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Multivariate Morphometric Differentiation of Butterflies in Gunung Tumpa Grand Forest Park, North Sulawesi, Indonesia

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Abstract. Sulawesi supports a taxonomically distinctive butterfly fauna, yet trait-based information that can complement conventional biodiversity inventories remains limited. Previous studies in Gunung Tumpa Grand Forest Park have primarily emphasized species diversity, abundance, and pollinator communities, leaving morphometric differentiation among co-occurring taxa comparatively unexplored. This study quantified morphological differentiation among ten butterfly taxa recorded from Gunung Tumpa, North Sulawesi, using eleven linear morphometric variables describing wing, body, antenna, and leg dimensions. Measurements were standardized as z-scores and analyzed using principal component analysis (PCA) and Ward's hierarchical clustering based on Euclidean distance. The first three principal components explained 93.22% of the total standardized variance (PC1 = 60.72%, PC2 = 18.51%, and PC3 = 13.99%). PC1 represented an integrated size-and-appendage gradient, with the strongest positive contributions from antenna length, abdomen length, thorax length, midleg length, and wing dimensions. *Troides helena* was strongly separated along PC1, *Idea blanchardii* along PC2, and *Papilio sp.* along PC3. Ward's clustering corroborated this hierarchical pattern of differentiation: *T. helena* was the most morphometrically distinct taxon, whereas seven taxa formed a relatively compact core cluster before *Papilio sp.* and *I. blanchardii* joined at greater linkage distances. These results provide an exploratory trait-space baseline for butterflies in Gunung Tumpa and demonstrate that local taxonomic diversity is accompanied by pronounced morphological differentiation.

Key words: Butterfly ecomorphology; Lepidoptera; Gunung Tumpa Grand Forest Park; Multivariate morphometrics; Principal component analysis

INTRODUCTION

Butterflies are functionally important components of terrestrial ecosystems and are increasingly used to investigate organismal trait responses to environmental heterogeneity. Beyond species richness, morphology provides a mechanistic dimension because wing size and shape, body dimensions, and appendage proportions can influence flight capacity, thermoregulation, resource use, and movement. Comparative studies have shown that butterfly wing morphology is associated with flight behavior and ecological performance, while the vertical structure of forests can generate predictable interspecific differences in allometry and flight morphology among tropical butterflies (Le Roy et al., 2019; Mena et al., 2020). Wing compartments may also evolve with a degree of independence, indicating that morphological variation cannot be reduced to a single axis of body size (Owens et al., 2020). At broader spatial scales, habitat differences, elevation, thermal regimes, and colonization history may be associated with measurable variation in wing morphology (Jugovic et al., 2018; Taylor-Cox et al., 2020; Montejo-Kovacevich et al., 2021; Shilpa et al., 2023).

North Sulawesi provides a particularly relevant setting for trait-based butterfly research because it encompasses heterogeneous forest, forest-edge, agricultural, and urban landscapes within the biogeographically distinctive Sulawesi region. Recent surveys have documented marked differences in butterfly composition among habitat conditions in the Sangihe and Talaud Islands, urban forests of North Minahasa, Rayow Waterfall, and Bogani Nani Wartabone National Park (Koneri & Nangoy, 2019; Koneri et al., 2019; Koneri et al., 2020; Koneri et al., 2022; Koneri et al., 2023). In Gunung Tumpa Grand Forest Park, Antoni et al. (2024) recorded high Nymphalidae diversity, whereas Koneri et al. (2024) demonstrated that pollinator-insect composition differs among forest, forest-edge, shrub, and agricultural habitats. Pontororing et al. (2024) also provided species-level morphological information for *Troides helena* in North Sulawesi. Collectively, these studies establish a strong taxonomic and ecological foundation, but they do not explain how multiple linear morphological traits jointly differentiate sympatric butterfly taxa in Gunung Tumpa.

This gap is important because community inventories and multivariate trait analyses address different ecological questions. Functional-trait studies indicate that butterfly assemblages may be structured by habitat gradients and anthropogenic change (Spaniol et al., 2019; Kuussaari et al., 2021; Mahata et al., 2023), whereas experimental research has shown that temperature and larval diet can alter adult morphology and flight-related performance (Günter et al., 2020; Soule et al., 2020). Movement strategies themselves are also associated with differences in flight morphology (Bhaumik & Kunte, 2020; Freedman et al., 2020). Consequently, morphological differences observed in the field may contain signals of evolutionary history, environmental plasticity, or both. Morphometric measurements should therefore be interpreted as phenotypic evidence rather than as direct measures of genetic variability unless they are validated with molecular data. This distinction is particularly important in conservation-oriented research, because equating phenotype with genotype can lead to biologically overstated conclusions.

The novelty of this study lies in integrating eleven linear morphological variables into a single multivariate trait-space analysis for ten butterfly taxa recorded in Gunung Tumpa Grand Forest Park. Rather than assigning taxa a priori to size categories, the study applies PCA to standardized data and Ward's hierarchical clustering to identify the principal axes of morphological differentiation and the hierarchical structure of intertaxon similarity. Specifically, this study aims to (1) characterize and compare the morphometric profiles of ten taxa, (2) identify the variables and major axes that contribute most strongly to differentiation among taxa, and (3) evaluate morphological similarity among taxa using hierarchical clustering. The resulting baseline is expected to complement existing biodiversity inventories and provide a reference for future specimen-level, ecological, and molecular studies of Sulawesi butterflies.

METHODS

Study site and research design

The study was conducted in Gunung Tumpa Grand Forest Park, Manado, North Sulawesi, Indonesia. This protected landscape is characterized by heterogeneous vegetation and occurs within a mosaic of forest, forest-edge, shrub, and agricultural habitats, as documented by recent insect surveys (Antoni et al., 2024; Koneri et al., 2024). The study area forms part of a conservation forest with high biodiversity and vegetation ranging from relatively open cover to dense stands.

Butterfly sampling and taxonomic identification

Butterflies were obtained through field sampling in Gunung Tumpa Grand Forest Park and were subsequently subjected to morphometric measurement. Comparable studies in North Sulawesi have used standardized transect-based field sampling to relate butterfly communities to habitat conditions (Koneri et al., 2022; Koneri et al., 2023). Ten taxa were included in the analytical matrix: *Troides helena*, *Idea blanchardii*, *Papilio sp.*, *Cyrestis strigata*, *Parantica cleona*, *Ideopsis vitrea*, *Hypolimnas bolina*, *Euploea core*, *Danaus ismare*, and *Catopsilia scylla*.

Morphometric measurements

Linear morphometric measurements were obtained using a digital caliper with a resolution of 0.01 mm. The eleven morphometric characters measured were forewing length (PSD), hindwing length (PSB), forewing width (LSD), hindwing width (LSB), head length (PK), thorax length (PTH), abdomen length (PABD), antenna length (PAN), foreleg length (PKK1), midleg length (PKK2), and hindleg length (PKK3). All morphometric characters were measured in millimeters (mm). The eleven variables were analyzed using their original dataset codes: PSD, PSB, LSD, LSB, PK, PTH, PABD, PAN, PKK1, PKK2, and PKK3. Collectively, these variables represent wing length and width, head and body dimensions, antenna length, and leg dimensions.

Data analysis

The analysis used a numerical matrix containing one morphometric profile for each of the ten taxa. Because the morphometric variables were measured on different anatomical structures and exhibited substantially different numerical ranges, each variable was standardized to a z-score before multivariate analysis: $z_{ij} = (x_{ij} - \bar{x}_j) / s_j$, where x_{ij} is the value of variable j for taxon i, $\bar{x}_j$ is the mean of variable j, and s_j is its standard deviation. Standardization ensured that variables with larger absolute scales did not dominate the covariance structure. PCA was then applied to the standardized matrix to reduce dimensionality and identify orthogonal axes that maximize explained variance, following current recommendations for exploratory multivariate analysis (Jolliffe & Cadima, 2016).

Component interpretation was based on explained variance, taxon scores, and the magnitude and direction of variable loadings. Morphological similarity was independently evaluated using agglomerative hierarchical clustering based on Euclidean distances among standardized profiles and Ward's linkage method. Ward's clustering minimizes the increase in within-cluster variance at each agglomeration step and is appropriate for standardized continuous variables when the distance assumptions are considered during interpretation (Strauss & von Maltitz, 2017; Randriamihamison et al., 2021). The dendrogram was interpreted hierarchically without imposing an arbitrary number of clusters. Because the current analytical matrix contains only ten taxon-level profiles and eleven variables, PCA and clustering were treated as exploratory descriptive analyses rather than inferential tests of population-level differences. The analyses reported in this revision were reproduced in Python 3.13 using scikit-learn 1.8.0 for standardization and PCA and SciPy 1.17.0 for hierarchical clustering. Explained-variance values and linkage distances are reported to two decimal places.

RESULTS

Morphometric profiles of the ten taxa

The available dataset revealed substantial among-taxon variation across the eleven measured traits (Tables 1 and 2). *Troides helena* had the highest values for PSD (77.6 mm), LSD (59.5 mm), PTH (17.3 mm), PABD (32.9 mm), PAN (59.2 mm), and PKK2 (56.3 mm), yielding a profile consistently shifted toward larger dimensions across several body and appendage variables. *Idea blanchardii* also exhibited large values for several wing dimensions, whereas *Papilio sp.* had the highest PSB value (51.8 mm). By contrast, *Hypolimnas bolina*, *Euploea core*, *Danaus ismare*, and several other taxa occupied lower ranges for many size-related variables. These differences in raw values demonstrate pronounced scale heterogeneity among traits and support the need for standardization prior to multivariate analysis. Values in the tables are reported exactly as provided in the available dataset and should be cross-checked against the original measurement sheets before journal submission.

Table 1. Wing and body morphometric measurements (mm) for ten butterfly taxa in the available analytical matrix (PSD: forewing length; PSB: hindwing length; LSD: forewing width; LSB: hindwing width; PK: head length; PTH: thorax length; PABD: abdomen length).

Species	PSD	PSB	LSD	LSB	PK	PTH	PABD
Troides helena	77.6	43.6	59.5	30.7	4.1	17.3	32.9
Idea blanchardii	65.9	45.3	42.5	35.5	2	7.8	24.1
Papilio sp.	52.6	51.8	21.8	18.1	2.1	6.5	17.8
Cyrestis strigata	49.2	38.3	33.1	28.8	3.4	8.3	21.8
Parantica cleona	39.5	24.8	23.9	23.2	2.9	7.2	18.7
Ideopsis vitrea	47.9	30	36.4	28.3	3.1	7.2	18.9
Hypolimnas bolina	36.6	25.5	22.5	20.2	3.6	6.6	13.6
Euploea core	35.1	29.4	20.2	26.4	3	7.8	12.8
Danaus ismare	44.3	30.3	19.8	29.9	2.4	6.8	15.4
Catopsilia scylla	48.4	35.5	29.8	28.6	2.7	7.7	16.2

Table 2. Antenna and leg morphometric measurements (mm) for ten butterfly taxa in the available analytical matrix (PAN: antenna length; PKK1: foreleg length; PKK2: midleg length; PKK3: hindleg length).

Species	PAN	PKK1	PKK2	PKK3
Troides helena	59.2	33	56.3	26.2
Idea blanchardii	20.8	2.7	21.8	18.5
Papilio sp.	18.3	29.7	14.7	24.7
Cyrestis strigata	17.4	24.2	19.9	22.9
Parantica cleona	15.1	25.3	27.8	21.2
Ideopsis vitrea	14.2	15.1	15.5	16.6
Hypolimnas bolina	13.4	14.5	14.2	16.4
Euploea core	15.2	16.4	13.8	18.2
Danaus ismare	13.6	16.3	14.8	14.6
Catopsilia scylla	17.7	17.5	15.5	15.9

Principal component analysis

PCA of the standardized matrix produced a low-dimensional representation with a strong concentration of variance. PC1 explained 60.72% of the total standardized variance, PC2 explained 18.51%, and PC3 explained 13.99%; cumulatively, the first three axes accounted for 93.22% (Table 3). PC1 had positive loadings for all variables and was most strongly associated with PAN (0.373), PABD (0.371), PTH (0.366), PKK2 (0.363), LSD (0.351), and PSD (0.345). This pattern indicates that PC1 primarily represents an integrated size-and-appendage axis rather than a single wing variable. PC2 was dominated by a positive loading for LSB (0.576), contrasted mainly with PKK1 (-0.547), PK (-0.337), and PKK3 (-0.307), whereas PC3 was dominated by PSB (0.628), opposed to PK (-0.538), with a secondary positive contribution from PKK3 (0.350).

Table 3. Explained variance and variable loadings for the first three principal components.

Variable	PC1	PC2	PC3
PSD	0.345	0.255	0.178
PSB	0.208	0.152	0.628
LSD	0.351	0.216	-0.128
LSB	0.145	0.576	-0.224
PK	0.183	-0.337	-0.538
PTH	0.366	-0.057	-0.193
PABD	0.371	0.120	0.027
PAN	0.373	-0.047	-0.076
PKK1	0.194	-0.547	0.164
PKK2	0.363	-0.087	-0.157
PKK3	0.282	-0.307	0.350
Explained variance (%)	**60.72**	**18.51**	**13.99**
Cumulative variance (%)	**60.72**	**79.23**	**93.22**

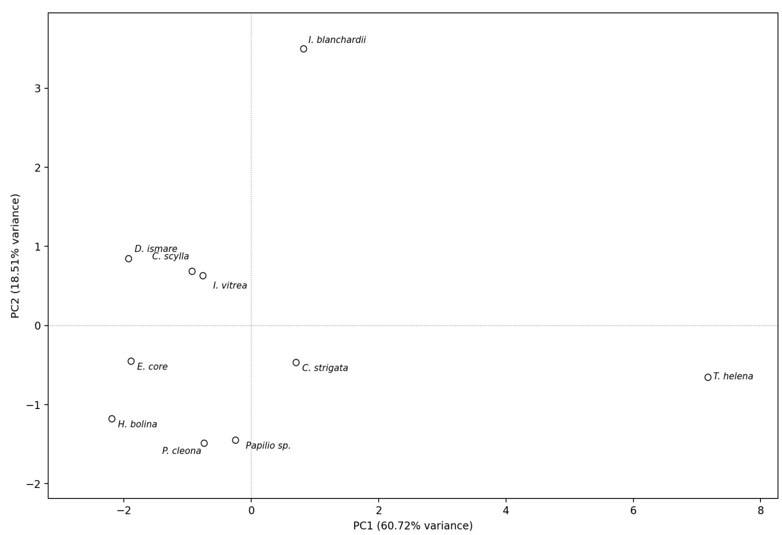

Figure 1. Principal component scores of ten butterfly taxa based on eleven morphometric variables standardized as z-scores. PC1 and PC2 together explain 79.23% of the total standardized variance.

Taxon scores further supported this interpretation (Figure 1). *Troides helena* was strongly separated from all other taxa along PC1 (score = 7.17), indicating that its multivariate profile was not merely somewhat larger but occupied a distinct position along the primary integrated size axis. *Idea blanchardii* was most prominent on PC2 (3.50), whereas *Papilio sp.* was most prominent on PC3 (3.33). The remaining taxa were concentrated closer to the central-to-negative region of PC1 and within a narrower range of PC2. Thus, most among-taxon differentiation in the available matrix was captured by a dominant size-related gradient, with additional shape and proportional contrasts expressed on PC2 and PC3.

Ward's hierarchical clustering

The Ward dendrogram provided a complementary representation of the same trait structure (Figure 2). The closest initial pair was *Ideopsis vitrea* and *Catopsilia scylla* (linkage distance = 1.25), followed by *Euploea core* and *Danaus ismare* (1.79). These pairs subsequently merged into a compact core cluster together with *Hypolimnas bolina*, *Cyrestis strigata*, and *Parantica cleona*. *Papilio sp.* joined this seven-taxon core cluster at a substantially greater distance (5.46), *Idea blanchardii* joined at 5.87, and *Troides helena* merged only at the greatest linkage distance (10.81). Accordingly, the data do not support the previously simplified grouping of all taxa into three equivalent ecological size classes. Instead, they reveal hierarchical morphometric differentiation characterized by a compact seven-taxon cluster, two progressively more distinct profiles, and one pronounced outlier, *T. helena*.

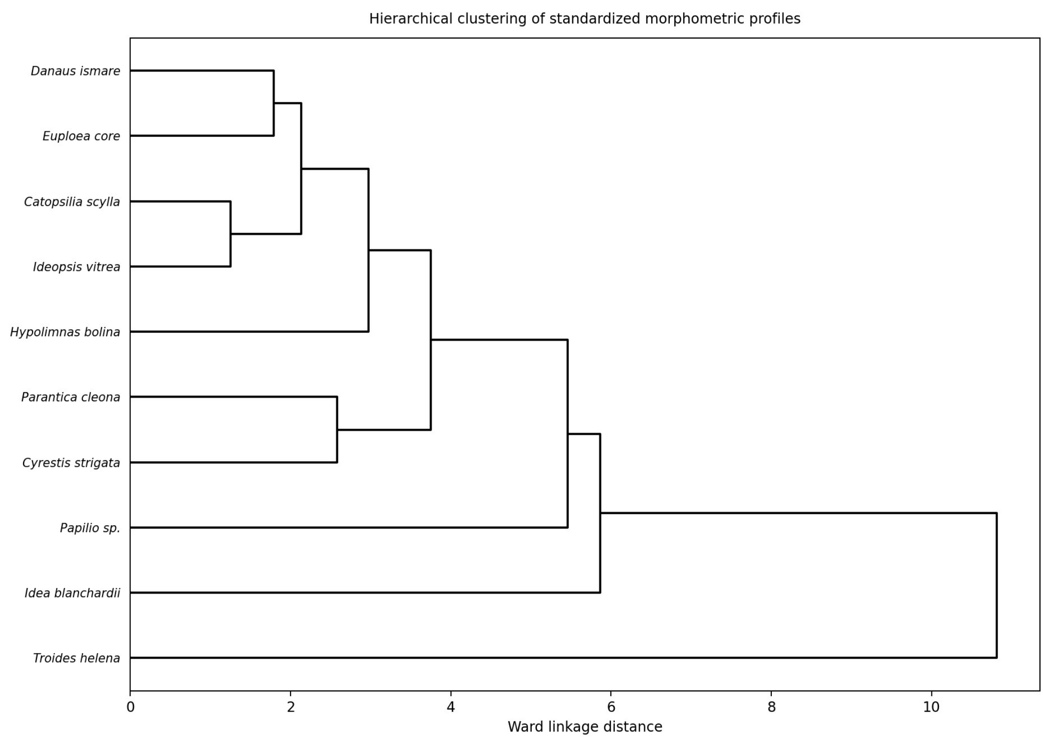

Figure 2. Ward's hierarchical clustering of ten butterfly taxa using Euclidean distances based on morphometric variables standardized as z-scores. Greater linkage distances indicate higher multivariate morphological dissimilarity.

DISCUSSION

The principal finding of this study is that the ten butterfly taxa from Gunung Tumpa occupy a structured morphometric trait space, with most standardized variation concentrated along an integrated axis of wing, body, antenna, and leg dimensions. This pattern is biologically plausible because flight-related morphology is inherently multivariate: wing dimensions interact with body-mass distribution, thoracic investment, appendage structure, and behavior rather than functioning as isolated characters. Le Roy et al. (2019) emphasized that the evolution of wing shape should be interpreted through the functional relationship between morphology and flight behavior, whereas Mena et al. (2020) showed that tropical forest stratification is associated with coordinated changes in allometry and flight morphology. The present findings extend this trait-based perspective to a conservation landscape in North Sulawesi by showing that intertaxon differences in Gunung Tumpa are more appropriately summarized as a multivariate trait continuum than as a set of isolated univariate measurements. Importantly, the first axis does not imply that every species differs in the same manner; PC2 and PC3 retain substantial information on proportional contrasts, consistent with the evolutionary modularity of forewings and hindwings demonstrated by Owens et al. (2020).

Troides helena provides the clearest example of this integrated differentiation. The taxon occupies an extreme positive position on PC1 and joins the remaining taxa only at the greatest Ward linkage distance. This result is consistent with species-specific measurements from North Sulawesi reported by Pontororing et al. (2024), who likewise highlighted the conspicuous size and morphological characteristics of *T. helena*. Nevertheless, ecological interpretation should remain cautious. Large wing and body dimensions may be associated with flight performance and movement strategy, but size alone does not demonstrate greater dispersal capacity, sensitivity to fragmentation, or habitat specialization. Comparative and experimental studies indicate that movement-related morphology can vary with dispersal strategy and evolutionary history: migratory or range-expanding butterflies may have longer or more elongated wings, whereas reduced migration may be accompanied by smaller wing size (Bhaumik & Kunte, 2020; Freedman et al., 2020; Taylor-Cox et al., 2020). Environmental conditions may also alter flight performance independently of overall body size; for example, diet and rearing temperature affect wing morphology and flight ability in monarch butterflies under controlled conditions (Soule et al., 2020). Therefore, the extreme profile of *T. helena* is best interpreted as evidence of morphological distinctiveness that generates testable ecological hypotheses, rather than as direct evidence of a particular response to dispersal or fragmentation.

The separation of *Idea blanchardii* on PC2 and *Papilio sp.* on PC3 further demonstrates that among-taxon differentiation cannot be reduced to a simple large-medium-small classification. PC2 contrasts hindwing-related width with leg and head dimensions, whereas PC3 is dominated by the PSB axis opposed to head length. Such proportional contrasts are expected when different anatomical modules are subject to distinct functional and evolutionary constraints. Owens et al. (2020) found that forewing and hindwing characteristics in Papilio exhibit partly independent evolutionary dynamics, while Jugovic et al. (2018) demonstrated habitat-associated differences in both classical and geometric wing morphometrics in *Coenonympha oedippus*. Shilpa et al. (2023) likewise reported elevation-associated phenotypic wing variation in *Tirumala septentrionis*. These studies support the interpretation that secondary PCA axes can contain ecologically meaningful information on proportional variation even when the overall size gradient dominates PC1. However, in the present dataset, the absence of within-species replication prevents testing whether these proportional differences represent stable population-level characteristics or are influenced by the particular specimens summarized in the matrix.

The local ecological context further underscores the value of this trait-based baseline. Gunung Tumpa supports diverse butterfly and pollinator communities, and community composition varies with vegetation condition (Antoni et al., 2024; Koneri et al., 2024). Similar habitat-dependent patterns have been reported elsewhere in North Sulawesi, including Sangihe, Talaud, urban forests of North Minahasa, Rayow Waterfall, and Bogani Nani Wartabone National Park (Koneri & Nangoy, 2019; Koneri et al., 2019; Koneri et al., 2020; Koneri et al., 2022; Koneri et al., 2023). Those studies primarily quantified taxonomic composition, abundance, or diversity. Morphometric trait space provides a complementary layer of information because two communities with similar species richness may nevertheless differ in the distribution of functional characteristics. This interpretation is supported by broader research showing that butterfly functional traits and phylogenetic structure respond to anthropogenic gradients (Spaniol et al., 2019), that mobility and habitat specificity mediate species responses to urbanization (Kuussaari et al., 2021), and that microclimate and vegetation structure strongly influence butterfly assemblages in tropical forests (Mahata et al., 2023).

Morphological traits may have an inherited basis, but field morphology cannot be equated with genetic variability. Montejo-Kovacevich et al. (2021) showed that elevation-associated wing shape in tropical butterflies has a genomic basis involving polygenic variation; such direct evidence was possible because morphological data were explicitly integrated with genomic analyses. By contrast, Günter et al. (2020) demonstrated that genotype-by-environment interactions and phenotypic plasticity jointly shape butterfly responses to temperature. Even thermoregulatory structures and behavior can influence wing function under different environmental conditions (Tsai et al., 2020). These findings indicate that morphometric patterns in Gunung Tumpa may reflect evolutionary divergence, phylogenetic history, developmental plasticity, sex, age, environmental history, measurement structure, or combinations of these processes. The scientifically defensible conclusion is therefore the presence of phenotypic or morphometric differentiation. Genetic diversity must be assessed independently using molecular markers or genome-scale data and subsequently integrated with morphological information to test phenotype-genotype correspondence.

The clustering results also require methodological caution. Ward's clustering is designed to minimize within-cluster dispersion at each agglomeration step, but the dendrogram itself does not constitute evidence for a particular number of biologically discrete groups (Strauss & von Maltitz, 2017; Randriamihamison et al., 2021). In this reanalysis, seven taxa form a relatively compact core cluster, *Papilio sp.* and *I. blanchardii* join at greater distances, and *T. helena* is the most pronounced outlier. This hierarchical pattern is more consistent with the observed distance structure than forcing three groups labeled according to body size or presumed habitat adaptation. PCA and the dendrogram yield mutually consistent results: the taxon located farthest along PC1 is also the last to merge hierarchically. This convergence strengthens descriptive confidence in the dominant trait pattern but does not replace the need for statistical replication. PCA itself is an exploratory dimension-reduction method whose interpretation depends on sampling structure and the quality of variable measurement (Jolliffe & Cadima, 2016).

CONCLUSION

This study achieved its objectives by demonstrating structured morphometric differentiation among ten butterfly taxa from Gunung Tumpa Grand Forest Park based on eleven standardized linear traits. The first three principal components explained 93.22% of the total variance, with PC1 (60.72%) representing a dominant integrated gradient of wing, body, antenna, and leg dimensions, while PC2 and PC3 captured additional proportional contrasts. Ward's clustering independently supported the same hierarchy, identifying *Troides helena* as the most morphometrically distinct taxon, followed progressively by the increasingly distinct profiles of *Idea blanchardii* and *Papilio sp.*, whereas the remaining seven taxa formed a relatively compact core cluster. These findings establish a quantitative trait-based baseline that complements existing butterfly inventories in North Sulawesi and provides a foundation for designing subsequent ecomorphological studies.

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REFERENCES

Antoni, N., Koneri, R., & Maabuat, P. V. (2024). Keanekaragaman kupu-kupu Nymphalidae di kawasan Taman Hutan Raya Gunung Tumpa, Manado-Sulawesi Utara. Jurnal Bios Logos, 14(2), 117–126. https://doi.org/10.35799/jbl.v14i2.55224

Bhaumik, V., & Kunte, K. (2020). Dispersal and migration have contrasting effects on butterfly flight morphology and reproduction. Biology Letters, 16(8), 20200393. https://doi.org/10.1098/rsbl.2020.0393

Freedman, M. G., Dingle, H., Strauss, S. Y., & Ramírez, S. R. (2020). Two centuries of monarch butterfly collections reveal contrasting effects of range expansion and migration loss on wing traits. Proceedings of the National Academy of Sciences of the United States of America, 117(46), 28887–28893. https://doi.org/10.1073/pnas.2001283117

Günter, F., Beaulieu, M., Freiberg, K. F., Welzel, I., Toshkova, N., Žagar, A., Simčič, T., & Fischer, K. (2020). Genotype-environment interactions rule the response of a widespread butterfly to temperature variation. Journal of Evolutionary Biology, 33(7), 920–929. https://doi.org/10.1111/jeb.13623

Jolliffe, I. T., & Cadima, J. (2016). Principal component analysis: A review and recent developments. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 374(2065), 20150202. https://doi.org/10.1098/rsta.2015.0202

Jugovic, J., Zupan, S., Bužan, E., & Čelik, T. (2018). Variation in the morphology of the wings of the endangered grass-feeding butterfly *Coenonympha oedippus* (Lepidoptera: Nymphalidae) in response to contrasting habitats. European Journal of Entomology, 115, 339–353. https://doi.org/10.14411/eje.2018.034

Koneri, R., & Nangoy, M. J. (2019). Butterfly community structure and diversity in Sangihe Islands, North Sulawesi, Indonesia. Applied Ecology and Environmental Research, 17(2), 2501–2517. https://doi.org/10.15666/aeer/1702_25012517

Koneri, R., Langoy, M. D., Nangoy, M. J., & Wakhid. (2024). Pollinator insects in the Mount Tumpa Forest Park, Manado, North Sulawesi, Indonesia. Biodiversitas, 25(6), 2415–2426. https://doi.org/10.13057/biodiv/d250610

Koneri, R., Maabuat, P. V., & Nangoy, M. J. (2020). The distribution and diversity of butterflies (Lepidoptera: Rhopalocera) in various urban forests in North Minahasa Regency, North Sulawesi Province, Indonesia. Applied Ecology and Environmental Research, 18(2), 2295–2314. https://doi.org/10.15666/aeer/1802_22952314

Koneri, R., Nangoy, M. J., Maabuat, P. V., Saroyo, & Wakhid. (2022). Diversity and composition of butterflies in three habitats around Rayow Waterfall, Minahasa District, North Sulawesi, Indonesia. Biodiversitas, 23(2), 1091–1098. https://doi.org/10.13057/biodiv/d230253

Koneri, R., Nangoy, M. J., Maabuat, P. V., & Wakhid. (2023). Butterfly species in Bogani Nani Wartabone National Park, North Sulawesi, Indonesia. Biodiversitas, 24(2), 1242–1251. https://doi.org/10.13057/biodiv/d240266

Koneri, R., Nangoy, M. J., & Siahaan, P. (2019). The abundance and diversity of butterflies (Lepidoptera: Rhopalocera) in Talaud Islands, North Sulawesi, Indonesia. Biodiversitas, 20(11), 3275–3283. https://doi.org/10.13057/biodiv/d201121

Kuussaari, M., Toivonen, M., Heliölä, J., Pöyry, J., Mellado, J., Ekroos, J., Hyyryläinen, V., Vähä-Piikkiö, I., & Tiainen, J. (2021). Butterfly species' responses to urbanization: Differing effects of human population density and built-up area. Urban Ecosystems, 24, 515–527. https://doi.org/10.1007/s11252-020-01055-6

Le Roy, C., Debat, V., & Llaurens, V. (2019). Adaptive evolution of butterfly wing shape: From morphology to behaviour. Biological Reviews, 94(4), 1261–1281. https://doi.org/10.1111/brv.12500

Mahata, A., Panda, R. M., Dash, P., Naik, A., Naik, A. K., & Palita, S. K. (2023). Microclimate and vegetation structure significantly affect butterfly assemblages in a tropical dry forest. Climate, 11(11), 220. https://doi.org/10.3390/cli11110220

Mena, S., Kozak, K. M., Cárdenas, R. E., & Checa, M. F. (2020). Forest stratification shapes allometry and flight morphology of tropical butterflies. Proceedings of the Royal Society B: Biological Sciences, 287(1937), 20201071. https://doi.org/10.1098/rspb.2020.1071

Montejo-Kovacevich, G., Salazar, P. A., Smith, S. H., Gavilanes, K., Bacquet, C. N., Chan, Y. F., Jiggins, C. D., Meier, J. I., & Nadeau, N. J. (2021). Genomics of altitude-associated wing shape in two tropical butterflies. Molecular Ecology, 30(23), 6387–6402. https://doi.org/10.1111/mec.16067

Owens, H. L., Lewis, D. S., Condamine, F. L., Kawahara, A. Y., & Guralnick, R. P. (2020). Comparative phylogenetics of Papilio butterfly wing shape and size demonstrates independent hindwing and forewing evolution. Systematic Biology, 69(5), 813–819. https://doi.org/10.1093/sysbio/syaa029

Pontororing, H. H., Rampe, H. L., & Wahyudi, L. (2024). Karakteristik kupu-kupu spesies *Troides helena*, kupu-kupu dilindungi dan terancam punah di Sulawesi Utara. Jurnal Bios Logos, 14(2), 39–45. https://doi.org/10.35799/jbl.v14i2.52864

Randriamihamison, N., Vialaneix, N., & Neuvial, P. (2021). Applicability and interpretability of Ward's hierarchical agglomerative clustering with or without contiguity constraints. Journal of Classification, 38(2), 363–389. https://doi.org/10.1007/s00357-020-09377-y

Shilpa, M. P., Anand, P. P., Shibu Vardhanan, Y., & Manogem, E. M. (2023). High and lowland dependent wing phenotypic variation of the dark blue tiger butterfly, *Tirumala septentrionis* (Butler, 1874) (Lepidoptera: Nymphalidae) with FE-SEM wing scales nanomorphology. Zoologischer Anzeiger, 302, 131–145. https://doi.org/10.1016/j.jcz.2022.12.002

Soule, A. J., Decker, L. E., & Hunter, M. D. (2020). Effects of diet and temperature on monarch butterfly wing morphology and flight ability. Journal of Insect Conservation, 24(6), 961–975. https://doi.org/10.1007/s10841-020-00267-7

Spaniol, R. L., Duarte, L. D. S., Mendonça, M. S., Jr., & Iserhard, C. A. (2019). Combining functional traits and phylogeny to disentangling Amazonian butterfly assemblages on anthropogenic gradients. Ecosphere, 10(8), e02837. https://doi.org/10.1002/ecs2.2837

Strauss, T., & von Maltitz, M. J. (2017). Generalising Ward's method for use with Manhattan distances. PLOS ONE, 12(1), e0168288. https://doi.org/10.1371/journal.pone.0168288

Taylor-Cox, E. D., Macgregor, C. J., Corthine, A., Hill, J. K., Hodgson, J. A., & Saccheri, I. J. (2020). Wing morphological responses to latitude and colonisation in a range expanding butterfly. PeerJ, 8, e10352. https://doi.org/10.7717/peerj.10352

Tsai, C.-C., Childers, R. A., Shi, N. N., Ren, C., Pelaez, J. N., Bernard, G. D., Pierce, N. E., & Yu, N. (2020). Physical and behavioral adaptations to prevent overheating of the living wings of butterflies. Nature Communications, 11, 551. https://doi.org/10.1038/s41467-020-14408-8