) second only to Muridae among mammals (Lack and Van Den Bussche 2010). Vespertilionids as a group are nearly cosmopolitan (Kawai et al. 2002; Gardner 2007), and so are distributed in every continent except Antarctica, and in all major islands except Greenland (Gardner 2008). The greatest diversity of the family is concentrated in warm regions of the world; however, due to their metabolic and behavioral adaptations, these bats dominate bat assemblages of temperate regions (Hoofer and Van Den Bussche 2003; Stevens 2004). Nearly all members of this family are exclusively insectivorous, and despite their diversity, vespertilionids exhibit relatively modest interspecific morphological variation (Nowak 1999; Lack and Van Den Bussche 2010).

Vespertilionid bats from southern South America represent an interesting study group given the latitudinal variation in species composition, and the variation of morphofunctional structure of those assemblages. Species richness increases from the polar to tropical regions generating a ubiquitous latitudinal gradient of biodiversity with tropical latitudes supporting relatively more life zones than cool or temperate environments (Patterson et al. 2003; Willig et al. 2003; Stevens 2004, 2006). South America spans the most extensive continuous latitudinal gradient in the Southern Hemisphere, and bat species diversity has responded to this gradient (Koopman 1982; Stevens 2004; Stevens et al. 2006). The morphofunctional structure of these assemblages may have been shaped by any one of the following three processes: 1) a simple increase in the total morphological space occupied, chiefly due to the addition of new divergent species or lineages; 2) an increase in the degree of species packing (Patterson et al. 2003; Moreno et al. 2006; Villalobos and Arita 2014); 3) a discernible combination of the former two alternatives occurs in a given environment, such that both packing and volume are affected.

The vespertilionid bat fauna of the South American Southern Cone represents an interesting opportunity to investigate properties of morphofunctional spaces, such as packing and volume, in the context of broad latitudinal variation. In this region, vespertilionids are widely distributed and tend to dominate the local bat assemblages (Koopman 1982; Stevens 2004). Although little is known about the diversity of vespertilionid bats in the temperate regions of the Southern Cone, specifically Patagonia, the reported diversity is low compared with subtropical areas of the same region (Barquez et al. 1999; Barquez 2006). Patagonia *sensu lato* harbors endemic species and unique populations of otherwise widespread species, and here several vespertilionid species reach their southern distributional limit (Barquez et al. 1999).

It is productive to approach the study of assemblages varying across the geographic space, such as those of Southern Cone vespertilionid bats, from an ecomorphological perspective. This approach relies on the assumption that a functional relationship exists between variation in the morphology of individuals or taxa and their ecological variation including patterns of resource use (e.g., Wainwright 1994). It is assumed that ecological requirements and evolutionary histories must have determined the size, shape, and associated functions of living organisms (Wainwright 1994; Moreno et al. 2006). Morphological variation often has helped provide insight into ecological function within and among bats species (Freeman 1981; Findley and Black 1983; Patterson et al. 2003). In particular, craniodental morphology, given its direct relationship with diet and resource partitioning, has been extensively studied in bats (Freeman 1981; Swartz et al. 2003; Nogueira et al. 2009; Santana et al. 2012).

Evolutionary history can determinate the structure of a contemporary assemblage (Simmons 2000). This becomes apparent when we consider that aspects of an organism's performance, such as functional morphology, ecology, and behavior, may have been shaped by adaptive evolution since the origin of a given lineage, and preserved by common ancestry in descendant species. The evolutionary history of Vespertilionidae is complex and the phylogenetic relationships within the family still being resolved (Jones et al. 2002; Lack and Van Den Bussche 2010; Van Den Bussche and Lack 2013). Vespertilionids represent an interesting case of evolutionary radiation given its worldwide species richness (see above), but as a group they exhibit relatively modest morphological disparity (Van Den Bussche and Lack 2013). Thus, we expect that phylogenetic relationships among the vespertilionid bats are fundamental in understanding the segregation of species in morphofunctional space and in the way it maps onto the real-world ecological space.

Here, we studied morphospace structure of the Southern Cone vespertilionid assemblage in an explicit phylogenetic framework. We subdivided the analysis in Patagonian vs. extra-Patagonian vespertilionid assemblages from Argentina, thus representing the major geographic patterning due to the strong latitudinal gradient of the whole region, and defined a multivariate morphofunctional space using cranial variables. We assessed the importance of evolutionary history and its impact on depauperate (Patagonian) versus rich (extra-Patagonian) neighboring assemblages as determinant of morphospace structure in this group. We show that species packing, and to a lesser extent morphospace volume (species disparity), are the chief structural aspects affected primarily by phylogeny and also biogeography, and suggest that this may represent a key in the evolutionary history of Vespertilionidae, the most diverse clade of bats.

Materials and Methods

Study region

We sampled specimens primarily from Argentina and also from Uruguay, which together comprise much of the actual Southern Cone, defined as the vast extra-tropical (Southern) region of South America. This region presents an extremely diverse topography, climate (subtropical to polar), and vegetation, both considering composition and physiognomy. According to the biogeographic scheme of Burkart et al. (1999), 15 continental eco-regions are represented in Argentina, mainly subtropical and temperate environments (Figure 1). To those, at least one distinct eco-region is added in Uruguay (see below and Figure 1). Vespertilionid bats inhabit all these eco-regions (see Barquez 2006). The Eastern or cis-Andean Patagonian region, located south of the Colorado River in Argentina, ranges from the 39° S to 55° S (León et al. 1998).The fluvial basins of Río Colorado and Río Negro mark the limit between the subtropical summer rain regime and the mid-latitude winter rain regime (Mancini et al. 2005). For this reason, rainfall in Patagonia is concentrated mainly in winter (much as snow) with a marked rainfall gradient from west to east (León et al. 1998; Paruelo et al. 1998). Climate is cool-temperate with a mean annual temperature range from 12°C in the north to 3°C in the south, with strong predominant eastward-direction winds (Paruelo et al. 1998). These climatic factors have generated a steep vegetation gradient such that two main eco-regions are recognized: the Patagonian Forest (austral forest) and Patagonian Steppe (cool desert; León et al. 1998).

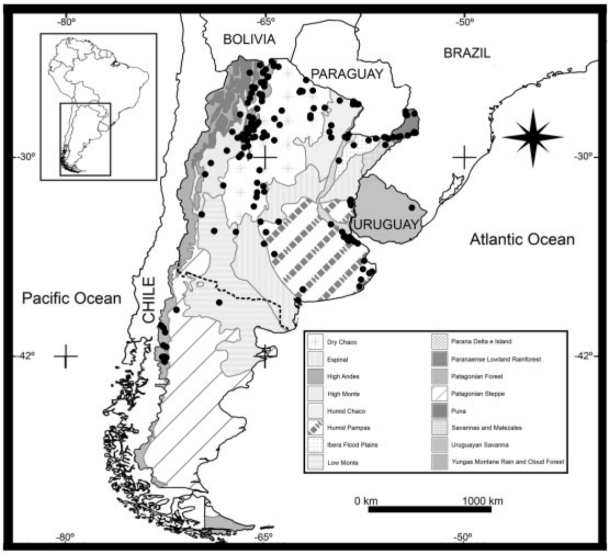

Figure 1. Study region and localities for vespertilionid bats from the Southern Cone. Eco-regions following Burkart et al. (1999) and Olson et al. (2001). Dotted line demarks the North Patagonian boundary (Río Colorado).

Marginally, the Low Monte eco-region is also represented in the NW of Patagonia (sensu Burkart et al. 1999). These conditions generate a climatic barrier causing to a marked decrease in mammals diversity in Patagonian environments, and even the isolation of Patagonian populations in some species (e.g., *Histiotus macrotus*, *Lyncodon patagonicus*, Schiaffini et al. 2013; Giménez et al. 2015) as well as the emergence of endemism (e.g., *Histiotus magellanicus*, *Lasiurus varius*, *Myotis chiloensis*, Barquez et al.1999). On this basis, we classified the species and specimen according to their record localities as Patagonian or extra-Patagonian. Provenance of extra-Patagonian specimens included the following eco-regions: Yungas Montane Rain and Cloud Forest, Paranaense Lowland Rainforest, Dry Chaco, Hummed Chaco, Low Monte, High Monte, Parana Delta and Islands, Ibera Flood Plains, Savanna and Malezales, Humid Pampas, Puna, and Espinal. We also included the Uruguayan Savanna eco-region (sensu Olson et al. 2001) because we included a specimen of *Eptesicus brasiliensis* from Uruguay.

Specimens and taxonomic considerations

The vespertilionid bat fauna in Argentina (Barquez 2006) includes *Eptesicus brasiliensis* (Desmarest 1819); *E. chiriquinus* Thomas 1920; *E. diminutus* Osggod, 1915; *E. furinalis* (d'Orbigny and Gervais 1847); *Histiotus laephotis* Thomas, 1916; *H. macrotus* (Poeppig 1835), *H. magellanicus* Philippi, 1866; *H. montanus* (Philippi and Landbeck 1861), *H. velatus* (I. Geoffroy Saint-Hilaire 1824); *Lasiurus blossevillii* (Lesson and Garnot 1826); *L. cinereus* (Palisot de Beauvois 1796); *L. ega* (Gervais 1856); *L. varius* Poeppig, 1835; *Myotis albescens* (Geoffroy Saint-Hilaire 1806); *M. chiloensis* (Waterhouse 1840); *M. dinellii* Thomas, 1902; *M. keaysi* Allen, 1914; *M. levis* (Geoffroy Saint-Hilaire 1824); *M. nigricans* (Schinz 1821); *M. riparius* Handley, 1960; *M. ruber* (Geoffroy 1806) and *M. simus* Thomas, 1901. Some systematic instability surrounds the validity of *M. aelleni* as species separate from *M. chiloensis*, and of *Dasypterus* as a genus distinct from *Lasiurus*, and *Histiotus* as a genus distinct from *Eptesicus*. First, *Myotis* is the most diverse genus from Argentina and includes one questionable Patagonian endemic *M. aelleni* (Baud 1979). Specimens attributed to this name are known only from two close localities in Patagonia; no new specimens have been captured since the original collection, and one of the authors (ALG) has collected in both localities, as well as the entire region, to obtain only typical *Myotis chiloensis*. Most likely *M. aelleni* is a synonym of *M. chiloensis* (Barquez et al. 1999) and so we excluded this taxon from the Patagonian species list. Second, the lack of the minute first upper premolar has led several authors to segregate *Lasiurus ega* in *Dasypterus* (Gardner 2007; Kurta and Lehr 1995). Previous, karyotypic and phylogenetic studies have shown that *L. ega* is close to the rest of Lasiurini (Baker et al. 1988; Morales and Bickham 1995; Hoofer and Van Den Bussche 2003), thereby provisionally supporting the synonymy of *Dasypterus* (Allen 1894) under *Lasiurus* (Gray 1831), and thus the recognition of a single genus in the tribe (Hoofer and Van Den Bussche 2003). Recently, Baird et al. (2015) recovered distinct clades of yellow (*Dasypterus*), red (*Lasiurus*), and hoary (*Aeorestes*) bats; we follow Baird et al. (2015) and recognize *D. ega, L. blossevillii, L. varius* and *A. villosissimus* (formerly *L. cinereus villosissimus*) for the Southern Cone. Third, *Histiotus* has been consistently recovered nested inside *Eptesicus*, sister to the Neotropical clade of brown bats, and considered a subgenus of the latter (Hoofer and Van Den Bussche 2003, Roehrs et al. 2010). Here we used *Histiotus* informally (pending a thorough taxonomic review of *Eptesicus*) to distinguish the large-eared brown bats from morphologically typical *Eptesicus*.

Specimens and variables

We examined 453 skulls from specimens that represented the 22 recognized species of vespertilionids that occur in Argentina (see above; Figure 1). Our sample included specimens from all eco-regions of the study area, although the eastern steppe is underrepresented in systematic collections. However, species from the few recorded eastern bat localities are the same as in the western localities we sampled. The specimen list with localities of occurrence is given in Supplementary Appendix 1. Data were obtained from specimens stored in the following mammalian collections of Argentina: Colección de Mamíferos Lillo (CML), Tucumán; Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA), Mendoza; Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Buenos Aires; Museo de La Plata (MLP), Buenos Aires; Fundación de Historia Natural Félix de Azara (CFA), Buenos Aires; Museo Municipal de Ciencias Naturales Lorenzo Scaglia (MMMP), Mar del Plata, Buenos Aires; Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB-M), Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Chubut. In addition, we measured specimens of the Mammal Collection of American Museum of Natural History (AMNH), New York, USA. This set represented all the specimens available to us from the study area. We included 51 additional specimens of seven species with relatively small samples ($n < 10$) from localities outside the study area, in the sensitivity analysis described below (catalog identification and provenance of these specimens in Supplementary Appendix 2).

We selected 18 craniodental variables that accurately represented the size and shape of the vespertilionid bat skull and its major structures (Figure 2). Many of these variables were taken or modified from Simmons and Voss (1998), Barquez et al. (1999), and Giménez and Giannini (2011). The variables included were: Condylobasal length (CBL); Postorbital constriction (PC); Zygomatic breadth (ZB); Mastoid breadth (MB); Length of rostrum (LR); Height of braincase (HB); Length of palate (LP); Length of maxillary toothrow (CM^3); Breadth across molar (MM); Breadth across canines (CC); Length of mandibular (LM); Length of mandibular toothrow (CM_3); Height of mandibular body (HM); Length of upper canine (LUC); Length of lower canine (LLC); Height of coronoid process 1 (HC1); Height of coronoid process 2 (HC2); height of coronoid process 3 (HC3). Measurements were taken with a digital caliper to the nearest 0.01 mm.

On the basis of the geographical coordinates of collection localities we assigned each specimen to an eco-region following the classification of Burkart et al. (1999) using the program DIVA-GIS (Hijmans et al. 2005). In addition, for those specimens we defined the categories "Patagonian" (with locality records ranging from 39° S to 55° S) and "extra-Patagonian" (with records located North of 39° S within the study area). We included in the first group specimens of the Patagonian endemic species *Histiotus magellanicus*, *Lasiurus varius* and *Myotis chiloensis*, as well as Patagonian specimens of *H. macrotus* and *H. montanus*. The remainder of specimens are included in the extra-Patagonian group (Table 1). A single record exists for *Aeorestes villosissimus* in northern Patagonia (see Barquez et al. 1999); we considered this record as marginal and so the species was included only in the extra-Patagonian set.

Data analysis

We used principal component analysis (PCA) to represent the morphofunctional space occupied by vespertilionid specimens of our sample. This analysis was performed upon a variance–covariance matrix of untransformed morphometric data for all 453 specimens. The PCA was performed with the statistic software InfoStat v. 2010 (Di Rienzo et al. 2010). We traced two minimum polygons on the PCA ordination diagram, each joining specimens from either the Patagonian or extra-Patagonian set.

In order to evaluate the *pattern* of species packing of each vespertilionid set (Patagonian vs. non-Patagonian) in the craniodental morphospace, we followed Schiaffini and Prevosti (2014) and calculated the Clark-Evans Index (CEI; Clark and Evans 1954). This index measures the departure of the spatial distribution of objects a random distribution, with the distance from one specimen to its nearest neighbor as a measure of spacing (Clark and Evans 1954). The CEI values vary between 0 and 2.15; the values near 0 correspond to a clustered distribution (maximum aggregation), values

Table 1. Number of adult specimens used in this study broken down by regions

Species	Patagonian	Extra-Patagonian
Eptesicus brasiliensis	—	1
Eptesicus chiriquinus	—	1
Eptesicus diminutus	—	8
Eptesicus furinalis	—	67
Histiotus laephotis	—	8
Histiotus macrotus	30	15
Histiotus magellanicus	7	—
Histiotus montanus	4	4
Histiotus velatus	—	4
Lasiurus blossevillii	—	38
Lasirius varius	8	—
Aeorestes villosissimus	—	32
Dasypterus ega	—	17
Myotis albescens	—	40
Myotis chiloensis	24	—
Myotis dinellii	—	46
Myotis keaysi	—	8
Myotis levis	—	50
Myotis nigricans	—	22
Myotis riparius	—	21
Myotis ruber	—	5
Myotis simus	—	2

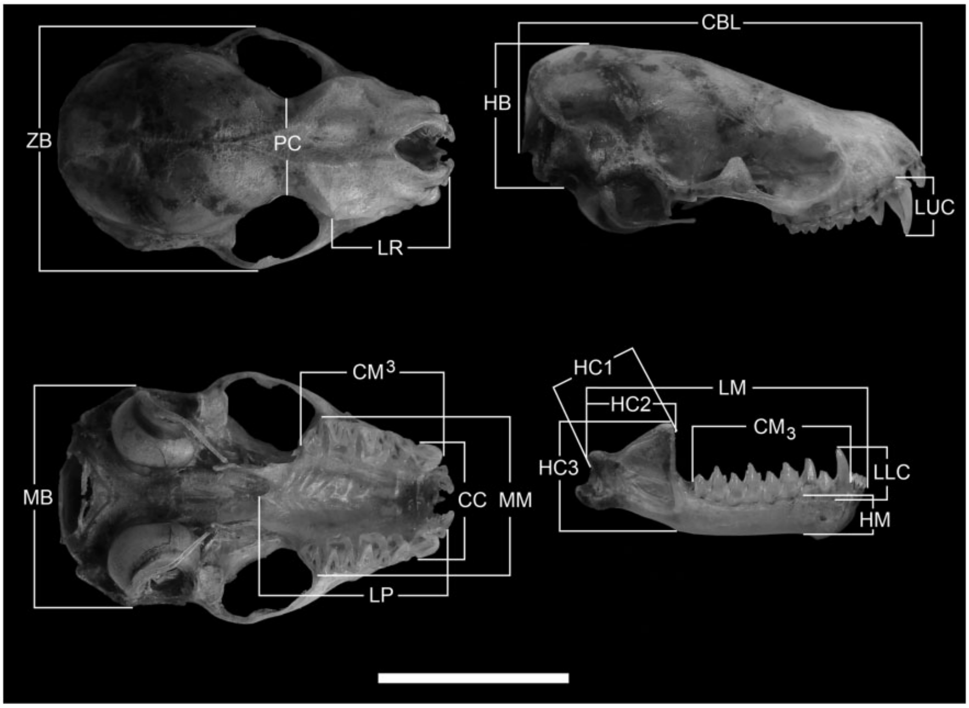

Figure 2. Skull variables measured in vespertilionid bats from Argentina, show on a *Histiotus macrotus* specimen (LIEB-M 851 ♀). See text for abbreviations. Scale 10 mm.

near 1 correspond to a random distribution, and values near 2.15 correspond to a systematic (orderly) distribution (individuals equidistant from each other; Clark and Evans 1954). The CEI was calculated upon the centroid of species on the reduced PCA space (planes axis 1 and 2) with 4,999 permutation using the package Spatstat (Baddeley and Turner 2005) in software R 3.1.3 (R Core Development Team, 2015). In addition, for each specimen set (Patagonian versus extra-Patagonian) we measured the degree of species packing calculated simply as the species density Ds = S/A with S = species richness and A = area in reduced morphospace (plane of PC axes 1 and 2, calculated in DIVA-GIS, Hijmans et al. 2005) as modified from Karr and James (1975; note that the authors used the somewhat counterintuitive expression A/S instead). This index was calculated in software InfoStat v. 2010 (Di Rienzo et al. 2010). The quantity A is measured in arbitrary units in morphospace so Ds was used only for inter-set (Patagonian vs. non-Patagonian) comparisons.

To assess whether variation at the eco-regional scale (*sensu* Burkart et al. 1999) may have influenced the morphological variation between groups, we applied redundancy analysis (RDA; Rao 1964; ter Braak 1995). RDA is the canonical form of PCA (Rao 1964; ter Braak 1995), an ordination technique with a linear constraint represented by the exploratory variables of an external matrix (ter Braak 1995). In this study, the main matrix was our morphological matrix represented by our 453 measured specimens (of all 22 vespertilionid species) by the 18 craniodental variables. The external matrix was composed by variables that contained the binary assignment of the 453 specimens to each eco-region (sensu previous section). This is a biogeographic approach in which we first tested each eco-region individually with 4,999 Monte Carlo unrestricted permutations (alpha level 0.01), and then we included the significant eco-regions in a model using a forward stepwise selection procedure (ter Braak and Šmilauer 1998).

We used a phylogenetic comparative method, canonical phylogenetic ordination (CPO; Giannini 2003), to evaluate effect of interspecific (historical) relationships on the morphofunctional variation between groups. CPO is a form of canonical ordination, here RDA, that uses main and external matrices (Giannini 2003). The main matrix was our morphological matrix, and the external matrix was composed by the set of 19 binary variables each representing a partition of the phylogenetic tree in Figure 3 as an unrooted network; tree partition are equivalent to clades when the network is rooted, so these variables encoded clade membership of each terminal. As in the previous RDA, each tree partition was tested individually using 4999 unrestricted permutations of Monte Carlo (Giannini 2003) and included in a final model using a forward stepwise selection procedure (ter Braak and Šmilauer 1998). This variable set represented a reduced tree matrix that best explained the phylogenetic effect on morphofunctional total variation without redundance (see Giannini 2003). The phylogenetic tree (Figure 3) was based on Jones et al. (2002); Hoofer and Van Den Bussche (2003), Bickham et al. (2004), Stadelmann et al. (2007), Lack and Van Den Bussche (2010), Lack et al. (2010), Roehrs et al. (2010). A more recent work (Shi and Rabosky 2015) shows a phylogeny consistent with the one used in this study.

We followed Morales and Giannini (2010) and Schiaffini and Prevosti (2014) in using the same multivariate framework to assess the possible co-variation between phylogeny (tree partitions) and biogeography (eco-regions) using partial CPO (Giannini 2003). We performed this analysis including three matrices: main morphological matrix, the external matrix of eco-regional, and the external matrix of non-redundant tree partitions (reduced tree matrix). All canonical analyses were carried out using CANOCO 4.5 (ter Braak and Šmilauer 1998).

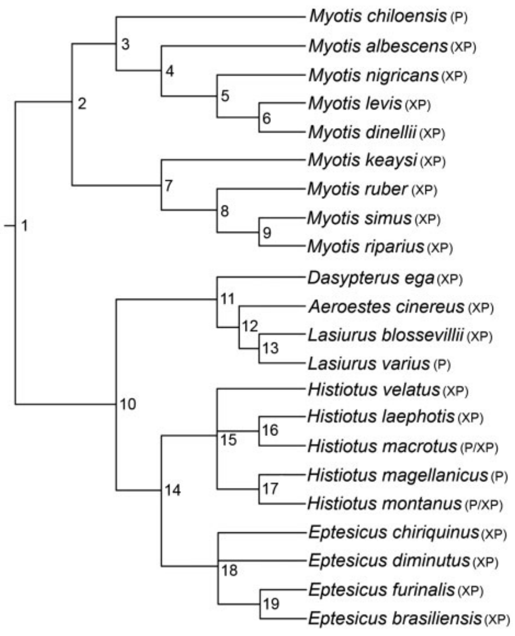

Figure 3. Cladogram of vespertilionid bats from Argentina based on Jones et al.2002; Hoofer and Van Den Bussche (2003), Bickham et al. (2004), Stadelmann et al. (2007), Lack and Van Den Bussche (2010), Lack et al. (2010), Roehrs et al. (2010). Tree partitions are indicated with numbers and correspond to clades used in canonical phylogenetic ordination. Each taxon presents the clasification of Patagonian (P) or extra-Patagonian (XP). See "Materials and Methods" section.

Finally, because some analyzed species were poorly represented in collections (with specimens from Study Area) we applied a scheme of sensitivity analysis to evaluate the effect of small samples in the morphological patterns of Patagonian and extra-Patagonian assemblages. We generated two additional datasets: 1) adding to the sample more specimens for species with $n < 10$ from localities outside the study area (Table 2); and 2) removing from the original dataset those rare species with smallest samples ($n < 5$; i.e., *Eptesicus chiriquinus*, *Eptesicus brasiliensis*, *Histiotus velatus*, and *Myotis simus*). In both cases, we performed the same analyses as above (Table 2) and compared the results with those of our main analysis, so evaluating the strength of patterns obtained for the study area.

Results

The first two principal components explained 92.7% of the total variation in the craniodental morphospace (λPC1 = 73.1% and λPC2 = 19.6%). The variables best positively correlated with CP1 were condylobasal length (CBL), length of mandible (LM), and zygomatic breadth (ZB); the PC2 axis was positively correlated with length of rostrum (LR) and length of palate (LP), and negatively with breadth across canines (CC), postorbital constriction (PO), and height of braincase (HB; see Supplementary Material S1, and Figure 4).

The general structure of morphospace was determined by interspecific size variation along PC1; gracile versus robust skulls defined the trend along PC2 (Figure 4A). Mapping Patagonian and

Table 2. Number of adult specimens used in each of three multivariate analyses

		Sensitivity analysis	
Species	Main analysis	More specimens	Fewer specimens
Eptesicus brasiliensis	1	14	–
Eptesicus chiriquinus	1	5	–
Eptesicus diminutus	8	12	12
Eptesicus furinalis	67	67	67
Histiotus laephotis	8	8	8
Histiotus macrotus	35	35	35
Histiotus magellanicus	7	7	7
Histiotus montanus	9	11	11
Histiotus velatus	4	6	–
Lasiurus blossevillii	38	38	38
Lasiurus varius	8	12	12
Aeorestes villosissimus	32	32	32
Dasypterus ega	17	17	17
Myotis albescens	40	40	40
Myotis chiloensis	24	24	24
Myotis dinellii	46	46	46
Myotis keaysi	8	11	11
Myotis levis	50	50	50
Myotis nigricans	22	22	22
Myotis riparius	21	21	21
Myotis ruber	5	5	5
Myotis simus	2	8	–

Main analysis included all specimens available of vespertilionid bats from patagonian and extra-patagonian assemblages of Southern Cone. The first sensitivity analysis included all specimens plus 51 additional specimens from other regions of the South America of species represented in the previous sample by <10 specimens. Sample sizes are shown in the second data column ("more specimens"). Specimen details in Supplementary Appendix 1 and 2. The second additional analysis included all the specimens in the first analysis minus the species *Eptesicus brasiliensis, E.chiriquinus, E.diminutus* and *H.velatus* (all with $n < 5$).

extra-Patagonian sets via minimum polygons showed a similar pattern for both assemblages; smaller species (*Myotis* spp., *Lasiurus blossevillii* and *L. varius*) toward the negative end of PC1 and larger species (*Eptesicus* spp., *Histiotus* spp., *Aeorestes villosissimus* and *Dasypterus ega*) placed toward the positive end of PC1. In turn, species with slender skulls (*Myotis* spp., *Eptesicus* spp., and *Histiotus* spp.) were located toward the positive end of PC2 and species with short, robust skulls appeared toward the negative end of PC2 (*Lasiurus* spp.; Figure 4A and B). The morphospace area occupied by Patagonian vespertilionids was about 30% smaller (7.33 arbitrary area units) than the extra-Patagonian space (10.52 area units). If the marginally Patagonian specimen of *Aeorestes villosissimus* was included, differences between sets are smaller. For reasons outlined above, the specimen was excluded and so the main differences between sets are the lack in Patagonia of 1) very small species, and 2) larger species of lasiurines (i.e., *Aeorestes villosissimus* and *Dasypterus ega*; Figure 3). Patagonian species or specimens tend to be larger than their closer extra-Patagonian relatives (i.e., *M. chiloensis* vs. sister species of *Myotis*, *Lasiurus varius* vs. *L. blossevillii*, Patagonian vs. extra-Patagonian *Histiotus*). Variation along PC2 did not allow a clear distinction of Patagonian vs. extra-Patagonian vespertilionids, overall, the former set was nested within the extra-Patagonian space. In addition, non-realized morphospace (i.e., empty areas among sampled specimens) corresponded largely to spacing among genera in both the Patagonian and extra-Patagonian sets, but it was more evident in the former due to its lack of species of *Eptesicus* sensu stricto (Figure 4).

Pattern of species packing, as estimated by the Clark–Evans Index (CEI), indicated that both groups had clustered species distributions although CEI was lower for the extra-Patagonian as compared to the Patagonian group ($\text{CEI} = 0.0488$, $P = 0.0004$; $\text{CEI} = 0.1951$ $P = 0.0004$, respectively). Degree of species packing, as estimated by species density Ds, was 2.7 times greater for the extra-Patagonian set as compared with the Patagonian counterpart ($\text{Ds} = 0.68$ and $\text{Ds} = 1.81$, respectively).

Redundancy analyses (RDA) showed that two Patagonian eco-regions (Forest and Steppe), together with three non-Patagonian eco-regions (Humid Pampas, Savanna and Malezales, and Puna) significantly ($P < 0.01$) explained ~13% of the total morphological variation (Table 3). The eco-regions that presented higher contribution (> 1.5%) were Patagonian Forest and Steppe, and Humid Pampas (Table 3). Phylogeny was the most important factor to explain the morphofunctional variation with all clades individually significant ($P < 0.01$, Table 4), and ten clades selected to compose the reduced external matrix (clades: 2, 13, 18, 11, 19, 6, 4, 3, 5 and 9, with $P < 0.01$; Table 4). Just the best three tree partitions explained together as much as 66.9% of total morphological variation, those of clade 2, separating *Myotis* from species from the rest of vespertilionids; clade 13, which includes *L. varius* and *L. blossevillii*; and clade 18, which includes *Eptesicus* species (Figure 3). Partial CPO showed a small but significant fraction of morphological variation associated with eco-regions that was independent of phylogeny (just 1.2%). The two more important eco-regions were again Patagonian Forest and Steppe.

Sensitivity analyses

The first additional analysis including 51 specimens of rare species from localities outside the study area showed essentially the same pattern of assemblages (Patagonian and extra- Patagonian) in the multivariate morphofunctional space (cf. Figure 4 with Supplementary Material S2). The amount of variation explained by PC axes 1 and 2 was practically the same (see Figure 4 and Supplementary Material S2). The first additional RDA, showed similar results, indicating as important the Patagonian Forest (4%) and Humid Pampas (2.7%) eco-regions (Supplementary Material S3). Likewise, partial CPO confirmed these results and included an additional important eco-region (Guianan Moist Forest sensu Olson et al. 2001) due to geographic expansion of study area. Phylogeny was again the most important factor affecting the morphological pattern of assemblages mostly due to the same tree partitions as in the main analysis. The first two partitions selected were the same, with clade 2 (*Myotis*) and 13 (*Lasiurus*) explaining the great majority (57.8%) of morphofunctional variation, only slightly less than in the main analysis (~ 59.7%; see Supplementary Material S4).

The additional analysis excluding rare species ($n < 5$; see above), showed a morphofunctional pattern of species identical to the previous analysis (*cf*. S5 with Figure 4 and Supplementary Material S2). The second additional RDA selected the same eco-regions but with different importance (Humid Pampas = 4%, and Patagonian Forest = 2.7%, respectively; Supplementary Material S6). The partial CPO analysis showed Humid Pampas and Low Monte as the most important eco-regions. Likewise, the second additional CPO showed a strong influence of phylogeny and the tree partitions that explain the most variation were the same (clades 2 and 13 clades; see Supplementary Material S7) as in the main analysis.

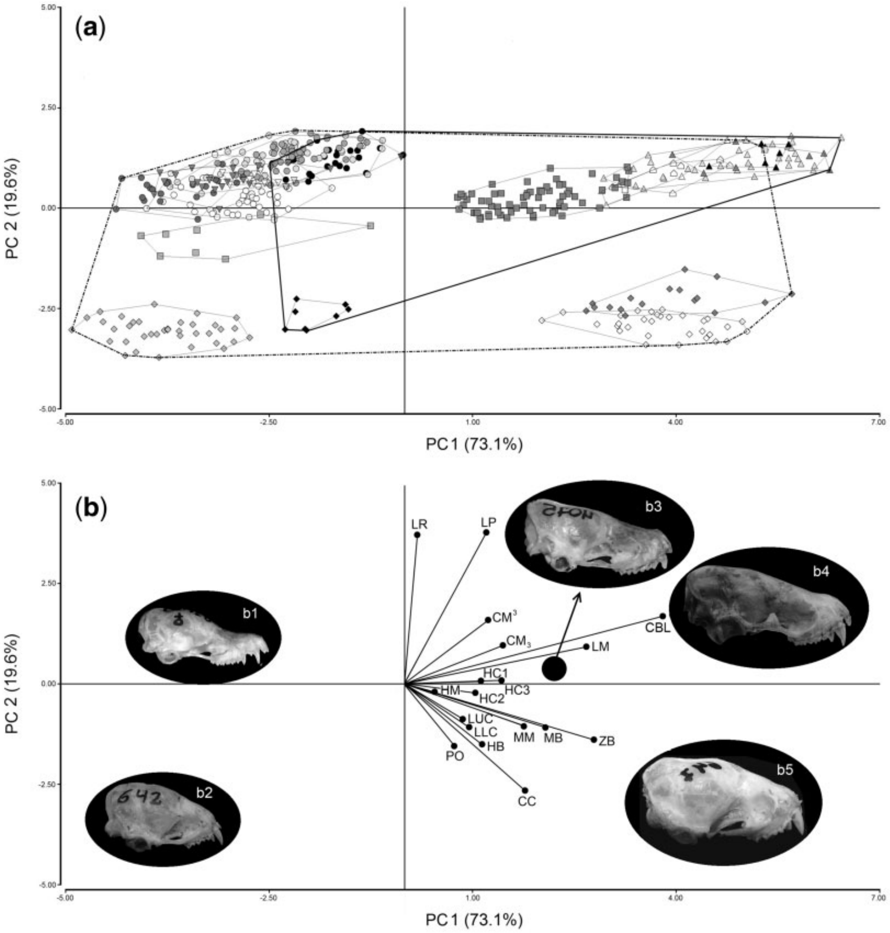

Figure 4. Ordination diagram of principal components analysis. (**A**) Segregation of the Patagonian and extra-Patagonian vespertilionid species from Argentina; polygons include patagonian (continuous line) and extra-patagonian (dotted line) species. Black symbols: endemic species from Patagonia. *Eptesicus brasiliensis* (open square), *E. chiriquinus* (■), *E. diminutus* (■), *E. furinalis* (■); *Histiotus laephotis* (⌂), *H. macrotus* (▲), *H. magellanicus* (▲), *H. montanus* (▲), *H. velatus* (△), *Lasiurus blossevillii* (♦), *L. varius* (♦), *Aeorestes villosissimus* (◊), *Dasypterus ega* (♦), *Myotis albescens* (○), *M. chiloensis* (●), *M. dinellii* (●), *M. keaysi* (white ▼), *M. levis* (●), *M. nigricans* (●), *M. riparius* (▼), *M. ruber* (▼), *M. simus* (▼). **B**) Vectors show the strengh of correlation of each variable with the plane of PC1 and PC2, and morphotypes ends for each component (b1: *M. levis* ICM 2120; b2: *L. blossevillii* MMPM 642; b3: ICM 4075; b4: *H. macrotus* LIEB-M 851; b5: *D. ega* MMPM 647). See text for abbreviations.

Table 3. Results of redundancy analysis for patagonian and extra-patagonian vespertilionid from argentina

Analysis	Variables	Variance	*F*-value	*P*-value
Individual	Patagonian Forest	0.057	27.063	0.0002
	Humid Pampas	0.030	13.716	0.0002
	Dry Chaco	0.020	8.968	0.0008
	Patagonian Steppe	0.012	5.515	0.0054
Forward stepwise selection	**Patagonian Forest**	0.057	27.063	0.0002
	Humid Pampas	0.031	15.045	0.0002
	Patagonian Steppe	0.017	8.283	0.0002
	Savanna and Malezales	0.012	6.002	0.004
	Puna	0.013	6.365	0.0008

Values significant at the $P = 0.01$. In bold the most important eco-regions selected by the model.

In conclusion, our additional analyses, which constituted effective tests of the results seen in our main analyses, demonstrated that the effect on the results of sample size in rare species was negligible.

Discussion

Vespertilionid bats are key components of all Neoptropical chiropteran assemblages. This represents the only one bat family that has been able to diversify in cold environments as extreme as Patagonia (Koopman 1982; Lack and Van Den Bussche 2010). Only one species from another bat family, the molossid *Tadarida brasiliensis* is widely recorded in Patagonia (Barquez et al. 1999), co-occurring with vespertilionid bats here and elsewhere in the American continent. The vespertilionid Patagonian assemblage is distinctive in having fewer (just five) species than other Neotropical assemblages, including two endemics (*Lasiurus varius* and *Histiotus*

Table 4. Results of canonical phylogenetic ordination for patagonian and extra-patagonian vespertilionid bats from Argentina

Analysis	Variables	Variance	*F*-value	*P*-value
Individual	2	0.326	281.294	<0.001
	10	0.368	218.294	<0.001
	14	0.271	168.043	<0.001
	15	0.265	163.168	<0.001
	3	0.235	138.562	<0.001
	4	0.206	117.326	<0.001
	12	0.189	105.372	<0.001
	16	0.173	94.421	<0.001
	11	0.157	83.986	<0.001
	13	0.155	82.713	<0.001
	5	0.135	70.568	<0.001
	6	0.088	43.385	<0.001
	17	0.067	32.571	<0.001
	19	0.051	24.070	<0.001
	7	0.036	16.986	<0.001
	18	0.036	16.950	<0.001
	9	0.030	13.864	<0.001
	8	0.029	13.482	<0.001
Forward stepwise selection	**2**	0.326	218.294	<0.001
	13	0.271	303.605	<0.001
	18	0.072	97.313	<0.001
	11	0.067	113.961	<0.001
	19	0.004	36.079	<0.001
	6	0.010	18.461	<0.001
	4	0.009	16.916	<0.001
	3	0.008	15.580	<0.001
	5	0.003	5.741	<0.001
	9	0.002	3.376	0.0054

Clades are numbered as in Figure 3. Values significant at the $P = 0.01$. In bold is the most important partition tree selected by the model.

magellanicus), one nearly endemic species (*Myotis chiloensis*), and two species with distinct (larger) Patagonian populations (*Histiotus macrotus* and *H. montanus*). Redundancy analyses (see below) also demonstrated statistically that the Patagonian assemblage is a natural one. In contrast, extra-Patagonian vespertilionid assemblages are characteristically richer, with many species shared across several eco-regions. As many as 17 species inhabit those eco-regions and just two species (*H. macrotus* and *H. montanus*) are shared with Patagonia.

Patagonian exclusive or semi-exclusive species, as well as distinct populations of widespread species, are best described as vicariant with respect to closely related extra-Patagonian species or populations. Specifically, *Myotis chiloensis* is sister to a group containing the extra-Patagonian neighbors *M. albescens*, *M. nigricans* and *M. levis* (Ruedi et al. 2013), and *Lasiurus varius* is a very distinctive species but most similar to the extra-Patagonian, widespread *L. blossevillii* of which the former was long considered a junior synonym (see Barquez et al. 1999). Likewise, although a comprehensive phylogeny of *Histiotus* is still lacking, the endemic *H. magellanicus* was recently accepted as a valid species with respect to *H. montanus* (see Giménez et al. 2012 and citations therein), and *H. macrotus* may prove to be a composite taxon with separate populations in Patagonia (Giménez et al. 2015). Of these Patagonian vicariant events, two have been dated the one involving *Myotis chiloensis* at 5.5 My (Ruedi et al. 2013), and the one involving *Lasiurus varius* at ~7 My (Baird et al. 2015; both cases are point estimates of relatively wide time intervals).

In ecomorphological terms, the Patagonian assemblage structurally is a subset of the extra-Patagonian group. The former occupies a widely overlapping portion of morphospace that is only about 30% smaller than the area covered by the considerably richer extra-Patagonian assemblage. The Patagonian set is depauperate in species and this is directly reflected in the degree of species packing. Thus, the occupied morphospace is roughly similar, with the same pattern of packing (clustered distributions), different degree of packing, and some functionally important differences. Specifically, the Patagonian set lacks representatives of large lasiurine species, *Aeorestes villosissimus* and *Dasypterus ega* (with the former only marginally present in northern Patagonia), so the space region of relatively large vespertilionids with robust skulls, which is a morphology often related to a durophagous diet (i.e., consumption of large hard-bodied prey such as large beetles; Freeman 1979, 1981) appeared empty. Second, the absence of morphologically typical (i.e., not long-eared) *Eptesicus* species generates a greater portion of potential but presently unrealized morphospace inside the Patagonian polygon. This is more remarkable considering that typical *Eptesicus* species from other continents commonly occupy temperate or cold regions to some extent comparable to Patagonia (e.g., North American *E. fuscus*, Kurta and Baker 1990). Regarding degree of species packing, the extra-Patagonian assemblage is 3.4 times richer in species within a morphospace that is only some 40% larger than the space occupied by the Patagonian assemblage, which results in 2.7 times greater species density (Ds) in the former. Often such differences have been related with environmental productivity (Currie et al. 2004) as this factor grossly determines the availability of resources in each environment (Currie et al. 2004; Stevens 2004; Buckley et al. 2010; McNab 2010). Some of the extra-Patagonian eco-regions (e.g., Southern Yungas Montane Rain and Cloud Forest, Dry Chaco) exhibit much more favorable climatic conditions and concomitantly, higher productivity, which may translate into a greater availability of food resources throughout the year, thus packing more species of different sizes and ecological roles. In contrast, Patagonian environments (i.e., Patagonian Forests and Steppe), with a colder, strongly seasonal climate, and lower productivity, may exhibit great fluctuations in insect abundance throughout the year (Mazía et al. 2006; Ruggiero et al. 2009) which might not allow the maintenance of many resident species and abundant populations. These factors are known to profoundly affect bat survival and size of bat populations (Glanz 1982; McNab 1982; Speakman and Thomas 2003; Boyles et al. 2008). Through their likely physiological effects, these factors may also explain the fact that Patagonian vespertilionid species or specimens are larger than their closest extra-Patagonian vicariants (e.g., *L. varius* larger than *L. blossevillii*, *M. chiloensis* larger than extra-Patagonian species of its sister group).

Despite these clear differences, both species sets showed a comparable morphofunctional structure, with a clustered species distribution (low CEI values) that depicted a strong sub-aggregated pattern largely due to spacing among genera. For this reason, phylogeny explained much of the observed morphofunctional pattern, as revealed by the phylogenetic comparative analysis (CPO). In fact, the structure of this space was so embedded in phylogeny that the only overlapping groups were *Eptesicus* and *Histiotus*, which are today classified as congeneric (Hoofer and Van Den Bussche 2003; Roehrs et al. 2010; Van Den Bussche and Lack 2013). The tree partition that separated *Myotis* from the remainder of species was the more important one. At a global scale, *Myotis* represents one of the greatest diversifications among mammals (Hoofer and Van Den

Bussche 2003; Stadelmann et al. 2007; Ruedi et al. 2013, 2015) despite being one of the most conservative clades within the family (e.g., conservative, unreduced dental formula, ancestral karyotype, etc.; Bickham 1979; Hoofer and Van Den Bussche 2003; Bickham et al. 2004; Wilson 2007). *Myotis* is also an ancient clade dated between 30 Ma (back in the early Oligocene of Europe; Hoofer and Van Den Bussche 2003; Lim 2009) and 26 Ma (Ruedi et al. 2013). The endemic New World clade originated ~12 Ma (Ruedi et al. 2013), while the South American branch of this group emerged some 7–10 Ma in the middle Miocene (Stadelmann et al. 2007), i.e., prior to the Great American Biotic Interchange maximum. In our study area, *Myotis* is the most diverse genus within the family; in both the Patagonian and extra-Patagonian sets the morphospace occupied by *Myotis* species is not shared with any other vespertilionid genus. Except for the related *Eptesicus* and *Histiotus*, this is true for all other genera, so this pattern in the Southern Cone likely reflects a larger, perhaps global pattern for the family, which is thought to vary morphologically only modestly among lineages, even among its most distantly related members (Lack and Van Den Bussche 2010; Van Den Bussche and Lack 2013). Because Vespertilionidae experienced an early diversification that included a rapid evolution in temperate environments following a quick cosmopolitan expansion, the need of specialized divergence was reduced (Lack and Van Den Bussche 2010) and the morphospace structure never really expanded to radically new morphotypes, as in several other bat groups (e.g., phyllostomid bats; Baker et al. 2012).

The variation of morphological patterns observed in morphospace was only limitedly affected by biogeography, i.e., by the classification in eco-regions (only ~13% of total variation). However, it is remarkable that even if marginal, this variation was primarily related to the Patagonian Forest and Steppe eco-regions. The eco-regional variation was very low (just 1.2%) but still statistically significant when evaluated independently of phylogeny. This means that biogeography largely co-varied with phylogeny, as demonstrated in many vespertilionoid clades (e.g., *Miniopterus*, Appleton et al. 2004; *Myotis*, Ruedi et al. 2013), and that the former contributed some to explain the morphological variation of vespertilionid bats in the South American Southern Cone.

In conclusion, we showed that the Patagonian assemblage is a structurally similar but depauperate ecomorphological vicariant of those assemblages from richer eco-regions located immediately North of Patagonia, regions that encompass temperate and subtropical environments that may have acted as sources of species, and together with Patagonia comprise the extra-tropical Neotropics or the South America Southern Cone. Historically, the Patagonian assemblage seems to have formed by successively adding vicariant species or populations sister to corresponding species or lineages in extra-Patagonian eco-regions, which were characteristically richer. This process is demonstrably old, particularly older than the GABI maximum. The harsh environmental conditions of Patagonia may have prevented the success of possibly many colonization events so that the present species richness remains low; still, representatives of several key morphotypes, corresponding to specific vespertilionid lineages, did establish in Patagonia so the morphofunctional structure of the assemblage remained quite similar to the original extra-Patagonian assemblages. However, degree of species packing was comparatively very low, which may reflect the combined effect of limited dispersal success and relatively poor local conditions for bat populations to establish in Patagonia.

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Supplementary material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

References

Appleton BR, McKenzie JA, Christidis L, 2004. Molecular systematics and biogeography of the bent–wing bat complex *Miniopterus schreibersii* (Kuhl, 1817) (Chiroptera: Vespertilionidae). *Mol Phylogenet Evol* **31**:431–439.

Baddeley A, Turner R, 2005. Spatstat: an R package for analyzing spatial point patterns. *J Stat Softw* **12**:1–42.

Baird AB, Braun JK, Mares MA, Morales JC, Patton JC et al., 2015. Molecular systematic revision of tree bats (Lasiurini): doubling the native mammals of the Hawaiian Islands. *J Mammal* **96**:1255–1274.

Baker RJ, Patton JC, Genoways HH, Bickham JW, 1988. Genic studies of *Lasiurus* (Chiroptera: Vespertilionidae). *Occas Pap Mus Tex Tech Univ* **117**:1–15.

Baker RJ, Bininda-Emonds OR, Mantilla-Meluk H, Porter CA, Van Den Bussche RA, 2012. Molecular timescale of diversification of feeding strategy and morphology in New World leaf-nosed bats (Phyllostomidae): a phylogenetic perspective. In: Gunnell GF, Simmons NB, editors. *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge: Cambridge University Press, 386–409.

Barquez RM, 2006. Orden Chiroptera Blumenbach, 1779. In: Barquez RM, Díaz MM, editors. *Mamíferos de Argentina: Sistemática y Distribución*. Tucumán: Sociedad Argentina para el Estudio de los Mamíferos, 56–86.

Barquez RM, Mares MA, Braun JK, 1999. *The Bats of Argentina*. Lubbock: Special Publications of the Museum of Texas Tech University.

Baud JF, 1979. *Myotis aelleni*, nov. spec., chauve-souris nouvelle d’ Argentine (Chiroptera: Vespertilionidae). *Rev Suisse Zool* **86**:267–278.

Bickham JW, 1979. Chromosomal variation and evolutionary relationships of vespertilionid bats (Mammalia: Chiroptera). *J Mammal* **60**:350–363.

Bickham JW, Patton JC, Schlitter DA, Rautenbach IL, Honeycutt RL, 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). *Mol Phylogenet Evol* **33**:333–338.

Boyles JG, Storm JJ, Brack VJr, 2008. Thermal benefits of clustering during hibernation: a field test of competing hypotheses on *Myotis sodalis*. *Funct Ecol* **22**:632–636.

Buckley LB, Davies TJ, Ackerly DD, Kraft NJB, Harrison SP et al., 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proc R Soc Lond B* **277**:2131–2138.

Burkart R, Bárbaro NO, Sánchez RO, Gómez DA, 1999. *Eco-regiones de la Argentina*. Buenos Aires: Administración de Parques Nacionales, Programa Desarrollo Institucional Ambiental.

Clark PJ, Evans FC, 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**:445–453.

Currie DJ, Mittelbach GG, Cornell HV, Field R, Guégan JF et al., 2004. Predictions and tests of climatebased hypotheses of broad-scale variation in taxonomic richness. *Ecol Lett* **7**:1121–1134.

Di Rienzo JA, Casanoves F, Balzarini MG, Gonzalez L, Tablada M et al., 2010. *InfoStat*. Argentina: Grupo InfoStat, FCA, Universidad Nacional de Córdoba.

Findley JS, Black H, 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* **64**:625–630.

Freeman PW, 1979. Specialized insectivory: beetle-eating and moth-eating molossid bats. *J Mammal* **60**:467–479.

Freeman PW, 1981. Correspondence of food habits and morphology in insectivorous bats. *J Mammal* **62**:166–173.

Gardner AL, 2007. *Mammals of South America*, Vol. **1**: *Marsupials, Xenarthrans, Shrews, and Bats*. Chicago: University of Chicago Press.

Giannini NP, 2003. Canoncial phylogenetic ordination. *Syst Biol* **52**:684–695.

Giménez AL, Giannini NP, 2011. Morphofunctional and geographic segregation among species of lasiurine bats (Chiroptera: Vespertilionidae) from the South American Southern Cone. *Mammalia* **76**:173–179.

Giménez AL, Giannini NP, Schiaffini MI, Martin GM, 2012. New records of the rare Histiotus magellanicus (Chiroptera, Vespertilionidae) and other bats from Central Patagonia. *Argentina Mastozool Neotrop* **19**:213–224.

Giménez AL, Giannini NP, Schiaffini MI, Martin GM, 2015. Geographic and potential distribution of a poorly known South American bat *Histiotus macrotus* (Chiroptera: Vespertilionidae). *Acta Chiropt* **17**:143–158.

Glanz WE, 1982. The terrestrial mammal fauna of Barro Colorado Island: censuses and long-term changes. In: Leigh EG, Rand AS, Windsor DM, editors. *The Ecology of a Tropical Forest*. Washington: Smithsonian Institute Press, 239–251.

Hijmans RJ, Guarino L, Mathur P, Jarvis A, Rojas E et al., 2005. DIVA-GIS version 7.5.0.0. http://www.diva-gis.org.

Hoofer SR, Van Den Bussche RA, 2003. Molecular phylogenetics of the Chiropteran family Vespertilionidae. *Acta Chiropt* **5**:1–63.

Jones KE, Purvis A, MacLarnon A, Bininda-Emonds ORP, Simmons NB, 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biol Rev* **77**:223–259.

Karr JR, James FC, 1975. Ecomorphological configurations and convergent evolution. In: Cody ML, Diamond JM, editors. *Ecology and Evolution of Communities*. Cambridge: Belknap Press, 258–291.

Kawai K, Nikaido M, Harada M, Matsumura S, Lin LK et al., 2002. Intra- and Interfamily relationships of Vespertilionidae inferred by various molecular markers including SINE insertion data. *J Mol Evol* **55**:284–301.

Koopman KF, 1982. Biogeography of the bats of South America. In: Mares MA, Genoways HH, editors. *Mammalian Biology in South America*. Pennsylvania: University of Pittsburgh, 273–302.

Kurta A, Baker RH, 1990. *Eptesicus fuscus*. *Mamm. Species* **356**:1–10.

Kurta A, Lehr GC, 1995. *Lasiurus ega*. *Mamm. Species* **515**:1–7.

Lack JB, Van Den Bussche RA, 2010. Identifying the confounding factors in resolving phylogenetic relationships in Vespertilionidae. *J Mammal* **91**: 1435–1448.

Lack JB, Roehrs ZP, Stanley CE Jr, Ruedi M, Van Den Bussche RA, 2010. Molecular phylogenetics of *Myotis* suggests familial-level divergence for the genus *Cistugo* (Chiroptera). *J Mammal* **91**:976–992.

León RJC, Bran D, Collantes M, Paruelo JM, Soriano A, 1998. Grandes unidades de vegetación de la Patagonia extra andina. *Ecol Austral* **8**:125–144.

Lim BK, 2009. Review of the origins and biogeography of bats in South America. *Chirop Neotrop* **l**:391–410.

Mancini MV, Paez MM, Prieto AR, Stutz S, Tonello M et al., 2005. Mid-Holocene climatic variability reconstruction from pollen records (32°–52°S, Argentina). *Quat Int* **132**:47–59.

Mazía CN, Chaneton EJ, Kitzberger T, 2006. Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. *J Arid Environ* **67**:177–194.

McNab BK, 1982. Evolutionary alternatives in the physiological ecology of bats. In: Kunz TH, editor. *Ecology of Bats*. USA (NY): Springer, 151–200.

McNab BK, 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia* **164**:13–23.

Morales JC, Bickham JW, 1995. Molecular systematics of the genus *Lasiurus* (Chiroptera: Vespertilionidae) based on restriction-site maps of the mitochondrial ribosomal genes. *J Mammal* **76**:730–749.

Morales MM, Giannini NP, 2010. Morphological patterns in neotropical felids: species co-existence and historical assembly. *Biol J Linn Soc* **100**: 711–724.

Moreno CE, Arita HT, Solis L, 2006. Morphological assembly mechanisms in Neotropical bat assemblages and ensembles within a landscape. *Oecologia* **149**:133–140.

Nogueira MR, Peracchi AL, Monteiro LR, 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. *Funct Ecol* **23**:715–723.

Nowak RM, 1999. *Walker's Mammals of the World*. 6th edn, Vol. **I**. Baltimore: Johns Hopkins University Press.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN et al., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* **51**:933–938.

Paruelo JM, Beltrán A, Jobbágy E, Sala OE, Golluscio RA, 1998. The climate of Patagonia: general patterns and controls on biotic processes. *Ecol Austral* **8**:85–101.

Patterson BD, Willig MR, Stevens RD, 2003. Trophic strategies, niche partitioning, and patterns of ecological organization. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. Chicago and London: The University of Chicago Press, 536–579.

R Development Core Team, 2015. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rao CR, 1964. The use and interpretation of principal component analysis in applied research. *Sankhya A* **26**:329–358.

Roehrs ZP, Lack JB, Van Den Bussche RA, 2010. Tribal phylogenetic relationships within Vespertilioninae (Chiroptera: Vespertilionidae) based on mitochondrial and nuclear sequence data. *J Mammal* **91**: 1073–1092.

Ruedi M, Stadelmann B, Gager Y, Douzery EJP, Francis CM et al., 2013. Molecular phylogenetic reconstructions identify East Asia as the cradle for the evolution of the cosmopolitan genus *Myotis* (Mammalia, Chiroptera). *Mol Phylogenet Evol* **69**:437–449.

Ruedi M, Csorba G, Lin LK, Chou CH, 2015. Molecular phylogeny and morphological revision of *Myotis* bats (Chiroptera: Vespertilionidae) from Taiwan and adjacent China. *Zootaxa* **3920**:301–342.

Ruggiero A, Sackmann P, Farji-Brener AG, Kun M, 2009. Beetle abundance-environment relationships at the Subantarctic-Patagonian transition zone. *Insect Conserv Diver* **2**:81–92.

Santana SE, Grosse IR, Dumont ER, 2012. Dietary hardness, loading behavior, and the evolution of skull form in bats. *Evolution* **66**:2587–2598.

Schiaffini MI, Martin GM, Giménez AL, Prevosti FJ, 2013. Distribution of Lyncodon patagonicus (Carnivora, Mustelidae): changes from the Last Glacial Maximum to the present. *J Mammal* **94**:339–350.

Schiaffini MI, Prevosti FJ, 2014. Trophic segregation of small carnivorans (Carnivora: Mustelidae and Mephitidae) from the southern cone of South America. *J Mamm Evol* **21**:407–416.

Shi JJ, Rabosky DL, 2015. Speciation dynamics during the global radiation of extant bats. *Evolution* **69**:1528–1545.

Simmons NB, 2000. Bat phylogeny: an evolutionary context for comparative studies. In: Adams RA, Pedersen SC, editors. *Ontogeny, Functional Ecology, and Evolution of Bats*. New York: Cambridge University Press, 2–58.

Simmons NB, 2005. Order Chiroptera. In: Wilson DE, Reeder DM, editors. *Mammals Species of the World: A Taxonomic and Geographic References*. Baltimore (MD): Johns Hopkins University Press.

Simmons NB, Voss RS, 1998. The mammals of Paracou, French Guiana, a Neotropical lowland rainforest fauna. *Part 1, Bats Bull Am Mus Nat Hist* **237**:1–219.

Speakman JR, Thomas DW, 2003. Physiological ecology and energetic of bats. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. Chicago and London: The University of Chicago Press, 430–490.

Stadelmann B, Lin LK, Kunz TH, Ruedi M, 2007. Molecular phylogeny of New World *Myotis* (Chiroptera, Vespertilionidae) inferred from mitochondrial and nuclear DNA genes. *Mol Phylogenet Evol* **43**:32–48.

Stevens RD, 2004. Untangling latitudinal richness gradients at higher taxonomic levels: familial perspectives on the diversity of New World bat communities. *J Biogeogr* **31**:665–674.

Stevens RD, 2006. Historical processes enhance patterns of diversity along latitudinal gradients. *Proc R Soc B* **273**:2283–2289.

Stevens RD, Willig MR, Strauss RE, 2006. Latitudinal gradients in the phenetic diversity of New World bat communities. *Oikos* **112**:41–50.

Swartz SM, Freeman PW, Stockwell EF, 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. In: Kunz TH, Fenton MB, editors. *Bats Ecology*. Chicago and London: The University of Chicago Press, 257–292.

ter Braak CJF, 1995. Ordination. In: Jongman RHG, ter Braak CJF, Van Tongeren OFR, editors. *Data Analysis in Community and Landscape Ecology*. Cambridge: Cambridge University Press, 91–173.

ter Braak CFJ, Šmilauer P, 1998. *CANOCO Reference Manual and User'S Guide to CANOCO for Windows: Software for Canonical Community Ordination*, version 4.0. Ithaca (NY): Microcomputer Power.

Van Den Bussche RA, Lack JB, 2013. Bat molecular phylogenetics: past, present, and future directions. In: Adams RA, Pedersen SC, editors. *Bat Evolution, Ecology, and Conservation*. New York: Springer Science+Business Media, 111–128.

Villalobos F, Arita HT, 2014. Morphological diversity at different spatial scales in a Neotropical bat assemblage. *Oecologia* **176**:557–568.

Willig MR, Patterson BD, Stevens RD, 2003. Patterns of range size, richness, and body size in the Chiroptera. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. Chicago and London: The University of Chicago Press, 580–615.

Wilson DE, 2007. Genus *Myotis* Kaup, 1929. In: Gardner AL, editor. *Mammals of South America, vol. 1, Marsupials, Xenarthrans, Shrews, and Bats*. Chicago: University of Chicago Press, 469–481.

Wainwright PC, 1994. Functional morphology as a tool in ecological research. In: Wainwright PC, Reilly SM, editors. *Ecological Morphology: Integrative Organismal Biology*. Chicago and London: The University of Chicago Press, 42–59.