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Insect morphometrics in ecology and evolution: Principles, techniques, and insights from Odonata

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Abstract

Morphometry is the quantitative study of form, including the measurement and analysis of size and shape of biological organisms. It plays an important role in understanding morphological variation, species identification, and evolutionary relationships. In insects, morphometric analysis has been widely used to examine structural differences, ecological adaptations, and developmental patterns. Insect morphometry is particularly useful in distinguishing closely related species and studying phenotypic variations influenced by environmental and genetic factors.

Morphometric methods are broadly classified into traditional and geometric approaches. Traditional morphometry is based on linear measurements such as length, width, and ratios of different body parts, providing basic information about size-related traits. In contrast, geometric morphometry focuses on shape analysis using landmark-based techniques, preserving the spatial relationships among structures and allowing more precise comparisons.

Both approaches have significantly contributed to biological research; however, geometric morphometry offers greater accuracy in analyzing shape and size variation. Overall, morphometric techniques provide a powerful framework for studying insect morphology, supporting taxonomic, ecological, and evolutionary investigations.

Keywords: Morphometry, geometric morphometry, traditional morphometry, insects, wing shape, odonata

Introduction

Morphometric analysis is one of the useful tools for identification of insect groups. It is quantitative analysis of form, involving measurement and analysis of geometric features, shape descriptors and surface characters (Daly, 1985; Digo *et al.,* 2015) [1, 2]**.** Morphometrics enhances taxonomic reliability by involving quantitative measurements, reducing subjective bias, and enabling objective comparisons. Also helpful in determining species relationships and growth variability, comparing life history and morphological trends across populations (Elahi *et al.,* 2017) [3].

The morphometry has proven to be highly significant in detecting species misidentifications that might arise from traditional morphological approaches and is also helpful in resolving ambiguities in closely related or cryptic species (Bickford *et al.,* 2006) [4]. Morphometric analysis enhances the accuracy of species classification by providing precise and quantifiable measurements, thereby providing more reliable taxonomic framework (Azrizal-Wahid *et al.,* 2016) [5]. Morphometric methods are enhanced by advanced statistical tools like null models and ordination techniques, which help analyze patterns in biological data (Chase *et al.,* 2011) [6].

Morphometry is widely used as an effective tool for quantifying and visualizing interspecific variation in insects, particularly through the analysis of wing shape. By examining specific anatomical landmarks on insect wings, this approach captures the spatial relationships within wing structures and provides a clearer understanding of both shape and size variation (Johansson *et al.,* 2009) [7].

Insects exhibit remarkable morphological diversity, which can be quantitatively analyzed using morphometric approaches. Variations in body structures such as wings, exoskeleton, and segmentation contribute to differences in size and shape across species (Kumar *et al.,* 2024) [8]. The structure and design of insect wings are integral to their flight mechanics. In dragonflies, the distinctive wing morphology—marked by intricate venation patterns and a balance between rigidity and flexibility—enables exceptional control during hovering and maneuvering. Such morphological adaptations not only enable efficient flight but also highlight the evolutionary pressures shaping these traits (Ellington, 1984) [9].

Morphometric Methods

Traditional Morphometry

Morphometric methods, both traditional and geometric, have significantly contributed to our understanding of arthropod morphology. During the 1960s and 1970s, biometricians increasingly applied advanced multivariate statistical methods to analyze variations in biological shape across and within groups. This approach, commonly referred to as traditional (Marcus, 1990) [10] or multivariate morphometrics involves examining multiple morphological measurements simultaneously. Traditional morphometrics is primarily focuses on studying size-related traits, providing basic quantitative measurements of organisms. The measurements usually lengths and widths of structures and distances between specific anatomical landmarks. In some cases, angles and ratios are also used to describe morphological variation. Such methods have been widely applied in studies of allometry, which examines changes in shape with respect to size, and in size correction techniques that allow comparison of shape differences among organisms standardized to a common size (Adams *et al.,* 2004) [11].

Geometric Morphometry

Geometric Morphometry can be defined as the study of form in two- or three-dimensional spaces and utilizes powerful and comprehensive statistical procedures to analyse shape differences of a morphological feature, using either homologous landmarks or outlines of the structure. It is used to understand sexual selection, species-specific traits, evolutionary, developmental and/or ecological patterns among different species (Rohlf and Marcus, 1993, Eagderi *et al.,* 2015, Adams *et al*., 2004) [11–13]. Geometric morphometrics is widely used to quantify morphological variation across different fields such as biology, anthropology and paleontology. It has been applied to assess shape differences among taxa, examine relationships between morphology and phylogeny, and study spatial variation in form (Cooke and Terhune, 2015) [14].

The integration of geometric morphometry into taxonomy bridges the gap between traditional morphological studies and modern analytical techniques, providing insights into evolutionary and ecological dynamics (Tuzun, 2009) [15].

Table 1: Comparison of Traditional Morphometry and Geometric Morphometry

Aspect	Traditional Morphometry	Geometric Morphometry	Key Advantages / Differences	References
Definition	Quantitative analysis focused on size-related traits using linear measurements (lengths, widths, distances, angles, ratios)	Study of shape in 2D or 3D space using homologous landmarks or outlines, preserving spatial relationships	Traditional emphasizes size; Geometric isolates pure shape by removing size, position, and orientation effects	Marcus (1990) [10], Rohlf & Marcus (1993) [12], Bookstein (1991) [16]
Core Measurements	Linear distances between anatomical points, widths, lengths, ratios, and simple angles	Homologous landmarks (e.g., vein intersections on wings), outlines, Procrustes superimposition	Geometric uses coordinate-based data; Traditional uses raw scalar measurements	Adams et al. (2004) [11], Klingenberg (2010) [17]
Statistical Tools	Multivariate statistics, allometry, size-correction techniques, ratios	Procrustes superimposition, relative warp analysis, thin-plate spline deformation, ordination techniques	Geometric removes statistical artifacts from ratios; Traditional can produce false correlations	Chase et al. (2011) [6], Atchley et al. (1976) [18], Rohlf (2004a,b) [19,20]
Applications in Insects	Basic quantification of body parts, allometric growth, size variation across populations	Wing shape analysis, venation patterns, sexual dimorphism, environmental and phylogenetic variation	Geometric provides higher precision for shape differences in cryptic species and ecomorphology	Tuzun (2009) [15], Klingenberg (2010) [17], Mutanen et al. (2007) [21]
Software Commonly Used	Basic statistical packages (e.g., for ratios and multivariate analysis)	tpsDig, tpsUtil, MorphoJ (landmark digitization and analysis)	Geometric requires specialized landmark software; Traditional can use general statistics tools	Rohlf (2004a and b) [19,20]
Strengths	Simple, quick, requires minimal equipment; good for initial size comparisons	High accuracy in shape analysis, removes size bias, visually intuitive deformation grids	Geometric offers greater statistical power and reproducibility for complex structures like wings	Adams et al. (2004) [11], Cooke & Terhune (2015) [14]
Limitations	Sensitive to size effects; ratios can create statistical artifacts; less effective for subtle shape differences	Requires more training and equipment (digital imaging); landmark choice can be subjective	Traditional may mask true shape variation; Geometric is more time-intensive but more powerful	Klingenberg (2010) [17], Atchley et al. (1976) [18],
Examples	Linear measurements of wing length, body length, and ratios in Odonata	Landmark-based analysis of forewing shape in *Heliozela resplendella* vs. *H. hammoniella* and *Argia sedula*	Geometric clearly separated species and revealed sexual dimorphism after size correction	Mutanen et al. (2007) [21], Stewart & Vodopich (2018) [22]

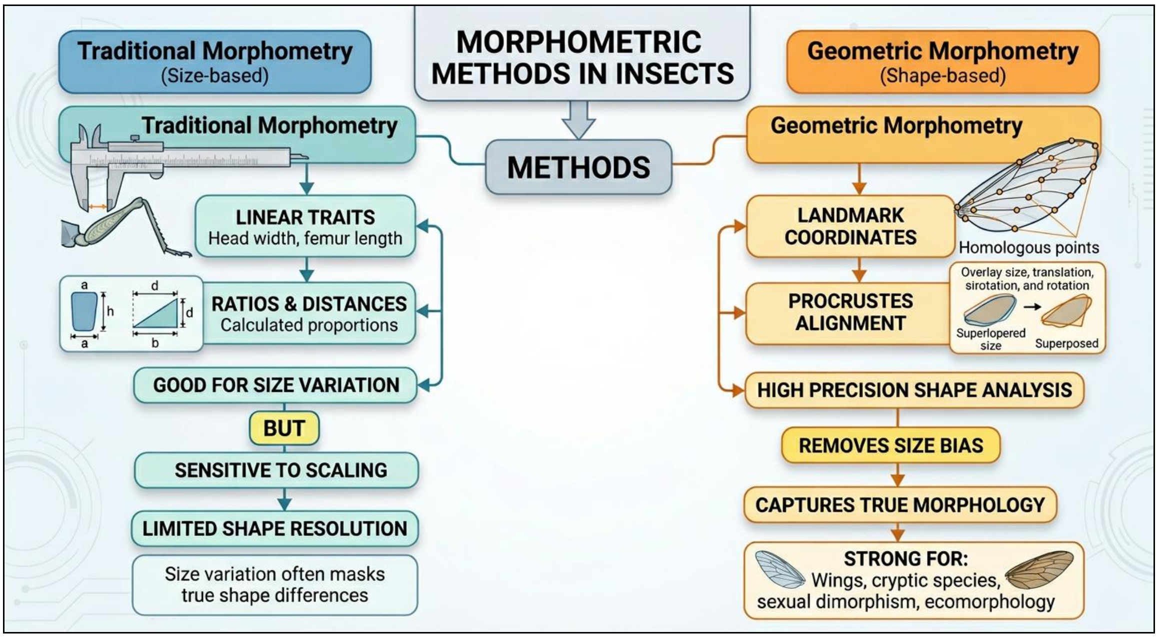

Fig 1: Comparison of traditional and geometric morphometric methods in insects

Traditional morphometry (left) relies on linear measurements (e.g., head width, femur length) and derived ratios/distances to quantify variation, making it suitable for assessing overall size differences but sensitive to scaling effects and limited in resolving true shape variation. In contrast, geometric morphometry (right) utilizes landmark-based coordinates of homologous points, followed by Procrustes alignment to remove non-shape variation (size, position, and orientation), enabling high-precision analysis of morphological shape. This approach captures subtle morphological differences and is particularly effective for studies of wing shape, cryptic species discrimination, sexual dimorphism, and ecomorphological adaptation.

Geometric morphometrics is to analyze the variations in shape and the relationships between shape and several independent variables. Comparative morphological analysis is a valuable tool for distinguishing between problematic groups of insects. Numerical taxonomy has been widely used to assist in the identification of numerous insect species (Daly, 1985; Baylac *et al.,* 2003) [1,23].

The use of ratios has been a longstanding practice in morphometric studies, particularly in biological research, where they are often applied to scale variables and eliminate size effects. In taxonomy, ratios are widely used to remove size-related variation and focus on shape; they can produce false correlations and statistical artifacts (Atchley *et al.,* 1976) [18]. In geometric morphometrics, Procrustes superimposition rotates, translates, and scales landmarks so that they are aligned, and this allows examination of pure shape variations (Bookstein, 1991) [16].

Landmark-based geometric morphometric analysis of insect wings is a transformative tool in species identification. It enables detailed and accurate quantification of wing shape and venation patterns and provides a statistically robust alternative to traditional techniques. It complements classical morphology and enhances the accuracy of species identification, 16 particularly for taxa where conventional methods face limitations (Klingenberg, 2010; Tuzun, 2009) [15,17].

Geometric morphometric methods along with advanced statistical tools were used to study the shape and patterns of the forewings in *Heliozela resplendella* and *H. hammoniella* to confirm differences more clearly. The forewings of *H. resplendella* were found to have a proximal dorsal spot that is more hook-shaped and bends towards the wing's tip, whereas *H. hammoniella* has a rounded spot. This difference was highlighted by relative warp analysis, a technique that helps isolate shape differences by removing any variations due to size or orientation (Mutanen *et al.,* 2007) [21]. The analysis done by the software shows that males of both species exhibited more consistent differences in wing shape than females, showing significant sexual dimorphism (Rohlf, 2004a&b) [19,20]. Geometric morphometric on *Argia sedula* revealed significant shape differences attributable to environmental and seasonal factors. The technique effectively isolates allometric effects, enabling a precise analysis of shape independent of size variations (Klingenberg, 2010; Stewart and Vodopich, 2018) [17,22].

Applications of Morphometry in insects

The diversity and distribution of insects are influenced by various ecological and environmental factors. A study conducted across six sandal provenances in Southern India highlighted the roles of habitat characteristics such as altitude, rainfall, soil type, and temperature, in shaping species diversity (Sharma *et al.,* 2007) [24]. The distribution is highly dependent on the particle sizes of the substrate, the nature of organic detritus and food availability under different conditions. Odonata larvae depend on specific habitat features, including sediment quality, water clarity, and vegetation. Alterations in these features, often caused by pollution or human activity, significantly affect their distribution and morphology (Burcher and Smock, 2002) [25].

a. Taxonomic and Phylogenetic Application

Morphometric techniques, particularly geometric approaches, have become powerful tools for taxonomic identification and phylogenetic inference in insects, especially when dealing with cryptic or closely related species.

Phylogenetic and morphological traits serve as diagnostic characters for species identification within the genus *Trithemis*. For instance, body coloration, wing venation, and habitat preference play key roles in distinguishing species. Red-bodied species, such as *T. annulata*, are typically associated with open, temporary water habitats, while dark-bodied species, like *T. africana,* inhabit cooler, shaded streams (Damm *et al.,* 2010) [26]. Distinct groups have also been identified based on wing venation, suggesting that morphological traits can be highly indicative of species relationships, which is supported by molecular analyses (Kalkman *et al.,* 2008; Damm *et al.,* 2010) [26,27].

Community Structure and Morphometrics

Hierarchical clustering and similarity indices, such as the Bray-Curtis index, are useful tools for analyzing community structures and identifying different morphotypes within a population (Clarke and Warwick, 2001; Chase *et al.,* 2011) [6,28]. The Bray-Curtis index is a statistical measure that assesses the similarity between two datasets, typically used in ecology and biology to compare species composition in different environments. It calculates a dissimilarity index (0-1) based on species abundance and presence/absence. This index helps researchers understand differences and similarities in species composition, informing conservation and management decisions. These methods can be applied to dragonfly morphometric data to distinguish between species and identify unique diagnostic traits that define each species. Alternative community states formed under varying environmental conditions, such as uniform (homogeneous) or diverse (heterogeneous) settings, highlight the importance of subtle morphological differences in accurately differentiating species (Hubbell, 2006) [29].

Predation and Evolutionary Pressures

Predation is a strong driving force behind the evolution of morphological and physiological traits. Therefore, examining the mechanics of predation can reveal selective pressures underlying key structure–function relationships (Combes *et al.,* 2012) [30].

Species Identification and Phylogeny

Phylogenetic and morphological traits serve as diagnostic characters for species identification within the genus *Trithemis.* For instance, body coloration, wing venation, and habitat preference play key roles in distinguishing species. Red-bodied species, such as *T. annulata,* are typically associated with open, temporary water habitats, while dark-bodied species, like *T. africana,* inhabit cooler, shaded streams (Damm *et al.,* 2010) [26]. Distinct groups have also been identified based on wing venation, suggesting that morphological traits can be highly indicative of species relationships, which is supported by molecular analyses (Kalkman *et al.*, 2008; Damm *et al.*, 2010) [26,27].

Table 2: Applications of Morphometric Analysis in Insects

Application Area	Description / Key Concepts	Specific Examples from Insects (Odonata focus)	Methods / Techniques Used	References
Taxonomic & Phylogenetic Applications	Distinguishing cryptic or closely related species; resolving misidentifications; inferring evolutionary relationships using morphological traits	Wing venation patterns and body coloration in *Trithemis* spp. (*T. annulata* vs. *T. africana*); identification of diagnostic characters in dragonflies	Landmark-based geometric morphometrics, multivariate analysis, Bray-Curtis similarity index, hierarchical clustering	Bickford et al. (2006) [4], Baylac et al. (2003) [23], Damm et al. (2010) [26], Kalkman et al(2008) [27].
Sexual Dimorphism & Reproductive Ecology	Quantification of sex-specific differences in size, shape, and structures linked to mating, territoriality, fecundity, and flight performance	Male vs. female differences in wing shape (*Plathemis lydia* territorial chases), abdominal width (*Ceroglossus chilensis*), and wing size (*Phlebotomus ariasi* females larger for dispersal)	Geometric morphometrics on wings and body parts, Procrustes superimposition, relative warp analysis	Digo et al. (2015) [2], Johansson et al. (2009) [7], Prudhomme et al. (2016) [31], Rubio et al. (2024) [32], Andersson (1994) [33]
Ecomorphological Adaptation & Environmental Drivers	Morphological variation driven by habitat, climate, altitude, fragmentation, and ecological pressures; links between wing shape and flight ecology	Wing shape differences in *Trithemis* across forest/open-water and running/standing habitats; migratory dragonflies with longer/slender wings and higher aspect ratios; altitude and seasonal effects in *P. ariasi* and *Argia sedula*	Geometric morphometrics, allometry, comparison of populations across environmental gradients	Johansson et al. (2009) [7], Prudhomme et al. (2016) [31], MacLeod et al. (2022) [34], Henriquez et al. (2009) [35], Combes & Daniel(2001) [36]

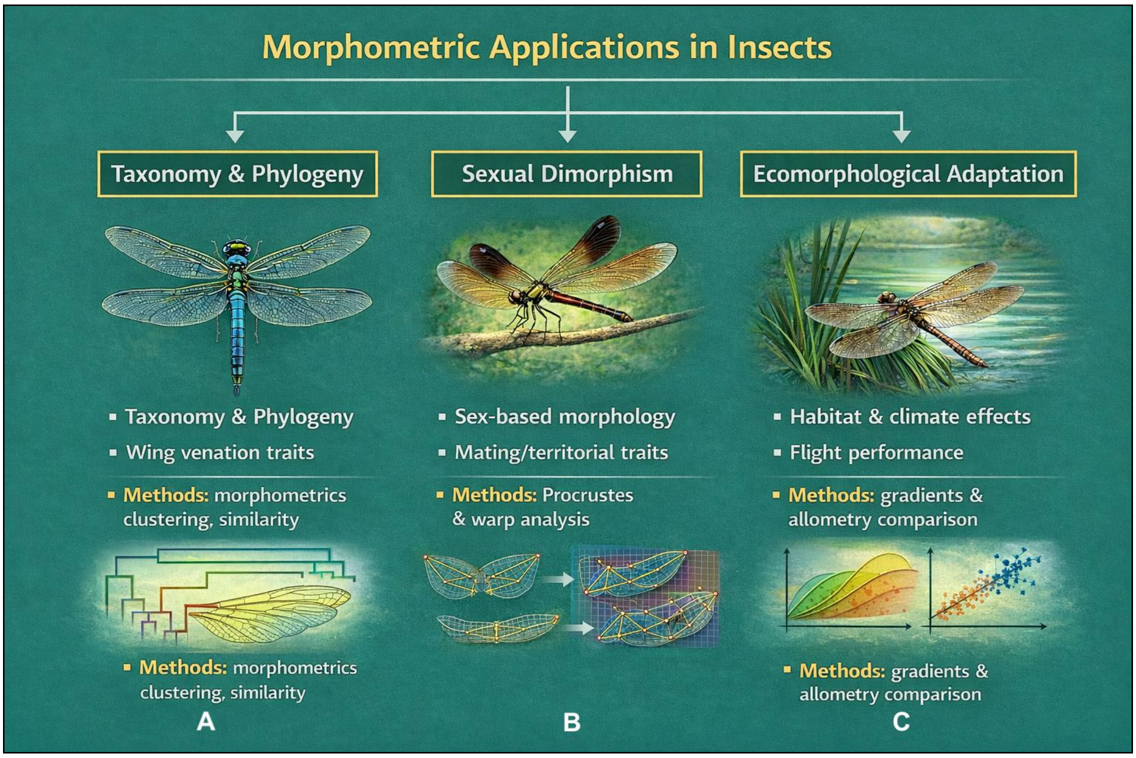

Fig 2: Morphometric Approaches to Insect Taxonomy, Dimorphism, and Adaptation

Schematic overview illustrating three principal domains of insect morphometric analysis. (A) Taxonomy and phylogeny: wing venation and shape traits are used to resolve species boundaries and evolutionary relationships through clustering and similarity-based morphometric methods. (B) Sexual dimorphism: sex-specific morphological variation, including traits associated with mating and territorial behavior, is quantified using geometric morphometric approaches such as Procrustes superimposition and deformation (warp) analysis. (C) Ecomorphological adaptation: variation in morphology in response to environmental gradients (e.g., habitat and climate) is examined to infer functional traits such as flight performance, commonly analyzed through allometric scaling and gradient-based comparisons.

a. Sexual Dimorphism and Reproductive Ecology

Sexual dimorphism in insects, particularly in Odonata, is frequently quantified using morphometric methods and has clear links to reproductive ecology, territorial defense, and flight performance

Sexual Dimorphism

Sexual dimorphism refers to the differences in morphological traits between males and females that arise due to reproductive and evolutionary pressures (Digo *et al.,* 2015) [2]. In insects, including Odonata, these differences are often reflected in body size, wing shape, and coloration. Such variations play an important role in mating behavior, survival, and ecological adaptation.

Among animals' morphological traits, body size is probably the single most ecologically relevant trait, as it relates to multiple dimensions of species' performance and ecological niches (Peters, 1986) [37]. In Odonata, body size is linked to thermoregulation (May, 1976) [38], energy requirements, and habitat use (Worthen and Jones, 2007) [39], among others. Body mass is the most informative measure of body size, but it is only available for a handful of odonate species (Aromaa *et al.,* 2019) [40]. Thus, most ecological studies use more indirect proxies, such as wing length or body length (Oliveira-Junior *et al.,* 2021) [41], derive body volume from scientific illustrations (Pinkert *et al.,* 2017) [42], or estimate body mass using allometric regressions from known species (Aromaa *et al.,* 2019) [40].

Besides body size, Odonate species' ecology is strongly influenced by traits that determine flight performance, as flight is essential for all Odonate activities. For instance, wing size affects manoeuvrability and size of anal triangle improves gliding and species' ecology (Johansson *et al.,* 2009; Suarez-Tovar and Sarmiento, 2016) [7,43]. Wing loading, relationship between body mass and wing area, is another essential trait that affects flying in animals. Species with a high wing loading exhibit higher stall speed and thus less manoeuvrable flight (Eagle, Vultures, bats etc), whereas those with a low wing loading exhibit more agile flight (Hummingbird, Dragonflies etc) (Wainwright and Reilly, 1994, Norberg and Rayner, 1987) [44,45].

Reproductive Success and Fecundity

Sexual dimorphism was evident in the species, with females' wider abdomens likely enhancing fecundity and reproductive success (Andersson, 1994) [33].

Territorial Defense and Wing Morphology

In *Plathemis lydia*, Male-male territorial chases are energetically costly, and having wings that maximize abilities associated with territorial defense is essential (Rubio *et al.,* 2024) [32].

Flight Dynamics and Morphology

In *P. ariasi,* females exhibited significantly larger wings than males, a trait likely linked to the increased energetic demands of blood-feeding and dispersal. The medial wing regions, critical for flight dynamics, showed marked differences between sexes, emphasizing functional adaptations. Geometric morphometry provides an objective means to quantify these differences, offering insights into the evolutionary pressures shaping sexual dimorphism across insect taxa (Prudhomme *et al.,* 2016) [31].

b. Ecomorphological Adaptation and Environmental Drivers

Environmental conditions act as strong drivers of morphological variation in insects, and morphometric analyses have proven effective in disentangling the effects of habitat, climate, and ecological pressures on phenotype

Environmental Pressures and Morphological Traits

Morphological variations in *Ceroglossus chilensis* were significant between populations in mature and second-growth forests. Males demonstrated wider pronotums, whereas females had wider abdominal sternites, highlighting distinct sex-based differences (Benitez *et al.,* 2011) [46]. These differences were attributed to environmental influences and local adaptations within the fragmented habitats. Environmental stress and habitat fragmentation also played a role in shaping the morphological traits of both sexes across different geographic locations (Henriquez *et al.,* 2009) [35].

Morphology in Ecological Adaptation

Wing morphology plays a pivotal role in ecological adaptation, particularly for insects that rely on fight for survival, reproduction, and dispersal. The shape, size, and structural features of wings are often closely linked to environmental factors, influencing an insect's ability to navigate its habitat and interact with its ecosystem. For instance, elongated and narrower wings are associated with greater aerodynamic efficiency, which aids in sustained flight and manoeuvrability in open or windy environments (Combes and Daniel, 2001) [34]. In contrast, broader wings may enhance stability and thrust generation, which are advantageous in cluttered or calm habitats.

Morphological adaptations such as wing shape have profound implications for dispersal and fitness. Insects with streamlined wings are often better adapted for long-distance dispersal, which is essential for colonizing new habitats and avoiding local extinctions under changing climatic conditions (Johansson *et al.,* 2009) [7].

During flight, many insect wings undergo dramatic deformations, which are largely controlled by the wing's architectural structure (Combes and Daniel, 2003) [36]. Wing design is often a compromise between multiple functions. The wings of butterflies, for instance, serve various purposes, including sexual and territorial display, in cryptic or warning defense, thermoregulation and in a wide range of flight patterns that reflect their complex behaviour (Kingsolver, 1985) [47].

Insect wing veins are the primary supporting structures in wings. Notably, the pleated, grid-like arrangement of leading-edge veins in dragonfly wings provides critical reinforcement, helping to strengthen the wing to spanwise bending (Wootton, 1991) [48]. The arrangement of veins and complexity of vein branching varies widely among insects, and venation pattern is often used to characterize orders and families.

Body size and wing shape influence their ecological roles and evolutionary dynamics. Morphometric analyses, employing both traditional and geometric approaches, provide insights into the relationships between size, shape, and various biological factors, including sexual dimorphism, environmental adaptation, and ecological interactions (Bybee *et al.,* 2016) [49].

Morphology in Evolution Adaptation

Morphological shape is the most evidential aspect of an organism's phenotype providing a strong linkage between species' genotype and its environment (Ricklefs and Miles, 1994) [50].

Morphological variations are also observed in migratory dragonflies, which 12 often display longer and slender wings with higher aspect ratios, optimized for energy-efficient long-distance flight (Norberg, 1989; Kalkman *et al.,* 2008) [27, 51]. These dragonflies exhibit notable adaptations in the intricate network of wing veins, which play a crucial role in enhancing flight efficiency (Wootton and Newman, 2008) [52]. The nodus contributes significantly to stability during wing strokes, whereas the pterostigma minimizes energy loss, both of which are essential for sustained migratory flights.

Migratory dragonflies also exhibit structural optimizations, such as enlarged forewing apices, associated with enhanced thrust during flight, and more prominent anal lobes of the hindwings, contributing to improved stability during sustained long-distance flights (Dudley, 2000; Johansson *et al.,* 2009) [7,53]. These adaptations are accompanied by allometric variations in body and hindwing lengths, providing a clear distinction from non-migratory species (Sacchi and Hardersen, 2013) [54]. Furthermore, dragonflies exhibit significant morphological variation in their thoracic muscle mass, which supports their diverse flight strategies (Dudley, 2000; Jongerius and Lentink, 2010) [53,55]. The structural adaptations, such as the V-shaped wing position during migratory glides, enable functional efficiency in long-distance travel (Wakeling and Ellington, 1997a; Drake and Reynolds, 2012) [56, 57].

Morphological traits, including wing venation, thoracic patterns, and appendage structures, form the cornerstone of dragonfly identification (Ahmed and Kareem, 2019) [58]. For example, *Orthetrum sabina* is characterized by its tiger-like thoracic stripes and unique abdominal markings, while *Diplacodes trivialis* is distinguished by its pruinescence and mid-dorsal stripes. Intraspecific variation in dragonflies is primarily caused by environmental factors, and individuals' ability to buffer against environmental stresses plays a significant role in determining these variations (Talu *et al.,* 2012) [59]. Understanding these morphological variations is crucial for elucidating the relationship between closely related taxa and identifying populations within and between species of insects (Baylac *et al.,* 2003; Tuzun, 2009) [15,23]. The choice of morphometric analysis methods can significantly impact the detection of ecomorphological variations in dragonfly wings (MacLeod *et al.,* 2022) [60].

Factors Affecting in Morphology

Morphological differences in organisms arise from the interaction of genetic architecture and environmental conditions. These differences are prominent across species and within species, driven by selection pressures. Strong divergent selection, often influenced by ecological or reproductive factors, can lead to variations in morphology between sexes (Andersson, 1994) [33].

Environmental stress and habitat fragmentation also played a role in shaping the morphological traits of both sexes across different geographic locations (Henriquez *et al.,* 2009) [35]. Most of the morphological variations in moth and butterflies are due to the environmental effects, whether through phenotypic responses or those acting during ontogenetic development (Mutanen *et al.,* 2007) [21].

Environmental factors play a crucial role in shaping the phenotypes of organisms. The dynamic interplay of abiotic and biotic environmental conditions influences key physiological, morphological, and behavioural traits, enabling organisms to adapt and survive in their unique habitats (Digo *et al.,* 2015) [2].

Table 3: Factors Influencing Insect Morphology

Factor Category	Description	Effects on Morphology	Specific Examples from Manuscript	References
Genetic Architecture	Inherited traits and developmental programs	Determines baseline shape and size; interacts with environment to produce variation	Intraspecific variation in wing venation and thoracic patterns in dragonflies	Baylac et al(2003) [23], Ricklefs & Miles (1994) [50]
Environmental Conditions	Abiotic (temperature, altitude, precipitation, habitat quality) and biotic (predation, competition) factors	Induces phenotypic plasticity, fluctuating asymmetry, and local adaptations	Wing shape changes with altitude/slope in *P. ariasi*; reduced wing reticulation at higher temperatures; habitat fragmentation effects in *Ceroglossus chilensis*	Prudhomme et al. (2016) [31], Henriquez et al. (2009) [35], Shortess (1929) [61], MacLeod et al(2022) [60].
Habitat Fragmentation & Disturbance	Deforestation, pollution, riparian vegetation loss	Alters community structure and drives morphological shifts in sensitive species	Changes in Odonata species composition and wing morphology due to deforestation and water quality	Burcher & Smock(2002) [25], De Marco et al. (2015) [62], Oliveira-Junior & Juen (2019) [63]
Developmental Conditions	Larval nutrition, temperature, water quality during ontogeny	Directly affects adult body size, wing shape, and symmetry	Adult morphology depends on larval nutrients and local conditions (e.g., temperature, water quality)	Mutanen et al. (2007) [21], Corbet (1999) [64], Lee & Lin (2012) [65]
Seasonal & Climatic Variation	Temporal changes in temperature, rainfall, and resource availability	Produces seasonal phenotypic plasticity in wing shape and size	Shape differences in *Argia sedula* between June and July; climatic shifts in African *Trithemis* during Plio-Pleistocene	Stewart & Vodopich (2018) [22], Damm et al. (2010) [26], Prudhomme et al. [31] (2016)
Evolutionary Pressures	Predation, sexual selection, migratory demands	Selects for optimized wing design, venation, and body proportions	Predation drives wing pigmentation and shape in Calopterygidae; migratory dragonflies show longer/slender wings and enlarged anal lobes	Combes et al. (2012) [30], Norberg (1989) [51], Sacchi & Hardersen (2013) [54], Siva-Jothy (1999) [66]
Interaction of Factors	Combined genetic × environment effects	Leads to ecomorphological variation and sexual dimorphism	Stronger environmental influence on wing morphology than phylogeny in recent studies	Digo et al. (2015) [2], Andersson (1994) [33], MacLeod et al. (2022) [60],

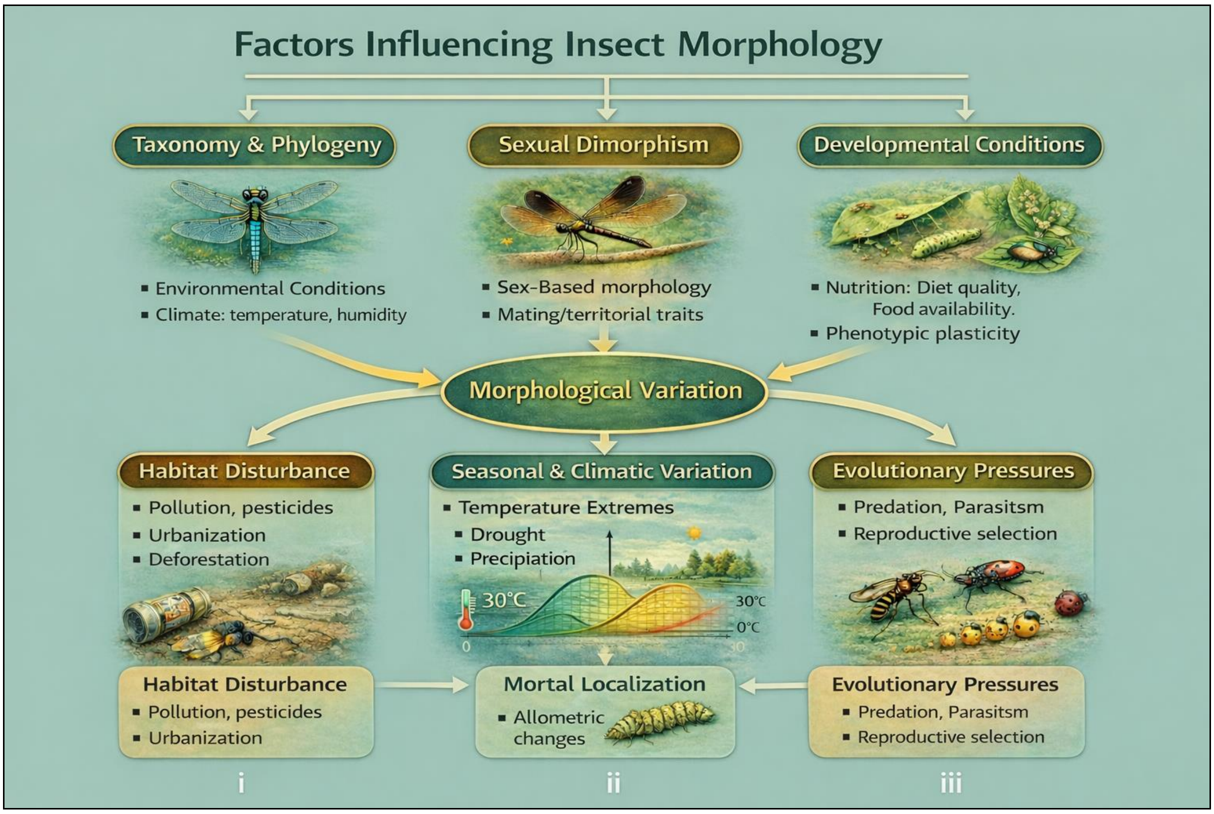

Fig 3: Determinants of Morphological Variation in Insects

Primary drivers include (i) environmental conditions (e.g., temperature, humidity), which directly affect physiological performance and phenotypic expression; (ii) sexual dimorphism, reflecting sex-specific traits associated with mating and territorial behaviors; and (iii) developmental conditions, particularly nutrition and resource availability, which influence growth trajectories and phenotypic plasticity. These factors interact to generate morphological variation, further modulated by external pressures such as habitat disturbance (e.g., pollution, pesticides, urbanization, deforestation) and seasonal or climatic fluctuations (e.g., temperature extremes, drought, flooding). Evolutionary forces, including predation, parasitism, and reproductive selection, act on this variation, leading to adaptive responses such as allometric changes and local adaptation.

Insects, being ectothermic, are particularly sensitive to environmental fluctuations, and their morphology often reflects adaptive responses to these pressures. For instance, in P. ariasi populations, wing shape and size varied significantly with altitude and slope. Environmental factors also induce seasonal phenotypic changes. The shape differences were noted between June and July, coinciding with shifts in climatic conditions (Prudhomme *et al.,* 2016) [31].

Developmental conditions dictate much of the morphological variation in the adult stage. For example, adult body size and shape depend on nutrients available to larvae and local 33 environmental conditions, including temperature and water quality (Corbet, 1999; Lee and Lin, 2012) [64,65].

Environmental stressors, such as temperature and habitat quality, contribute to fluctuating asymmetry in morphology. For example, in *Ceroglossus chilensis* beetles, fragmented habitats drive adaptations to localized conditions (Henriquez *et al.,* 2009) [35]. Recent studies suggest that environmental factors have a stronger influence on wing morphology than phylogeny (MacLeod *et al.,* 2022) [60].

Major environmental disturbances modify environmental and/or spatial factors, leading to the elimination of sensitive local species and alterations in community organization (Oliveira junior and Juen, 2019) [41]. Alterations to habitat structure caused by deforestation affect trophic dynamics and may alter Odonata species composition and diversity.

Environmental factors, such as riparian vegetation and physical-chemical properties of water, significantly affect Odonata communities, especially in Zygoptera species (De Marco *et al.,* 2015) [62]. Climatic shifts influence the morphology of dragonflies, as seen in *Trithemis* species adapting to fluctuating water conditions in Africa during the Plio-Pleistocene (Damm *et al.,* 2010) [26]. Environmental factors, such as temperature and precipitation, shape dragonfly wing morphology. A stronger correlation has been observed between higher temperatures and reduced wing reticulation (Shortess, 1929) [61].

In Calopterygidae damselflies, wing shape and ornamentation are influenced by environmental factors, such as predation and conspecific interactions (Rantala *et al.,* 2011) [67]. Wing pigmentation, based on melanin, is costly to produce and condition-dependent, and has been positively selected in male-male territorial contests and by female choice (Siva-Jothy, 1999) [66]. Certain wing shapes improve both flight performance and ornament display, and the quality of the ornamental signal (Srygley, 1999) [68]. Adult odonates emerge with empty guts and minimal fat but gain mass rapidly during adulthood, often doubling their weight in weeks (Anholt et al., 1991) [69].

Conclusion

Morphometric analysis has become an important tool for studying insect diversity, structure, and evolutionary relationships. By allowing accurate measurement of size and shape, these techniques have improved the reliability of species identification, especially in cases where species are closely related or difficult to distinguish using traditional morphology alone. While traditional morphometry provides useful baseline data through linear measurements and ratios, geometric morphometry offers a more detailed understanding of shape by retaining the spatial arrangement of morphological features.

The combination of these approaches with statistical methods such as multivariate analysis and Procrustes superimposition has made it possible to interpret complex patterns of variation more effectively. In addition, morphometric studies have contributed to understanding ecological adaptations, sexual dimorphism, and evolutionary trends in insects. It is also evident that environmental conditions and developmental factors play a significant role in shaping morphological traits, reflecting the interaction between genetic and external influences.

In summary, morphometry forms a link between classical taxonomy and modern analytical approaches. With the growing use of digital imaging and advanced analytical tools, its applications are likely to expand further. Future developments, particularly in areas such as image analysis and machine learning, may provide more refined and efficient ways to study insect morphology and its ecological and evolutionary significance.

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