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ORIGINAL ARTICLE

# Is the niche shift a driver of invasion success? Case study of the large hairy armadillo (*Chaetophractus villosus*) in a Sub-Antarctic ecosystem

## ¿Es el cambio de nicho un motor del éxito de las invasiones? Estudio de caso del peludo (*Chaetophractus villosus*) en un ecosistema subantártico

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## ABSTRACT

The large hairy armadillo (*Chaetophractus villosus*) is native to Paraguay, Bolivia, Argentina, and Chile. It was introduced to Isla Grande de Tierra del Fuego (TdF), an island shared by Chile and Argentina, in 1982. Its rapid spread in TdF poses a threat to native species. We evaluated the species' potential niche shift and expansion in the island ecosystem. Using species occurrence records, bioclimatic variables, and modeling frameworks (COUE and n-dimensional hypervolumes), we compared the climatic niches of the native and invasive ranges. Our results suggest that *C. villosus* has encountered new climatic conditions in TdF, showing niche differentiation while retaining similarities to its native range. Species Distribution Models (SDMs) under current and future climate scenarios (ssp126 and ssp585) predict southward expansion, driven by climate change. These findings highlight the species' adaptability and potential for further colonization, emphasizing the need for proactive management to mitigate its ecological impact on TdF's fragile ecosystem.

**Keywords:** armadillos, Chlamyphoridae, climate change, invasive species, niche shift.

## RESUMEN

El armadillo peludo (*Chaetophractus villosus*) es una especie nativa de Paraguay, Bolivia, Argentina y Chile. Fue introducido en la Isla Grande de Tierra del Fuego (TdF), una isla compartida por Chile y Argentina, en 1982. Su rápida expansión representa un peligro para las especies nativas. Evaluamos el potencial cambio de nicho y expansión de la especie en el ecosistema insular. Usando registros de ocurrencia de la especie, variables bioclimáticas y técnicas de modelado (COUE e hipervolúmenes n-dimensionales), comparamos los nichos climáticos de las áreas nativa e invadida. Nuestros resultados sugieren que *C. villosus* ha encontrado nuevas condiciones climáticas en TdF, mostrando un cambio de nicho mientras conserva similitudes con su rango nativo. Los Modelos de Distribución de Especies (SDMs) bajo escenarios climáticos actuales y futuros (ssp126 y ssp585) predicen una expansión hacia el sur, impulsada por el cambio climático. Estos hallazgos destacan la adaptabilidad de la especie y su potencial para una mayor colonización, subrayando la necesidad de una gestión proactiva para mitigar su impacto ecológico en el frágil ecosistema de TdF.

**Palabras claves:** armadillos, cambio climático, cambio de nicho, Chlamyphoridae, especies invasoras.

## INTRODUCTION

An invasive species can be defined as a taxon introduced by humans to a habitat outside its natural range, where it manages to establish and disperse (Alford *et al.* 2009). Although introductions can occur in a variety of ecosystems, they are of particular importance in Antarctic and sub-Antarctic ecosystems which, compared to other regions of the planet, have historically had little exposure to species introductions (Hughes *et al.* 2015).

The phylogenetic niche conservatism proposes that the evolution of climatic niches is constrained by the ancestral attributes of the clade to which the species or genus belongs (Gomez-Rodríguez *et al.* 2015; Olalla-Tárraga *et al.* 2011; Hadly *et al.* 2009). Niche conservatism does not always occur in invasive species. It is crucial because such species can adapt to a new climate if they have high plasticity (Pearman *et al.* 2008; Araujo & Guisan 2006; Guisan & Zimmermann 2000). With global climate change, it has become increasingly important not only to describe the climatic realized niches of species, but also to understand whether or not these may change rapidly between different geographic areas or time periods (Peterson 2011).

Evolutionarily and geographically isolated ecosystems, such as oceanic islands, are particularly vulnerable to biological invasions (Kowarik 1995). The Tierra del Fuego (TdF) archipelago, located at the southern tip of South America, between the Atlantic and Pacific oceans, is an island prone to colonization by invasive species due to its proximity to the mainland, lack of predators, and low species diversity with high endemism (Jaksic *et al.* 2002; Mittermeier *et al.* 2002; Benitez *et al.* 2019). The large hairy armadillo (*Chaetophractus villosus*; Mammalia, Cingulata, Chlamyphoridae) is the last mammal introduced to TdF. Its global distribution includes parts of Bolivia, Paraguay, Argentina, and Chile (Gallo *et al.* 2022). Both the fossorial habits of *C. villosus*, which allow it to cope with fluctuations in environmental temperature (McNab 1985, 1979), and its omnivorous diet (Gallo *et al.* 2019) give it a remarkable adaptive capacity to inhabit regions with diverse climates and food resources (Poljak *et al.* 2010). According to Abba *et al.* (2014), the recent southward expansion of *C. villosus* on the Patagonian mainland was likely facilitated by anthropogenic factors, including land use changes and the construction of roads and bridges that eased the species' dispersal. This hypothesis highlights the role of human activities in the observed rapid spread of *C. villosus* in southern Patagonia and provides a framework for understanding its introduction to Tierra del Fuego. The species was introduced on Isla Grande of TdF in 1982 from the Argentinian side (Ballari *et al.* 2016), and evidence of its rapid spread on the island has been documented both in Argentina and Chile (Cabello *et al.* 2017; Gallo *et al.* 2020).

In this study, we modeled the distribution of the large hairy armadillo in its global native distribution ("mainland") and within TdF ("island") and compared both climatic niches to assess potential niche shifts. We also evaluated its potential distribution under different climate change scenarios, highlighting the significance of understanding how invasive species adapt to new environments, the interplay between climate change and biological invasions, and the need for proactive ecological management to mitigate impacts on fragile ecosystems.

## MATERIALS AND METHODS

### SPECIES OCCURRENCE RECORDS

A database of georeferenced records of the large hairy armadillo throughout its distribution, including Isla Grande of Tierra del Fuego, was created. This information was compiled from publications (Gallo *et al.* 2021, 2020; Santos *et al.* 2019; Pasutti 2017), field work performed by one of the authors (RPM), and records provided by the civil society and locals.

A total of 1517 georeferenced occurrence records were compiled, all with a maximum record age of 30 years. To address spatial clustering and reduce the overrepresentation of environmentally redundant records, we applied geographic thinning using the 'spThin' R package (Aiello-Lammens *et al.* 2015), retaining only one occurrence per pixel at the spatial resolution of the bioclimatic variables (2.5 arc-min; see below). Although recent studies have questioned the overall benefit of thinning for species distribution modeling (e.g., Ten Caten & Dallas 2023), it is still considered a useful step in cases of strong spatial sampling bias. In this case, a bias toward accessible areas, particularly near roads, was evident based on an analysis using the 'sampbias' R package (Zizka *et al.* 2021; see Supplementary Fig. S1). Thus, thinning was applied as a preliminary measure to partially mitigate this bias and reduce the risk of model overfitting. The resulting dataset was then split into two subsets: one from the native mainland range (n = 846), and one from the invaded island region (n = 47).

### CLIMATIC VARIABLES

Twenty-one environmental variables were obtained from the CHELSA v2.1 dataset (Karger *et al.* 2022), including the 19 standard bioclimatic variables, as well as annual gross primary productivity (NPP) and growing season precipitation (GSP; Supplementary Table S1). These two additional variables were selected from a larger set provided by CHELSA because they are available across the entire study area and include future projections under climate change scenarios (explained in more detail in a later subsection). All variables correspond to the historical period 1981–2010 and were retrieved at a spatial resolution of 2.5 arc-minutes (approximately 4.6 km × 3.8 km, representing average pixel dimensions across the latitudinal range of the study area, from Bolivia to southern South America). Descriptive statistics for these variables in the native and invasive ranges of *C. villosus* are presented in Tables S2A and S2B, respectively, including measures such as mean, variance, and coefficient of variation.

## Comparison of niches in the environmental climate space

### Centroid shift, Overlap, Unfilling, and Expansion (COUE) framework

Using the COUE framework, the niches were compared in a two-dimensional space using Schoener's D metric of niche overlap (Broennimann *et al.* 2012). To construct this space, the 21 environmental variables derived from the CHELSA dataset were first standardized (centered and scaled), then reduced to their principal components (PCs) through a Principal Component Analysis (PCA). The environmental space was then divided into a 100 × 100 grid of cells and the density of occurrences within the environmental space was estimated using a kernel density estimator (Parravicini *et al.* 2015; Broennimann *et al.* 2012). Schoener's D metric quantified the degree of overlap of the two niches between 0 (no overlap) and 1 (complete overlap) (Broennimann *et al.* 2012; Warren *et al.* 2008).

Additionally, niche equivalence and similarity tests were performed. The null hypothesis that the niches are equivalent was rejected if the observed D was below the 5th percentile of the null distribution. The niche similarity test assessed whether the observed D was significantly different from that of a null distribution of 1000 metric D generated when the geographic availability of environmental conditions was accounted for (randomly distributing one niche over its background while the other did not change). The null hypothesis that niches are different was rejected if the observed D was greater than the 95th percentile of the null distribution (Broennimann *et al.* 2012; Warren *et al.* 2008).

COUE metrics of niche stability, niche expansion, and niche unfilling were analyzed (Guisan *et al.* 2014). All metric calculations as well as niche similarity and equivalence tests were performed using the 'ecospat' R package (Di Cola *et al.* 2017). All metrics of the COUE framework can only be calculated by two PCs at a time, so the first two PCs that collected the most information (70.4%) were used.

### N-dimensional hypervolume frame

The *n*-dimensional hypervolume framework was used to assess niche differences within a multidimensional environmental space (Blonder *et al.* 2014; Hutchinson 1957), unlike the COUE framework that uses a space of only two dimensions.

The top five PCs of the bioclimatic variables (91% of the variance) were used to construct multidimensional hypervolumes for the native and invaded niche. Hypervolumes were generated using the Gaussian kernel density estimation method (Blonder *et al.* 2014). To assess differences between niches, the Jaccard index and the Sørensen-Dice index were calculated and compared to a null distribution of 1000 iterations. All analyses related to the estimation and comparison of n-dimensional niches were conducted using the 'hypervolume' R package (version 3.1.5; Blonder *et al.* 2014).

## Potential, current and future distribution

The potential current and future geographic distribution of *C. villosus* in Tierra del Fuego and on the mainland was estimated using Species Distribution Models (SDMs). The Continuous Boyce Index CBI was used to evaluate the performance of the species distribution models (Hirzel *et al.* 2006; Di Cola *et al.* 2017). This metric is particularly appropriate for models calibrated using presence-only data, as it does not rely on absence or background data and instead assesses how predictions differ from a random distribution of presences across the prediction gradient. The SDMs were developed using Bayesian Additive Regression Trees (BART), a modern machine learning method that provides highly accurate predictions without generating overfitting to particular observations or noise (Carlson 2020). To estimate the current geographic distribution, the SDMs were calibrated using species occurrences as response variable and seven variables from the CHELSA dataset plus a sampling rate layer as predictors. Each bioclimatic variable was first assessed independently in models with a single predictor using the BART algorithm with default hyperparameters (i.e., the modelling options of the BART algorithm). Variables with the highest predictive performance, based on CBI, were selected. From this subset, we excluded those with high pairwise correlation (Pearson's |r| ≥ 0.7) to minimize multicollinearity in the final model (Dormann *et al.* 2013). The sampling rate variable corresponds to the geographic sampling bias due to human accessibility. It was estimated using the 'sampbias' R package (Zizka *et al.* 2021), based on the species occurrence records prior to geographic thinning. This method applies a Bayesian framework to quantify the spatial influence of biasing factors (such as roads, airports, cities, and rivers) on the likelihood of a site being sampled. The resulting sampling rate raster was resampled to match the spatial resolution of the bioclimatic variables (2.5 arc-min) using the Lanczos interpolation method (Lanczos 1988).

The hyperparameters of the BART algorithm were optimized to achieve the best predictive performance of each SDM, following the recommendations of Carlson (2020). Each combination of hyperparameters was tested within a five-fold spatial block cross-validation framework using the *blockCV* R package (Valavi *et al.* 2019). This approach has been increasingly adopted in recent species distribution modeling studies due to its robustness in accounting for spatial structure and improving model transferability (Erazo *et al.* 2024; Meyer & Pebesma 2022). This spatial partitioning between training and validation datasets reduces the risk of model overfitting to geographically clustered occurrences and aims to produce more generalized predictions. In each training iteration, the number of randomly generated pseudo-absences matched the number of presence records, as recommended for decision tree–based models such as BART (Barbet-Massin *et al.* 2012). The final models retained the hyperparameter configuration that yielded the highest CBI values.

The SDMs were fitted using the 'bart2' function of the 'dbart' R package (Dorie 2024).

The future distribution of *C. villosus* was estimated using projected CHELSA variables for the 2081-2100 period according to two scenarios (ssp126 and ssp585), which are associated with the lowest and highest intensity in terms of projected greenhouse gas emissions, respectively. The projected CHELSA variables were determined through the ensemble of mean values of 5 general circulation models (GCMs) from the Coupled Model Intercomparison Project-6 (CMIP6), which are available in the CHELSA database.

To mitigate the influence of sampling bias during projection, both current and future SDM predictions were generated using a constant value of zero for the sampling rate predictor. This approach prevents the extrapolation of spatial sampling patterns and ensures that model outputs reflect only species–environment relationships. By removing the effect of biasing factors during projection, the model becomes more capable of generalizing to unsampled areas (e.g., Pouteau *et al.* 2023). Occurrence probabilities were interpreted using a threshold that maximized the sum of sensitivity (the proportion of correctly classified presences) and specificity (the proportion of correctly classified absences), known as the maxSSS criterion (Liu *et al.* 2013). This threshold was used to distinguish suitable from non-suitable areas in both present and future projections. As the model was calibrated using occurrence records from the present, and all projections are generated on the same probability scale, the same threshold can be consistently applied across time. This procedure is commonly used in species distribution modeling (e.g., Lee *et al.* 2021).

## RESULTS

The climatic space that the large hairy armadillo occupies on the continent (Fig. 1A, light green) is limited compared to the entire available climatic gradient. In Tierra del Fuego, the species has been able to colonize areas with environmental conditions similar to those of its native range (Fig. 1A, blue areas). However, part of the niche that the species occupies on the mainland has not yet been colonized in Tierra del Fuego (Fig. 1A, dull green).

The analysis of the COUE framework revealed that the native and invasive niches are not equivalent. Although the algorithm reports a p-value of 0.98 (based on a right-to-left cumulative rank), this corresponds to the 2nd percentile of the null distribution. This indicates that the observed overlap is significantly lower than expected by chance, providing sufficient evidence to reject the null hypothesis of niche equivalence between the native and invaded ranges (Fig. 1B)

The observed value of Schoener's D (0.5) for niche similarity was higher than 92% of the simulated niches (Fig. 1C) with a p-value of 0.08. This result indicates that the niches are not significantly more similar than expected by chance.

The five-dimensional hypervolume (Fig. 2) shows that the native and invaded niches have reduced overlap compared to the results obtained from the COUE framework (Fig. 1A). When comparing combinations of PC1 to PC5, the centroids of the native (continent) and invaded (Tierra del Fuego) niches appear visually close in several dimensions, but the dispersion and coverage of environmental space differ between both ranges.

The observed values of the Jaccard and Sørensen-Dice indices indicate that the similarity between native and invaded niches is significantly lower than expected by chance ($p = 0$ for both metrics), supporting the conclusion that there is minimal shared environmental space between the two hypervolumes (Figs. 2B, 2C).

The final and optimized SDM achieved a CBI of 0.93, indicating excellent predictive performance. Values close to 1 reflect a strong ability to distinguish suitable from unsuitable areas, meaning that the model assigns higher predicted suitability to sites where the species has been observed compared to random background locations (Hirzel *et al.* 2006).

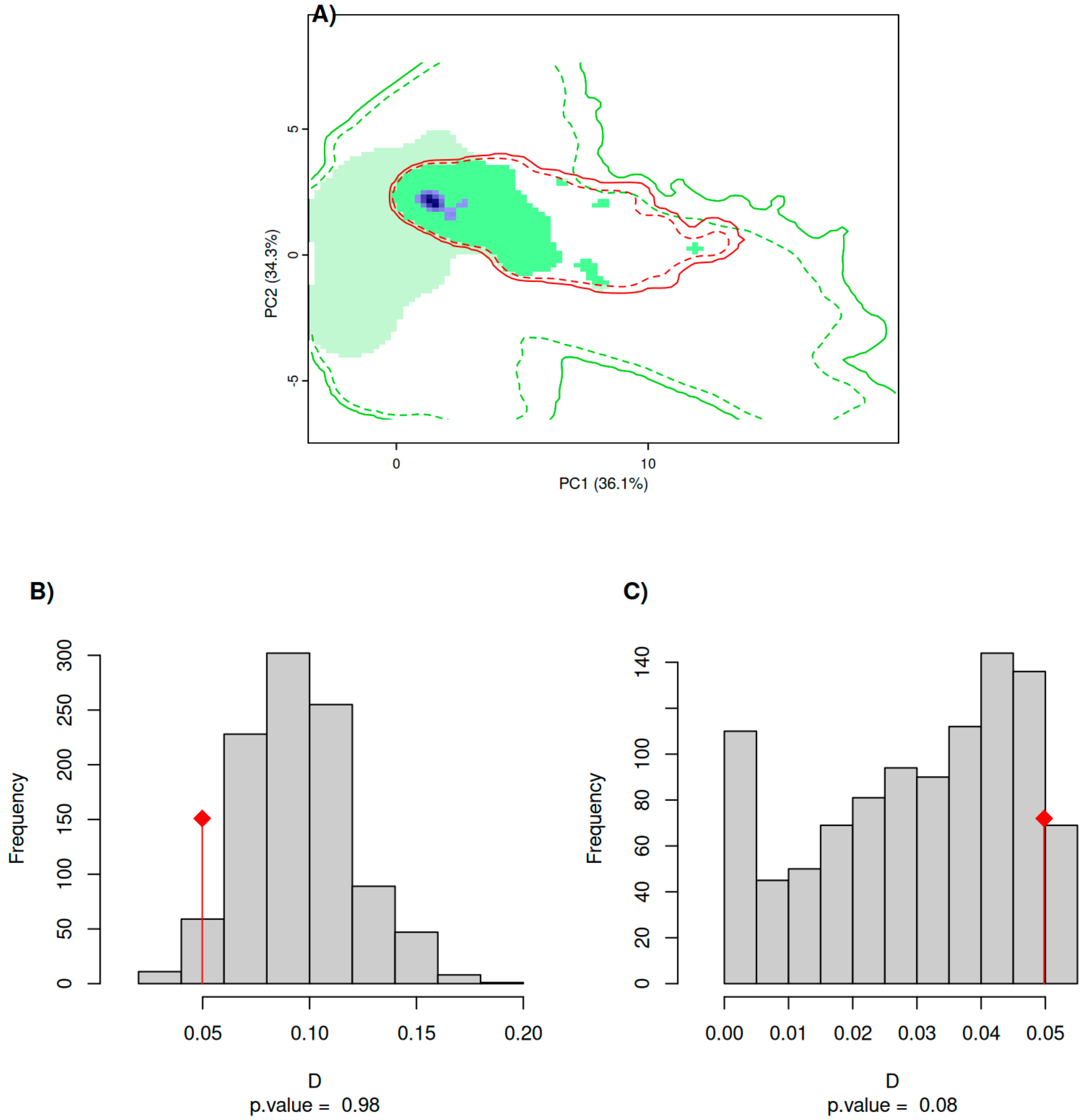

**Figure 1.** A) Niche comparison in two-dimensional principal component space of large hairy armadillos (*Chaetophractus villosus*). Blue area: overlapping niches. Shading: occurrence density. Dull green: unshared native niche. Light green: unoccupied native niche in the introduced range. Solid and dashed lines: 100% and 85% of the available environmental space in the native (green) and introduced (red) ranges, respectively. B) Histogram of the null distribution of Schoener's D metric for 1000 iterations compared to the observed value (red diamond) for niche equivalence. C) Histogram of the null distribution of Schoener's D metric for niche similarity. / A) Comparación de nichos en un espacio bidimensional de componentes principales de los peludos (*Chaetophractus villosus*). Área azul: nichos superpuestos. Sombreado: densidad de ocurrencia. Verde opaco: nicho nativo no compartido. Verde claro: nicho nativo no ocupado en el rango introducido. Líneas sólidas y discontinuas: 100% y 85% del espacio ambiental disponible en los rangos nativo (verde) e introducido (rojo), respectivamente. B) Histograma de la distribución nula del métrico D de Schoener para 1000 iteraciones comparado con el valor observado (diamante rojo) para la equivalencia de nicho. C) Histograma de la distribución nula del métrico D de Schoener para la similitud de nicho.

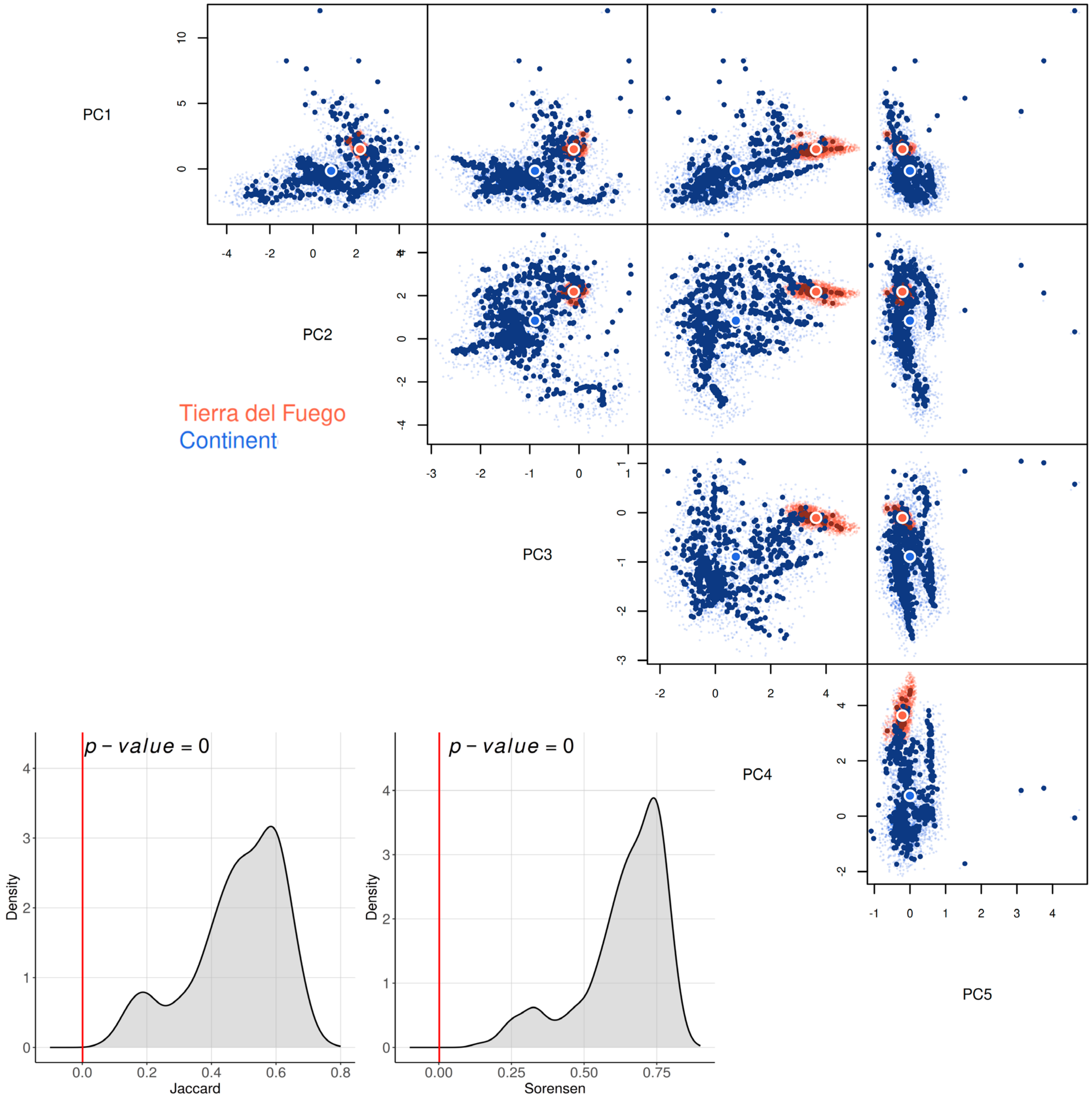

**Figure 2.** A) Five-dimensional hypervolume in a two-dimensional pairwise space comparing the native (blue) and invaded area (red) of large hairy armadillos (*Chaetophractus villosus*). Filled circles indicate the centroids of the hypervolumes for each range. B) Histogram of the Sørensen-Dice index. C) Histogram of the Jaccard index. / A) Hipervolumen de cinco dimensiones en un espacio bidimensional de pares que compara el área nativa (azul) y el área invadida (rojo) de los peludos (*Chaetophractus villosus*). Los círculos rojos indican los centroides de los hipervolúmenes para cada rango. B) Histograma del índice de Sørensen-Dice. C) Histograma del índice de Jaccard.

In the current scenario, central Argentina, particularly the Pampas region, presents the most climatically suitable conditions for *C. villosus*, with suitable areas also extending into parts of northern Patagonia and Tierra del Fuego, where the species is already established (Fig. 3A). The niche overlap (Fig. 1) and the potential current distribution (Fig. 3B and 3C) suggest that the species may encounter similar environmental conditions in the introduced areas compared to its native range, potentially facilitating its establishment and expansion. However, it is important to note that *C. villosus* is a semi-fossorial mammal that depends heavily on soil characteristics for burrowing and shelter (Abba *et al.* 2014), and it tends to avoid rocky or flood-prone soils (Gallo *et al.* 2020). Therefore, areas predicted as climatically suitable may not be equally accessible or favorable for the species if soil conditions are limiting.

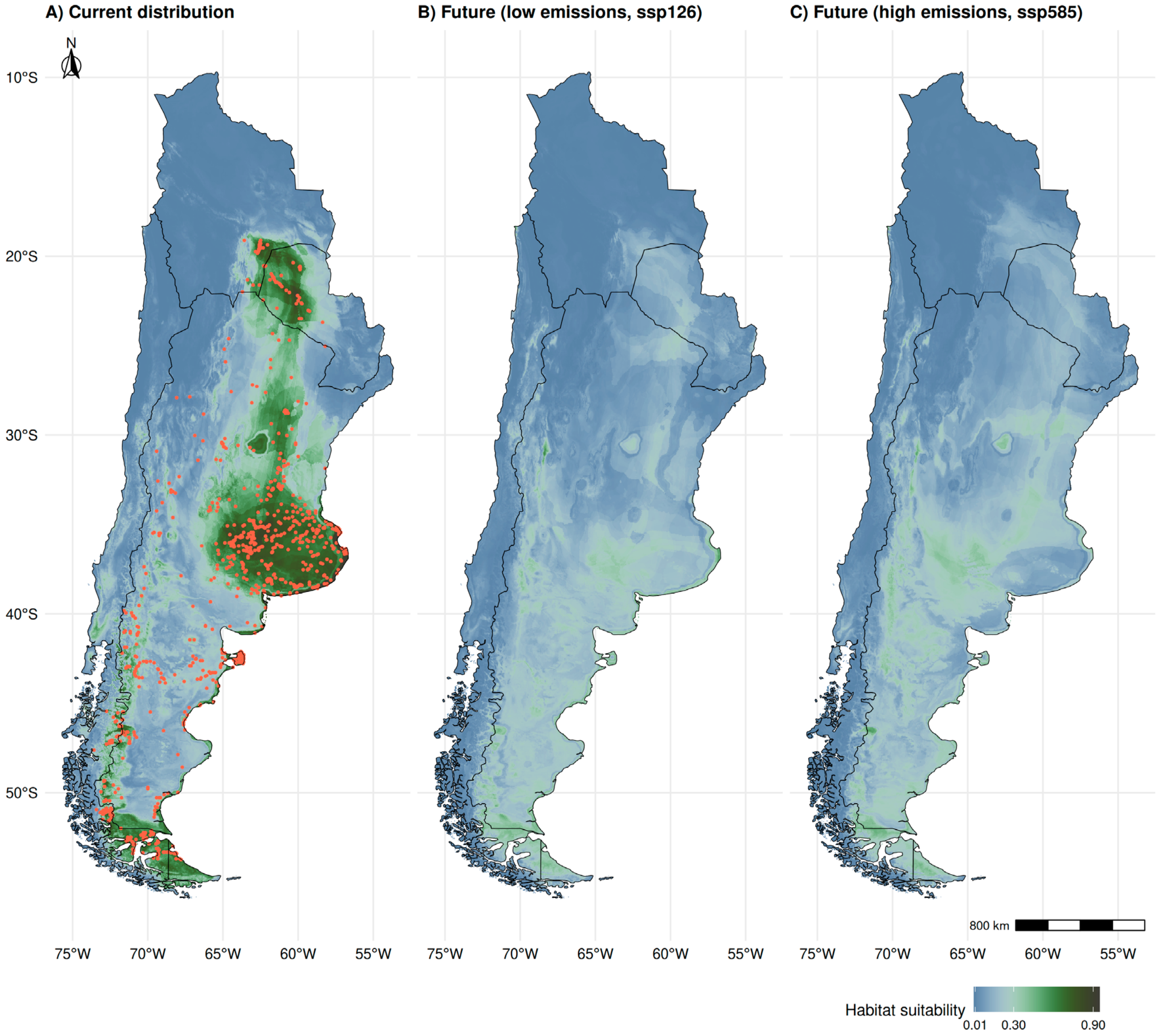

**Figure 3.** Current potential geographic distribution of *Chaetophractus villosus* (A) and future potential range for the end of the 21st century estimated by SDM, under a scenario of low (B) and high (C) GHG emissions, respectively. It is important to note that the habitat suitability threshold of 0.3 corresponds to the value determined by the MaxSSS criterion, which distinguishes between suitable and unsuitable areas. The orange dots correspond to records of the species' presence. / Distribución geográfica potencial actual de *Chaetophractus villosus* (A) y distribución potencial futura para finales del siglo XXI estimada mediante SDM, bajo un escenario de bajas (B) y altas (C) emisiones de GEI, respectivamente. Cabe destacar que el umbral de idoneidad del hábitat de 0,3 fue determinado según el criterio MaxSSS, utilizado para diferenciar áreas idóneas de aquellas no idóneas. Los puntos naranjos corresponden a registros de presencia de la especie.

The projected distribution towards the end of the 21st century under a low GHG emissions scenario (Fig. 3B) shows an important reduction of suitable areas in central and northern Argentina, particularly in the species current range. In southern Patagonia and Tierra del Fuego, there is also a reduction of the suitable areas, with no significant increases projected in those regions.

Under a high GHG emissions scenario (Fig. 3C), the contraction of suitable areas in the north and center of Argentina becomes even more pronounced. While some suitable areas persist in parts of southern Patagonia and Tierra del Fuego, no new climatically suitable regions emerge. The models suggest that *C. villosus* is likely to experience a net contraction of its suitable climatic envelope under future climate change scenarios, with no compensatory expansion into new southern areas beyond those already colonized.

## DISCUSSION

Biological invasions offer a unique opportunity to study how species colonize new environments (Kueffer *et al.* 2013; Sax *et al.* 2007; Pysek & Richardson 2007) and whether they retain their climatic niche in a new range (Pearman *et al.* 2008). In this study we found that the large hairy armadillo does not retain its climatic niche in the invaded area. This result highlights the importance of considering the unoccupied niche that could be exploited in the future, especially with the uncertainty that climate change brings into future climate scenarios.

### NICHE SHIFT AND POTENTIAL EXPANSION OF *C. VILLOSUS* IN ISLA GRANDE DE TIERRA DEL FUEGO

The niche of the large hairy armadillo on the island is not equivalent to that of its native range on the continent. In other words, the species has managed to establish itself on Isla Grande de Tierra del Fuego by occupying a subset of climatic conditions that partially overlap with those used in its original range but also show differences. There are still many areas in both territories that are not being utilized by the species.

The limited overlap between the native and invaded niche, along with shifts in centroid and niche breadth, could indicate a differentiation between the climatic spaces occupied in each region. The fact that the species has found a suitable environment in Tierra del Fuego suggests that there are certain climatic similarities between the two ranges. Our analyses suggest that the large hairy armadillo is using distinct portions of its climatic niche, potentially expanding it or taking advantage of previously underutilized conditions. This supports the idea that invasive species, when confronted with a new environment, may use different portions of their niche or even expand it (Guisan *et al.* 2014). Similar observations have been reported from other species (Pack *et al.* 2022; Zhang *et al.* 2020).

The unoccupied niche on the island represents another important observation. Although these climatically suitable areas are not being utilized by the species on Tierra del Fuego, they are on the mainland. However, it is important to consider that the establishment and distribution of *C. villosus* is not determined solely by climatic variables. This semi-fossorial species strongly depends on the characteristics of the soil (Gallo *et al.* 2020) and tends to avoid rocky and/or floodable areas, which may limit its colonization of certain regions predicted as suitable based on climate alone. These findings highlight the importance of monitoring potential areas of *C. villosus* expansion on the island (Cabello *et al.* 2017).

These findings also suggest a degree of niche conservatism, as the climatic conditions currently occupied by *C. villosus* in the invaded range appear largely nested within its native environmental space. Rather than supporting a complete niche shift, the observed pattern may reflect a process of niche expansion or adjustment within the broader climatic envelope already available to the species. Nevertheless, changes in niche centroid and breadth can still represent ecologically meaningful shifts, even in the absence of total niche displacement (Broennimann *et al.* 2012; Sexton *et al.* 2017).

### IMPACT OF CLIMATE CHANGE ON THE DISTRIBUTION OF *C. VILLOSUS*

Projected analyses under different greenhouse gas (GHG) emission scenarios reveal changes in climatically suitable areas for *C. villosus* toward the end of the 21st century. Under a low-emission scenario, a substantial loss of suitable areas is projected in central and northern Argentina, indicating that these regions will no longer provide favorable climatic conditions for the species. The models also suggest the persistence of suitable conditions in southern Patagonia and Tierra del Fuego, although no clear expansion is projected into new areas within these regions. This pattern contrasts with expansion behaviors observed in other species under accelerated climate change scenarios (Pack *et al.* 2022; Pauchard *et al.* 2016; Smith *et al.* 2017). While the loss of suitable habitats in temperate and arid regions of central Argentina presents clear challenges, the projections do not suggest compensatory climatic gains in the far south.

In the case of Tierra del Fuego, the predicted suitability likely reflects, at least in part, the current presence of the species, which was introduced through anthropogenic means.

Monitoring areas already colonized, particularly those that appear marginal under future scenarios, remains relevant to assess the long-term persistence of invasive populations and their potential ecological impacts.

### Practical implications for management

Our findings have implications for the management and conservation of fragile ecosystems such as Tierra del Fuego (Lizarralde *et al.* 2004). The ability of *C. villosus* to adapt and occupy distinct climatic niches in the invaded area and the potential to expand to other areas within the island that it is not currently occupying poses a considerable risk for wildlife (Gallo *et al.* 2020).

Effective management efforts should prioritize areas within Tierra del Fuego that have not yet been colonized by *C. villosus*. These areas represent unoccupied portions of the species' potential niche. Likewise, peripheral zones at the southern edges of the current known distribution may act as expansion fronts under favorable conditions. Focusing control strategies in these zones would allow for early detection of new colonization events and more efficient allocation of monitoring and mitigation efforts. Preventing the colonization of these areas is essential to limiting species spread and mitigating its ecological impact (Davidson *et al.* 2011).

## CONCLUSIONS

Our findings indicate that *Chaetophractus villosus* has successfully established in Tierra del Fuego. Its current distribution on the island appears to be nested within the environmental space it occupies on the mainland, although with measurable changes in niche centroid and breadth that may reflect ecological adjustment or expansion.

Despite the limited climatic overlap between ranges, *C. villosus* shows the ability to persist and potentially expand into still unoccupied but climatically suitable areas. Although future climate projections do not predict the emergence of new favorable regions in the south, they do show a contraction of the species' core range. The availability of suitable soil types and other non-climatic factors will ultimately determine whether these areas become occupied.

These results underscore the importance of proactive management strategies that anticipate potential expansions, particularly at the southern and eastern edges of the current distribution and integrate long-term monitoring of areas not yet colonized. Considering the adaptability of the species and the fragile nature of the sub-Antarctic ecosystem, conservation efforts should prioritize early detection in order to prevent and mitigate the potential ecological impacts that this invasive species could have on local biodiversity.

## SUPPLEMENTARY MATERIAL

The supplementary material includes the following information:

- Sampling bias analysis, Figure S1.
- Description of the bioclimatic variables used for niche comparison in the environmental climate space, Table S1.
- Descriptive statistics of bioclimatic variables in the native range of *C. villosus*, including standard deviation, variance, and coefficient of variation, Table S2A.
- Descriptive statistics of bioclimatic variables in the invaded range of *C. villosus* on Isla Grande de Tierra del Fuego, Table S2B.
- Overlap and niche dynamics indices for *Chaetophractus villosus* in native and invasive areas, Table S3.

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