

Research Article

Wing shape changes as a proxy for invasion success in Antarctica: case study of *Psychoda albipennis* (Psychodidae) using geometric morphometrics

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Abstract

Invasions of exotic species in fragile and pristine ecosystems, such as those of Antarctica, is a growing ecological concern. *Psychoda albipennis*, a cosmopolitan saprophagous fly, has recently become established in the Maritime Antarctic South Shetland Islands archipelago, raising questions about its potential for adaptation and expansion. This study analyses wing morphological variation amongst Maritime Antarctic and Magellanic sub-Antarctic populations of *P. albipennis* using geometric morphometrics to infer rapid adaptive responses to the extreme Antarctic environment. The data obtained reveal significant differences in wing shape and size, with Maritime Antarctic flies exhibiting narrower and more elongated wings, an aerodynamic configuration likely favoured under stronger wind conditions. Additionally, interannual reduction in wing size in the Maritime Antarctic population suggests an adaptive thermoregulatory strategy, partially consistent with the temperature–size rule. These morphological changes are likely to be associated with selective pressures, such as wind strength and minimum temperatures, which explained 46% and 2.74% of the shape variation, respectively. Our findings support the hypothesis of rapid phenotypic response processes, reflecting an early stage of successful adaptation. Given the species' potential ecological impact, including alterations in decomposition processes and trophic networks, we emphasise the need to implement early detection and preventative management strategies. This research highlights the value of geometric morphometrics as a cost-effective and practically applicable tool for identifying adaptive patterns in biological invasions and supports the application of integrative approaches combining morphological, genomic and physiological data to anticipate and mitigate the consequences of future invasions in Antarctica.

Key words: Biological invasion, King George Island, moth flies, non-native species, phenotypic plasticity

Introduction

Exotic species represent one of the most significant threats to biodiversity in natural systems (Frenot et al. 2005). This phenomenon is a direct consequence of various anthropogenic activities, such as the globalisation of trade, increasing tourism, wildlife trafficking and land-use change, amongst others (Hulme 2009; Stavert et al. 2017; Hayes et al. 2025). These activities not only facilitate the introduction of new species, but also contribute to the degradation of ecosystems worldwide. In this context, Antarctic ecosystems are often considered amongst the least disturbed on the Planet. The intrinsic characteristics of this continent, such as its extreme climate and geographic isolation, have served as natural barriers against the dispersal and establishment of new species by natural processes (Frenot et al. 2005; Duffy et al. 2017).

However, in recent decades, the influence of climate change, together with the progressive (and largely unregulated) increase in human activities in the region, has paved the way for the entry of exotic species with invasive potential (Hughes et al. 2025). As a result, a total of 112 terrestrial exotic species have been reported in Antarctica, with over 240 records, primarily concentrated in the Antarctic Peninsula region. Of these, at present 18 species are known to have established in the natural Antarctic environment for at least some period (Hughes et al. 2025), all in the Maritime Antarctic region, with a small number of other species present in synanthropic situations in research stations. Notably, since the onset of human presence in the Maritime Antarctic region, there has been no evidence of any successful natural establishment events, although occasional vagrant individuals and propagules have been recorded. On King George Island in the South Shetland Islands, the establishment of synanthropic species, such as *Plodia interpunctella* Hübner, 1813 (Pyralidae), has been documented, along with species that were initially confined (or thought to be) to synanthropic environments, but have recently been confirmed to be present in natural habitats, such as *Trichocera maculipennis* Meigen, 1818 (Trichoceridae) and *P. albipennis* (Zetterstedt, 1850) (Volonterio et al. 2013; León et al. 2021; Benitez et al. 2024; Hernandez-Martelo et al. 2024).

Psychoda albipennis, a cosmopolitan dipteran of the family Psychodidae, commonly known as the moth fly, typically inhabits environments rich in decaying organic matter. Although populations have been reported in South America (Argentina and Chile) (Elgueta and Jezek 2014), no previous records existed for the Magellanic sub-Antarctic region. On Navarino Island, the absence of evidence confirming its native status suggests it may be an introduced or naturalised species, consistent with its cosmopolitan distribution. This species has gained scientific attention due to its ability to adapt to the extreme climatic conditions of Antarctica, where it is a non-native species. Since its first record on the continent in 2019 (SCAR 2022), its persistence and recent observations in natural habitats suggest not only a successful adaptation process, but also expansion into new environmental conditions, raising concerns about its potential impacts on the fragile Antarctic ecosystem (Hernandez-Martelo et al. 2024). Unravelling the adaptive mechanisms that have facilitated its integration into the Antarctic ecosystem is now a priority.

An exotic or non-native species is defined as any taxon present and reproducing beyond its native range, having been transported and introduced either intentionally or accidentally as a result of anthropogenic activities (Blackburn et al. 2011). Not all such species become invasive and only those that are able to overcome

ecological filters (comprising both abiotic and biotic factors), establish, spread and produce negative impacts on the recipient ecosystem are considered as such. This distinction has led many researchers in the field of invasion biology to ask the central question of what makes an exotic species become invasive (Blackburn and Duncan 2001). One approach to addressing this question suggests that invasion success represents a major challenge for an exotic species and requires adaptation to new ecological conditions (Keller and Taylor 2008; Pluess et al. 2012).

The adaptive processes observed during biological invasions may be mediated, primarily, by mechanisms of accommodation or phenotypic plasticity (Debat and David 2001). These operate at the individual level, are reversible and non-heritable, yet enable functional responses (morphological, physiological, genetic or behavioural) to variable environmental stimuli (Hulme 2008; Nyamukondiwa et al. 2010; Davidson et al. 2011; Molina-Montenegro et al. 2012; Kelley 2014; Marin et al. 2020). However, adaptation can also occur through genetic assimilation, where a shift in allele frequencies takes place within a population in response to selective pressures, resulting in rapid evolutionary changes observable within just a few generations (Rivera-Marchand et al. 2012; Rayner et al. 2019). Unlike plasticity, these changes are permanent, heritable and occur at the population level, playing a decisive role in the establishment and spread of species in novel environments (Debat and David 2001; Fox et al. 2019; Miller et al. 2023).

The use of morphometric markers has historically been a key tool employed as a proxy for adaptation, contributing to our understanding of biological diversity and to the identification of morphological responses associated with invasion processes (Azzurro et al. 2014) in relation to the environment and species lifestyles (ecomorphology) (Adams et al. 2004; Betz 2006; Lemic et al. 2021). In winged insects, wings are reference morphological structures in evolutionary and ecological studies, as their high plasticity makes them sensitive to environmental, anthropogenic and other selective pressures (e.g. sexual selection). These pressures may induce adaptive shape changes and size-related effects (allometry) that enhance fitness under adverse conditions (Mikac et al. 2019; Gemmellaro et al. 2024). Furthermore, wings play a crucial role in dispersal and the colonisation of new areas, key aspects of geographic expansion processes (Lemic et al. 2021). These properties make them ideal models for morphometric studies, as they allow precise delimitation of anatomical reference points (landmarks) at the intersections of wing veins, which are essential for the structural support of the wing (Chazot et al. 2016).

In this context, given that changes in wing morphology can significantly influence the success or failure of a species during the processes of establishment, dispersal and colonisation of new areas, quantifying these morphological disparities can provide a key proxy for adaptive and invasive potential. To this end, approaches, such as geometric morphometrics (GM), have been developed, a technique that combines multivariate statistical tools with data that accurately capture the geometry of biological structures (Bookstein 1986; Rohlf and Marcus 1993). Unlike traditional methods, GM allows for the simultaneous analysis of shape and size, based on landmarks, which are specific, equivalent and homologous points on a studied biological structure (Bookstein 1986). Additionally, GM is based on the Generalised Procrustes Analysis (GPA), which enables the extraction of shape information by eliminating components of variation, namely scale, rotation and orientation (Rohlf and Slice 1990; Benítez and Püschel 2014).

In recent years, geometric morphometrics (GM) has become recognised as an effective tool for assessing traits related to the invasiveness of exotic species. For example, Lemic et al. (2023) analysed wing variation in *Cydalima perspectalis* (Walker, 1859) (box tree moth), demonstrating that wing shape is key indicator of invasive potential, flight capability and dispersal risk. Similarly, Mikac et al. (2016) examined the morphology of hind wings in European populations of *Diabrotica virgifera virgifera* (LeConte, 1868), associating wing shape with invasion processes and multiple introduction events. Likewise, Lemic et al. (2021) quantified variation in the wing shape of *Ceratitis capitata* amongst various European geographic populations, encompassing different crops and comparing wild populations with laboratory-reared specimens.

Given the importance of understanding the mechanisms that allow an exotic species to disperse, colonise and establish in new environments, this research takes on a strategic role. Such knowledge is key to designing, implementing and optimising strategies for the prevention, mitigation and eradication of invasive species, particularly in environmental management programmes promoted by governmental agencies in Antarctica, with an emphasis on King George Island (COMNAP 2008; Terauds et al. 2012; Hughes et al. 2019). This study analyses the morphological adaptive patterns of *P. albipennis* in to the context of the extreme conditions faced on King George Island. We hypothesise that, as an exotic species in a colonisation phase, the fly will require rapid wing morphological modifications in order to survive, establish and disperse in the Antarctic ecosystem. Our primary objective is to quantify morphological differences between Antarctic populations and, due to their cosmopolitan nature, compare them with populations from the South American continental sub-Antarctic region, considered the gateway to Antarctica.

Material and methods

Study area and sample collection

This study focused on three localities where populations of the non-native *Psychoda albipennis* are established: two in Maritime Antarctica, the Chilean Professor Julio Escudero Station and the Uruguayan Artigas Station, both located on King George Island (South Shetland Islands) and one in the Magellanic sub-Antarctic region, the City of Puerto Williams on Navarino Island (Cape Horn Biosphere Reserve, south of the Tierra del Fuego Archipelago) (Fig. 1). Adult flies were collected during 2024 and 2025 using light traps, Malaise traps and manual sampling. A total of 429 specimens were collected: 157 from Escudero, 168 from Artigas and 104 from Puerto Williams and subsequently preserved in 70% ethanol. Subsequently, in the Laboratorio de Ecología y Morfometría Evolutiva, the samples were identified using both morphological and molecular approaches (see Hernandez-Martelo et al. (2024) and sexed by examining the abdominal apex, following the criteria described by Jezek (1983). The left and right wings were dissected from each individual and damaged or incomplete wings were excluded from the study. After this process, 241 individuals out of the 429 were selected and their wings were mounted on microscope slides and labelled according to established guidelines.

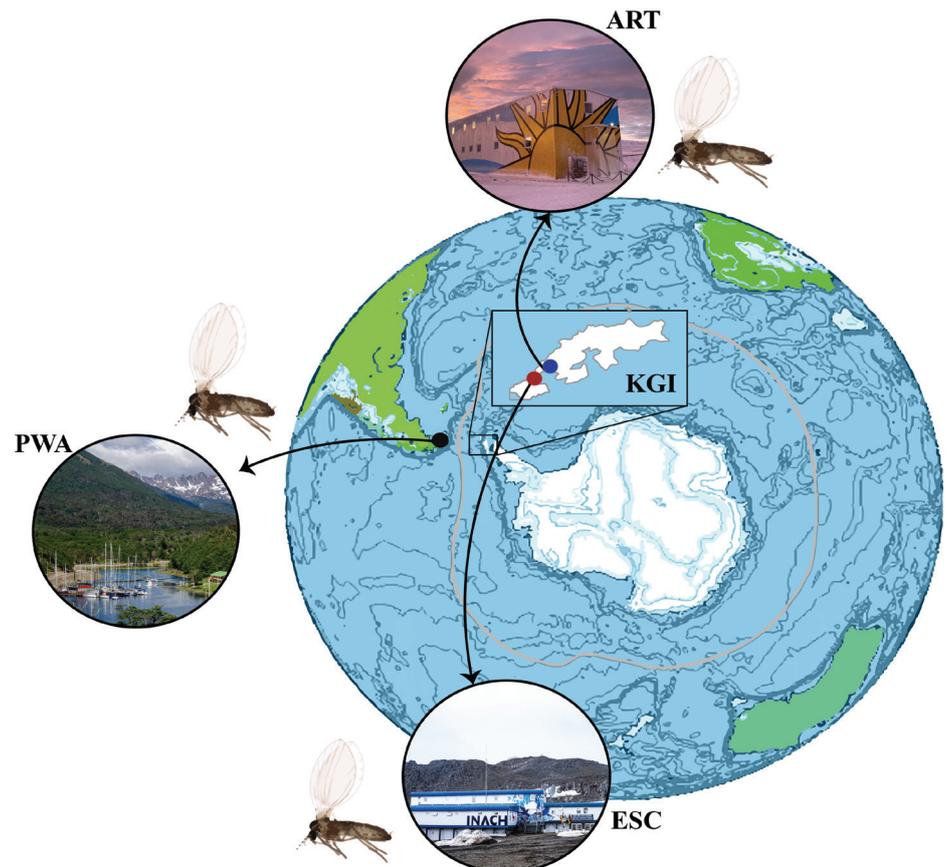


Figure 1. Map showing the sampling locations of *Psychoda albipennis*. Samples were obtained from three locations: Professor Julio Escudero Station (ESC; 62.20140°S, 58.96156°W), Artigas Station (ART; 62.18472°S, 58.90333°W), both located on King George Island (KGI) and Puerto Williams (PWA; 54.93161°S, 67.57350°W), on Navarino Island. Credits: under the CC BY-SA 3.0 Unported licence.

Data processing

Digitised images of a total of 482 wings (left and right wings of each fly) of *P. albipennis* were obtained using an Axiocam 208 camera coupled to a Zeiss Stemi 305 stereomicroscope. These images were scaled and converted to TPS format using TPSutil v.1.81 software (Rohlf 2015). Subsequently, 14 landmarks were placed following criteria of structural homology, consistency in relative position, adequate coverage of the biological shape, repeatability and co-planarity (Toro Ibacache et al. 2010) (Fig. 2). The digitisation of landmarks was performed using TPSdig2 v.2.17 software (Rohlf 2013). Specifically, for insect wings, reference points are commonly located at the junctions or termini of veins (Camara et al. 2006; Kadoić Balaško et al. 2021).

Data analysis

Prior to the main analyses, left and right wings were assessed for bilateral asymmetry. Exploratory analyses revealed a high correspondence in both centroid size and shape, with near-complete overlap in the morphospace (PCA). In the absence of meaningful directional asymmetry, both wings were treated as equivalent and pooled for subsequent morphometric analyses.

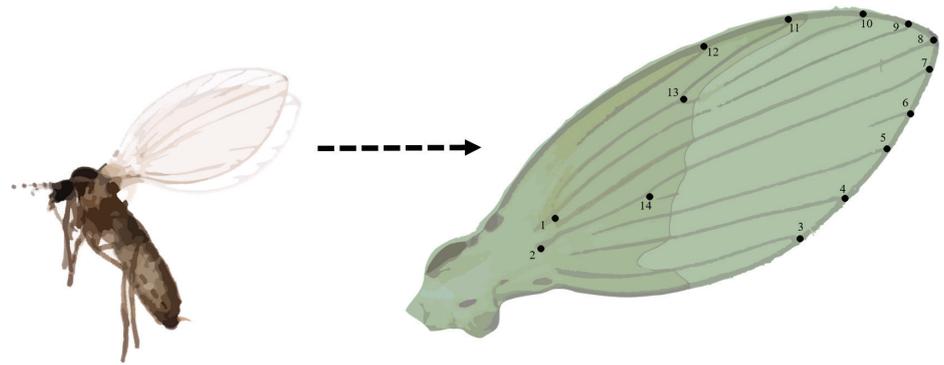


Figure 2. Representation of the wing shape of *Psychoda albipennis*, showing the 14 landmarks used for morphometric analysis.

All analyses were performed using the software MorphoJ v. 1.07a and the R package geomorph within the R-Studio platform (Klingenberg 2011; Adams and Otárola-Castillo 2013). First, the raw data, Procrustes coordinates and classifiers (location, sex and year) were extracted from MorphoJ. These data were imported into R and a Procrustes analysis was conducted using the “`gpagen()`” function from geomorph to transform the data by removing mathematical properties of size, rotation and orientation that do not affect shape (Rohlf and Slice 1990). This allows the calculation of the mean configuration that summarizes all landmark configurations, thereby enabling the description and comparison of specimen shapes (Rohlf and Slice 1990; Klingenberg et al. 2002).

To estimate measurement error, samples were digitised twice and evaluated through a Procrustes ANOVA, verifying that the mean squares associated with individuals were greater than those of the error (Arnqvist and Martensson 1998). Variation in wing shape was explored via principal component analysis (PCA), which represents the morphospace of geometric shapes, based on the covariance matrix relative to the mean wing shape (Jolliffe 2002). To visually represent differences in wing shape, Procrustes coordinates were imported into R and mean shapes for each classifier were calculated using the “`mshape()`” function from geomorph. Given that shape is closely associated with size (allometry), a multivariate regression was performed considering centroid size as the independent variable and shape as the dependent variable (Monteiro 1999). Adjusted values were interpreted as morphological variables with an allometric component, while residuals represented shape variation independent of size, i.e. the non-allometric component (Benítez et al. 2013). To examine differences in geometric size between locations and sexes, violin plots, based on centroid size, were constructed, complemented with regressions using the classifier “Sex”. Statistical significance was assessed through ANOVA and permutation tests with 10,000 iterations.

Influence of environment on wing shape

To explore the influence of environmental variables (temperature and wind speed) on geometric shape, a two-block Partial Least Squares (PLS) analysis was applied, which estimates the covariation between both matrices (Rohlf and Corti 2000; Hernandez et al. 2022). Additionally, linear models were fitted using randomised residual permutation procedures (RRPP) implemented in geomorph to evaluate the effect of the variables on shape (Adams and Otárola-Castillo 2013). In both cases,

shape was used as the dependent variable and combinations of variables served as predictors. Specifically, minimum and maximum temperatures, along with maximum wind speed, were evaluated as potential stress factors. Environmental data were obtained from the Antarctic Multiparametric Station Latitudinal Network of the Chilean Antarctic Institute (INACH) for Escudero and Artigas (https://www.redsensoresinach.cl/index.php?proj_pag=contact&p_cod=rlema, accessed 4 June 2025) and from the Chilean General Directorate of Civil Aeronautics (DGAC) for Puerto Williams (<https://climatologia.meteochile.gob.cl/application/diariob/visorDeDatosEma/550001>, accessed 3 June 2025). These standard meteorological measurements were taken at 2.5 m above ground level and cover a temporal scale corresponding to the austral summers of November 2023 to March 2024 and November 2024 to March 2025, coinciding with the study's sampling periods. Additionally, environmental variables were statistically compared between the Antarctic Region (Escudero and Artigas bases) and Navarino Island (Puerto Williams), with the aim of determining whether significant differences exist between the two regions. Environmental variables were treated as locality-level predictors and were linked to individual wing-shape data by assigning each individual the corresponding environmental timeseries of its sampling locality, thereby avoiding the use of environmental measurements as independent observations at the individual level.

These analyses allowed us to assess the relative contribution and statistical significance of each environmental variable to shape variation and to evaluate the association between environmental variability and individual wing shape. In contrast, comparisons of environmental variables between the Antarctic Region (Escudero and Artigas) and the sub-Antarctic Region (Puerto Williams) were conducted to provide a broader environmental context for the observed morphological patterns, rather than to directly model individual-level shape responses.

Furthermore, to better understand these relationships, we tested whether regional environmental differences were associated with the observed morphological patterns. Environmental comparisons were based on daily timeseries recorded during the austral summers of 2023–2024 and 2024–2025 for each locality. These datasets provided multiple observations per variable (minimum temperature, maximum temperature and maximum wind speed), allowing a robust statistical comparison between the Antarctic Region (Escudero and Artigas) and the sub-Antarctic Region (Puerto Williams) using the Mann–Whitney U test, as the assumptions of normality and homoscedasticity required for the Student's t-test were not met.

Results

The Procrustes ANOVA confirmed the reliability of landmark digitisation, showing that the mean squares (MS) for individuals (3.20073×10^{-5}) greatly exceeded that associated with error (3.8493×10^{-6}). The first three principal components (PCs) of the PCA explained 66.5% of the variation in wing shape of *P. albipennis* (PC1: 40.2%, PC2: 17.5%, PC3: 8.8%) (Fig. 3), representing the majority of shape variation, as the remaining PCs (PC4 and PC24) accounted for only 33% of the total shape variation. The results show clear differences in wing shape between the Magellanic sub-Antarctic population (Puerto Williams) and the two Antarctic populations (Escudero and Artigas). The latter populations also showed distinct separation.

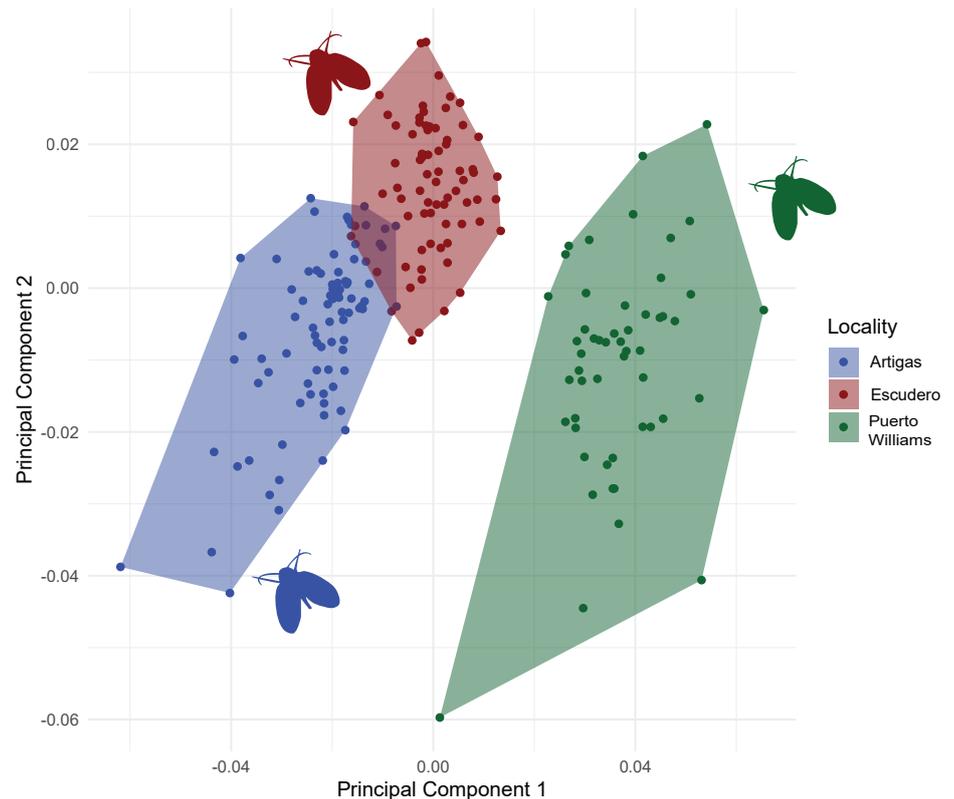


Figure 3. Principal Component Analysis (PCA) illustrating wing shape variation in *Psychoda albipennis* amongst the three sampling locations.

The superimposition of mean shapes revealed clear differences amongst the three sampling locations (Fig. 4A). Individuals from the two King George Island populations were characterised by narrower and more elongated wings, contrasting with the Navarino Island population, whose wings were more compact and flattened. At Artigas, downward shifts were observed in landmarks 1, 2, 3, 4 and 14 and upward shifts in landmarks 9, 12 and 13. The landmarks showing the greatest deformation were 3, 11 and 13, corresponding respectively to the first radial vein, the first cubital vein and the intersection between the third medial vein and the first cubital vein (Fig. 4B). In contrast, at Escudero, an upward displacement of landmark 3 (first radial vein) was observed, which gives the wings a slightly wider shape compared to those from Artigas. Although landmarks 4, 5 and 6 showed a tendency towards upward shifts, these did not reach significant deformation values as observed for landmark 13, similar to the wings from Artigas (Fig. 4D). Individuals from Puerto Williams exhibited the highest levels of deformation at landmarks 8, 10 and 11, corresponding to the cubital vein, showing displacement towards the distal region. Additionally, landmarks 3 and 12 exhibited shifts in opposite directions, tending to widen the wing (Fig. 4C).

The violin plot revealed that wings of females tended to be larger than those of males, except for Escudero where a low number of males were sampled (Fig. 5). Two-way ANOVA assessing the effects of sex and location on centroid size (Table 1) identified highly significant differences between the centroid sizes of males and females ($F = 48.613$, $p = 1.68e^{-10}$). Significant differences were also evident between locations, with Puerto Williams exhibiting the lowest values ($F = 12.037$, $p = 1.68e^{-05}$). Additionally, a significant interaction between sex and

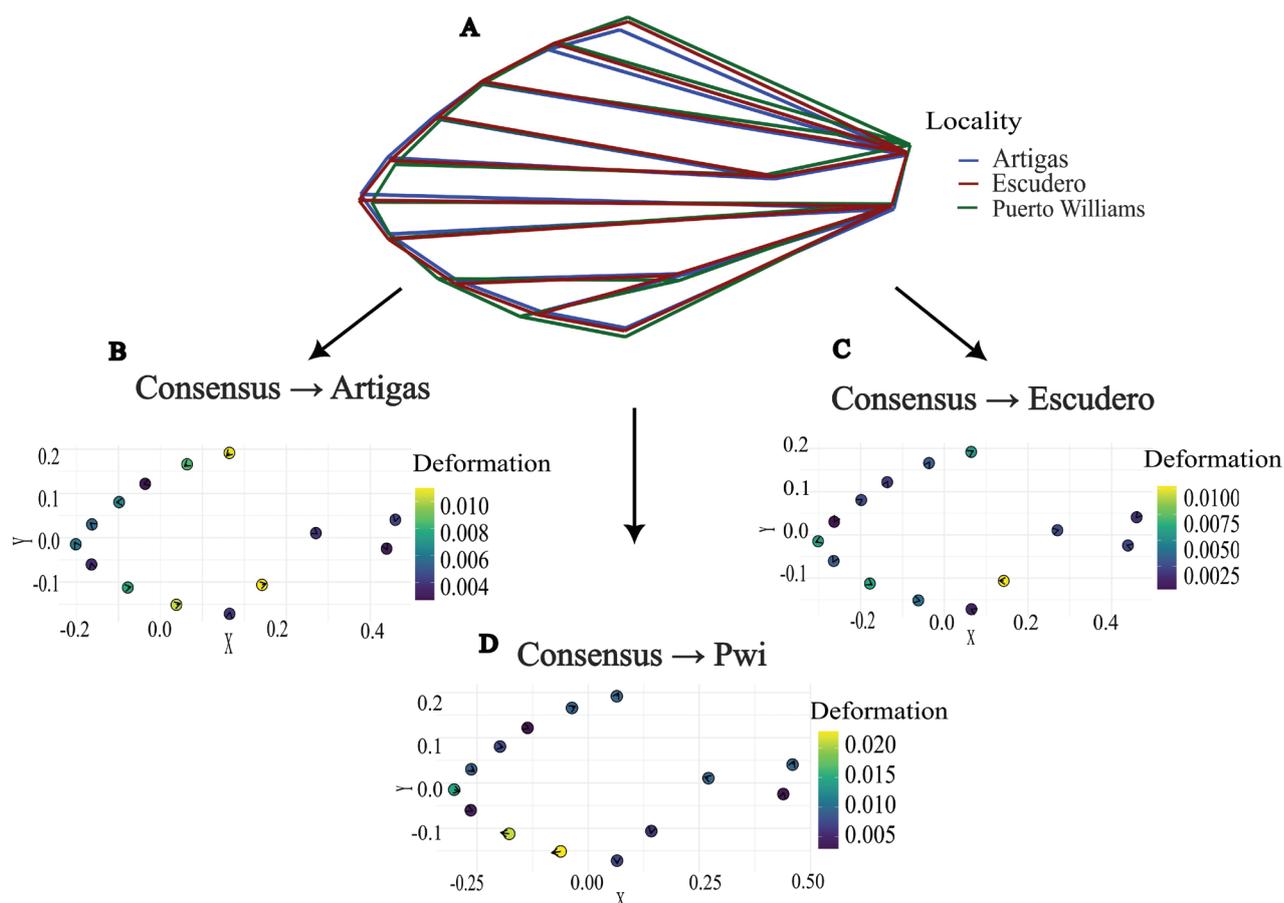


Figure 4. Superimposition and deformation of the average wing shape of *Psychoda albipennis* across the three sampling locations. **A.** Superimposition of the mean landmark configurations for individuals from the three locations: Artigas (blue), Escudero (red), Puerto Williams (green); **B–D.** Deformation grids showing shape differences between the overall consensus and each location: **(B)** Artigas, **(C)** Puerto Williams and **(D)** Escudero. Colour gradients represent the magnitude of deformation at each landmark, with higher values indicating greater displacement from the consensus shape.

location was detected in relation to centroid size ($F = 8.402$, $p = 0.00038$). Given this significant interaction, a “post hoc” test was conducted to identify specific comparisons where differences occurred. The Puerto Williams population had significantly smaller centroid size values compared to Artigas ($p = 0.0008$) and Escudero ($p = 0.0009$), while no significant difference was detected between Escudero and Artigas ($p = 0.933$). Comparison of wing shape between sexes revealed that female wings were slightly broader than those of males at all three locations (see Suppl. material 1).

The multivariate regression of size on shape using location as a classifier revealed an allometric influence of 12.39%, indicating a certain degree of association between wing size and shape. Three clearly-separated groups were observed along the shape axis (Regression Score), suggesting distinct morphologies and two groups differentiated along the size axis (Centroid Size) (Fig. 6A). Given the evident size differences amongst the Maritime Antarctic locations, additional multivariate regressions were conducted comparing samples obtained from 2024 and 2025 at Artigas and Escudero. In Escudero samples, the allometric effect was 3.27% ($p = 0.0001$), indicating a low influence of size on wing shape. In contrast, in Artigas, the effect was 12.32% ($p = 0.0001$), suggesting an allometric influence. At both locations, a difference in centroid

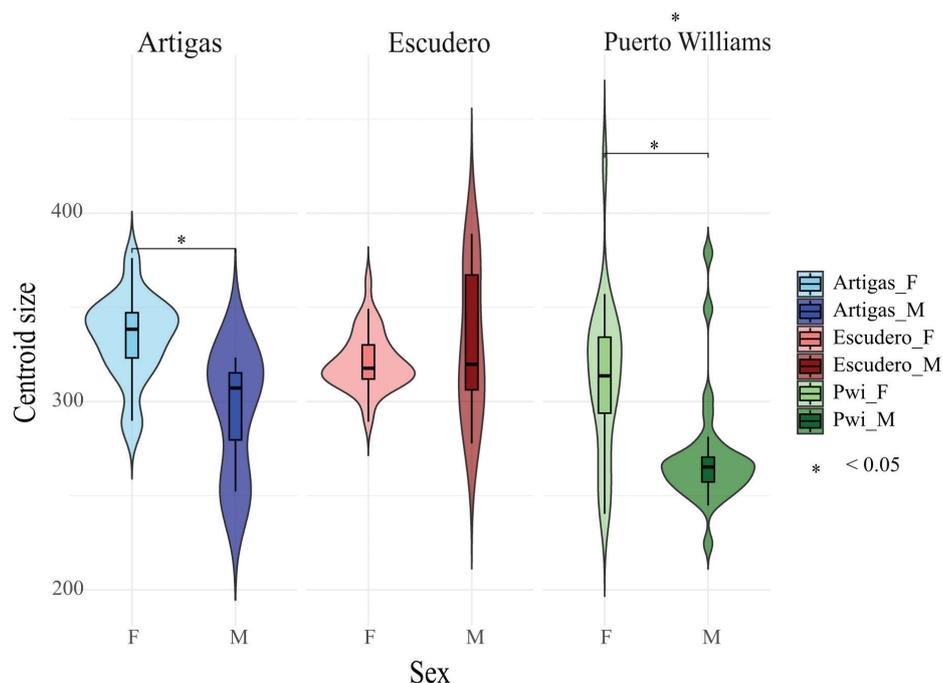


Figure 5. Distribution of wing centroid size by sex (F = females, M = males) across three localities (Artigas, Escudero and Puerto Williams). Violin plots illustrate the data distribution, while embedded boxplots show the median (central line), interquartile range (box) and whiskers representing 1.5 times the interquartile range. An asterisk (*) indicates statistically significant differences between sexes within each locality ($P < 0.05$).

Table 1. Two-way Analysis of Variance (ANOVA) for the centroid size of *Psychoda albipennis*, considering sex, sampling location and their interaction as factors. Significant effects were detected for both sex and location, as well as their interaction. Df = Degrees of Freedom, MS = Mean Squares and SS = Sum of Squares. A single asterisk (*) indicates statistically significant effects ($P < 0.05$).

Group	Df	SS	MS	F	P(> F)
Sex	1	39492	39492	48.613	$1.68e^{-10}$ *
Location	2	19557	9778	12.037	$1.68e^{-05}$ *
Sex*Location	2	13651	6826	8.402	0.00038*
Residuals	123	99922	812	–	–

size between years was apparent, with wings from 2024 being larger than those from 2025 (Fig. 6B, C). To assess whether these differences were statistically significant, separate Procrustes ANOVAs were performed for each location. In both localities, Escudero ($F = 2112.10$, $p < 0.0001$) and Artigas ($F = 1434.51$, $p < 0.0001$), the results were highly significant, indicating clear interannual variation in wing size. In both cases, the effect of year on centroid size was strong, highlighting consistent temporal changes across populations.

The Mann-Whitney test revealed significant differences in minimum and maximum temperatures between Antarctica and Puerto Williams (Navarino Island). Specifically, Antarctica exhibited considerably lower minimum temperatures ($W = 53$, $p < 2.2e^{-16}$), while Puerto Williams recorded higher maximum temperatures ($W = 0$, $p < 2.2e^{-16}$), confirming that this locality is warmer than Antarctica. Regarding wind speed, Puerto Williams experienced significantly stronger maximum winds during the analysed period ($W = 603.5$, $p = 1.564e^{-09}$).

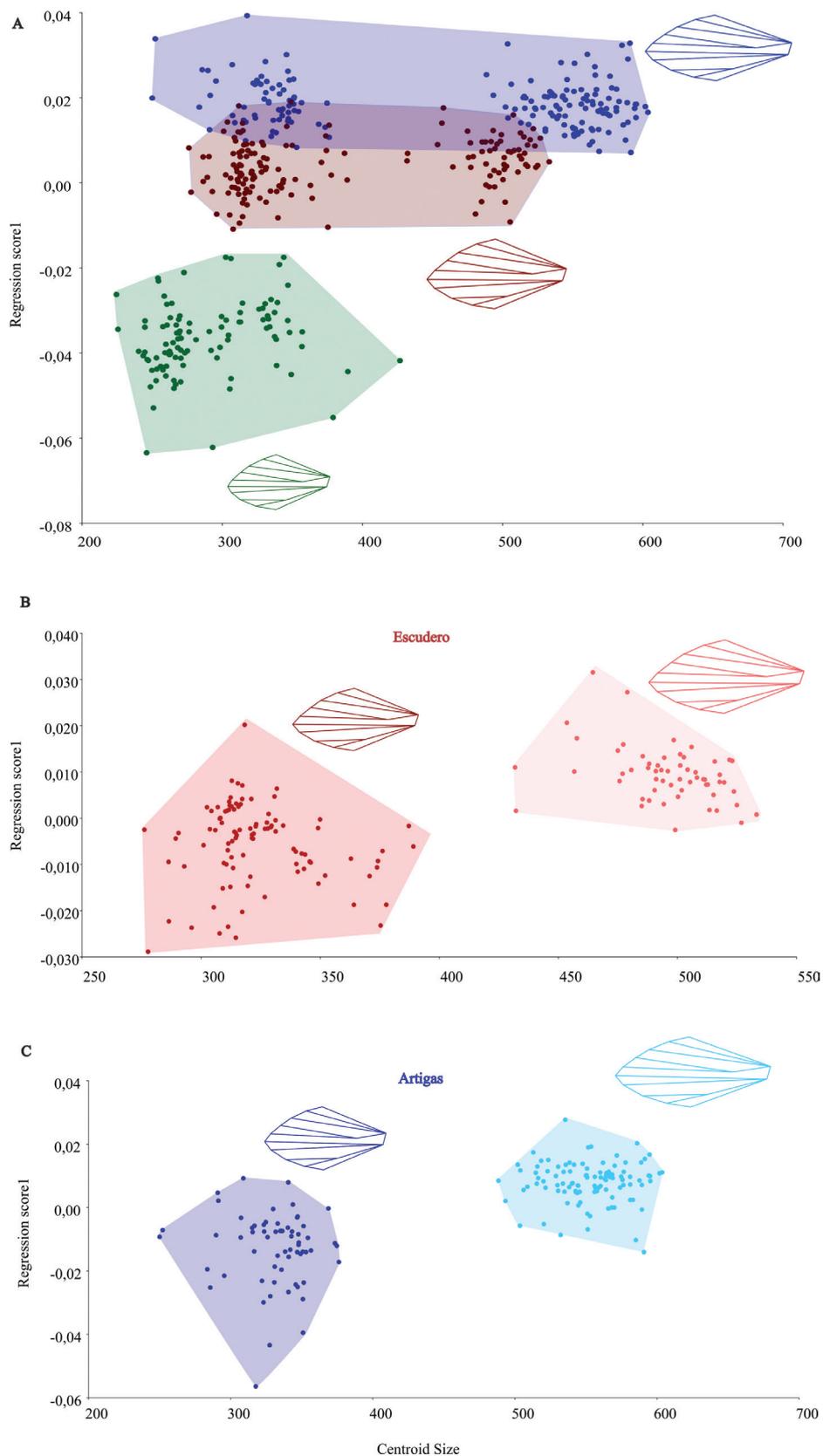


Figure 6. Multivariate regression between wing shape and centroid size of *Psychoda albipennis*. **A.** Analysis using sampling location as classifier. Green: Puerto Williams, blue: Artigas, dark red: Escudero; **B.** Analysis of Escudero samples using year as classifier. Dark red: 2025, pink: 2024; **C.** Analysis of Artigas samples using year as classifier. Dark blue: 2025, light blue: 2024.

Partial least squares (PLS) regression analyses identified the standard meteorological variables exerting the greatest influence on the three non-native populations of *P. albipennis* sampled. Results indicated that maximum wind speed explained 46% of the variation in wing shape, while minimum temperature explained 2.74%, with both being highly significant ($p < 0.001$) (Table 2). Similarly, maximum wind speed explained 46% of variation when analysed in combination with maximum temperature, which also explained 2.74% of the variation (Table 3). These findings suggest that both temperature and wind speed may act as selective pressures modulating wing morphology.

Table 2. Partial Least Squares (PLS) Regression Analysis. Results from the model fitted using “lm.rpp()” with a residual permutation procedure (RRPP, 1000 permutations). The effects of minimum temperature (tempmin) and maximum wind speed (windMax) on the wing shape of *Psychoda albipennis* were evaluated. R^2 values indicate the proportion of variation explained by each predictor. Df = Degrees of Freedom, MS = Mean Squares, SS = Sum of Squares, R^2 = proportion of total shape variation.

Effect	Df	SS	MS	R^2	F	Z	P(> F)
windMax	1	0.055	0.055	0.46	110.451	6.483	0.001
tempmin	1	0.003	0.003	0.027	6.589	4.595	0.001
Residuals	123	0.062	0.0005	0.512	–	–	–
Total	125	0.121	–	–	–	–	–

Table 3. Partial Least Squares (PLS) Regression Analysis. Results of the model fitted using “lm.rpp()” with a residual permutation procedure (RRPP, 1000 permutations). The effects of maximum wind speed (windMax) and maximum temperature (tempmax) on the wing shape of *Psychoda albipennis* are shown. R^2 values indicate the proportion of variation explained by each predictor. Df = Degrees of Freedom, MS = Mean Squares, SS = Sum of Squares, R^2 = proportion of total shape variation.

Effect	Df	SS	MS	R^2	F	Z	P(> F)
windmax	1	0.055	0.055	0.460	110.45	6.483	0.001
tempmax	1	0.003	0.003	0.027	6.589	4.595	0.001
Residuals	123	0.062	0.0005	0.512	–	–	–
Total	125	0.121	–	1.000	–	–	–

Discussion

This study documents clear patterns of morphological differentiation amongst non-native localities of *Psychoda albipennis* examined, all thought to be recent introductions. The observed wing shape variation suggests divergence amongst localities during an invasion process, potentially reflecting early-stage phenotypic differentiation, without implying the rate at which these changes occurred. These patterns, detected through geometric morphometric analyses, reflect the influence of environmental pressures with selective effects. They allow for the inference of both accommodation processes (the initial plastic response to a new environment) and assimilation (the progressive genetic fixation of traits that were initially plastic due to sustained selective pressures) (Pfennig et al. 2010).

An alternative explanation for the observed wing morphological variation is the presence of cryptic genetic structure amongst populations. Although all examined specimens were assigned to *Psychoda albipennis* based on morphology and mitochondrial COI sequences, these data alone do not allow cryptic differentiation

or incipient divergence to be fully ruled out. Thus, the observed morphological differences may reflect early phenotypic differentiation associated with the invasion process, cryptic population structure or a combination of both. Further genomic analyses with higher resolution markers would be necessary to disentangle these alternatives and to assess population structure in greater detail.

The extreme climatic conditions of Antarctica, including low temperatures and strong winds, are widely recognised as ecological barriers that limit the arrival and establishment of non-native species. However, once a species arrives and becomes established, these same conditions become selective pressures that can shape its phenotype (Kelley 2014). In winged insects, such as *P. albipennis*, wing morphology and flight capacity are key traits in the context of biological invasion, as they directly influence fundamental processes, such as dispersal, reproduction and the colonisation of new habitats (Azzurro et al. 2014). Leihy and Chown (2020) emphasise that, in insular environments, wind plays a crucial role in insect flight capacity by increasing the associated energetic costs and influencing the maintenance of wing structures. Turbulence caused by strong winds can significantly restrict flight performance (Combes and Dudley 2009). For introduced or colonising species in Antarctica, such as *P. albipennis*, sustained exposure to such pressures may induce adaptive responses in order to optimise aerodynamic performance and maintain functional fitness under more extreme environmental conditions (Whitney and Gabler 2008).

Our data reveal the presence of three morphologically differentiated non-native populations of *P. albipennis* in the Magellanic sub-Antarctic and Maritime Antarctic regions. Our analyses highlight marked contrasts in wing shape between the Magellanic sub-Antarctic populations and the more recently introduced populations in the maritime Antarctic, suggesting morphological differentiation associated with local adaptation to the new and more extreme environment. Maritime Antarctic individuals had wings that are narrower along the dorsoventral axis and elongated from the thoracic insertion to the apex (Fig. 4). Li and Nabawy (2022) noted that this type of aerodynamic configuration enhances flight performance in environments with high exposure to strong winds, suggesting that this new wing shape may be associated with greater dispersal and colonisation capacity (Leihy and Chown 2020).

Although the average maximum wind speed was significantly higher in Puerto Williams (18.13 km/h) compared to Antarctica (11.92 km/h; $p = 1.564e^{-09}$), this pattern does not necessarily translate into greater selective pressure on wings in the sub-Antarctic zone. Populations of *P. albipennis* in Puerto Williams inhabit environments with dense vegetation cover (mainly shrubs and forests) that buffer direct wind exposure. In contrast, Antarctic populations are exposed to open, vegetation-free landscapes, which increase their vulnerability to wind, even at lower average speeds. This direct exposure is likely to exert stronger selective pressure on flight-related morphological traits, such as wing shape and proportions. Therefore, from an eco-evolutionary perspective, it is likely that effective wind exposure rather than absolute wind speed is the main factor influencing the morphological differences observed between these regions.

Psychodid flies are characterised by limited flight capacity, typically performing short, erratic movements and often being easily carried by wind gusts (Munstermann 2019; Tonelli et al. 2021). However, the wing shapes observed in the Maritime Antarctic populations of *P. albipennis* studied here may represent a morphological adjustment that, together with the presence of setae on their wings, enhances flight performance in this environment (Engels et al. 2021). A similar pattern was

reported by Duckhouse (1971) in other psychodids (*Psychoda acutipennis* (Tonnoir, 1920) and *P. brachyptera* (Quate, 1964) inhabiting the sub-Antarctic Bounty, Antipodes and Campbell Islands. These species were described as having reduced, narrow and sharply pointed wings. The author suggested that this wing configuration might be related to their endemic status, although no evidence was provided to support this claim. Nevertheless, such wing morphology could indicate an adaptive process to the particular ecological context of these islands. Likewise, Ortega Ancel et al. (2017) demonstrated that wing shape and orientation significantly influence flight aerodynamics, showing that a greater wingspan (i.e. longer distance between wing tips) improves lift, reduces drag and facilitates more efficient gliding. In this context, the more elongated wings observed in *P. albipennis* from the Maritime Antarctic may confer more efficient aerodynamics, compensating for their limited flight ability in wind-exposed environments and enhancing both passive and controlled dispersal under windy conditions.

Our data also revealed differences in wing morphology between the two Maritime Antarctic populations. In particular, individuals from Escudero had slightly broader wings along the dorsoventral axis compared to those from Artigas. This morphological variation may again be associated with the degree of wind exposure or other environmental conditions experienced by the different populations. While specimens from Escudero are typically found in more sheltered areas, such as within or close to buildings, at Artigas, they are more frequently observed in natural habitats where they are directly exposed to more extreme environmental conditions (Hernandez-Martelo et al. 2024). Nevertheless, direct evidence is still needed to support this hypothesis, such as comparable meteorological measurements between the two stations or microclimatic data from the specific habitats where the flies are observed.

Flies from Navarino Island (Magellanic sub-Antarctic) exhibited broader, but less elongated wings compared to those from the Maritime Antarctic. This wing configuration aligns with lower exposure to strong winds (18.13 km/h Puerto Williams vs. 11.92 km/h in Antarctica, $p = 1.564e^{-09}$), which is plausible given the dense vegetation surrounding Puerto Williams that likely buffers wind impact.

Changes in wing morphology may also be driven by selective pressures related to sexual selection (Gidaszewski et al. 2009). Although our analyses did not reveal sexual dimorphism in wing shape, marked size dimorphism was apparent. Specifically, the violin plot showed that the centroid size of female wings was significantly larger than that of males (Fig. 5). This pattern is consistent with reports in numerous insect species, in which females tend to have larger body sizes (de Camargo et al. 2015; Benítez and Vargas 2017; Zhou et al. 2020; López-Mercadal et al. 2021).

This difference in wing size may be related to greater energetic investment by females in reproductive functions, which would be reflected not only in body size (Frazier et al. 2008), but also in the development of structures, such as wings (Berger et al. 2008). Moreover, larger body and wing sizes can influence egg size and, consequently, reproductive success (Yanagi and Tuda 2012). Furthermore, our analyses revealed significant differences in wing size between the study locations, with those from Puerto Williams being significantly smaller.

The latter observation variation may be an illustration of the temperature–size rule, which states that individuals of a given species developing in cold environments grow more slowly and, therefore, reach larger sizes due to reduced metabolic rates (Atkinson 1994; Forster and Hirst 2012; Klok and Harrison 2013). These results are also consistent with the findings of Frazier et al. (2008), who demonstrated that flies reared at low

temperatures develop relatively larger wing sizes in relation to body mass, improving performance under cold conditions. Similarly, Rendoll-Cárcamo et al. (2023) evaluated variation in body and wing size in native species of the orders Ephemeroptera and Plecoptera on Navarino Island, finding that several species exhibited patterns consistent with the predictions of this rule. Although their study was conducted along an altitudinal gradient, this may provide a proxy for understanding the modulatory role of temperature across larger scale geographical environmental gradients.

The observed differences in wing shape and size illustrate an allometric influence, explaining 12.39% ($p = 0.001$) of the morphological variation. The general multivariate regression (Fig. 6A) reinforces the size differences between Magellanic sub-Antarctic and Maritime Antarctic populations as well as revealing significant spatial variation. In particular, the location-specific analyses (Fig. 6B, C) demonstrate interannual reduction in wing size in the Escudero and Artigas population, with this effect being more pronounced at Artigas. This pattern could be interpreted as an adaptive adjustment, modulated by temperature as, although it may initially appear to contradict the temperature–size rule, various studies have documented that, in certain contexts, a reduction in body or wing size can function as a thermoregulatory mechanism (Angilletta et al. 2002; Chown and Nicolson 2004; Santos et al. 2024).

In this case, a reduction in wing size could represent a functional advantage by decreasing heat loss or improving aerodynamic performance under variable thermal conditions (Combes and Dudley 2009). Moreover, the reduction in wing size could also reflect decreased flight activity or a functional inhibition of flight due to constant wind exposure. For instance, Leihy and Chown (2020) showed that in sub-Antarctic regions, characterised by strong and persistent winds, secondary flight loss has evolved repeatedly across multiple insect lineages. In such environments, reduced flight propensity or diminished wing structures may offer an adaptive advantage by preventing wind-induced displacement and lowering the energetic costs of maintaining flight capacity.

The PLS regression analyses support this hypothesis, showing that wind and minimum temperature explain 46% and 2.74% of wing shape variation, respectively. This suggests that both factors exert distinct selective pressures on wing morphology. Thus, our results suggest that temperature, alongside wind exposure, not only helps explain morphological differences between the Magellanic sub-Antarctic and Maritime Antarctic regions, but may also drive a progressive reduction in wing size within Antarctic populations themselves. This pattern could be interpreted as part of an adaptive adjustment response involving both thermoregulatory and aerodynamic functions. Although the mechanisms may differ, this perspective resonates with the ideas of Kingsolver and Koehl (1985), who proposed that insect wings may have originally evolved as thermoregulatory structures and were later refined for flight, becoming aerodynamically optimised.

Taken together, our data and analyses suggest the occurrence of phenotypic accommodation and assimilation processes, providing evidence of adaptive responses of *P. albipennis* to the more extreme conditions of the Maritime Antarctic. The observed variation in wing shape and size represents a functional adjustment that may enhance the fly's dispersal and colonisation capacity, reinforcing its invasive potential and indicating an increasing risk to the health of its newly-colonised ecosystem. This potential may be further amplified by specific life-history traits, such as the ability to enter diapause and the presence of parthenogenetic morphotypes (Jezek 1983), which will further facilitate the species' establishment, persistence and expansion. The low

terrestrial biodiversity of Maritime Antarctic ecosystems may make them particularly vulnerable to the negative impacts of invasive species (Hughes et al. 2025).

The potential expansion of *P. albipennis* into new Antarctic habitats could have significant impacts on local biodiversity and ecosystem functions, including alterations in species composition, trophic networks and key processes, such as decomposition, given its saprophagous role. A notable illustration of this is provided by the chironomid midge, *Eretmoptera murphyi*, whose introduction to Maritime Antarctic Signy Island from its native sub-Antarctic South Georgia has led to a four- to fivefold increase in inorganic nitrogen levels in the soil compared to uncolonised areas (Bartlett et al. 2023). Similarly, the example of *Trichocera maculipennis*, first observed on King George Island in 2007, exemplifies the dispersal and colonisation potential of exotic insects in Antarctica, as it has progressively expanded its distribution on the Island (Volonterio et al. 2013).

These precedents underscore the urgent need to implement early detection and control measures against biological introductions and emphasise the importance of biosecurity procedures being preventative rather than reactive. Deepening knowledge of phenotypic adaptive patterns and complementing these with genomic studies during the initial stages of invasion are essential for anticipating expansion scenarios, assessing risks and designing effective management plans. Understanding these dynamics enables the development of scientifically-grounded solutions not only for the development of new control programmes, but also for strengthening and optimising existing management strategies.

Conclusions

The establishment and expansion of a non-native species depend on its adaptive capacity to overcome the ecological filters of the recipient ecosystem. In this study, adaptive responses in *P. albipennis* are identified, such as wing size reduction and the development of a more aerodynamic wing configuration in Maritime Antarctic populations, likely in response to selective pressures of wind and temperature. The size difference observed between Magellanic sub-Antarctic and Maritime Antarctic populations of this non-native fly are consistent with the temperature–size rule, while the interannual change in wing size amongst Maritime Antarctic populations suggests an adaptive thermoregulatory strategy. These results not only reinforce the invasive potential of *P. albipennis*, but also raise concern about its possible ecological impacts in the fragile terrestrial ecosystems of the Maritime Antarctic, where its presence could alter key processes, such as decomposition, modify trophic networks and affect the structure of local biodiversity.

This study also highlights the value of geometric morphometrics as a cost-effective, precise and powerful tool to identify adaptive phenotypic patterns, particularly applicable in sustainable long-term monitoring programmes. To deepen understanding of the invasion process, it is essential to complement these morphological analyses with future genomic and physiological studies, in order to clarify key aspects, such as the genetic structure of populations, potential invasion routes, the presence of genes under selection and the physiological mechanisms involved in adaptive plastic responses to temperature. Taken together, these findings underscore the urgency of implementing effective surveillance and preventative management strategies, grounded in robust scientific evidence, to mitigate potential negative effects before invasions with irreversible ecological consequences become established.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Conceptualization: HAB, JCHM. Data curation: MG, KCV, JCHM. Formal analysis: JCHM. Funding acquisition: HAB, TC. Investigation: JPG, JCHM, FCJ. Methodology: JCHM. Project administration: HAB. Resources: HAB, TC. Software: JCHM. Supervision: JPG, PC, HAB, TC. Validation: MG, HAB, PC, GMMK. Visualization: JCHM. Writing - original draft: JCHM. Writing - review and editing: KCV, PC, JPG, JCHM, FCJ, TC, HAB, GMMK, MG.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Sexual dimorphism

Authors: Jordan Hernandez-Martelo

Data type: png

Explanation note: Multivariate regression to represent the sexual shape and size dimorphism in *P. albipennis*. The dependant variable is the wing shape and the independant variable is the centroid size.

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