

Article

Wing Shape Variation in *Drosophila suzukii* Associated with Host Plants and Geographic Origin

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Abstract

This study investigates the effects of host plant and geographic origin on wing shape variation in *Drosophila suzukii* populations from Serbia using geometric morphometrics. A total of 421 left wings, each representing a different adult individual collected across five host plants and multiple localities, were analyzed to assess patterns of phenotypic variation. Principal component analysis revealed substantial overlap among groups, indicating that neither host plant nor geographic origin alone produces distinct morphological clusters. However, canonical variate analysis, deformation grids, and Procrustes distances detected subtle but consistent differences in wing shape. Procrustes ANOVA confirmed significant effects of both host plant and locality, with geographic origin explaining a larger proportion of the variation, and a significant interaction between factors indicating context-dependent morphological responses. Shape changes were primarily concentrated in distal and posterior wing regions, suggesting potential implications for flight performance and dispersal capacity. Our findings indicate that wing shape variation in *D. suzukii* is associated with host plant and geographic origin, suggesting that multiple ecological factors may contribute to the observed morphological differences. The observed patterns are consistent with the species' invasion success, reflecting ecological flexibility rather than discrete morphological differentiation. These findings provide a foundation for future studies investigating the mechanisms underlying host- and locality-associated wing shape variation in *D. suzukii*.

Keywords: geometric morphometrics; phenotypic variation; host plant effects; invasive species; wing morphology; spotted wing drosophila



Academic Editor: Eliseu José Guedes Pereira

Received: 9 July 2026

Revised: 1 August 2026

Accepted: 15 August 2026

Published: 18 August 2026

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1. Introduction

The spotted wing drosophila (*Drosophila suzukii* (Matsumura, 1931)) is an invasive pest of considerable economic importance in global fruit production systems [1,2]. Its invasion dynamics have been extensively documented. Unlike most species of the genus *Drosophila*, which oviposit exclusively in overripe or fermenting substrates, *D. suzukii* can lay eggs in intact, ripening fruits due to its strongly sclerotized and serrated ovipositor [1]. This adaptation causes substantial direct and indirect economic losses in soft-skinned fruit crops [3,4]. Native to East and Southeast Asia, *D. suzukii* has rapidly expanded its distribution across multiple continents [2,5], with its potential range further supported by predictive modeling across different climatic regions [6]. After its initial detection in Europe in 2008, the species spread rapidly throughout the continent [3,7]. It is now recognized as one of the most economically significant pests of berry and stone fruit crops [2,4,8].

The invasion success of *D. suzukii* is closely linked to its broad host range. The species exploits a wide variety of cultivated and wild host plants [1,8], with alternative hosts playing an important role in supporting population persistence outside managed systems [9–11]. This polyphagy enhances population stability and may also support dispersal across heterogeneous environments. From an integrated pest management perspective, this broad host use is important because it enables population persistence outside treated crops and facilitates seasonal movement between cultivated and non-crop habitats. Consequently, effective management of *D. suzukii* requires not only crop-level interventions, but also a better understanding of how host plants, local environmental conditions, and landscape structure influence population movement and recolonization risk.

In addition, *D. suzukii* exhibits high reproductive capacity and rapid development. Females may lay several hundred eggs during their lifetime, depending on environmental conditions, and development from egg to adult can be completed in as little as 8–10 days under optimal thermal conditions [12,13]. Temperature is a key abiotic factor influencing these processes, including development, survival, and reproduction [12,13]. The capacity of *D. suzukii* to respond to environmental variability is further reflected in its phenotypic plasticity. Phenotypic plasticity, defined as the ability of a single genotype to produce different phenotypes under varying environmental conditions [14], is an important mechanism enabling rapid responses to environmental variability. Its evolutionary significance has been widely discussed, particularly in relation to adaptation to environmental variability [15]. In *D. suzukii*, phenotypic plasticity has been proposed to contribute to invasion success [16]. Plastic responses in this species have been documented in developmental, behavioural, and reproductive traits [12], highlighting its ability to cope with diverse environmental conditions [16]. Such responses are shaped by both abiotic and biotic factors, including temperature and host plant [12,17].

Among morphological traits, insect wings represent a particularly suitable system for investigating phenotypic plasticity and environmentally induced variation. Geometric morphometrics has become a standard approach for quantifying shape variation [18] and has been widely applied in insect studies [19–23]. Experimental studies have demonstrated associations between wing morphology and flight performance [24]. However, the functional significance of naturally occurring wing shape variation in field populations remains largely unresolved. In *D. suzukii*, the relationship between wing morphology and flight performance has been experimentally explored under varying thermal conditions [25]. Experimental evidence shows that these conditions affect both wing morphology and flight parameters, including speed and acceleration, suggesting a potential functional relationship between wing plasticity and flight performance [25]. Dispersal-related traits are relevant because *D. suzukii* populations can move between non-crop hosts, surrounding vegetation and commercial orchards, affecting crop colonisation and reinfestation risk.

Therefore, understanding traits potentially associated with movement may complement ecological monitoring based on trapping, infestation data, host phenology and landscape context [4,26]. Because wing morphology in *D. suzukii* has been experimentally linked to flight-related parameters under different developmental conditions, morphometric variation may provide additional ecological information for interpreting dispersal-related phenotypic variation [25]. Similar environmentally driven changes in wing morphology have been documented in other insect species, highlighting the role of agroecological conditions in shaping phenotypic variation [20,21,27–29].

From an evolutionary perspective, a recent study has shown that wing shape evolution in *D. suzukii* is not strongly constrained by ancestral genetic covariances, indicating a relatively high degree of evolutionary flexibility [30]. Consequently, wing morphology can respond readily to environmental variation and may show subtle divergence among populations. However, phenotypic plasticity is not uniform across morphological structures. While wings exhibit substantial responsiveness to environmental variation, other functionally specialised traits may be more constrained. The ovipositor of *D. suzukii*, despite its role in host exploitation, exhibits relatively limited phenotypic plasticity, suggesting the presence of functional constraints on its morphological variation [31,32]. This highlights that functional specialisation can restrict phenotypic plasticity in certain traits.

In Serbia, *D. suzukii* was first recorded in 2014 on raspberry, blackberry, grapevine and fig [33], and subsequent monitoring has confirmed its continued spread and establishment in the country [34,35]. Similar patterns of population dynamics have been reported in neighbouring regions, where population fluctuations are associated with host plant phenology [36]. Despite increasing knowledge of the ecology, invasion biology, and environmental responses of *D. suzukii*, little is known about how wing shape varies among field-collected adults captured in different crop-associated orchards and geographic localities. Previous studies have rarely considered crop context and geographic origin simultaneously, although both may contribute to morphological variation under natural agroecological conditions. This gap limits our understanding of how wing morphology varies across real fruit-production landscapes.

The aim of the present study is to examine wing morphometric variation in *D. suzukii* in relation to host plants and geographic regions in Serbia, with particular attention to its potential relevance for dispersal. Based on current knowledge of phenotypic plasticity and wing morphology in this species, the following hypotheses were formulated: (H1) wing shape varies among individuals associated with different host plants; (H2) wing morphology varies among geographically distinct populations; and (H3) host plant and geographic origin interact in shaping wing morphology.

2. Materials and Methods

2.1. Data Collection

Specimens were collected in 2021 from five host plants across several regions in Serbia where economic damage to fruits had been recorded (Figure 1). The sampling localities lie within the temperate continental climatic zone of Serbia, characterized by cold winters, warm to hot summers, and pronounced seasonal variation. Novi Sad and Ruma represent northern lowland sites with typical Pannonian continental conditions and a relatively uniform seasonal climate. Požarevac represents an eastern continental site, generally characterized by warmer summers and comparatively drier conditions. Čačak and Kraljevo are located in central Serbia, where temperate continental conditions are accompanied by somewhat more humid local climatic characteristics. Niš and Leskovac represent southern localities, characterized by warmer summers, stronger seasonal thermal contrasts, and more irregular precipitation during the vegetation period.

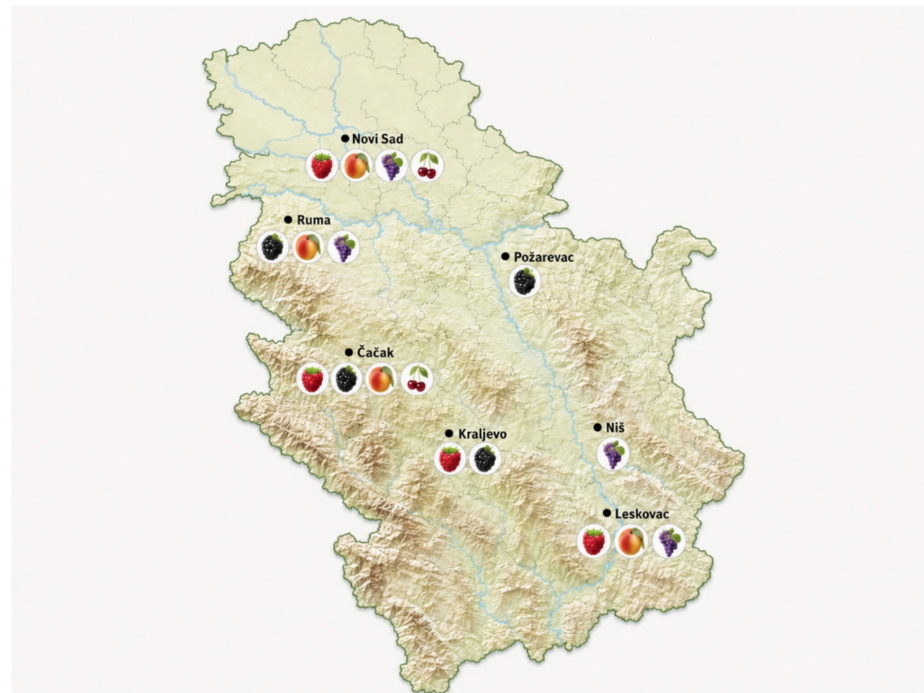


Figure 1. Sampling localities and host plants of *Drosophila suzukii* in Serbia.

Sampling was conducted during the fruit-ripening and harvest period of each host plant. Sweet cherry orchards were sampled in June, raspberry in June–July, blackberry and peach in July–August, and grapevine in August. One apple vinegar trap was installed in the central part of each orchard to minimize edge effects. Each trap remained in the field for one month and was inspected weekly, with captured insects collected every seven days. The collected flies were preserved in 70% ethanol prior to identification. Species and sex identification of *D. suzukii* was carried out according to the recommendations of the European and Mediterranean Plant Protection Organization [37]. A total of 430 adult *D. suzukii* were collected (20–25 per host per location). Both the left and right wings were removed from each specimen and slide-mounted using Euparal (Australian Entomological Supplies, Melbourne, VIC, Australia), following standard methods [38], for subsequent geometric morphometric analysis. Slide-mounted wings were photographed using a Leica (Wetzlar, Germany) DFC295 digital camera (3 megapixel) on a trinocular mount of a Leica MZ16a stereomicroscope and saved in JPEG format using the Leica Application Suite version 3.8.0 (Leica Microsystems, Australia). On each photograph of the *D. suzukii* wing, 14 landmarks were placed at the nodes or ends of the veins. The landmarks were placed on the wings according to a well-defined arrangement (according to Bookstein [39]) in the software package tpsDig232 (Figure 2). For all geometric morphometric analyses, only the left wing of each specimen was used, ensuring that each individual was represented only once in the statistical analyses. After quality control, the final analytical dataset comprised 421 left wings from 421 individuals.

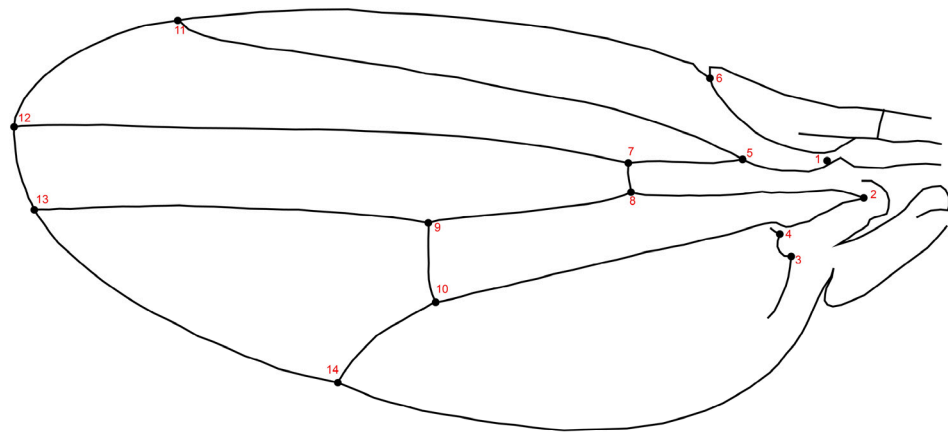


Figure 2. Landmark configuration used for geometric morphometric analysis.

2.2. Multivariate Analyses of Size and Shape

To assess measurement error associated with landmark digitization, a random subset of 40 left wings was independently digitized twice by the same observer under identical conditions. Measurement error was quantified using a Procrustes ANOVA following standard geometric morphometric procedures.

After quality control, landmark configurations were analyzed using a Generalised Procrustes Analysis (GPA) to remove the effects of size, position, and orientation, retaining only shape information [40]. The relationship between wing shape and centroid size was evaluated to assess the potential influence of allometry. A multivariate regression of Procrustes shape coordinates on centroid size was performed using permutation tests (10,000 iterations) in MorphoJ. The proportion of shape variation explained by centroid size (R^2) was used to quantify the magnitude of the allometric effect. In addition, the effects of sex and the interaction between sex and centroid size on wing shape were evaluated using Procrustes ANOVA with residual randomization (10,000 permutations).

Principal Component Analysis (PCA) was then used as an exploratory tool to summarize the major axes of variation and to visualize the distribution of individuals according to host plant and geographic origin. To evaluate group differentiation more explicitly, Canonical Variate Analysis (CVA) was conducted using host plant and locality as grouping factors, both independently and in combination [41]. Differences in mean wing shape among groups were quantified using pairwise Procrustes distances, which were organized into distance matrices and visualized as heat maps, with colour intensity representing the magnitude of morphological divergence among groups. Warmer colours indicate higher Procrustes distances, allowing direct comparison of shape differentiation among localities and host plants. Shape changes associated with group differences were visualized using thin-plate spline deformation grids and heat maps, enabling identification of localised regions of landmark displacement. The statistical significance of shape variation was assessed using Procrustes ANOVA with residual randomization procedures, including host plant, locality, and their interaction as explanatory factors. All multivariate analyses were performed in MorphoJ 1.08a [42] and in R 4.6.0 [43] using the package geomorph [44] for geometric morphometric analyses and ggplot2 [45] for data visualization.

3. Results

The digitization error was negligible relative to the biological variation among individuals, indicating high repeatability of landmark placement.

A significant relationship between wing shape and centroid size was detected ($R^2 = 0.0428$, $F = 18.74$, $p < 0.0001$), indicating a statistically significant but relatively weak allometric effect. Centroid size explained only 4.3% of the total shape variation.

Procrustes ANOVA also detected a significant effect of sex on wing shape ($R^2 = 0.0230$, $F = 10.21$, $p < 0.0001$), indicating weak sexual dimorphism. However, sex explained only 2.3% of the total shape variation. Furthermore, the interaction between sex and centroid size was not significant ($p = 0.384$), indicating similar allometric trajectories in males and females. Given the relatively small effect sizes, males and females were pooled for all subsequent analyses.

Principal component analysis of wing shape showed overlap among host plants when all individuals were considered collectively. The first two principal components explained a substantial proportion of the shape variation, with PC1 accounting for 59.21% and PC2 for 18.40% of the variance (Figure 3A). Although these components captured most of the variation, individuals associated with different host plants showed considerable overlap in morphospace, indicating that distinct clusters based solely on host use were not evident. The distribution of points along PC1 and PC2 suggests that most of the variation reflects continuous shape changes rather than host-specific differentiation.

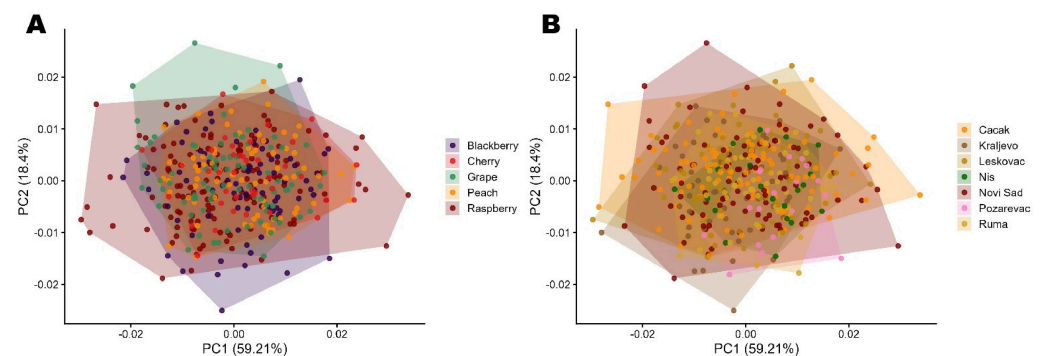


Figure 3. Principal component analysis of the wing shape in *Drosophila suzukii*, panels represent: (A) hosts plants and (B) sampled localities in Serbia.

A similar pattern emerged when the PCA was conducted by locality. Individuals from the sampled localities also showed substantial overlap in the morphospace defined by the first two principal components, indicating that geographic origin alone does not produce distinctly separated wing-shape clusters. Although certain localities displayed broader dispersion along PC1 or PC2, the overall morphospace structure was characterized by extensive overlap, suggesting that shape differences among local populations are subtle rather than categorical (Figure 3B).

Canonical variate analyses (CVAs) were conducted to identify multivariate shape differences within a defined group. When individuals were grouped by host plant within localities, the CVA showed greater separation among groups than principal component analysis (PCA), particularly along the first canonical axis. Certain host groups exhibited partial segregation; however, overlap persisted, suggesting that host-associated shape differences are present but moderate in magnitude (Figure 4).

Similarly, CVA by locality within host plants revealed clearer differentiation among some localities, particularly along the first canonical variate, although overlap among groups persisted (Figure 5). The CVA provided a visual representation of group separation, whereas the statistical significance of group differences was evaluated independently using Procrustes ANOVA and pairwise Procrustes distances.

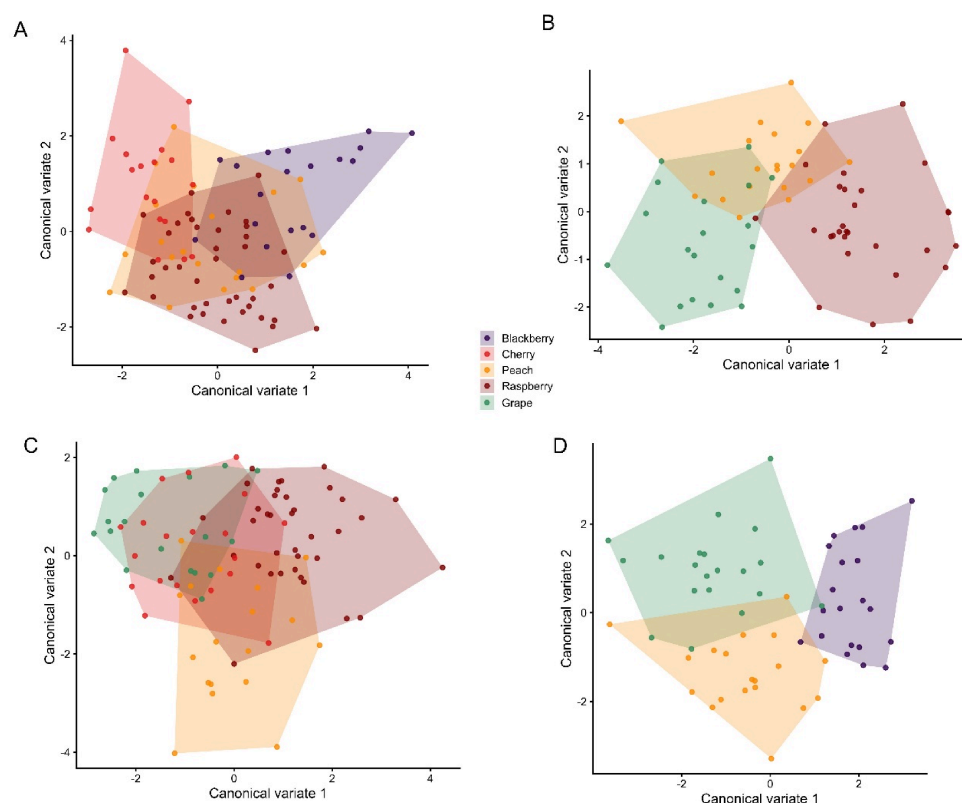


Figure 4. Canonical variate analyses of the *Drosophila suzukii* wing shape among different host plants by localities. (A): Čačak, (B): Leskovac, (C): Novi Sad, (D): Ruma.

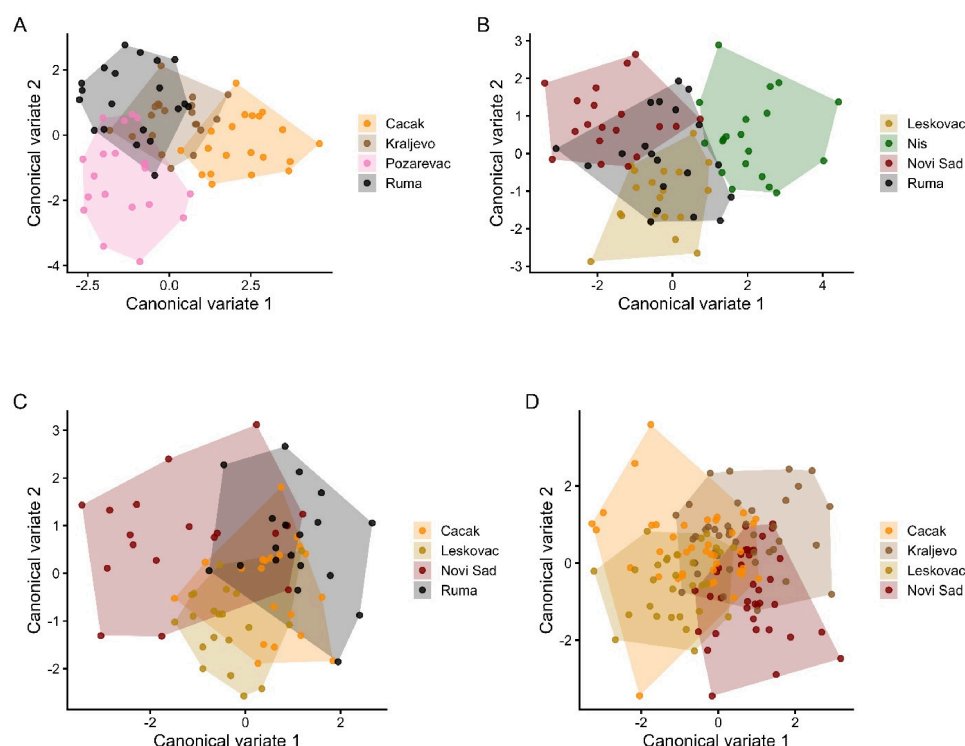


Figure 5. Canonical variate analyses of the *Drosophila suzukii* wing shape among different localities by host plants. (A): Blackberry, (B): Grape, (C): Peach, (D): Raspberry.

Analysis of mean wing shapes and deformation heat maps indicated that shape differences among localities were primarily expressed as coordinated displacements of landmarks in the distal and posterior regions of the wing. Deformation patterns across

localities consistently involved changes in the relative positions of distal vein junctions, with pronounced effects on the apical region and posterior margin. In several localities, including Požarevac and Niš, greater deformation magnitudes were concentrated at distal vein intersections, suggesting localized expansion or contraction of the wing outline in this area. Additionally, subtler deformations were detected along the central portion of the wing, involving shifts in landmarks associated with the median veins, which implies minor modifications in vein spacing rather than abrupt structural changes (Figure 6).

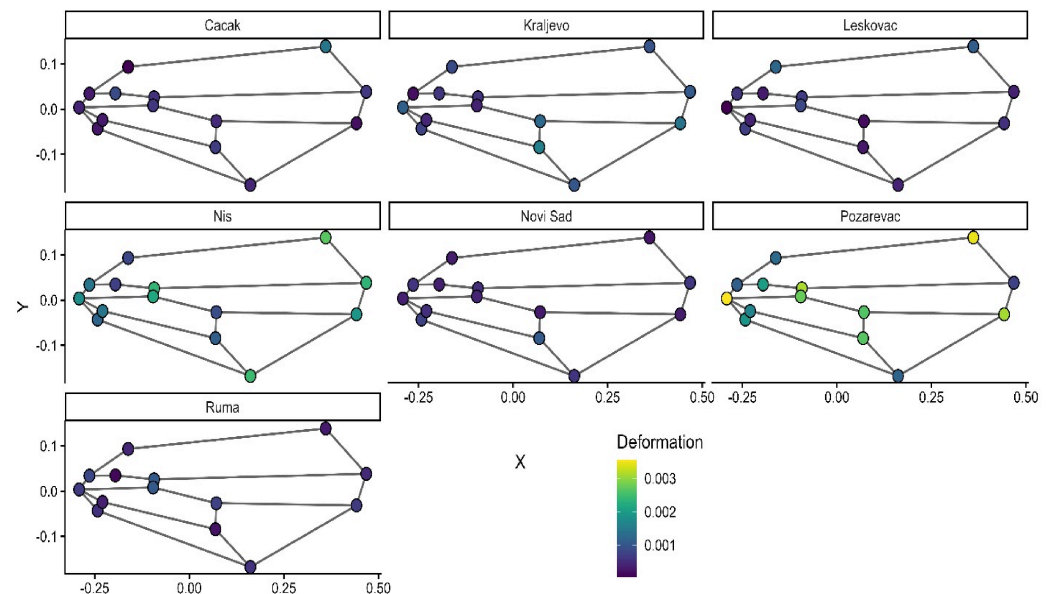


Figure 6. Deformation heat maps of mean wing shape in *Drosophila sukukii* by locality. Color intensity represents the magnitude of landmark displacement relative to the overall mean shape, with warmer colors indicating higher deformation values.

A similar pattern emerged when mean wing shapes were compared across host plants. Heat maps showed that host-associated shape differences were concentrated in the distal and posterior regions of the wing, with moderate deformation magnitudes distributed across the same vein junctions identified in the locality analysis. Specifically, individuals associated with cherry and raspberry exhibited higher deformation intensities around distal landmarks at apical vein intersections, whereas peach and grape showed greater displacement along the posterior wing margin and adjacent vein junctions. In contrast, blackberry showed lower overall deformation magnitudes, with more evenly distributed and subtle landmark shifts across the wing. These findings suggest that host-related variation affects a common set of wing regions, although the magnitude and spatial distribution of deformation vary among host plants (Figure 7).

Procrustes distances among mean shapes quantified the magnitude of wing shape differences identified in the deformation analyses. Distances among localities indicated heterogeneous levels of shape divergence, with pairs involving Požarevac exhibiting the highest Procrustes distances compared with several other localities, particularly Čačak, Kraljevo, and Leskovac. Moderate divergence was also observed between Niš and Leskovac, while other locality pairs displayed lower and more uniform distances. These quantitative patterns corresponded closely with the spatial distribution of deformation intensities shown in the heat maps (Figure 8A). Procrustes distances among host plants similarly demonstrated consistent but moderate divergence in mean wing shape, with cherry and raspberry exhibiting higher distances than other hosts. Overall, Procrustes distance values remained within a relatively narrow range, indicating that both locality and host plant

contribute to wing shape variation, although the magnitude of these differences is subtle (Figure 8B).

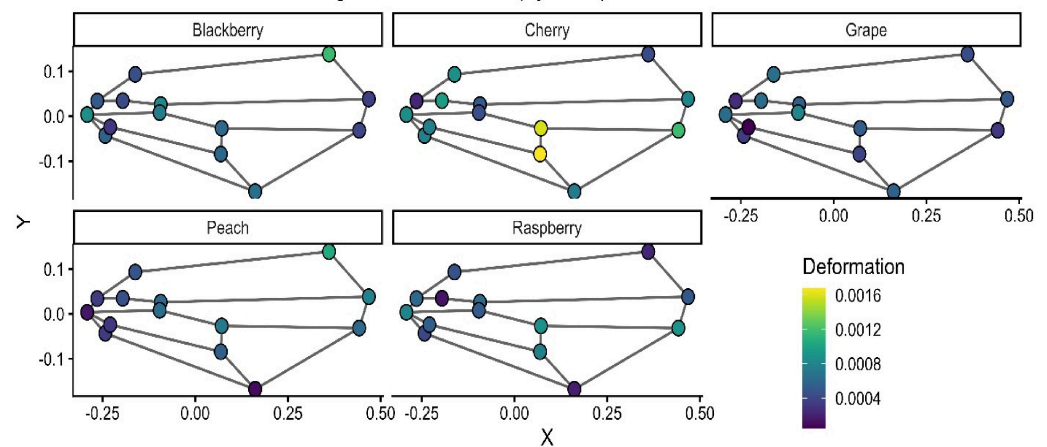


Figure 7. Deformation heat maps of mean wing shape in *Drosophila suzukii* by hosts. Color intensity represents the magnitude of landmark displacement relative to the overall mean shape, with warmer colors indicating higher deformation values.

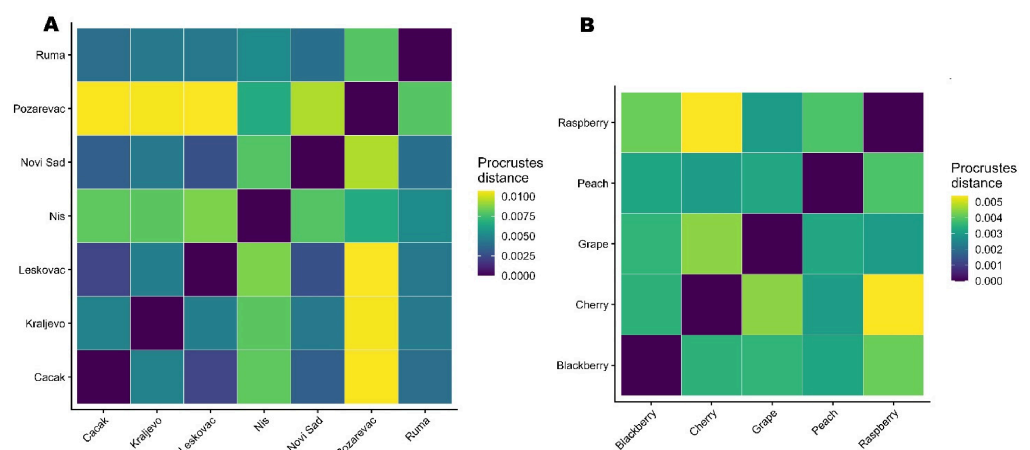


Figure 8. Procrustes distances among mean wing shapes. **(A)** Pairwise Procrustes distances among locality mean wing shapes. **(B)** Pairwise Procrustes distances among host plant mean wing shapes. Color intensity indicates the magnitude of shape divergence, with warmer colors representing larger Procrustes distances.

Finally, a Procrustes ANOVA based on residual randomization revealed significant effects of both host plant and geographic location on wing shape. Location explained the largest proportion of shape variation ($R^2 = 0.0346$, $F = 2.53$, $p = 0.0001$), indicating a statistically significant spatial component of wing shape variation. Host plant also had a significant, though smaller, effect on shape ($R^2 = 0.0167$, $F = 1.83$, $p = 0.0091$). Importantly, the interaction between host and location was significant ($R^2 = 0.0310$, $F = 1.94$, $p = 0.0010$), suggesting that host-associated shape differences are context-dependent.

4. Discussion

The present study showed that wing shape variation in *D. suzukii* in Serbia is associated with host context and geographic origin, with a significant host $\times$ locality interaction. Although the broad overlap observed in the PCA indicates that these effects do not produce discrete morphotypes, the CVA and deformation analyses provide a visual representation of group differences, whereas Procrustes distances and Procrustes ANOVA provide

statistical support for the observed moderate morphological structuring. This is an important finding because it demonstrates that field-collected populations of *D. suzukii* share a largely conserved wing morphology, but still exhibit subtle, statistically detectable shape differences associated with the host environment in which adults were captured and with geographic origin. Rather than indicating fixed or clearly separated morphotypes, the results point to fine-scale morphological variation within a mobile and ecologically flexible invasive species. This interpretation agrees with the broader view of *D. suzukii* as an invasive species whose success is strongly linked to ecological flexibility, broad host use, and pronounced phenotypic plasticity [1–4,12,16]. Therefore, the present study contributes field-based evidence that wing shape can reflect ecological and spatial structuring in natural fruit-production systems.

Our results indicate that adults captured in orchards of different fruit crops differed in wing shape. In the context of this study, the host category represents the fruit crop present at the capture site during ripening and harvest, rather than the confirmed larval developmental host of each individual. This distinction is important, because adults were collected using vinegar-baited traps and were not reared directly from infested fruits. Nevertheless, the observed capture-site-associated differences remain biologically relevant because they describe the morphology of adult flies occurring in different fruit-production environments at the time when each crop was susceptible to infestation. Such field-based information is valuable because adult *D. suzukii* populations in orchards are shaped not only by larval substrate, but also by adult movement, fruit phenology, local resource availability, and the surrounding agroecosystem. This interpretation is consistent with previous geometric morphometric work showing host-associated wing differences in *D. suzukii* developing on different fruit species [17], as well as with studies in other dipteran pests reporting host- or cultivar-associated morphological responses [21,23,46,47].

The effect of geographic origin was stronger than the host effect, indicating that wing shape variation in Serbian populations of *D. suzukii* is associated not only with the crop environment in which adults were captured, but also with locality-related factors. This is one of the clearest outcomes of the study and suggests that spatial context is an important component of morphological variation in these populations. In the present study, geographic origin should be interpreted as a composite field variable rather than as a single causal environmental factor. Although the explained variance was modest, this result remains biologically relevant because geometric morphometric variation in field-collected insects is typically influenced by substantial individual-level variability, developmental noise, and unmeasured environmental heterogeneity. Consequently, the detection of a significant locality effect, despite this natural variability, indicates that wing shape variation is not entirely random but shows spatial structure across Serbian fruit-growing regions.

The sampled localities covered different agroecological contexts, ranging from northern lowland areas with continental conditions to central valley systems and warmer southern localities with stronger seasonal thermal contrasts. These differences provide a plausible ecological background for interpreting the stronger locality effect. Environmental differences could potentially influence wing morphology through developmental pathways affecting larval and pupal development time, growth rate, adult body size, and allometric relationships between size and shape [48,49]. However, because these environmental variables were not measured directly in the present study, their influence should be interpreted as a plausible explanation rather than as a demonstrated causal mechanism. The observed pattern therefore suggests that wing shape variation is likely influenced by multiple environmental and biological factors, with crop/capture-site context and geographic locality representing only part of the overall morphological variability.

Temperature is particularly relevant in this species. Hamby et al. [12] summarized how temperature affects development, survival, and reproduction in *D. suzukii*, while Winkler et al. [50] reviewed the role of temperature and humidity in shaping population dynamics. Fraimout et al. [25] demonstrated experimentally that developmental temperature alters both wing shape and flight parameters, including speed and acceleration, directly linking the developmental environment with functional wing variation. Comparable temperature-induced effects on wing size and shape have been reported in other dipterans, including *D. simulans*, where allometric and non-allometric components of wing shape responded differently to developmental temperature [51,52], and *Aedes albopictus*, where rearing temperature significantly affected wing size and shape [53]. Altitude- and landscape-associated climatic gradients have also been linked to wing morphology in invasive insects such as the potato tuber moth, *Tecia solanivora* [54], and agroecological contrasts have been associated with wing shape variation in pests such as *Diabrotica virgifera virgifera* and *Ceratitis capitata* [20,21,27]. These studies provide a strong biological rationale for considering environmental heterogeneity as a potential contributor to the locality-associated wing shape variation observed here. In the present study, temperature and humidity were not directly measured at the orchard level; therefore, climatic explanations should be viewed as mechanistic hypotheses supported by the literature.

A particularly important result of this study is the significant interaction between crop/capture-site context and locality. This indicates that crop-associated differences in wing shape were not expressed uniformly across Serbian localities, but depended on the geographic context in which adults were collected. This interaction strengthens the ecological relevance of the results because it suggests that wing shape variation in field populations cannot be explained by host or locality alone. Instead, the observed morphology reflects the combined influence of host-associated habitat, local agroecological conditions, seasonal host availability, and population-level variation. This interpretation aligns with studies showing that host use, host succession, and landscape context influence seasonal population dynamics and movement of *D. suzukii* across cultivated and non-crop habitats [9–11,26,55–57]. Although the sampling design was not fully balanced across all host × locality combinations, this reflects the actual distribution of fruit crops under field conditions. Therefore, the interaction should be interpreted as a field-based ecological pattern. Within this framework, the significant interaction provides useful evidence that morphological variation in *D. suzukii* is context-dependent and spatially structured across fruit-production environments.

The deformation analyses are also biologically informative because they indicate that most variation is concentrated in distal and posterior wing regions, particularly around apical vein junctions and along the posterior margin. The fact that shape changes were concentrated in specific wing regions, rather than randomly distributed across the wing, supports the biological relevance of the detected morphometric differences. These regions are relevant to overall wing geometry and have been discussed in the broader literature on insect flight mechanics [24]. Fraimout et al. [25] showed under experimental conditions that developmental temperature can affect both wing morphology and flight-related parameters in *D. suzukii*. Comparable arguments have been made in other dipteran systems: Pieterse et al. [47] suggested that host-induced wing changes in fruit flies may be biologically meaningful even when their direct fitness consequences remain unresolved, and Pajač Živković et al. [23] discussed broader female wing shapes as potentially relevant to dispersal and oviposition efficiency in *Bactrocera oleae*.

In the present study, flight performance was not measured directly; nevertheless, we identify specific wing regions that may be important targets for future studies linking field morphometrics with flight performance, movement, or dispersal capacity. In this sense, the

deformation results provide more than a statistical description: they show where in the wing the main shape changes occur and generate biologically meaningful hypotheses for subsequent experimental work. The morphometric patterns detected here are still valuable because they provide a field-based baseline for identifying naturally occurring wing shape variation in Serbian *D. suzukii* populations. Previous experimental work in *D. suzukii* demonstrated that developmental conditions can affect both wing morphology and flight-related traits [25], but such relationships should be tested directly before being applied to natural populations. Thus, the present results should be viewed as an important first step: they document the existence, direction, and spatial distribution of wing shape variation, while future experimental studies can evaluate whether these differences correspond to measurable variation in flight performance or dispersal behaviour.

An important aspect of the present findings is that statistically significant effects were detected despite substantial overlap among groups and relatively small effect sizes. This result should be interpreted as a realistic representation of morphological variation in a mobile, invasive species sampled under natural field conditions. Rather than generating sharply delimited forms, environmental heterogeneity often produces subtle but repeatable shifts in morphospace. Similar outcomes have been documented in fruit flies and other Diptera by Pieterse et al. [47], Lemić et al. [20,21] and Gemmellaro et al. [58], where host, agroecological system, urbanization, elevation or geographic context generated significant shape variation without complete morphological segregation. At the same time, studies such as Schutze et al. [59] show that wing shape can have strong discriminative power when evolutionary divergence is deeper, underscoring that incomplete separation in the present study is consistent with fine-scale, within-species variation rather than taxonomic-level differentiation. Therefore, the modest explained variance supports a cautious but meaningful conclusion: crop/capture-site context and locality contribute to wing shape variation, but they represent only part of a broader set of biological, environmental, and stochastic factors influencing morphology.

From an invasion biology perspective, the pattern observed here is consistent with fine-scale morphological flexibility within a broadly distributed invasive pest. This interpretation agrees with the ecological profile of *D. suzukii*, which is characterized by broad host use, seasonal host tracking, high mobility, and persistence across heterogeneous fruit-production landscapes [1–4,12,16]. Little et al. [16] and Plantamp et al. [46] highlighted the importance of plasticity and adaptation in the invasion success of *D. suzukii*, while Olazcuaga et al. [55] showed that adaptation to seasonal host fruits can be rapid and transient. Fraimout et al. [30] further suggested that wing shape evolution in this species may be relatively flexible. The present study does not distinguish among phenotypic plasticity, genetic differentiation, local adaptation, maternal effects, or other mechanisms. However, it contributes field evidence that Serbian populations of *D. suzukii* display subtle but structured wing shape variation across crop-associated and geographic contexts. This is relevant because invasive species often maintain morphological cohesion while still showing local or ecological modulation of quantitative traits.

The present findings may have practical relevance as complementary ecological information. *Drosophila suzukii* persists across cultivated and non-crop hosts in heterogeneous landscapes, where host succession, wild host availability, and landscape context can influence seasonal population dynamics, local pest pressure, and population persistence [10,11,26,57]. In this context, the observed locality effect and crop/capture-site $\times$ locality interaction suggest that crop identity alone is insufficient to explain morphological variation in field-collected populations. Although wing shape should not be considered a standalone marker for monitoring or IPM decision-making, it may provide

useful supporting information when combined with population, landscape, environmental, and genetic data in future studies.

5. Conclusions

This study demonstrates that wing shape variation in field-collected Serbian populations of *D. suzukii* is significantly associated with crop/capture-site context and geographic origin, with locality showing a stronger effect and a significant interaction between the two factors. Although the detected differences were subtle, they reveal fine-scale morphological structuring across heterogeneous fruit-production environments. These findings highlight the value of geometric morphometrics for detecting ecological patterns in invasive pest populations and provide a basis for future studies integrating controlled rearing, environmental covariates, genetic data, and flight-performance assays to clarify the mechanisms and potential functional relevance of wing-shape variation.

Author Contributions: Conceptualization, B.J., H.A.B., I.P.Ž. and D.L.; methodology, D.L., H.A.B. and I.P.Ž.; software, H.A.B., A.M., L.M.P. and R.Á.-V.; validation, D.L., H.A.B. and I.P.Ž.; formal analysis, B.J., L.M.P., A.M., A.I.Ć., M.K. and R.Á.-V.; investigation, B.J., L.M.P., A.M., A.I.Ć., M.K. and R.Á.-V.; resources, D.L., H.A.B. and I.P.Ž.; data curation, B.J., D.L., I.P.Ž. and H.A.B.; writing—original draft preparation, B.J., H.A.B., D.L. and I.P.Ž.; writing—review and editing, H.A.B., D.L., A.I.Ć., I.P.Ž., M.K. and R.Á.-V.; visualization, H.A.B., L.M.P., A.M., D.L. and R.Á.-V.; supervision, D.L., I.P.Ž., A.I.Ć. and M.K.; project administration, A.I.Ć. and M.K.; funding acquisition, D.L. and H.A.B. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: All data supporting the findings of this study are included in this published article. The original wing images used for the geometric morphometric analyses are available from the first author upon reasonable request.

Acknowledgments: H.A.B. and D.L. gratefully acknowledge the support of the collaborative grant ANID/ANILLO/ATE230025. During the preparation of this manuscript, the authors used ChatGPT (OpenAI, GPT-5.5 Thinking) for language editing and map generation. All AI-generated content was carefully reviewed and edited by the authors, who take full responsibility for the final content of the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

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