museu de ciències naturals de Barcelona

Animal Biodiversity and Conservation 49.1 (2026)
DOI: 10.32800/abc.2026.49.0005

Research paper

A quantitative comparison of the morphological diversity within beetles and true bugs: why immatures matter

F. Braig[1,2], C. Haug[1,3], E. Toman[1], Z. Sipos[1], T. Wabnitz[1], J. Joosten[1,4], F. Haxel[1], J. Mack[1], T. Haanraads[1,5], L. Ullmann[1], S. Hagn[1], C. Voith[1], K. Pröller[1], F. Meißner[1], B. Berninger[1], C. Stahlecker[1], S. L. Kliese[1,6], J. Preschl[1], L. Neuburger[1,4], L. Böckeler[1], S. Albach[1], M. Tellioglu[1], J. T. Haug[1,3]

Author affiliations:
[1] Biocenter, Ludwig-Maximilians-Universität München, Munich, Germany.
[2] University of Oulu, Linnanmaa, Finland.
[3] GeoBio-Center of the LMU Munich, Munich, Germany
[4] Munich, Germany.
[5] Uppsala University, Uppsala, Sweden.
[6] Technical University Vieanna, Vienna, Austria

Corresponding author:
Florian Braig: florian.braig@palaeo-evo-devo.info

Handling Editor:
Jorge M. Lobo

Received: 25/06/2025
Cond. acceptance: 07/11/2025
Final acceptance: 22/01/2026
Published: 26/02/2026

Cite:
Braig F, Haug C, Toman E, Sipos Z, Wabnitz T, Joosten J, Haxel F, Mack J, Haanraads T, Ullmann L, Hagn S, Voith C, Pröller K, Meißner F, Berninger B, Stahlecker C, Kliese SL, Preschl J, Neuburger L, Böckeler L, Albach S, Tellioglu M, Haug JT, 2026. A quantitative comparison of the morphological diversity within beetles and true bugs: why immatures matter. *Animal Biodiversity and Conservation* 49.1, e0005. DOI: https://doi.org/10.32800/abc.2026.49.0005

Abstract

A quantitative comparison of the morphological diversity within beetles and true bugs: why immatures matter. Measuring biodiversity is more important than ever due to the ongoing global mass extinction event, often done by counting species. A species number cannot fully reflect the structure of diversity within an ecosystem. In Coleoptera, the group of beetles, the larvae strongly differ morphologically and ecologically from their corresponding adults. We evaluate the morphological diversity of adult and larval beetles from their body shape in comparison to adult and immature true bugs (Heteroptera). The latter have about 10 % of the species richness of beetles and have immatures which are morphologically similar to the corresponding adults. With an elliptic Fourier analysis of the overall body shape, we reconstructed and compared the morphospaces occupied by adult and larval beetles and adult and immature true bugs. The morphological diversity of immature beetles is significantly larger than that of adult beetles, within true bugs it is comparably small. Such potentially ecologically relevant differences can hence be detected by using quantitative morphology.

Key words: Biodiversity, Quantitative morphology, Coleoptera, Heteroptera, Development

Introduction

In the face of an ongoing mass extinction event (Ceballos et al 2015, Briggs 2017, Cowie et al 2022), measuring the loss of biodiversity has become an increasingly important challenge for biologists over the past decades (e.g., Turak et al 2017b, and papers therein). Biodiversity is often measured by counting the number of species in a specific habitat and further processing these numbers (Maurer and McGill 2011, Birk et al 2012, Tilman et al 2014). While different measures emphasise different aspects, e.g., species richness (Simpson Index; Simpson 1949) or species evenness (Shannon Index; Shannon 1948), most of these are dependent on the taxonomic properties of a monitored habitat. Other types of diversity, such as genetic diversity, behavioural diversity, or morphological diversity (often referred to as disparity; Hopkins and Gerber 2017) may provide rather different insights in the structure of diversity of an ecosystem. Ultimately, these measures of diversity are often used as a proxy

© [2026] Copyright belongs to the authors, who license the journal *Animal Biodiversity and Conservation* to publish the paper under a Creative Commons Attribution 4.0 License.

ISSN: 1578-665 X **eISSN:** 2014-928 X

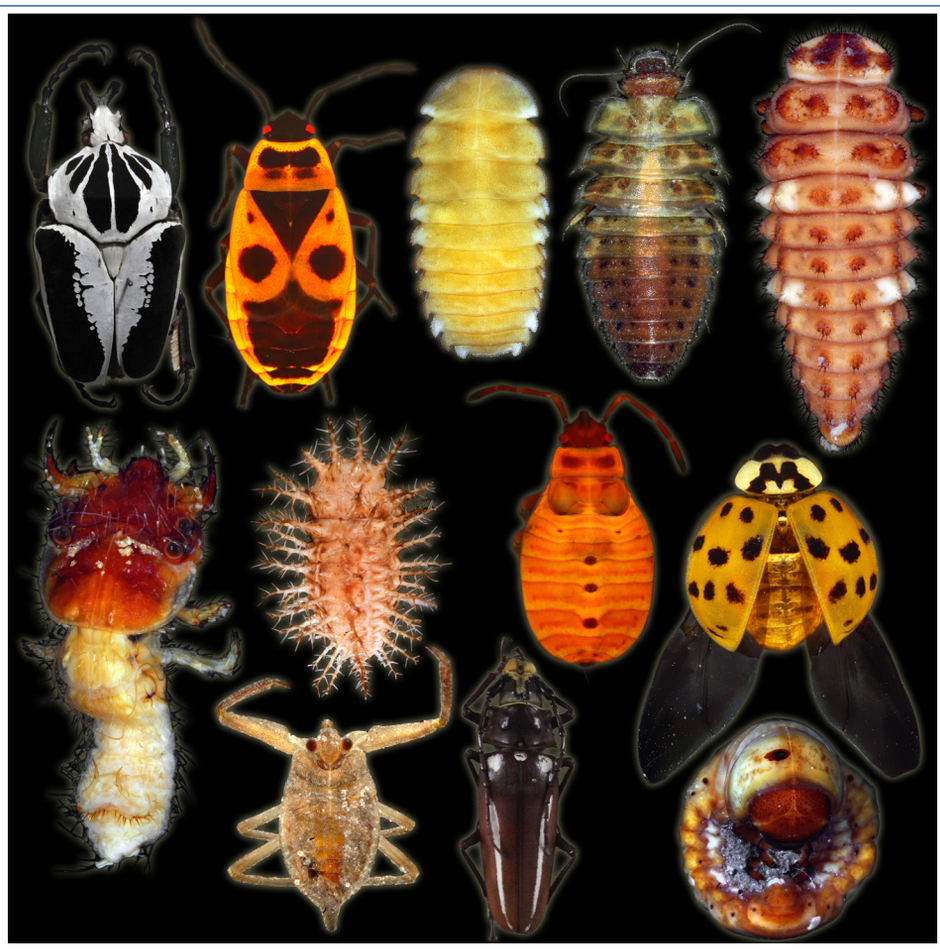

Fig. 1. Examples of different adult and immature beetles and true bugs to illustrate the morphological diversity.

for ecological diversity or, to put it more economically, ecosystem function diversity (Daily and Matson 2008, Tilman et al 2014).

A downside of species-based diversity indices is that ontogenetic changes cannot be considered, which can be especially problematic with insects. Coleoptera, the group of beetles, represents a major share of the continental animal species diversity, with more than 380,000 formally described species (Ślipiński et al 2011, McKenna et al 2019). Most adult beetles can be easily identified as such due to the specific organisation of the folded wings: the anterior pair of wings forms hardened elytra; when closed, these form a distinct midline (Evans and Bellamy 2000, McGavin 2002, Bouchard 2014; fig. 1), while most other folded wings in insects are "crossed" over each other.

Coleoptera is an ingroup of the hyper-species-rich group Holometabola, including also other super-diverse groups such as Hymenoptera (wasps and their relatives), Lepidoptera (moths) and Diptera (flies and their relatives), as well as different less diverse groups. The group Holometabola is often termed evolutionary successful, due to its high species richness (Friedrich and Beutel 2010, Beutel et al 2022). These results are among others attributed to a specification of their post-embryonic ontogeny: early post-embryonic stages differ morphologically and ecologically from their later adults (Wiegmann et al 2009, Beutel et al 2011). This differentiation allows them to reduce exploitation competition between different life phases. In the case of beetles, the immatures, usually called larvae (see discussion in Haug 2020), can appear quite different from the 'common' beetle appearance. The larval phase of life can also be quite long-lasting; some species develop through 30 larval stages and spend most of their life span in the larval phase. In some cases, the different larval stages may also differ from each other, often with highly mobile early larvae (often termed 'triungulin') and grub-like later larval stages. Such a type of development is often referred to as hypermetamorphosis (Pinto 2009). This type of ontogeny leads to species which have even more differentiated morphologies and ecological roles throughout their life.

Non-holometabolans are sometimes unfortunately still referred to as 'Hemimetabola' (see discussion in Haug et al 2016). It is generally assumed that non-holometabolans show less differentiation concerning morphology and ecology than holometabolans. Yet, several lineages of non-holometabolans have aquatic larvae and terrestrial

adults (Haug et al 2021c), already demonstrating that the case is not that simple. One very species-rich lineage of non-holometabolans is Heteroptera, the group of true bugs, with about 40,000 formally described species (e.g., Schaefer and Panizzi 2000, Henry 2017, and references therein). True bugs not only differ in their ontogeny from beetles, but also in other aspects. Most obviously are differences in the mouthparts, which form a distinct beak in true bugs, while in beetles this is not the case (with few exceptions, see Ślipiński 1991, Costa et al 1995, Balke 2005, Faucheux 2014). Despite these differences the overall appearance can be very similar. For example, true bugs of the group Plataspididae/Plataspidae can easily be mistaken for beetles of the group Coccinellidae (ladybugs/ladybirds), when viewed from dorsal (compare Eger et al 2010, Ali et al 2018).

As a side note, we use the term 'group' to refer to taxa above the species level (Haug et al 2024). The reason being that higher ranks, such as 'families' or 'superfamilies', lack objective criteria for their application (Hennig 1969, Griffiths 1976, Schaefer 1976, de Queiroz and Donoghue 1988, Minelli 2000, Ereshefsky 2002, Bertrand et al 2006, Avise and Liu 2011, Zachos 2011, Müller et al 2013, Lee et al 2020). This observation has of course been made before and discussed accordingly (Schaefer 1976, Minelli 2000). We therefore looked for other criteria based on which we chose the two groups.

In conclusion, Coleoptera and Heteroptera are prominent, species-rich, and similarly appearing representatives of holometabolans and non-holometabolans respectively, with different levels of differentiation in their development. They therefore are well suited for a comparison of intra-group variation of insect body morphology during ontogeny. Here, we quantitatively compare the morphological diversity between immatures and their adult counterparts in Coleoptera and Heteroptera respectively. Due to the presence of a holometabolan development we expect the morphological disparity in Coleoptera to be larger, when compared to the non-holometabolan group Heteroptera. We use body outlines as a proxy for overall morphology. We will furthermore compare the morphological variation within immatures and within adults. We expect adults to show larger morphological diversity in accordance with their ecological diversity. Since we compare morphological diversity within a group as well as between two groups with different numbers of species, we also hope to derive information on the relationship of taxonomic and morphological diversity.

Material and Methods

Material

The analysis is based on a sample of 1,000 specimens. These came from literature and public databases (published under CC BY 4.0 license). Used images depicted specimens in dorsal view, more rarely in ventral view. We selected 250 immature individuals (larvae) of Coleoptera. Subsequently, we searched for 250 corresponding adults. If no image of an adult was available for the exact same species, a closely related one was used. This procedure was necessary as there are still lineages of Coleoptera for which larvae are known but cannot be identified to species level (e.g., for representatives of the group Omma; Lawrence 1999). In other species-poor lineages larvae may be identified to species level, but adults have not been depicted with habitus images. Excluding any of these two cases would have led to several lineages not being represented in the data set. Therefore, while this approach may appear less 'sharp' on the species level, it leads to a better overall coverage of major lineages. The resulting data set covers roughly 50 % of the 183 extant beetle 'families' described (McKenna et al 2015). It was also necessary to have the same number of specimens for adults and immatures to not create biases due to sample size differences. While correction for sample sizes is possible (Haug et al 2020), this step adds variation to the results of the analysis. Balancing the sample size from the start is therefore advantageous.

Similarly, 250 immature individuals (nymphs) of Heteroptera were selected, then we searched for 250 corresponding adults. Again, if no adult of the exact same species was available, a closely related one was used. Again, we started the search with immatures as these are less often depicted in the literature in comparison to adults, hence starting search from the adult side would have often resulted in not finding any corresponding immatures (see discussion in Haug and Haug 2019). Ultimately, finding sufficient depictions of immatures proved to be the bottleneck. We tried to have a broad phylogenetic coverage of the larger groups, covering about 43 % of the 91 described extant 'families' of Heteroptera (Henry 2017), yet for the different ingroups of Coleoptera and Heteroptera the coverage is uneven to a certain degree due to limited availability of immatures for some ingroups. The resulting data set overall includes 1,000 specimens (listed in file S1; references listed in file S2).

Data generation

Of all 1,000 specimens selected, the outline of the entire body was redrawn as a vector graphic, anterior facing upwards. Appendages were omitted and wings were reconstructed in a closed position. To eliminate the influence of left-right asymmetry on the data set (which can otherwise dominate the analysis and conceal other differences), we only reconstructed the better-preserved half of the body and then duplicated, mirrored, and merged the two halves (Haug et al 2020). Vector graphic software used were Adobe Illustrator CS2 and the free software InkScape.

Statistical analysis

We created a mathematical representation of the body outline by applying elliptic Fourier transformation to the reconstructed outlines, using the free R-statistics environment (ver. 4.1.0; R Core Team 2021), using packages: ape (ver. 5.0; Paradis and Schliep 2019), dispRity (ver. 1.6.0; Guillerme 2018), Momocs (ver. 1.3.2; Bonhomme et al 2014), readxl (ver. 1.3.1; Wickham and Bryan 2019), and tidyverse (ver. 1.3.1; Wickham et al 2019).

Elliptic Fourier Analysis (EFA) uses the principle of the Fourier transformation to decompose a complex two-dimensional shape, i.e., the outline of the body, into a mathematical object, describing the original outline with so-called harmonics (Kuhl and Giardina 1982, Bonhomme

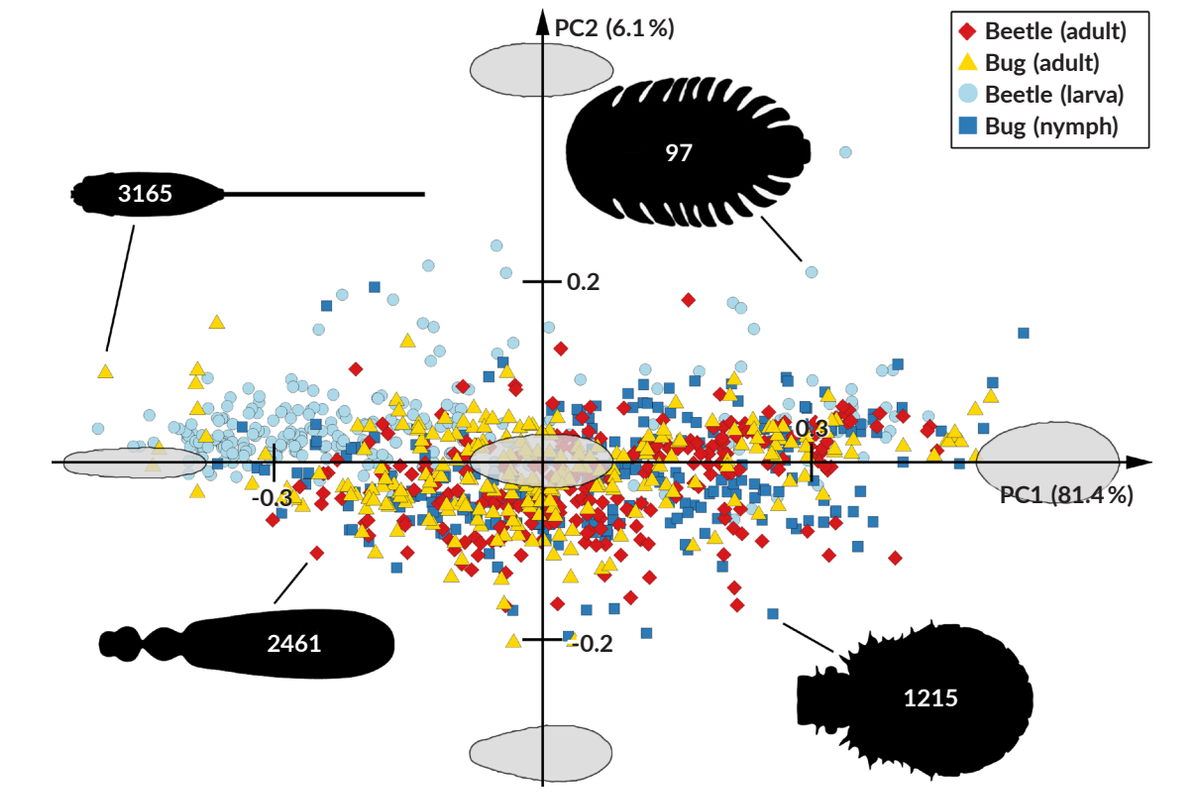

Fig. 2. Morphospace of PCA of the elliptic Fourier analysis on the body outlines of adult and larval beetles and adults and nymphs of true bugs. PC1 and PC2 plotted against each other. Grey shapes demonstrate mean and +/- 1 sd shape for every axis. Example outlines provided in black, with their respective identifiers for this study (see file S1).

et al 2014, Dujardin et al 2014, Braig et al 2024). We centered and scaled all shapes and aligned them using the bottom center of each shape as the homologous starting point. Using a calibration function, based on all specimens in the data set, we found 11 harmonics to describe over 99 % of variation of the shapes. We applied elliptic Fourier analysis on the complete data set. The elliptic Fourier descriptors (EFDs) representing all the specimens were then analysed with a principal component analysis (PCA). We chose to retain the first 12 PCs amounting to over 99 % variation. The resulting ordinated matrix was used for further analyses and as a morphospace.

We measured the diversity of each group by calculating the size they occupied in the morphospace. As a measure for size, we chose the sum of variance of each group across all dimensions, after a first investigation of the data set showed this measure to capture the size changes most effectively of all possible metrics (Guillerme et al 2020). We bootstrapped the data (n = 1,000) before comparing the resulting distributions for the metrics for adults and immatures using Welch's two-sample t-test. We also computed the relative position of the groups in relation to each other to estimate shared morphology. We calculated the Euclidean distance vectors between group centroids using the 50 % quantiles for each group (Guillerme et al 2020). Smaller distances equal more similar morphology. The code used for the analysis is provided in file S3.

Results

Shape analysis

The outline analysis of the data set resulted in 12 principal components (PCs) describing more than 99 % of variation on the body outline. PC1 explained 81.4 %, PC2 6.1 %, PC3 3.5 %, PC4 2.4 %, PC5 1.5 %, PC6 1.1 %, PC7 0.8 %, PC8 0.6 %, PC9 0.5 %, PC10 0.3 %, PC11 0.3 %, and PC12 0.2 % of variation of the body outline in the entire data set (differences due to rounding; for the graphical component loadings, see file S4). We describe the first three PCs in more detail below, as they amount to over 90 % of variation and will therefore be used for construction of morphospaces for graphical interpretation.

PC1 is dominated by the width of the body. Negative values indicate slim elongated bodies, positive values indicate wide, oval to circular bodies. The mean shape (as for all other PCs) describes an elliptic body shape that tapers more anterior than posterior (fig. 2).

PC2 is dominated by the position of the widest point of the body with an opposed straightened body end. Negative values indicate wider posterior ends and slimmer straightened anterior ends, positive values indicate slimmer straightened posterior ends and wider anterior ends (fig. 2).

PC3 is dominated by the position of the widest point of the body with an opposed pointed body end. Negative values indicate wider anterior ends and slimmer pointed

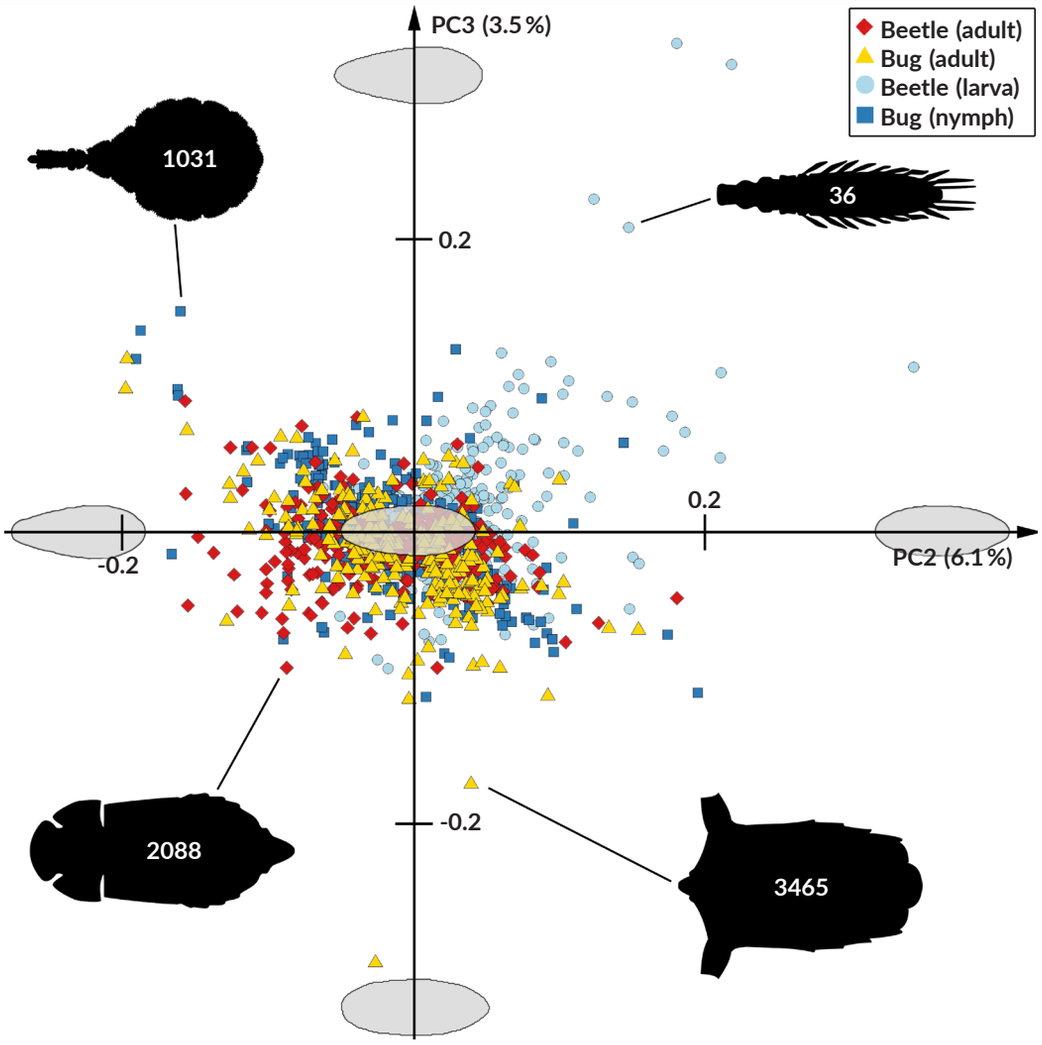

Fig. 3. Morphospace of PCA of the elliptic Fourier analysis on the body outlines of adult and larval beetles and adults and nymphs of true bugs. PC2 and PC3 plotted against each other. Grey shapes demonstrate mean and +/- 1 sd shape for every axis. Example outlines provided in black, with their respective identifiers for this study (see file S1).

anterior ends, positive values indicate slimmer pointed posterior ends and wider anterior ends (fig. 3).

Morphospace comparison of adults vs. immatures

The part of the morphospace represented by PC1 and PC2 showed a large overlap of the groups with the largest amount of variation along PC1 (fig. 2). The group of beetle larvae hereby showed the most distinct clustering, with a larger spread along the top side of the morphospace where rarely any other representatives plot, as well as a high density on the left of the morphospace. This pattern indicates a dominance of slim body morphologies with broader anterior ends among beetle larvae. Beetle larvae are more sparsely represented on the bottom and right side of the morphospace, where the adult beetles plot. The adult beetles are also more strongly represented in the centre and right side of the morphospace than the immature beetles, indicating their wider bodies and more tapering anterior ends. Between adult and immature true bugs, differences are not as pronounced. Both groups mostly plot in the centre, bottom, and right of the morphospace. However, immatures of true bugs plot slightly more towards the top of the morphospace, while adult true bugs plot more to the left. Generally, the position of both groups indicates a wider body morphology with broader posterior ends.

The part of the morphospace represented by PC2 and PC3 showed again a large overlap of all groups (fig. 3). Beetle larvae again showed the least overlap with other groups, plotting into the upper right quadrant of the morphospace. This position indicates individuals with slender necks and oval-shaped bodies. Adult beetles plot around the center and slightly towards the left of the morphospace, indicating smaller heads in relation to the rest of their bodies. The immatures of true bugs also plot around the center of the morphospace though slightly

Table 1. Overview of observed median values and Bonferroni corrected *p*-values of the pairwise two-sample t-tests for the sum of variance.

Subsets	Obs. median sum of variance
Beetle (larva)	0.066
True bug (nymph)	0.042
Beetle (adult)	0.034
True bug (adult)	0.045
Beetle (all)	0.062
True bug (all)	0.045
Comparison	***p*-value sum of variance**
Beetle (larva): beetle (adult)	<0.0001
True bug (nymph): true bug (adult)	<0.0001

extending towards the top, indicating generally oval bodies with slightly tapering anterior ends. Adults of true bugs mostly cover the same areas in the morphospace as their immatures, but extend more towards the bottom, indicating tapering posterior ends instead.

Size occupation and position of groups

Quantification of the results was achieved by measuring different metrics for the ordinated data set. The diversity of morphology was quantified by measuring the sum of variances of each group in the multidimensional morphospace. Significance testing showed that both in beetles and true bugs immatures and adults were significantly differing from each other in size (p-value < 0.001, Welch's two-sample t-test; table 1). Larvae of beetles occupied a larger area in the morphospace, compared to adult beetles. Nymphs of true bugs occupied a smaller area in the morphospace than adult true bugs (fig. 4A). The difference in size hereby was larger in beetles than it was in true bugs (fig. 4B).

Measuring the relative position of the groups showed that while the three other groups were plotting closer to each other, indicating more similar morphologies, beetle larvae plotted furthest away from all three. This position resulted in a smaller overlap of larval and adult beetles compared to nymphs and adults of true bugs. Consequentially, the distance between immature and adult beetles was larger than between immature and adult true bugs in the morphospace (fig. 4).

Discussion

Limitations of the approach

Due to the scarcity of graphic representations of immatures in the literature for both groups (Coleoptera, Heteroptera) (e.g., Danks and Smith 2009), we had to deviate from using conspecific immatures for each adult in our analysis. Instead, in cases where no direct counterpart was found for an immature specimen, we used an adult representative of a closely related species (in most cases representatives of the same 'family', although ranks in general are an arbitrary construct). Excluding all immature specimens without a direct counterpart in the adult sample would have significantly decreased the sample sizes of the groups, not allowing for a quantitative comparison anymore.

The final sample size is quite large, and the covered phylogenetic variation is rather broad. Yet, considering the large number of species present in both Coleoptera and Heteroptera, the overall number of 1,000 specimens appears still low. Therefore, the here shown morphospace only captures a part of the morphological diversity present in both groups. A larger data set should consequentially give a more detailed picture of the morphological diversity for the two groups. Still, due to the rather broad sampling including individuals from all major lineages of the groups, it seems unlikely that large parts of existing morphology are completely unrepresented.

Due to the approach selected here, we are also neglecting intra-specific variation. Since we are choosing one individual to represent the larval phase of a species, morphological variation within the larval phase is not captured in this analysis (e.g., in some ingroups of Neuroptera; Hoffman and Brushwein 1992). Similarly, sexual variation in the adult phase is also not captured. However, due to the overall sample size and the goals of this study to compare morphological change during development in two different groups, these effects should not bias the interpretation of results.

The outlines were created by several people potentially leading to a certain 'observer bias'. Due to the nature of the elliptic Fourier transformation, smaller individual variation is not expected to have a strong effect. Similar outlines of entire bodies have been used in other instances successfully (Baranov et al 2020, Haug et al 2021a, 2021b). Insect morphometry also has been shown to be reproducible in the past (Csösz et al 2020).

Morphological diversity: beetle adults vs. beetle immatures

As apparent in the morphospaces, beetle larvae differ significantly in their morphology from their corresponding adults (figs. 2, 3, table 1). There are large areas of the morphospace in which larvae plot, but no adults. This demonstrates that there are larval morphologies that differ strongly from their adults. Furthermore, the wide spread of the larvae indicates a larger morphological diversity compared to their adult counterparts. This larger morphological diversity could be a first indicator for a larger ecological diversity in the larvae compared to the adults. It has been generally attributed that adult and larval beetles differ in their ecology (Wiegmann et al 2009, Beutel et al 2011). They are therefore able to evolve different ecological specialisations independently from each other, at least to a certain degree (Scholtz 2005). The ecology of adult beetles is often constrained by the fact that most of them can fly, which demands certain morphological features. This condition potentially limits the degree to which the adult beetle morphology can become derived. Larvae do not have this type of restriction, allowing them to evolve morphological and ecological specialisations which differ from their adults. Consequentially, the body shapes of the larvae, which plot outside of the area occupied by the adults, are

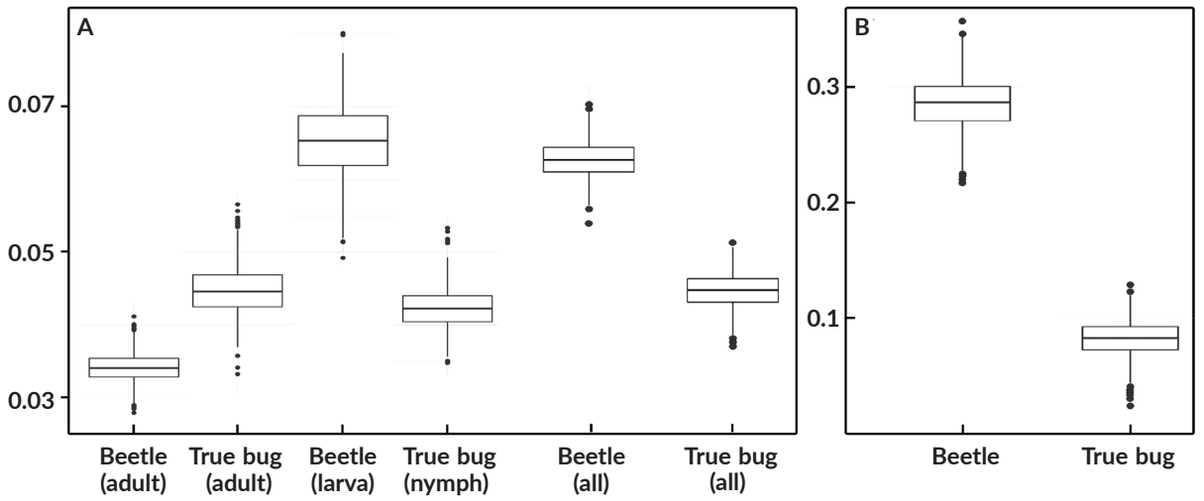

Fig. 4. Box plots of the disparity metrics measuring the morphological diversity, for each group across the first twelve principal components explaining over 99% of variation. A, box plots showing values for sum of variance of all four analysed groups, as well as adults and immatures combined for beetles and true bugs respectively; B, box plots showing Euclidean distances measured of the bootstrapped data set, between adult and immature beetles and adult and immature true bugs respectively.

characterised by rather elongated body shapes and quite prominent protrusions arising from the trunk. These larval specializations could therefore create a larger ecological diversity of the larvae. Of course, the adults themselves can express ecological diversification in aerial lifestyles that the larvae cannot. Further research into the differences between larvae and adults is needed.

Morphological diversity: true bug adults vs. true bug immatures

In true bugs, we only see an increase in the morphological diversity, but no shift. The morphological diversity of adults is significantly larger than that of nymphs (figs. 2, 3, table 1). However, the represented morphologies are more similar to each other than they are in beetles (fig. 4B). There are indeed few individual immatures that are more circular in outline than all of the adults and plot in a region of the morphospace in which no adult true bugs plot (bottom right of the morphospace; fig. 2). There are also few adults that have strongly expressed 'shoulders'; these specimens plot in a region of the plot in which no immature plots (bottom center of the morphospace; fig. 3). Still, the areas occupied by adult and immature true bugs largely overlap, indicating rather little differentiation in morphology between the two. This overlap could be a result of a similar ecology throughout their life cycle (e.g., Grevstad and Klepetka 1992, Ferran and Dixon 1993).

Differences in the differences

The comparison of the changes of the two groups, Coleoptera and Heteroptera, is congruent with the initial expectation: there is a significant change, quantitatively recognisable, of morphology in beetles, while this change is visibly quantifiably smaller in true bugs (fig. 4). Consequentially, beetles cover more morphological diversity during their life cycle than true bugs (fig. 4A). This pattern is to be expected for more representatives of Holometabola and non-holometabolans.

Structure of diversity and consequences for assessing diversity

Common diversity assessments often rely on aspects of species richness (Turak et al 2017a). Although some assessments, such as the Shannon Index, put more weight on evenness, such approaches factually strongly rely on counting species. The basic assumption behind such approaches is that each species is characterised by its own ecological niche, and therefore counting species provides a proxy for evaluating the diversity of ecological roles, or better of ecosystem functions (Nakazawa 2015, Turak et al 2017a).

However, we have shown here that the morphological diversity can differ from species to species significantly. Using species-number-based metrics for assessing diversity can therefore result in imprecise measures of diversity, as they fail to grasp diversity expressed during the life cycle of an organism. Furthermore, the approach shows that immature stages can play an important role in assessing biodiversity, as to be expected based on the knowledge of niche differentiation between adults and larvae in holometabolans (e.g., Klecka and Boukal 2012, and references therein). Common diversity assessments that operate with population and species assessments are not sensitive to this aspect.

Morphological diversity has the potential to provide a partially independent view onto diversity. It is a more quantitative approach compared to describing ecological functions of species in character matrices (Haug et al 2024), but not yet too complicated, meaning it could be employed in larger-scaled studies. The proxy we used here, body outline, is of course only one among many imaginable alternatives. The mouthpart shape (Đurđević et al 2016), for example, is expected to yield compa-

rable results to the body outline: It appears strikingly different between beetles and true bugs, but also shows little difference between immature and adult true bugs, while immature and adult beetles are expected to differ strongly. Our results possibly also point to a correlation between the body shape of the beetle larvae and their mouthparts: as the head is oriented more forward in beetle larvae than in many beetle adults, the anterior ends of the larvae may appear more pointed. With this, the body shape difference between adult and larval beetles might be correlated with differences in feeding strategies, hence ecology.

Our rather limited knowledge of immatures is also striking. As pointed out, the rather low number of known larvae in comparison to adults (Haug and Haug 2019, Zippel et al 2022) is disturbing, given the fact that many beetle larvae play important ecological roles and spend large parts of their lifetime in their larval forms while the adults live only for a short time (e.g., Kodada et al 2005, p. 472, Heijari et al 2008, Scholtz and Grebennikov 2016, p. 472). As the ecology of larvae differs often drastically from that of the adults, having a limited knowledge of larvae also means having a limited knowledge of their ecological impact.

Morphological diversity assessments show potential to reveal aspects of diversity not explorable by taxonomy-oriented approaches (Haug et al 2020, Haug et al 2021a, 2021b). It is planned to expand the here presented data, especially also to fossil representatives for facilitating comparisons through time.

References

Ali M, Ahmed K, Ali S, Raza G, Hussain I, Nafees MA, Anjum SI, 2018. An annotated checklist of Coccinellidae with four new records from Pakistan (Coleoptera, Coccinellidae). *ZooKeys* 803, 93-120. DOI: 10.3897/zookeys.803.22543

Avise JC, Liu JX, 2011. On the temporal inconsistencies of Linnean taxonomic ranks. *Biological Journal of the Linnean Society* 102(4), 707-714. DOI: 10.1111/j.1095-8312.2011.01624.x

Balke M, 2005. 7.6. Dytiscidae Leach, 1915. In: *Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), Teilband/ Part 38 Volume 1*: 90-116 (RG Beutel, RAB Leschen, Eds.) Walter de Gruyter, Berlin.

Baranov VA, Wang Y, Gašparič R, Wedmann S, Haug JT, 2020. Eco-morphological diversity of larvae of soldier flies and their closest relatives in deep time. *PeerJ* 8, e10356. DOI: 10.7717/peerj.10356

Bertrand Y, Pleijel F, Rouse GW, 2006. Taxonomic surrogacy in biodiversity assessments, and the meaning of Linnaean ranks. *Systematics and Biodiversity* 4(2), 149-159. DOI: 10.1017/S1477200005001908

Beutel RG, Friedrich F, Hörnschemeyer T, Pohl H, Hünefeld F, Beckmann F, Meier R, Misof B, Whiting MF, Vilhelmsen L, 2011. Morphological and molecular evidence converge upon a robust phylogeny of the megadiverse Holometabola. *Cladistics* 27(4), 341-355.

Beutel RG, Friedrich F, Economo EP, 2022. Patterns of morphological simplification and innovation in the megadiverse Holometabola (Insecta). *Cladistics* 38(2), 227-245.

Birk S, Bonne W, Borja A, Brucet S, Courrat A, Poikane S, Solimini A, van de Bund W, Zampoukas N, Hering D, 2012. Three hundred ways to assess Europe's surface waters: an almost complete overview of biological methods to implement the Water Framework Directive. *Ecological Indicators* 18, 31-41. DOI: 10.1016/j.ecolind.2011.10.009

Bonhomme V, Picq S, Gaucherel C, Claude J, 2014. Momocs: Outline Analysis - Using R. *Journal of Statistical Software* 56(13), 1-24. DOI: 10.18637/jss.v056.i13

Bouchard P, 2014. *The Book of Beetles: A Life-Size Guide to Six Hundred of Nature's Gems*. University of Chicago Press, Chicago.

Braig F, Haug C, Haug JT, 2024. Morphological diversity in true and false crabs reveals the plesiomorphy of the megalopa phase. *Scientific Reports* 14, 8682. DOI: 10.1038/s41598-024-58780-7

Briggs JC, 2017 Emergence of a sixth mass extinction? *Biological Journal of the Linnean Society* 122, 243-248. DOI: 10.1093/biolinnean/blx063

Ceballos G, Ehrlich PR, Barnosky A D, García A Pringle RM, Palmer TM, 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances* 1, e1400253. DOI: 10.1126/sciadv.1400253

Costa C, Ide S, Teixeira ÉP, 1995. Larvae of neotropical Coleoptera. XX: *Glyptolopus quadricostatus* Heinze (Cerylonidae, Ceryloninae). *Revista Brasileira de Entomologia* 39, 771-777.

Cowie RH, Bouchet P, Fontaine B, 2022. The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews* 97, 640-663. DOI: 10.1111/brv.12816

Csősz S, Seifert B, Mikó I, Boudinot BE, Borowiec ML, Fisher BL, Prebus M, Puniamoorthy J, Rakotonirina J-C, Rasoamanana N, Schultz R, Trietsch C, Ulmer JM, Elek Z, 2020. Insect morphometry is reproducible under average investigation standards. *Ecology and Evolution* 11, 547-559. DOI: 10.1002/ece3.7075

Daily GC, Matson PA, 2008. Ecosystem services: From theory to implementation. *Proceedings of the National Academy of Sciences USA* 105, 9455-9456. DOI: 10.1073/pnas.0804960105

Danks HV, Smith ABT, 2009. Insect Biodiversity in the Nearctic region. In: *Insect Biodiversity: Science and Society:* 35-46 (RG Foottit, PH Adler, Eds.) Blackwell Publishing, Oxford.

Dujardin JP, Kaba D, Solano P, Dupraz M, McCoy KD, Jaramillo-O N, 2014. Outline-based morphometrics, an overlooked method in arthropod studies? *Infection, Genetics and Evolution* 28, 704-714. DOI: 10.1016/j.meegid.2014.07.035

Đurđević A, Milošević D, Žiki V, 2016. The shape of mandibles in the Chironomidae family (Insecta: Diptera) as a predictor of feeding type. *12th Symposium on the Flora of Southeastern Serbia and Neighboring Regions:* 16-19 June, Kopaonik, Serbia.

Eger Jr JE, Ames LM, Suiter DR, Jenkins TM, Rider DA, Halbert SE, 2010. Occurrence of the Old World bug *Megacopta cribraria* (Fabricius) (Heteroptera: Plataspidae) in Georgia: a serious home invader and potential legume pest. *Insecta Mundi* 0121, 1-11.

Ereshefsky M, 2002. Linnaean ranks: Vestiges of a bygone era. *Philosophy of Science* 69(S3), 305-315. DOI: 10.1086/341854

Evans AV, Bellamy CL, 2000. *An Inordinate Fondness for Beetles*. University of California Press, Berkeley.

Faucheux MJ, 2014. Antennal sensilla of the primary larva of the false firefly beetle *Drilus mauritanicus* Lucas, 1849 (Coleoptera, Elateridae, Agrypninae, Drilini). *Bulletin de l'Institut Scientifique Rabat* 36, 57-64.

Ferran A, Dixon AFG, 1993. Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *European Journal of Entomology* 90(4), 383-402.

Friedrich F, Beutel RG, 2010. Goodbye Halteria? The thoracic morphology of Endopterygota (Insecta) and its phylogenetic implications. *Cladistics* 26(6), 579-612.

Grevstad FS, Klepetka BW, 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* 92(3), 399-404.

Griffiths G, 1976. The future of Linnaean nomenclature. *Systematics of Zoology* 25, 168-173. DOI: 10.2307/2412743

Guillerme T, 2018. dispRity: a modular R package for measuring disparity. *Methods in Ecology and Evolution* 9, 1755-1763. DOI: 10.1111/2041-210X.13022

Guillerme T, Puttick MN, Marcy AE, Weisbecker V, 2020. Shifting spaces: Which disparity or dissimilarity measurement best summarize occupancy in multidimensional spaces? *Ecology and Evolution* 10, 7261-7275. DOI: 10.1002/ece3.6452

Haug JT, 2020. Why the term "larva" is ambiguous, or what makes a larva? *Acta Zoologica* 101, 167-188. DOI: 10.1111/azo.12283

Haug JT, Baranov V, Braig F, Haug C, 2024. Morpho-ecospaces, or how to measure biodiversity in a different way. *Acta Zoologica* 105, 496-513. DOI: 10.1111/azo.12486

Haug GT, Baranov V, Wizen G, Pazinato PG, Müller P, Haug C, Haug JT, 2021a. The morphological diversity of long-necked lacewing larvae (Neuroptera: Myrmeleontiformia). *Bulletin of Geosciences* 96, 431-457. DOI: 10.3140/bull.geosci.1807

Haug JT, Haug C, 2019. Beetle larvae with unusually large terminal ends and a fossil that beats them all (Scraptiidae, Coleoptera). *PeerJ* 7, e7871. DOI: https://doi.org/10.7717/peerj.7871

Haug JT, Haug C, Garwood R, 2016. Evolution of insect wings and development – new details from Palaeozoic nymphs. *Biological Reviews* 91, 53-69. DOI: 10.1111/brv.12159

Haug GT, Haug C, Haug JT, 2021b. The morphological diversity of spoon-winged lacewing larvae and the first possible fossils from 99 million-year-old Kachin amber, Myanmar. *Palaeodiversity* 14, 133-152. DOI: 10.18476/pale.v14.a6

Haug GT, Haug C, Pazinato PG, Braig F, Perrichot V, Gröhn C, Müller P, Haug JT, 2020. The decline of silky lacewings and morphological diversity of long-nosed antlion larvae through time. *Palaeontologia*

Electronica 23, a39. DOI: 10.26879/1029
Haug JT, Müller P, Haug C, 2021c. Fossil dragonfly-type larva with lateral abdominal protrusions and implications on the early evolution of Pterygota. *IScience* 24, 103162. DOI: 10.1016/j.isci.2021.103162
Heijari J, Nerg AM, Kainulainen P, Noldt U, Levula T, Raitio H, Holopainen JK, 2008. Effect of long-term forest fertilization on Scots pine xylem quality and wood borer performance. *Journal of Chemical Ecology* 34, 26-31. DOI: 10.1007/s10886-007-9395-x
Hennig W, 1969. *Die Stammesgeschichte der Insekten*. Waldemar Kramer.
Henry TJ, 2017. Biodiversity of Heteroptera. In: *Insect Biodiversity: Science and Society, 2nd ed*: 279-335 (RG Foottit, PH Adler, Eds). Wiley: Hoboken, New York.
Hoffman KM, Brushwein JR, 1992. Descriptions of the larvae and pupae of some North American Mantispinae (Neuroptera: Mantispidae) and development of a system of larval chaetotaxy for Neuroptera. *Transactions of the American Entomological Society* 118(2), 159-196.
Hopkins MJ, Gerber S, 2017. Morphological disparity. In: *Evolutionary Developmental Biology:* 1-12 (L Nuño de la Rosa, GB Müller, Ed). Springer International Publishing, New York. DOI: 10.1007/978-3-319-33038-9_132-1
Klecka J, Boukal DS, 2012. Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. *Plos One* 7, e37741. DOI: 10.1371/journal.pone.0037741
Kodada J, Jäch M, 2005. 18.2. Elmidae Curtis, 1830. In: *Handbook of Zoology. Volume IV: Arthropoda: Insecta. Coleoptera, Beetles, Morphology and Systematics (Archeostemata, Adephaga; Myxophaga, Polyphaga partim), Part 38. Volume 1*: 471-496 (RG Beutel, RAB Leschen, Eds.). Walter de Gruyter, Berlin.
Kuhl FP, Giardina CR, 1982. Elliptic Fourier features of a closed contour. *Compututer Graphics and Image Processing* 18, 236-258. DOI: 10.1016/0146-664X(82)90034-X
Lawrence FJ, 1999. The Australian Ommatidae (Coleoptera:Archostemata): new species, larva and discussion of relationships. *Invertebrate Systematics* 13, 369. DOI: 10.1071/it99008
Lee KM, Zeegers T, Mutanen M, Pohjoismäki J, 2020. The thin red line between species–genomic differentiation of *Gymnosoma* Meigen, a taxonomically challenging genus of parasitoid flies (Diptera: Tachinidae). *Systematics of Entomology* 46(1), 96-110. DOI: 10.1111/syen.12450
Maurer BA, McGill BJ, 2011. Measurement of species diversity. In: *Biological Diversity: Frontiers in Measurement and Assessment*: 55-65 (AE Magurran, BJ McGill, Eds.). Oxford University Press, Oxford.
McGavin GC, 2002. *Smithsonian Handbooks: Insects*. DK Smithsonian Handbook, London.
McKenna DD, Shin S, Ahrens D, Balke M, Beza-Beza C, Clarke DJ, Donath A, Escalona HE, Friedrich F, Letsch H, Liu S, Maddison D, Mayer C, Misof B, Murin PJ, Niehuis O, Peters RS, Podsiadlowski L, Pohl H, Scully ED, Yan, EV, Zhou X, Ślipiński A, Beutel RG, 2019. The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences USA* 116, 24729-24737. DOI: 10.1073/pnas.1909655116
McKenna DD, Wild AL, Kanda K, Bellamy CL, Beutel RG, Caterino MS, Farnum CW, Hawks DC, Ivie MA, Jameson ML, Leschen RAB, Marvaldi AE, Mchugh JV, Newton AF, Robertson JA, Thayer MK, Whiting MF, Lawrence JF, Ślipinski A, Maddison DR, Farrell BD, 2015. The beetle tree of life reveals that Coleoptera survived end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution. *Systematic Entomology* 40, 835-880. DOI: 10.1111/syen.12132
Minelli A, 2000. The ranks and the names of species and higher taxa, or a dangerous inertia of the language of natural history. In: *Cultures and institutions of natural history, Essays in the history and philosophy of science:* 339-351 (MT Ghiselin, AE Leviton Eds.) California Academy of Sciences.
Müller M, Pander J, Geist J, 2013. Taxonomic sufficiency in freshwater ecosystems: Effects of taxonomic resolution, functional traits, and data transformation. *Freshwater Sciences* 32(3), 762-778. DOI: 10.1899/12-212.1
Nakazawa T, 2015. Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Population Ecology* 57, 347-354. DOI: 10.1007/s10144-014-0448-z
Paradis E, Schliep K, 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526-528. DOI: 10.1093/bioinformatics/bty633
Pinto JD, 2009. Chapter 128 – Hypermetamorphosis. In: *Encyclopedia of Insects, 2nd ed*: 484-486 (VH Resh, RT Cardé, Eds.). Academic Press. DOI: 10.1016/B978-0-12-374144-8.00137-5
de Queiroz K, Donoghue MJ, 1988. Phylogenetic systematics and the species problem. *Cladistics* 4, 317-338. DOI: 10.1111/j.1096-0031.1988.tb00518.x
R Core Team. 2021. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Schaefer CW, 1976. The reality of the higher taxonomic categories. *Zeitschrift für Systematische Zoologie und Evolutionsforschung* 14, 1-10.
Schaefer CW, Panizzi AR, 2000. *Heteroptera of Economic Importance*. CRC Press, Boca Raton.
Scholtz G, 2005. Homology and ontogeny: pattern and process in comparative developmental biology. *Theory in Biosciences* 124, 121-143.
Scholtz CH, Grebennikov VV, 2016. 15 Scarabaeoidea Latreille, 1802. In: *Handbook of Zoology. Volume IV: Arthropoda: Insecta. Coleoptera, Beetles, Morphology and Systematics (Archeostemata, Adephaga; Myxophaga, Polyphaga partim), Part 38. Volume 1, 2nd ed:* 443-525 (RG Beutel, RAB Leschen, Eds.). Walter de Gruyter, Berlin. DOI: 10.1016/j.biocon.2016.08.019
Shannon CA, 1948. Mathematical theory of communication. *Bell Systems Technological Journal* 27, 379-423.
Simpson EH, 1949. Measurement of Diversity. *Nature* 163, 688. DOI: 10.1038/163688a0
Ślipiński SA, 1991. A monograph of the world Cerylonidae (Coleoptera; Cucujoidea). Part 1: introduction and higher classification. *Annali del Museo Civico di Storia Naturale Giacomo Doria* 88, 1-273.
Ślipiński SA, Leschen RAB, Lawrence JF, 2011. Order Coleoptera Linnaeus, 1758. In: *Animal biodiversity: An out-line of higher-level classification and survey of taxonomic richness:* 203-208 (Z-Q Zhang, Ed). Zootaxa 3148. DOI: 10.11646/zootaxa.3148.1.39
Tilman D, Isbell F, Cowles JM, 2014. Biodiversity and ecosystem functioning. *Annual Reviews of Ecology, Evolution, and Systematics*, 45, 471-493. DOI: 10.1146/annurev-ecolsys-120213-091917
Turak E, Brazill-Boast J, Cooney T, Drielsma M, DelaCruz J, Dunkerley G, Fernandez M, Ferrier S, Gill M, Jones H, Koen T, Leys J, McGeoch M, Mihoub J-B, Scanes P, Schmeller D, Williams K, 2017a. Using the essential biodiversity variables framework to measure biodiversity change at national scale. *Biological Conservation* 213, 264-271. DOI: 10.1016/j.biocon.2016.08.019
Turak E, Regan E, Costello MJ, 2017b. Measuring and reporting biodiversity change. *Biological Conservation* 213, 249-251. DOI: 10.1016/j.biocon.2017.03.013
Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spine V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H, 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4, 1686. DOI: 10.21105/joss.01686
Wickham H, Bryan J, 2019. *readxl: Read Excel Files*. R package version 1.3.1. https://CRAN.R-project.org/package=readxl
Wiegmann BM, Kim JW, Trautwein MD, 2009. Holometabolous insects (Holometabola). *The Timetree of Life* 31, 260-263.
Zachos FE, 2011. Linnean ranks, temporal banding, and time-clipping: Why not slaughter the sacred cow? *Biological Journal of the Linnaean Society* 103, 732-734. DOI: 10.1111/j.1095-8312.2011.01711.x
Zippel A, Haug C, Hoffeins C, Hoffeins H-W, Haug JT, 2022. Expanding the record of larvae of false flower beetles with prominent terminal ends. *Rivista Italiana Paleontologia Stratigrafia* 128, 81-104. DOI: 10.54103/2039-4942/17084

Acknowledgements
We would like to thank Sofía I. Arce (LMU, Munich) for translation of the abstract into Spanish. We would also like to thank Yasmin Alieva, Alisa-Maria Bader, Annegret Bayer, Clara Berger, Alexander Eckerle, Júlia Feiner, Svenja Füchsle, Anna-Maria Grünziger, Alisa Gücker, Luisa Gutewort, Lukas Hartmann, Leonhard Hetzke, Sebastijan Jedrejcic, Marc Köhler, Alexander Kubryk, Julian Kurtenbach, Jenna Meßmer, Simon Oberhauser, Jiayi Qi, Alina Spemann, Theresa Stuffler, Julika Trüstedt, Marie Zilch, Tolga Zorlu, and further students from the Faculty of Biology of the LMU Munich for helping with generating data for this study. We thank J. Matthias Starck, LMU Munich, for long-standing support, and all people dedicating their free time to programming free software used for this study.

Author contributions
Conceptualization, **F Braig**, **C Haug** and **JT Haug**; methodology, **F Braig**, **C Haug** and **JT Haug**; formal analysis, **F Braig**, and **JT Haug**; investigation, **F Braig**, **E Toman**, **Z Sipos**, **T Wabnitz**, **J Joosten**, **F Haxel**, **J Mack**, **T Haanraads**, **L Ullmann**, **S Hagn**, **C Voith**, **K Pröller**, **F Meißner**, **B Berninger**, **C Stahlecker**, **SL Kliese**, **J Preschl**, **L Neuburger**, **L Böckeler**, **S Albach**, **M Tellioglu** and **JT Haug**; resources, **F Braig**, **C Haug**, **E Toman**, **Z Sipos**, **T Wabnitz**, **J Joosten**, **F Haxel**, **J Mack**, **T Haanraads**, **L Ullmann**, **S Hagn**, **C Voith**, **K Pröller**, **F Meißner**, **B Berninger**, **C Stahlecker**, **SL Kliese**, **J Preschl**, **L Neuburger**, **L Böckeler**, **S Albach**, **M Tellioglu** and **JT Haug**; writing-original draft preparation, **F Braig** and **JT Haug**; writing-review and editing, **C Haug**, **E Toman**, **Z Sipos**, **T Wabnitz**, **J Joosten**, **F Haxel**, **J Mack**, **T Haanraads**, **L Ullmann**, **S Hagn**, **C Voith**, **K Pröller**, **F Meißner**, **B Berninger**, **C Stahlecker**, **SL Kliese**, **J Preschl**, **L Neuburger**, **L Böckeler**, **S Albach**, **M Tellioglu** and **JT Haug**; visualisation, **F Braig**; funding acquisition, **C Haug** and **JT Haug**.

Supplementary Materials
The following are available online at https://zenodo.org/records/15211606. File S1. Information on the specimens included in the analyses; File S2. References for table in file S1; File S3. Code used for the statistical analysis; File S4. Graphical representation of the factor loadings of the principal component analysis; note that the anterior end of the bodies faces to the left.

Conflicts of interest
The authors declare no conflict of interest.

Funding
JT Haug is funded by the Volkswagen Foundation (Lichtenberg Professorship) and by the German Research Foundation (DFG HA 6300/3-3); **F Braig** received funding from Safeguarding biodiversity through interdisciplinary research on habitat restoration (SAFIRE) through University of Oulu and the Research Council of Finland PROFI8 funding.

Complete affiliations
F Braig, **C Haug**, **E Toman**, **Z Sipos**, **T Wabnitz**, **J Joosten**, **F Haxel**, **J Mack**, **T Haanraads**, **L Ullmann**, **S Hagn**, **C Voith**, **K Pröller**, **F Meißner**, **B Berninger**, **C Stahlecker**, **SL Kliese**, **J Preschl**, **L Neuburger**, **L Böckeler**, **S Albach**, **M Tellioglu**, **JT Haug**, Faculty of Biology, Biocenter, Ludwig-Maximilians-Universität München (LMU Munich), Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany.
F Braig, Ecology and Genetics Research Unit, University of Oulu, Pentti Kaiteran katu 1, Linnanmaa, Finland.
C Haug, **JT Haug**, GeoBio-Center of the LMU Munich, Richard-Wagner-Str. 10, 80333 Munich, Germany.
J Joosten, **L Neuburger**, Munich, Germany.
T Haanraads, Department of Medical Biochemistry and Microbiology, Uppsala University, Husargatan 3, Uppsala, Sweden.
SL Kliese, Faculty for Architecture and Planning, Technical University Vieanna (TU Vienna), Karlsplatz 13, 1040 Vienna, Austria.

Animal Biodiversity and Conservation es manté neutral respecte a les reclamacions jurisdiccionals sobre mapes publicats i afiliacions institucionals
Animal Biodiversity and Conservation se mantiene neutral con respecto a reclamaciones jurisdiccionales sobre mapas publicados y afiliaciones institucionales
Animal Biodiversity and Conservation remains neutral with regard to jurisdictional claims in published maps and institutional affiliations