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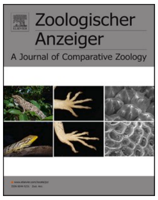

Evolving to invade: Using geometric morphometrics to assess wing shape variation in the Antarctic non-native fly *Trichocera maculipennis*

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ABSTRACT

Globalization has increased human movement, transforming ecosystems and introducing non-native species that threaten biodiversity, particularly in Antarctica. Due to its harsh climatic conditions, Antarctica has largely remained protected from biological invasions. However, rising human activity and environmental changes are facilitating the introduction of non-native species. The risks posed by species like *Trichocera maculipennis* are significant, as they can adapt and survive in new environments. This highlights the importance of understanding the adaptive factors that contribute to their success in order to prevent future invasions and protect the continent's unique ecosystem. The aim of this study was to quantify the wing morphological variation of *T. maculipennis* individuals associated with different Antarctic bases, analyzing this variation within a spatial and temporal context using morphometric tools. Samples were collected during Antarctic summer campaigns (2017/18 to 2019/20 and 2022/23) at the following research stations on King George Island: Artigas (Uruguay), Bellingshausen (Russia), Profesor Julio Escudero (Chile), and King Sejong (Korea). Morphometric analyses revealed changes in wing shape among study sites, with King Sejong individuals showing the most significant differences. Additionally, a temporal shift in wing size was observed, with specimens from 2017/18 and 2018/19 having larger average wings compared to those from 2019/20 and 2021/22. These results emphasize the importance of understanding the factors contributing to the success of non-native species to prevent future invasions and protect the unique ecosystem of Antarctica.

1. Introduction

Globalization and the growth of international trade and travel have facilitated increasing movement of humanity around the planet's biomes (Landschoff et al., 2013; Meyerson and Mooney, 2007). This has contributed to the transformation of ecosystems, loss of ecosystem services and high levels of non-native species introductions, often far in excess of natural dispersal rates (Landschoff et al., 2013). To date, the Antarctic continent's harsh environmental extremes (low temperatures, high wind speeds, etc.) and geographic isolation have enabled it to remain one of the least disturbed regions of the planet (Duffy et al., 2017), in particular protecting it from the scale of biological invasions seen elsewhere (Duffy et al., 2017; Frenot et al., 2005). However, the progressive breakdown of the continent's natural geographic barriers due to increased human activities (Convey, 2023; Tejedo et al., 2022), acting in synergy with the high rates of environmental change being

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experienced in some of its regions, records of establishment of non-native and in some cases potentially invasive species have increased (Bergstrom, 2022; Hughes et al., 2015), threatening the continent's unique biological diversity (Hughes et al., 2020).

A non-native species (also often referred to as alien, exotic, invasive) is one whose origin lies in a different region, which has been introduced into a new ecosystem by external factors. While dispersal and colonization leading to changes in range boundaries and the occupation of new locations are recognized natural processes, there is particular concern over the consequences of anthropogenically mediated movement of species to new locations, which can occur both intentionally or accidently, and in Antarctica is responsible for all known instances in the Antarctic continent and Peninsula and almost all (>98 %) in the milder sub-Antarctic islands (Capdevila-Argüelles et al., 2013). A majority of the non-native species that have managed to establish at an Antarctic location do not spread further or have negative impacts on the host ecosystem, and thus are not considered truly invasive, as is also noted more generally in the invasive species literature (Capdevila-Argüelles et al., 2013; Hughes, 2010).

The initial establishment and subsequent dispersal of a newly-arriving non-native species in a new environment is challenging, with success dependent on the ability to survive and reproduce under the new environmental conditions, and the presence of appropriate habitat, food and other resources. Studies such as those of Colautti and Lau (2015) and Molina-Montenegro et al. (2018) have emphasized that rapid evolutionary changes can be a key factor in establishment success of a species during biological invasions, while phenotypic plasticity is also considered important (Baker, 1974; Marin et al., 2020; Molina-Montenegro et al., 2018). Responses to different environmental drivers can be expressed as morphological, physiological, ethological, genetic and other changes (Freudiger et al., 2021).

Both environmental factors and an organism's genotype influence morphological variation. Thus, the measurement and analysis of anatomical characters have contributed to understanding biological diversity (Adams et al., 2004), including the proposal of adaptive hypotheses for the role of morphological shape variation in colonization processes (Betz, 2006; Lemic et al., 2021). Morphometric markers are widely applied to describe such variation, and are able to detect small and emerging changes (Lemic et al., 2021). One of the most widely used tools in this field is geometric morphometry (GM), which allows the study of the shape of organisms or biological structures. In GM, the definitions of landmarks at particular locations on the body generates a series of two-dimensional coordinates, which are then analyzed using multivariate statistics (Benítez and Püschel, 2014). In studies of insects, the wings are generally the most commonly used structures, as they directly individual dispersal and movement (Lemic et al. (2014).

In recent decades growing attention has been paid to the risks and consequences of the anthropogenic introduction of non-native species to Antarctica, due to the extremely high levels of species endemism characteristic of most terrestrial invertebrate groups and the very limited overall biological diversity present (Hughes, 2010). The Antarctic terrestrial flora, other than two species of flowering plant, comprises mosses and lichens, while the fauna consists of only two species of native insect (the winged chironomid midge, *Parochlus steinenii*, and the endemic brachypterous midge, *Belgica antarctica* (Contador et al., 2020; Rendoll-Cárcamo et al., 2020) and dominated in terms of diversity by microarthropods (mites and springtails) and microinvertebrates (nematodes, tardigrades, rotifers) (Convey and Biersma, 2024),

Parts of Antarctica, particularly the Antarctic Peninsula and Scotia Arc archipelagoes (Fig. 1), have experienced some of the most rapid rates of warming along with other environmental changes since the mid-Twentieth Century (Turner et al., 2009; Siegert et al., 2019), with predictions of continued and even accelerated warming throughout the current century. This is widely expected to facilitate the establishment and subsequent dispersal of non-native species to and within Antarctica (Siegert et al., 2019). The Maritime Antarctic biological region, which primarily includes the western coast of the Antarctic Peninsula, the South Shetland Islands and South Orkney Islands, is regarded as the most vulnerable to invasion (Chown et al., 2012; Hughes et al., 2020), and indeed is the only part of the area under Antarctic Treaty governance in which non-native species are known to be established in the natural environment (Hughes et al., 2015, in review). The risks posed by non-native species in Antarctica and their prevention, management and mitigation are a standing agenda item of the Committee for Environmental Protection (CEP) of the Antarctic Treaty Consultative Meetings (ATCM) (Hughes and Convey, 2010).

Two non-native dipterans are currently known to be established in specific parts of the Maritime Antarctic. These are the flightless midge,

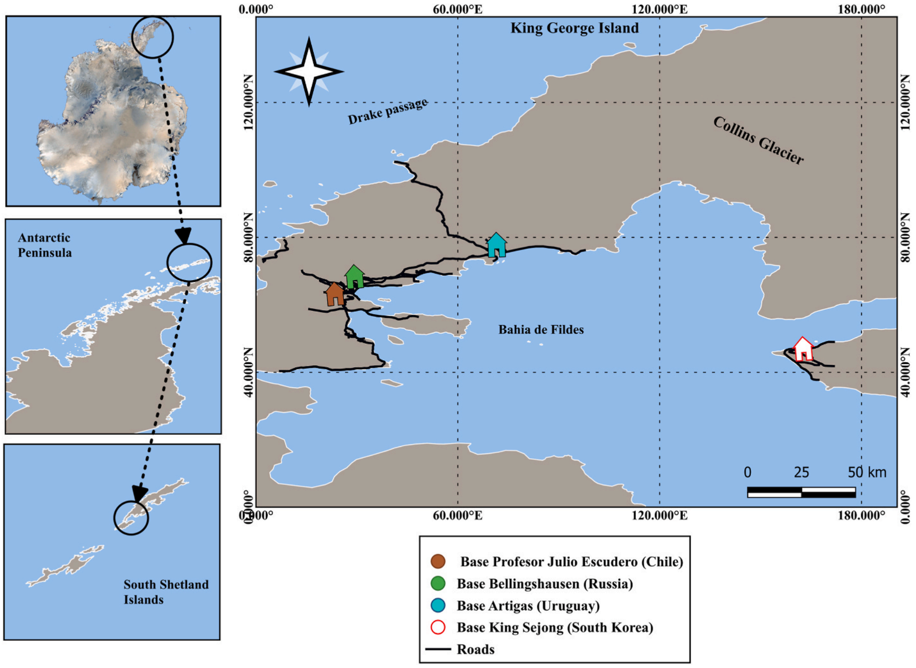

Fig. 1. Sampling locations on King George Island, South Shetland Islands, Maritime Antarctic.

Eretmoptera murphyi, a close relative of *B. antarctica*, which is endemic to sub-Antarctic South Georgia and became established in the 1960s on Signy Island (South Orkney Islands; Bartlett et al., 2019), and the boreal trichocerid fly, *Trichocera maculipennis* Meigen, 1818, which arrived on King George Island (South Shetland Islands in the late 2000s (Volonterio et al., 2013).

Since its first discovery, *T. maculipennis* has spread to several further locations on King George Island and, while most formal records come from close to established research stations (often linked with sewage treatment facilities), until recently there has been little or no dedicated survey effort, although since its first discovery it has been suggested that the fly is capable of surviving in the natural environment of the island (Volonterio et al., 2013; Potocka and Krzemińska, 2018; Remedios-de Léon et al., 2020), and this has most recently been positively confirmed (Benitez et al., in prep.). Given this species' rapidly increasing distribution on King George Island and its clear presence in natural habitats, it is now imperative to understand features contributing to its success, in order to help prevent the introduction of further non-native species, and to establish action plans that to minimize the risk of further dispersal where it is already established.

Morphological features of *T. maculipennis* include the presence of a ringed abdomen, the absence of wing spots and the presence of clearly darkened or clouded veins, which allow adult flies to be identified adult. The larvae are characterized by a strongly sclerotized head capsule. Larvae are saprophagous and sometimes coprophagous and, although typically terrestrial, they can be found in moist, semi-liquid, substrates (Potocka and Krzemińska, 2018). The species is native to the Holarctic region and is well adapted to cold environments, demonstrating a wide range of thermal tolerance compared to its congeners (Pertierra et al., 2021). The aim of this study was to quantify the wing morphological variation of *T. maculipennis* individuals associated with different Antarctic bases, analyzing this variation within a spatial and temporal context, using morphometric tools.

2. Materials and methods

2.1. Sample collection

Samples were collected during Antarctic summer campaigns (2017/18, 2018/2019,2019/20 and 2022/23) using ultra-violet (UV) traps, pitfall traps and sticky traps at the following research stations on King George Island: Artigas (Uruguay), Bellingshausen (Russia), Profesor Julio Escudero (Chile) and King Sejong (Korea) (Fig. 1).

2.2. Data analysis

The collected specimens were preserved in 95 % alcohol. A total of 294 *T. maculipennis* individuals from various localities, collected during multiple Antarctic expeditions, were subsequently processed. It is important to note that the study was based on data availability, as administrative and logistical limitations (permissions to collect from the different stations) prevented continuous temporal sampling across stations. Both wings of each individual were removed, mounted in an extended position, and prepared for morphometric analysis. Wing morphology was described using both the right and left wings of each fly, which were digitized with 35 landmarks placed at vein intersections and margins, ensuring clear homology and consistent identification (Fig. 2). Shape variation across the dataset was assessed using Principal Component Analysis (PCA) based on the covariance matrix of individual configurations, and an additional PCA using averaged shapes was conducted to identify general variation patterns in the morphospace (Jolliffe, 2002). To visualize differences in wing shape across the sampling localities, a Canonical Variate Analysis (CVA) was conducted. This discriminant analysis uses Procrustes coordinates to generate a set of new variables, known as canonical variables (CVs), which sequentially capture the maximum variance between groups relative to the variance within groups. To assess the morphological differences between groups, a permutation test (10,000 permutations) was conducted using Mahalanobis and Procrustes distances.

Since shape changes can be associated with changes in size, static allometry was evaluated using a multivariate regression of shape on centroid size (Monteiro, 1999). The predicted values were then used as morphological variables that account for the allometric component of shape, and the residuals were used to investigate the shape variation independent of size (i.e., the non-allometric component) (Benítez et al., 2013; Gidaszewski et al., 2009; Klingenberg, 2016). Finally, a violin plot was used to examine the distribution of samples based on geometric size (centroid size) across sampling years, enabling comparisons between different categories. Additionally, the assumptions of homoscedasticity and normality were verified as a prerequisite for statistical analysis. Subsequently, an analysis of variance (ANOVA) was conducted to determine the statistical significance of the differences between the samples.

Given that the sampling structure was more balanced across localities than across years, we adopted a differentiated analytical approach for the temporal and spatial scales: wing shape analyses focused on spatial differences, while analyses of size (centroid size) and allometry were conducted at the temporal scale. This methodological decision aimed to avoid biases associated with unequal sample sizes and to ensure a reliable interpretation of the observed morphological patterns.

All morphometric analyses were performed using the packages geomorph and gmshiny in the R environment (Adams and Otárola-Castillo, 2013; Baken et al., 2021) and MorphoJ 1.06d (Klingenberg, 2011).

3. Results

The PCA showed that the first three components of the morphospace explained 42 % of wing shape variance (PC1: 16.7 %, PC2: 14.0 %, and PC3: 11.4 %). After averaging the data, the PCA (Fig. 3) showed that the

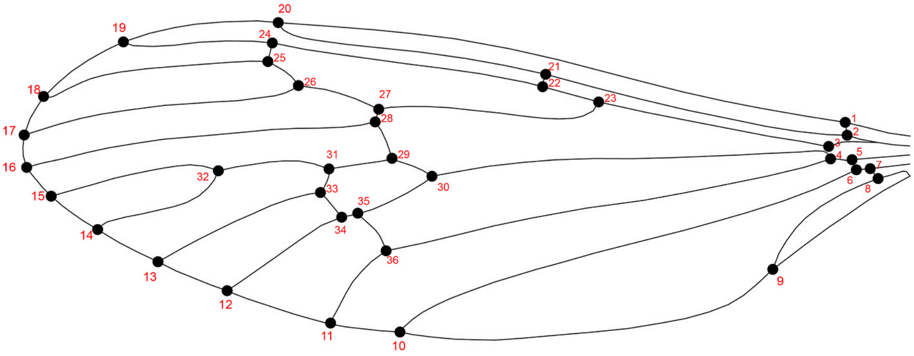

Fig. 2. Wing shape of *Trichocera maculipennis* illustrating the 35 landmarks selected.

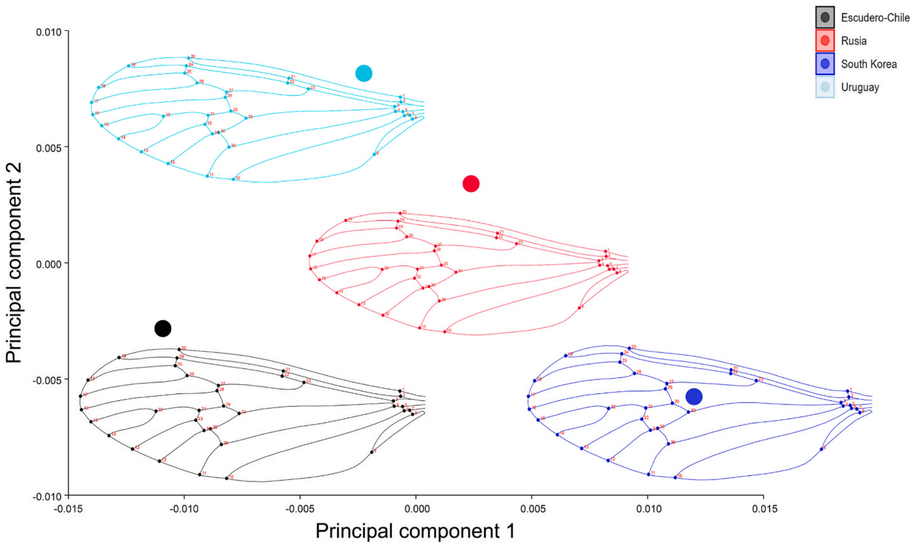

Fig. 3. Principal component analysis of the average wing shape of *Trichocera maculipennis*, illustrating differences between the four sampling locations (Bellingshausen, Artigas, Escudero and King Sejong stations).

locality from Bellingshausen and Artigas stations were most similar morphologically, followed by that from Escudero, with that from King Sejong displaying the most pronounced wing shape differences.

Compared with samples from the other three stations, specimens from King Sejong station exhibited subtle shifts in the positions of landmarks 9, 10, 11, 12 and 13, located in the ventral part of the wing, as well as downward movements of landmarks 1, 20 and 21 in the dorsal region. Downward shifts were also observed in landmarks 18 and 19, located in the apical region of the wing. Similarly, the wings of these individuals showed slight displacements towards the thoracic articulation, as reflected in landmarks 32, 29, 30, 27, 28 and 23, situated along the wing veins (Fig. 4). These differences result in the average wing shape of the King Sejong specimens being slightly narrower and shorter.

The (CVA) provided further support for the relatively minor variation between specimens from Bellingshausen, Artigas and Escudero and the distinct difference with those from King Sejong (Fig. 5)

The permutation test using Mahalanobis distances and Procrustes distances (Table 1) further validated these differences, under the null hypothesis that no significant differences exist between the groups, with all comparisons with the King Sejong specimens showing significant differences.

Finally, the multivariate regression of size on shape, analyzed from a temporal perspective (Fig. 6), showed an allometric effect of 3.88 %, indicating that there is no significant influence of size on shape (P = 0.0001). Additionally, a clear reduction in wing centroid size was

Fig. 5. Canonical Variate Analysis of the four studied *T. maculipennis* populations.

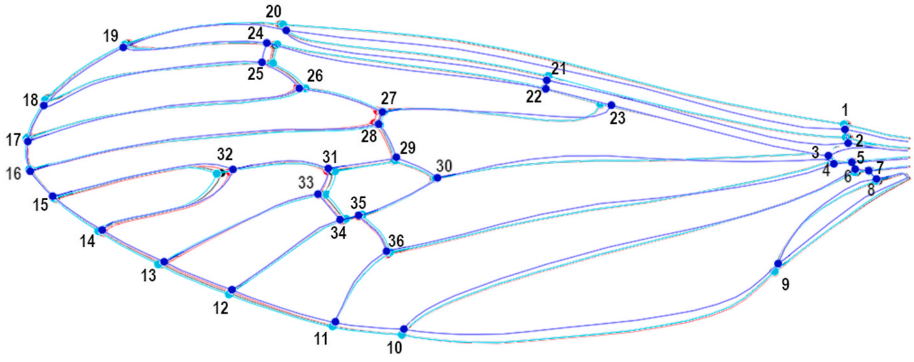

Fig. 4. Graphical representation of the superimposition of the average wing shape of the four sampled *Trichocera maculipennis* populations: Escudero (black), Bellingshausen (red), Artigas (light blue) and King Sejong (dark blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Mahalanobis and Procrustes Distances between populations of *Trichocera maculipennis* collected closet to the four Antarctic research station, with respective permutation comparison p-values.

Mahalanobis Distances/p-value	Escudero	Bellingshausen	King Sejong
Bellingshausen	2.2032		
	0.5652		
King Sejong	6.9066	7.0364	
	<.0001	**<.0001**	
Artigas	1.7569	3.8506	6.7322
	0.9976	<0.0001	**<.0001**
Procrustes Distances/p-value	Escudero-Chile	Russia	South Korea
Bellingshausen	0.0088		
	0.4793		
King Sejong	0.0189	0.0178	
	<.0001	**<.0001**	
Artigas	0.0081	0.0163	0.0218
	0.6526	**<.0001**	**<.0001**

observed over the five years of study.

The violin plot (Fig. 7) revealed significant differences in average wing size among individuals collected by year ($P = 0.0003$), highlighting that specimen from 2019/20 and 2022/23 had smaller wings compared to those collected in 2017/18 and 2018/19.

4. Discussion

This study provides insights into changes in phenotypic features between seasons and local populations of *T. maculipennis* on King George Island. Morphological variation in wing shape is likely to affect key attributes for invasiveness, such as flight capability and dispersal potential. Geometric Morphometric proved to be an effective tool for characterizing and analyzing insect wings, revealing morphological variation across the four sampling locations on King George Island. These patterns of variation appear to be modulated by the extreme Antarctic environment and the associated selective pressures.

The population near King Sejong station is geographically isolated

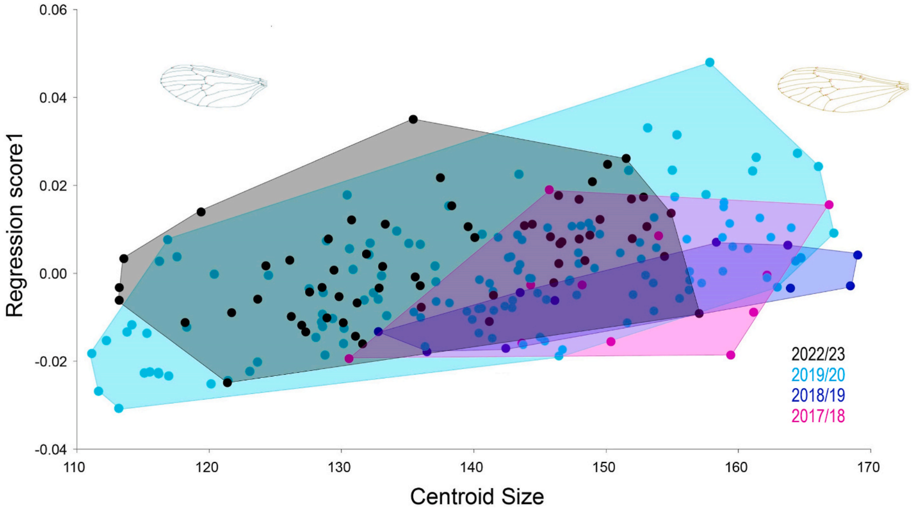

Fig. 6. Multivariate regression between wing shape and the centroid size of *T. maculipennis* individuals collected in the four separate study seasons.

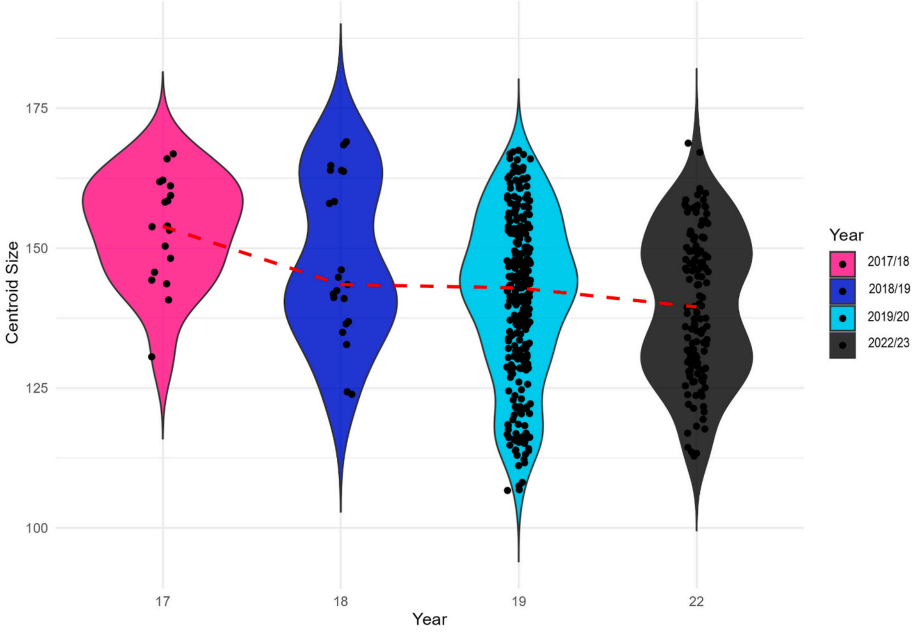

Fig. 7. Violin plot with a trend line showing the centroid size of *T. maculipennis* individuals and samples by year.

from the other three populations/station areas by the Collins Glacier and Fildes Bay, with connection provided only by anthropogenic maritime transport or independent aerial dispersal. Individuals in this population exhibited narrower and shorter wings, with a noticeable reduction in the distance between the wing apex and the thoracic articulation. Slatyer et al. (2020) noted that a reduction in gene flow across environmental gradients is generally needed for local adaptation to occur, and we hypothesize that these morphological changes reflect local adaptations to the specific conditions around King Sejong (Estoup et al., 2016; Kardum Hjort et al., 2024; Kawecki and Ebert, 2004). Field observations generally suggest that individuals *T. maculipennis* move around the spaces between rocks, often being unable to fly due to strong winds (pers. obs. Benitez and Contador) (Navarro, 2017; Yu et al., 2020) (see supplementary video). It is possible that the new morphological configuration, characterized by smaller, narrower, and more streamlined wings, emerges as an adaptive response to these strong winds. This wing morphology appears optimized to enhance aerodynamics, favoring dispersal and enabling higher speeds over short distances (Leihy and Chown, 2020). This could represent a fitness advantage for the population by increasing its capacity for colonization, access to resources, and reproductive opportunities in the Antarctic environment, as a response to the isolation they face.

In contrast, the specimens at Escudero, Bellingshausen and Artigas stations exhibited very similar wing shapes, suggesting an absence of isolation among them and, therefore, the existence of reproductive connectivity and gene flow (Cassel-lundhagen et al., 2011; Slatyer et al., 2020). The presence of transit routes between these three locations, along with the possibility of individuals moving between rocks or dispersing through human-facilitated means, supports this hypothesis. Another reinforcing factor is the similar and stable climatic conditions at the bases influenced by Fildes Bay. Since the isolated population (Korea) exhibited the greatest variation in wing shape, it can be inferred that the similarity in wing shape among these three locations may be attributed to reproductive connectivity and gene Flow (Clegg and Phillimore, 2010; Rundell and Price, 2009).

On the other hand, the allometric analysis showed that, throughout the analyzed time series (2017/18, 2018/19, 2019/20, and 2022/23), there were differences in both the centroid size and the wing shape. The multivariate regression and the violin plot revealed a significant reduction in the average wing size in the Antarctic populations of *T. maculipennis* over the years. However, it is important to note that sample sizes were smaller in the 2017/18 and 2018/19 seasons, which may limit the generalizability of the pattern observed in those particular years. Despite this, the consistency of the trend across the series supports the hypothesis of a biological tendency toward wing size reduction. This suggests the presence of selective pressures favoring individuals with smaller wings (Hoffmann et al., 2002). Hoffmann and Shirriffs (2002) and Alves et al. (2016) note that reduction in wing size in some insects is strongly associated with changes in environmental temperature, although it can also be underlain by the optimization of energy expenditure for thermoregulation or the diversion of energy towards reproduction (Rohner et al., 2019). Zera and Denno (1997) also highlight that the development of flight structures and active flight at low temperatures entails high energy costs, providing selection pressures towards flight loss. Similarly, Leihy and Chown (2020) emphasize that wind speed plays a key role in wing optimization and flight loss, especially in insects inhabiting insular, polar, or oceanic regions.

Establishment success by non-native species is predicated on their ability to overcome the ecological filters (biotic and abiotic) of the receiving ecosystem (Kelley, 2014). Multiple environmental stressors can be experienced, resulting in different levels of stress (Lalouette et al., 2011; Pajač Živković et al., 2018), which can select for changes in wing morphology (e.g. relating to wing load, structural changes), possibly facilitated by phenotypic plasticity (Chaiphongpachara et al., 2022; Nattero et al., 2015). Lemic et al. (2023) evaluated wing shape variation in the invasive lepidopteran, *Cydalima perspectalis* (box tree moth), in Europe, using this trait as a proxy for invasiveness, flight potential and the risk of further spread. They reported significant differences in wing shape between inland and coastal populations of the moth, concluding that these differences play a crucial role in the species' expansion into new habitats. Similarly, Mikac et al. (2016) analyzed the hind wing morphology of the invasive insect *Diabrotica virgifera virgifera* in Europe using GM, reporting that changes in wing shape and size were associated with multiple introduction events (propagule pressure) in Europe, with further support provided by genetic marker analyses.

Our data highlight the importance of unraveling adaptive mechanisms during the processes of colonization and invasion of new environments. This understanding has significant implications for the development of future comprehensive management strategies for non-native species, especially in ecosystems such as those of Antarctica with limited terrestrial biodiversity (Frenot et al., 2005; Hughes and Convey, 2010). Although guidelines have been developed to reduce the risk introduction of new species and control those already established in Antarctica (Chown et al., 2022), the limited biological, ecological and adaptive knowledge of such species, combined with the lack of enforcement mechanisms has to date proved largely ineffective (Hughes et al., 2020; Remedios-De León et al., 2020). Sixteen years after the introduction of *T. maculipennis* to King George Island the species appears to be accelerating in its invasion process and it is crucial to understand its capacity for adaptation in order to help develop effective biosecurity measures that can limit its further expansion into new environments.

CRediT authorship contribution statement

Jordan Hernández-Martelo: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mathias Jabs:** Writing – review & editing, Writing – original draft, Investigation, Data curation, Conceptualization. **Tamara Contador:** Writing – review & editing, Writing – original draft, Resources, Investigation, Conceptualization. **Sanghee Kim:** Writing – review & editing, Writing – original draft, Validation, Investigation, Conceptualization. **Sook young Lee:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Laura M. Pérez:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Mónica Remedios-De-León:** Writing – review & editing, Writing – original draft, Validation, Resources, Data curation, Conceptualization. **Enrique Morelli:** Writing – review & editing, Writing – original draft, Resources, Investigation, Data curation. **Peter Convey:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Investigation, Conceptualization. **Hugo A. Benítez:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jcz.2025.09.001.

Data availability

Data will be made available on request.

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