



Original Investigation

Climate fluctuations as a cause of rarity in fairy armadillos

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ABSTRACT

Despite having a moderately large distributional area, both the pink fairy armadillo (*Chlamyphorus truncatus*) and particularly the Chacoan fairy armadillo (*Calyptophractus retusus*), which are among the least known xenarthrans, appear to be rare or patchily distributed. Although low density in species with large range sizes has been associated with large body size, this is not the case for fairy armadillos. We propose that past climate variations may have caused their current low densities, and evaluate retractions and expansions of suitable areas of fairy armadillos by extrapolating the consensus of habitat suitability models fitted with current climatic conditions to past conditions. We found great variation in suitable area along time in both species, with a drastic reduction in the Last Interglacial (LIG) period when compared with current situation. Both the variations and the reduction during LIG were more pronounced in *Calyptophractus* than in *Chlamyphorus*. We postulate that past extreme reductions in suitable areas could cause a delay in the recovery of the populations, resulting in low densities despite climatic conditions during more benign times allowing a more widespread distribution.

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Introduction

The pink fairy armadillo (*Chlamyphorus truncatus*) and the Chacoan fairy armadillo (*Calyptophractus retusus*; Mammalia: Cingulata: Dasypodidae: Chlamyphorinae) are among the least known xenarthrans (Superina et al., 2014a,b), in part due to their small size (up to 100 g) and subterranean lifestyle, for which they are highly adapted (Gardner, 2008; Wetzel, 1985). Consequently, field research on these cryptic mammals is difficult and information on their ecology is scarce, with aspects as basic as their distributional range being incompletely known (Superina et al., 2014a). It is thus not surprising that both species are currently listed as Data Deficient in the IUCN Red List of Threatened Species (Abba and Superina, 2010).

The current known distributions of the two fairy armadillo species are allopatric (Delsuc et al. 2012). The occurrence records of *Chlamyphorus* extend over 350,000 km² in central Argentina, and are concentrated in the Monte and Espinal ecoregions (sensu Burkart et al., 1999). The scarce presence localities of *Calyptophractus* are distributed over 258,000 km² in the Gran Chaco region,

a tropical area encompassing northern Argentina, south-eastern Bolivia and western Paraguay (Fig. 1; Abba and Superina, 2010; Abba et al., 2012; Gardner, 2008). Despite their moderately large distributional area, fairy armadillos, and particularly *Calyptophractus*, are rare and patchily distributed (Abba and Superina, 2010). These low densities are also shared by some other insectivorous subterranean mammals living in arid sandy zones, such as the Australian notoryctids (Benshemesh and Burbidge, 2008; Dickman et al., 2008) and some golden moles (e.g., Jackson and Robertson, 2011). They cannot be attributed to the elusiveness of such species alone given that other insectivorous, strictly subterranean mammals, such as moles and most golden moles, are observed far more frequently (e.g., Bronner, 2008; Goszczynski, 1983; Nevo, 1979).

Although some factors, such as habitat loss and hunting by domestic dogs and cats (*Chlamyphorus*) or persecution and death due to local traditional beliefs (*Calyptophractus*), could have deleterious effects on some populations (Aguar and da Fonseca, 2008; Roig, 1995; Superina, 2006), there is no doubt that fairy armadillos are naturally rare (Chébez, 2008; Cuellar et al., 2014; Superina et al., 2014b). Natural factors associated with limited distribution or density include species traits such as low growth rates, long generation time, small litter size, large area requirements, high specialization and large body size, as well as ecosystem traits such as low carrying capacity or scarcity of suitable habitats (Flather and Sieg, 2007). This last factor seems to be an important constraint, as some

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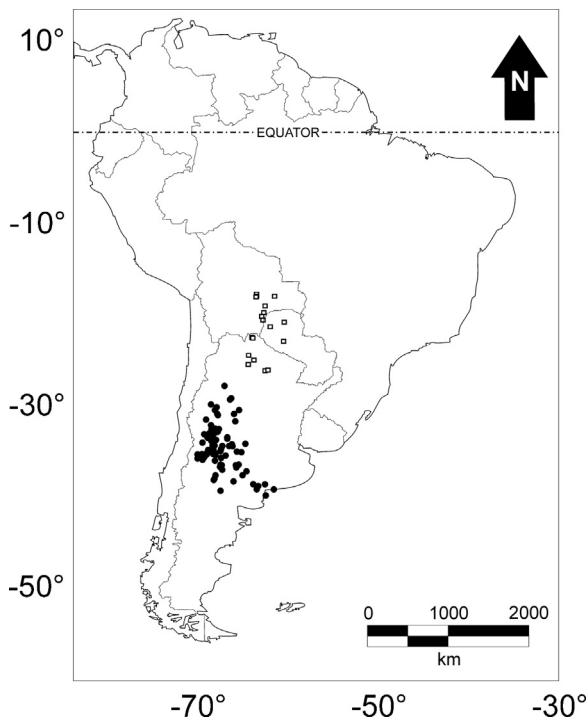


Fig. 1. Distribution of presence localities of *Chlamyphorus* (dark circles) and *Calyptophractus* (open squares). Geographic projection: Aitoff.

evidence suggests that species with very limited distributional ranges would be survivors of past climatic changes that currently persist only in those small areas where climates resemble conditions that were more widespread in the past (Ohlemüller et al., 2008). Rarity is, however, not determined solely by range size but also by population density (Flather and Sieg, 2007; Rabinowitz, 1981; Rabinowitz et al., 1986), and many species (such as fairy armadillos) can be regarded as “rare” for their low densities despite showing broad distributional areas. We postulate that low density in these species could be the consequence of extreme variations in range size and habitat suitability, caused in turn by extreme variations in past climates. In other words, after having suffered a drastic decrease in suitable areas as a consequence of a past climate change, species with high specialization and low dispersal capability (and possibly low productivity), such as fairy armadillos, could take an exceedingly long time to recolonize all suitable habitats once the climate becomes benign again.

We modeled the habitat suitability for fairy armadillos under current climate conditions and extrapolated these models to the projected past conditions (Last Interglacial, Last Glacial Maximum and Mid Holocene) to evaluate retractions and expansions of suitable areas according to changes in climate. Species typical of arid environments, such as the fairy armadillos, would have been more common and widespread when aridity predominated, while they would have rarefied with increasing humidity. The scarce information about the climate in the Last Interglacial period (LIG; ~140,000–120,000 yBP) in South America indicates warmer and more humid conditions than at present (Hammen, 1974). In the plains of southern South America the climate turned cold and dry during the Last Glacial Maximum (LGM; ~21,000 yBP), warming and wetting again at the end of this period and reaching higher values of temperature and precipitations than at present in the Mid Holocene (MH), around 8000–6000 yBP (Iriando and García, 1993). In southern tropical areas, however, the aridity and temperature increased from LGM to MH, with rains increasing to current levels during the Late Holocene (Burbridge et al., 2004; Mayle and

Beerling, 2004; Mayle et al., 2004). Thus, compared to the current distribution and assuming niche conservatism (*sensu* Wiens and Graham, 2005), for *Chlamyphorus* we expect an expansion of suitable areas in the LGM and a retraction in LIG and MH. This prediction follows the “zig-zag” hypothesis raised by Cione et al. (2003), which for the plains of southern South America postulates an expansion of open areas at the expense of forests during the cold and dry periods, and the inverse situation during warm and humid periods. On the other hand, for *Calyptophractus* we expect an expansion of suitable habitats from the LIG until the MH, followed by a retraction until today.

Material and methods

Occurrence records

Occurrence records of fairy armadillos were obtained from museum collections, localities cited in the bibliography, field observations, and personal reports from other researchers (see Supplementary Material 1). Three occurrence points for *Chlamyphorus* and one for *Calyptophractus* from newspaper reports with photographs and data about the locality of observation were also included. Records were filtered according to the date of collection (or observation); only records after 1950 were considered, given that the bioclimatic variables used for modeling (see below) represent the climate in the 1950–2000 period (Hijmans et al., 2005). The spatial error associated with the geographic location of the remnant localities was lower than the spatial resolution used for modeling (5 arc-minutes; see below) in all cases. Finally, all duplicate presence points (i.e., those records falling in cells already occupied by a previous record) were deleted.

Modeling techniques

Projecting habitat suitability models to the past requires dealing with the uncertainty associated mainly to the use of different modeling techniques and atmospheric General Circulation Models (GCM; Buisson et al., 2010; Diniz-Filho et al., 2009). To overcome this, Araújo and New (2007) proposed the use of ensembles of model forecasts, where models of the same species are developed with diverse techniques and considered together (e.g. Araújo et al., 2006, 2011; Prasad et al., 2006; Rodríguez-Soto et al., 2011). We used a consensus of three methods: Maximum Entropy (Maxent), Bayesian Classification and Mahalanobis Distance. These methods are known as “presence-only” methods because they do not require information about areas not occupied by the entity being modeled. However, strictly speaking only the Mahalanobis Distance is a presence-only method given that the other ones rely on differences in environmental conditions between the occurrence points and a sample of points taken at random from the study area. Further information on modeling techniques is provided in Supplementary Material 2.

Environmental variables and modeling procedures

Models were first fitted using the 19 bioclimatic variables from the WorldClim database (Hijmans et al., 2005), downloaded at a resolution of 5 arc-minutes for continental South America, plus three topographic variables: an elevation layer of South America, obtained at a resolution of 30 arc-seconds from the SRTM database (<http://srtm.usgs.gov>), and slope and aspect, derived from the elevation layer with the SURFACE module of Idrisi v17 Selva (Eastman, 2012). Given that fairy armadillos are associated to sandy soils (Aguar and da Fonseca, 2008), a categorical layer describing the percentage of sand at 0–20 cm depth was obtained at a resolution of 5 arc-minutes from the ISRIC-WISE database (Batjes, 2006; <http://>

www.isric.org) and was incorporated to the models. The spatial distribution of categories in this layer showed high agreement in South America with those of the percentage of sand at 20–40 cm depth from the same database (with kappa values of agreement for the same category between both layers varying between 0.73 and 1.00). Hence, we considered that the layer we used was a good descriptor of the percentage of sand from 0 to 40 cm depth. Models fitted with sand percentage were developed in order to evaluate the importance of soil-related constraints for the current distribution of fairy armadillos. The percentage of sand, however, is likely to have changed greatly between LGM, MH and the current situation; to allow comparisons, projections to past conditions were therefore made with models trained without the soil variable. Because the spatial autocorrelation (an inherent feature in datasets from museum collections and field observations) may influence the predictions of distribution models, a “bias grid” was created for each species as the inverse of the Euclidian distance to all occurrence points (Allouche et al., 2008; Elith et al., 2011) and was included in models as another environmental layer. All variables plus the bias grid were interpolated at a resolution of 5 arc-minutes.

Environmental variables are frequently intercorrelated (Graham, 2003), causing problems of multicollinearity, with models providing incorrect estimations of a given variable in the presence of collinear variables (Dormann et al., 2008). To deal with this, a variable selection process was performed with Maxent. An initial set of ten models was obtained for both species by randomly selecting 75% of the occurrence localities at each run for training, and leaving the remaining 25% for testing. Correlations between environmental variables were then tested by means of the Spearman r_s coefficient, considering only the cells with presence data. Only those pairs of variables with a r_s value >0.70 were considered to be significantly correlated. Based on the mean values of percent contribution of the environmental variables to the model (Phillips, 2010), the variables with the highest contribution were selected and all variables correlated to them were removed, which allowed obtaining a reduced set of uncorrelated environmental variables.

Ten replicates per modeling technique (Maximum Entropy, Bayesian Classification and Mahalanobis Distance) were performed with the reduced set of variables, again selecting at random 75% of occurrences for training and 25% for testing at each run. Performance of each technique was assessed by the mean value of the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Fielding and Bell, 1997; Manel et al., 2001; McPherson et al., 2004) for the test points (see Supplementary Material 2 for a full comparison between modeling techniques with two additional evaluation metrics).

Given that the continuous outputs of the different algorithms may have different meanings, they must be converted to binary outputs before combining them into a consensus model. Hence, the mean suitability value of all pixels of the prediction was used as threshold to define the presence of fairy armadillos (Liu et al., 2005). As this threshold does not rely on occurrence localities, it is adequate for obtaining binary outputs from past projections. Those areas coincident between the binary outputs of the three suitability models were considered as the “final consensus model”.

Past projections

Models fitted with current bioclimatic variables were projected onto the LGM and MH climatic conditions using the layers of precipitation, and maximum and minimum temperature available in the PMIP2 database (Braconnot et al., 2007). These layers were obtained as global coverages at a resolution of three degrees and were later cropped to the same extension (all of South America) and downscaled to the same resolution (5 arc-minutes) as the current environmental layers. Downscaling was performed following

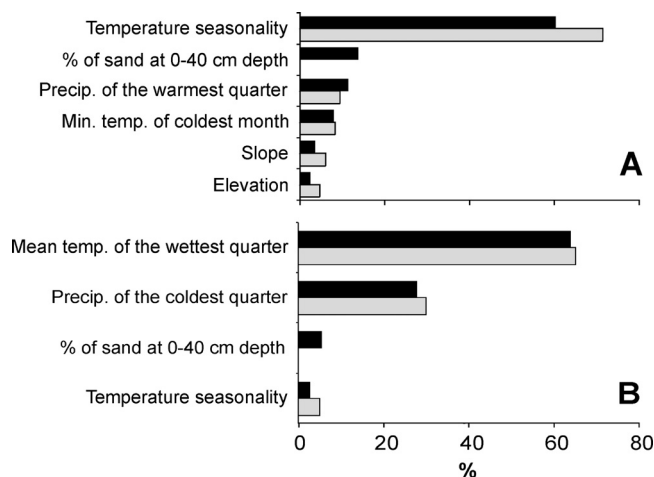


Fig. 2. Percent contribution of the relevant environmental variables to Maximum Entropy suitability models for (A) *Chlamyphorus* and (B) *Calyptophractus*. Gray bars correspond to models fitted without the soil variable (% of sand at 0–40 cm depth) whereas black bars indicate models including them.

the “delta method” (Ramírez-Villegas and Jarvis, 2010). Bioclimatic variables (*sensu* Hijmans et al., 2005) were later developed from the PMIP2 layers. Projections to past conditions were made by using the three GCMs with available data for all periods considered (FGOALS, IPSL-CM4 and MIROC). For each modeling technique we developed three projections, one for each GCM; these projections were averaged to obtain an “intermediate consensus model” for each modeling technique. The model was also projected to the LIG conditions with the climate layers developed by Otto-Bliesner et al. (2006) with the CCSM circulation model, which is the only climate simulation currently available for that period. These layers were also obtained from the Worldclim database at a resolution of 5 arc-minutes. The intermediate consensus models were then converted to binary maps and later assembled in a final consensus model for each period, following the same procedures than in the model for the present time.

A reasonable assumption for projecting to past conditions is that fairy armadillos have limited dispersal ability; thus, of the total area predicted for each period, only those areas coincident plus those adjacent to the areas predicted for the preceding period and/or the subsequent period were included. Isolated areas no more than 100 km distant of core areas in each period were also incorporated.

Results

A total of 133 presence localities for *Chlamyphorus* were compiled, 26 of which corresponded to records made prior to 1950 and were excluded from further analyses. A total of 107 localities were therefore used for modeling. Occurrence sites were concentrated in western Argentina, mainly in Mendoza province. For *Calyptophractus* 19 presence localities were found: eight in northern Argentina, eight in south-eastern Bolivia, and three in western Paraguay (Fig. 1 and Supplementary Material 1). Two of these localities in Argentina corresponded to citations before 1950 and were therefore not used in modeling.

Models showed a good performance in both species, with AUC values between 0.97 and 0.98 in *Chlamyphorus* and between 0.96 and 0.98 in *Calyptophractus*; in general, other validation metrics also showed higher values (Supplementary Material 2). The variable selection process revealed five relevant uncorrelated non-soil environmental variables for *Chlamyphorus* and three for *Calyptophractus*; the two species were quite different in their environmental requirements (Fig. 2). Temperature seasonality was the

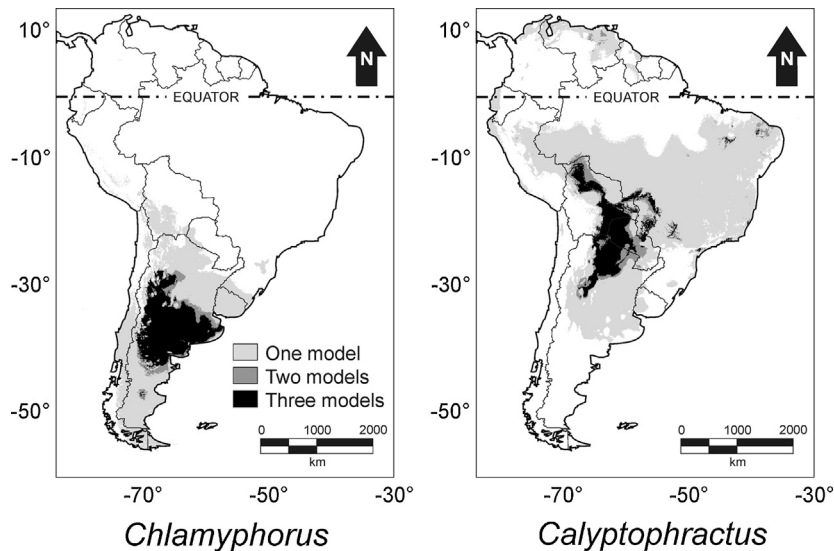


Fig. 3. Consensus of projections of three suitability models (Maximum Entropy, Bayesian Classification and Mahalanobis Distance) for fairy armadillos (geographic projection: Aitoff).

most important variable for *Chlamyphorus*, with higher values of suitability associated to sites with higher seasonality (see Fig. S1 in Supplementary Material 2). It contributed with 60.4% and 71.4% to models fitted with and without the sand percentage, respectively (Fig. 2). The most important variables for *Calyptophractus* were the mean temperature of the wettest quarter and precipitation of the coldest quarter, which together contributed with 91.6% and 95% to models with and without the sand percentage, respectively. Habitat suitability values for the Chacoan fairy armadillo were higher in sites with high temperatures during the wet season and zero precipitation during the dry season (Fig. S1). Inclusion of the percentage of sand did not influence the percent contribution of the non-soil-related variables when compared with models fitted without sand percentage. Sand percentage contributed only with 13.8% and 5% to models of *Chlamyphorus* and *Calyptophractus*, respectively, with *Chlamyphorus* selecting sites with higher percentages of sand than *Calyptophractus* (Fig. S1).

The spatial projections of the consensus models showed suitability areas that were in agreement with the distribution of occurrence points (Fig. 3). The distribution of suitable areas for *Chlamyphorus* covered 923,123 km² in the southwest of Santiago del Estero, center and east of Catamarca, La Rioja, San Juan and Mendoza, almost all of San Luis, the south and southeast of Córdoba, all of La Pampa, the east of Neuquén, and almost all of Río Negro and Buenos Aires provinces in Argentina. The consensus model also predicted some areas where the species was never sighted in the provinces of Chubut, Santa Fe, Santiago del Estero, the east and center of Buenos Aires and the southeast of Córdoba. Projections for *Calyptophractus* showed a distribution spanning over 1,016,139 km². It covered the known areas of presence (north of Santiago del Estero, west of El Chaco and east of Salta provinces in Argentina; all of Boquerón, and northwest of Presidente Hayes and Alto Paraguay departments in Paraguay; and Santa Cruz department in Bolivia), plus novel areas where the occurrence of the species is unknown in central and south-western Santiago del Estero, eastern Catamarca and La Rioja, and north-western Córdoba in Argentina, eastern Presidente Hayes and small areas in the San Pedro and Concepción departments in Paraguay, eastern Chuquisaca and Tarija, central Beni and small areas in La Paz departments in Bolivia, as well as some areas in the states of Mato Grosso and Mato Grosso do Sul in Brazil (Fig. 3).

A differential fluctuation of suitable areas was observed when models were projected to past conditions, although both species

coincided in a drastic reduction during the LIG (Figs. 4 and 5). This reduction was more prominent in *Calyptophractus*, whose suitable area during this period covered only 14,707 km². This area increased during the LGM, reached a maximum in the MH and then decreased to the current value. The suitable area for *Chlamyphorus* also showed a minimum in the LIG (33,509 km²) and an increment during the LGM, but later showed a severe reduction during the MH followed by a further increase to reach its maximum value in present time (Figs. 4 and 5).

Discussion

Understanding the causes of rarity in biological species is a main issue in conservation biology given that most threatened species have small range sizes and/or are low in numbers of individuals (Flather and Sieg, 2007). Low density in species with large range sizes has been mainly associated with large body size, as larger species (e.g., keystone predators) require more space and a wider range of resources (Arita et al., 1990). This relationship has, however, been called in question (Dobson and Yu, 1993; but see Gaston and Blackburn, 1995). We propose that, at least in small, numerically rare species with broad distributions such as fairy armadillos, past climate variations may have caused their current low densities.

Fluctuations in the extension of suitability areas for fairy armadillos according to climate variations became evident when suitability models were projected to past climatic conditions. These projections were obtained by extrapolating reliable consensus of habitat suitability models under current climatic conditions, which in turn were based on a comprehensive, updated database. The latter includes more than twice the number of presence localities for *Chlamyphorus* than the latest revisions of the occurrence of this species (Abba et al., 2012; Borghi et al., 2011) as well as the highest number of localities for *Calyptophractus* ever compiled (although the number of presence sites for the latter species remains very scarce). Although the performance of models across algorithms and evaluation parameters was good in both species, we are aware that the sample size for *Calyptophractus* was low. However, we used modeling algorithms that work well with small sample sizes (Elith et al., 2006; Tsoar et al., 2007); in the case of Maxent, reliable models can be obtained with only five presence localities (Pearson et al., 2007). Moreover, the between-run variability was not much greater than in *Chlamyphorus* (see Fig. S3 in Supplementary Material 2). We are aware that outputs of habitat suitability

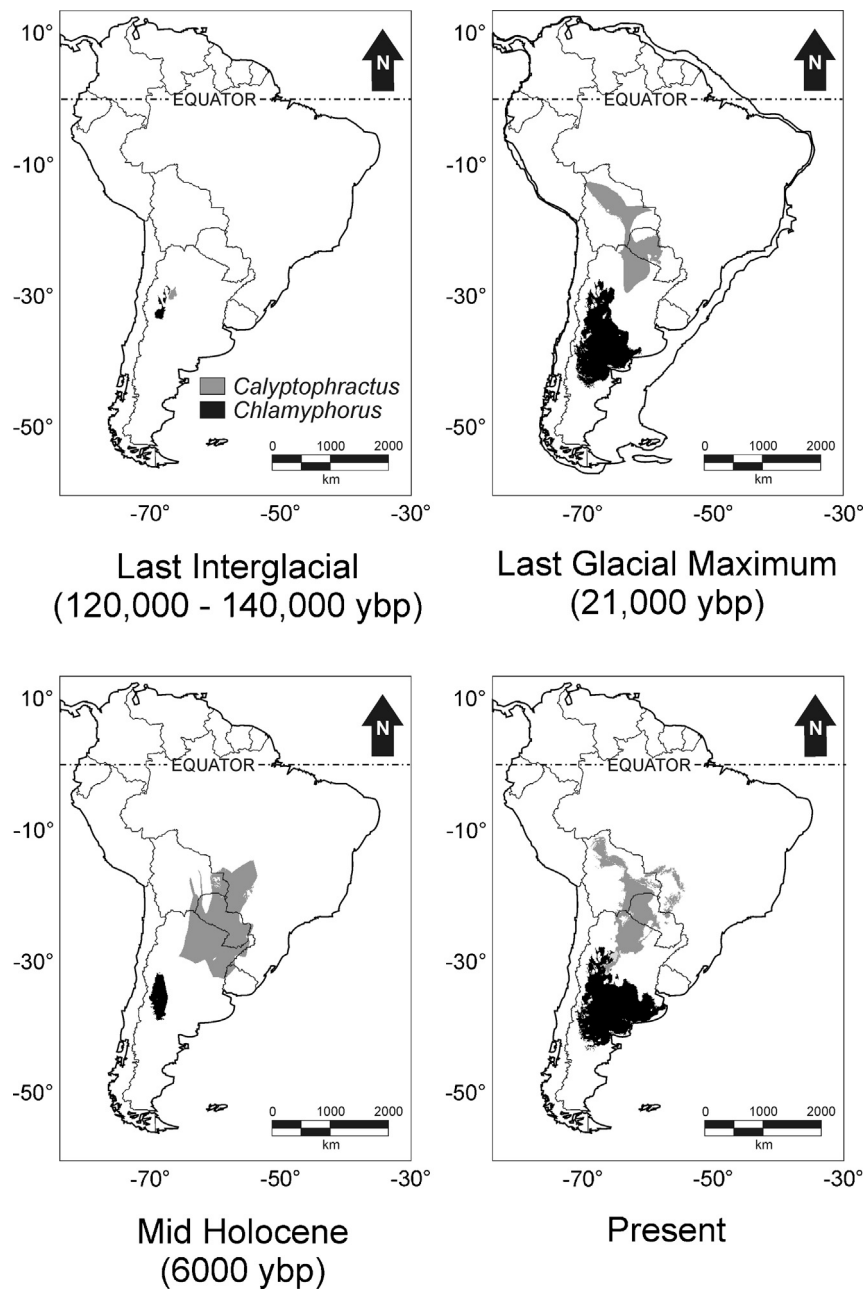


Fig. 4. Consensus of projections of suitability models to past and present conditions for fairy armadillos (geographic projection: Aitoff).

models that do not account for imperfect detection may represent areas where species are likely to be observed, rather than where they actually occur (Guillera-Arroita et al., 2015). We are, however, convinced that our models for fairy armadillos are reliable representations of the relative suitability given that both species use single habitat types (desert scrubs and Chacoan forests in pink and Chacoan fairy armadillos, respectively). Moreover, due to their fossorial lifestyle, it is unlikely that climatic variables are correlated with the detectability of fairy armadillos; thus, for each species a near constant detectability can be assumed.

In *Chlamyphorus*, the geographical projection from the consensus model for the present time provides a range of suitability areas that exceeds the previously delimited range maps drawn based on known occurrence localities (Abba and Superina, 2010; Borghi et al., 2011) and modeling (Abba et al., 2012). It does, however, closely fit the distribution of occurrence points used in this work. For *Calyptophractus*, the suitable area obtained offers a

counterintuitive picture, with a greater area than for *Chlamyphorus* while the inverse situation was expected given the distribution of known occurrence points.

Fluctuations of projected suitable areas from the LIG to the present differed considerably between species, reflecting the interspecific differences in the response to climate constraints. In fact, the current habitat suitability of *Chlamyphorus* is mainly positively affected by temperature seasonality. The same has been reported in another mammal living in the arid Monte Desert and Patagonian steppe of southern South America, the Patagonian weasel (*Lyncodon patagonicus*; Schiaffini et al., 2013), suggesting that both species are adapted to cope with the high inter-seasonal differences in temperature typical of extremely arid zones. In contrast to this, optimal habitats for *Calyptophractus* are mainly linked to high temperatures during the wettest quarter and no precipitation in the coldest month, a response similar to mammal species living in the Chaco ecoregion [e.g. the Chacoan peccary (*Catagonus wagneri*), the

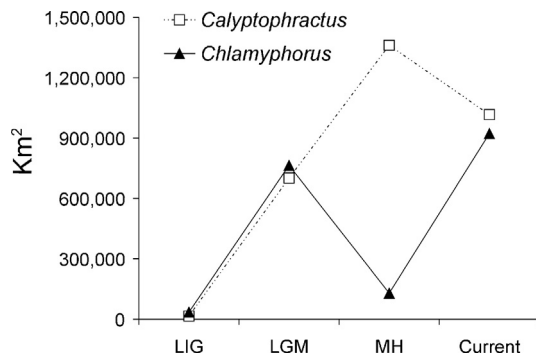


Fig. 5. Fluctuations in projected consensus of suitability areas for fairy armadillos (LIG = Last Interglacial; LGM = Last Glacial Maximum; MH = Mid Holocene).

giant armadillo (*Priodontes maximus*) and the maned wolf (*Chrysocyon brachyurus*) that are related to the same or similar variables with identical relationships (Torres and Jayat, 2010; Torres et al., 2013). The inverse response to precipitations in the coldest month is probably related to avoidance behavior to the severe frosts that normally occur in the Chaco during winter (Minetti, 1999). Despite the superficial resemblance in their morphology, both species seem to have diverged considerably in their ecological requirements after the postulated splitting of the distributional range of their common ancestor in Mid Miocene (Delsuc et al., 2012). Both species also differed in their dependence on sand, with *Chlamyphorus* having a more pronounced association to high percentages of sand than *Calyptophractus*. Our results, however, suggest that sand is not an important constraint for fairy armadillos at the scale of their entire distribution (although it probably determines their patchy distribution at a local scale; Abba and Superina, 2010). As a consequence, the projections to past provided here may be reliable representations of the true distribution of suitable habitats in these times even though they are based on models fitted without sand percentage.

The differences in habitat requirements were translated into differential fluctuation patterns. Variations in suitable areas over time in *Chlamyphorus* followed in part the “zig-zag” dynamics proposed by Cione et al. (2003), although the pattern was counterintuitive, with greater values in current times than in the LGM. Climatic suitability for *Chlamyphorus* is, however, mainly driven by temperature seasonality, which not necessarily covaries over time with variables directly expressing ambient temperature. On the other hand, suitability areas for *Calyptophractus* were positively affected by summer temperatures and fluctuated according to the recorded and projected variations in temperature in the southern tropics of South America (Burbridge et al., 2004; Mayle and Beerling, 2004; Mayle et al., 2004). In spite of such interspecific differences, both fairy armadillos coincided in an extremely severe reduction of high suitability areas during the LIG. We propose that, although climatic conditions in the LIG (and probably in all Pleistocene interglacial periods) were harshly adverse for fairy armadillos – and particularly for *Calyptophractus* – both species probably survived thanks to their strictly subterranean habits and the short duration of the LIG (from 130,000 to 116,000 yBP; Otto-Bliesner et al., 2006) when compared with the subsequent glacial period, a more favorable time spanning from the end of the LIG to 17,000 yBP in southern South America (McCulloch et al., 2005). A scheme where the reduction of suitable areas in the LIG was more critical for *Calyptophractus* than for *Chlamyphorus* fits perfectly with the current situation, with the former being numerically rarer than the latter. Despite the increase in suitable areas for *Calyptophractus* by four orders of magnitude from the LIG to MH, the recovery of its populations may have been delayed by low dispersal ability (and possibly low reproductive rate) and a strong founder effect, resulting in its current

numerical rarity. According to the only available estimates of the dispersal rate of fairy armadillos (0.85 and 0.72 km/y for pink and Chacoan fairy armadillos, respectively; Schloss et al., 2012), they should have been able to recolonize all suitable areas when the latter expanded at the end of LIG. These estimates, however, are based on the dispersal models provided by Sutherland et al. (2000), which used a comprehensive database (68 mammal species) that does not fully account for different lifestyles. In fact, although fossorial mammals are known for their lower vagility than other mammals (Nevo, 1995), only one strictly subterranean mammal species was included in Sutherland et al.’s (2000) database. Mechanisms driving dispersion are also positively related to population density, so that those populations that experienced severe reductions will show lower dispersal rates (Travis et al., 1999; Lachish et al., 2011). Theoretically, dispersal can even be null below a critical threshold (Travis et al., 1999). Future research should be directed toward testing the hypothesis raised above by means of phylogeographic analyses. For instance, the phylogeography of another numerically scarce species with large range size, the maned wolf, also suggests a bottleneck during the LIG (Prates, 2008).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2015.07.007>

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