

Article

The Relationship Between Category Richness and Morphological Diversity in Jewel Beetles

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Received: date; Accepted: date; Published: date

Abstract: Correlation between the category richness (CR) and morphological diversity (MD) of some communities at a local scale was found pendent, however, examination of a whole category using a large dataset are lacking. In this study, 1119 jewel species from around the world representing all existing subfamilies and 33.78% of Buprestidae genera were selected as a test group. A geometric morphometric analysis on the contour of homologous traits: pronotum and elytra was conducted to quantify morphological diversity. Correlations between MD and CR among subfamilies were found to be consistently positive with the exceptions of a pronotum genus-level test on the subfamily category. The correlation was also found to be higher at the genus-level than it on the species-level, in both pronotum and elytron measurements. Based on our analyses the hypothesis of positive correlations was expected in the genus-level test of jewel beetles but rejected in species-level test. The inconsistent correlation between morphological diversity and species richness revealed convergent morphological variation of pronotum under the similar functional diversity in Buprestidae. In addition, our test revealed variable correlation between MD and CR based on different groups and characters, which might be caused by morphological changes under coevolution with different ecological factors.

Keywords: Morphological diversity; species richness; jewel beetle; geometric morphometrics; elytron; pronotum

1. Introduction

Biodiversity plays a host of important roles in biosphere operations. Biodiversity is usually quantified via proxy indicators (e.g., morphological diversity, genes, species richness), and used to study changes in ecosystems. Use of different biodiversity indicators highlights the disparate nature of biodiversity investigations [1,2]. Among these, morphological diversity and species richness have often been used to explore patterns of biodiversity in different ecosystems [3,4]. Morphological diversity reflects biological feedback and ecosystem functionality [5]. Species richness reveals the number of species in a community or area and is one of the most widely used indicators of biodiversity. According to the information contained in both morphological diversity and species richness, analysis of the relationship between these two indicators has been tested widely, and has been applied to most animal groups, from unicellular organisms to mammals, as well as many plant groups [6-8]. Most studies revealed that morphological diversity was positively correlated with species richness [9-12]. However, this documented relationship has not always been consistent because of variation in the niche and status of an organism in ecosystem [13,14], which reminds us

that the relationship between these two indicators is not as simple as was initially thought. For instance, a biodiversity research of leaf-litter ants has suggested that morphological diversity decreased with latitude while the trend of species richness was opposite [15]. While most authors have compared the morphological diversity and species richness of a particular community at a local scale [16-22], few studies have focused on the comparison of these different facets simultaneously at a large cosmopolitan scale (but see Safi et al. 2011 and Lucie et al. 2018) [23,24]. Whether new data collection and data analysis approaches applied to a whole taxonomic category can also provide a positive insight into this correlation like it in the most specific community test is still unknown.

More than 14,000 described jewel beetles (Buprestidae) have been recorded [25]. Possession of the strong chitin exoskeleton and fairly complex life history improves the environmental adaptability of this community [25,26], making them one of the most successful beetle clades. Previous studies typically focused on aspects of the morphological comparison of mandibles, antenna, genitalia and hind wing [27-31]. The pronotum supports prothorax's muscle system and the locomotion of the prothoracic legs [32] whilst the elytron represents an autapomorphy of Coleoptera [33], which represents a major part of the body structure in dorsal view has typically been used as an index for body size, both of which contain evolutionary information [34]. The application of quantitative analysis methods in entomological research provides an opportunity for solving the problem that traditional taxonomy cannot accurately describe and distinguish such continuous traits [35-37]. Owing to the huge number and diverse array of morphological characters, buprestids have received comprehensive attention from researchers [33,38,39]. Their global distribution and complex habitat requirements make the Buprestidae an excellent group for biodiversity research. However, up to now, there has been no investigation focusing on the relationship between morphological diversity and species richness within Buprestidae based on a large dataset containing information on species from around the world, especially in which the morphological variation of the pronotum and elytron was involved.

In this study, the relationship between morphological diversity and species richness was explored based on a large dataset covering 1119 species of Buprestidae, including all 6 extant subfamilies and 175 genera (34% of extant genera), representing 7.5% of all known jewel beetles. Two major aspects of buprestid and beetle morphology were investigated in general. Geometric morphometrics, a useful approach to the quantitative analysis of morphological variation, was employed in this study to estimate morphological diversity and variations of the contour of pronotum and elytron; then the genus richness and species richness of all test subfamilies based on taxonomic factor were counted to explore the biodiversity of jewel beetles in different categories, and the correlation between morphological diversity and genus/species richness in different test categories was also explored.

2. Materials and Methods

2.1. Taxa Examined

This study analyzed 1119 species (1152 samples) including all six extant subfamilies (Polycestinae, Chrysochroinae, Buprestinae, Agrilinae, Agrilinae and Galbellinae) and 175 buprestid genera (approximately 33.78% of all described extant genera) around the world. Measurements collected from all species were based on published images [26] and the museum of the Institute of Zoology, Chinese Academy of Sciences. Standard dorsal views were selected for this study. Pronotum and elytron [40-42] from images that were not covered or blurry and with adequate resolution (the smallest one was 90 pixels) sufficient to facilitate accurate representation. All sample image-file names were assigned to taxonomic based on Suborder-Series-Superfamily-Family-Subfamily-Genus and species, so as to facilitate the subsequent morphological analysis (Table S1) [43].

2.2. Data Analysis

The objectivity of sample selection was taken into account in this experiment firstly to reflect the degree of difference in taxa diversity between test and worldwide groups. The worldwide

species/genus richness of each subfamily in Buprestidae was counted and the proportions of test/worldwide taxa richness under each subfamily in total test/worldwide group was also been obtained (Table S2, Table S3). All taxa diversities were converted by log10 to better display the test data discretely (Figure 1). Mann-Whitney U test was operated through SPSS Statistics (Version: 26) [44], to document the consistency of species/genus richness proportions between the worldwide dataset and test dataset.

Two curves were extracted from the left contours of pronotum and elytron to represent their external forms. Curve One was collected from the middle of pronotum anterior margin and ended up at the middle of pronotum posterior margin; Curve Two started from the front base of the left half elytron under the scutellum to the extreme of the left half part. Each curve was resampled into 25/50 equally spaced semi-landmarks respectively (Figure 2). The curves and semi-landmarks were digitized with TPS-DIG 2.05 [45]. Principal component analysis (PCA) and the geometric modelling of mathematical spaces formed by the PC axes were used to ordinate and interpret outline shape variation of the pronotum and elytron [46]. The shape-deformation patterns expressed by the first three principal components which accounted for a large observed shape variation were collected in this study. Each shape model was calculated at coordinate positions spaced at equal intervals along each PC axis from the minimum to maximum values of projected shapes (Figure 3).

Exploration of correlations between morphological diversity and species richness was achieved through Spearman correlation coefficient in SPSS Statistics (Version: 26) [44]. Morphological diversity was quantified as the total Procrustes variance in MORPHO J 1.06a (Table S3) [47,48], which measures the dispersion of all observations around the mean shape of the respective taxa [37,48]; the category richness value was obtained by counting the number of genera and species in different test groups (Figure 2).

3. Results

3.1. Test of Sampling Ratio in Genus and Species Category

Known global species richness values for the categories (6 subfamilies include 14,724 species and 518 genera), were counted to test differences between the sampling proportions of samples in test genus/species category and those in worldwide Buprestidae (Table 1). Four best-fit lines were used through ordinary least squares (OLS) and regression analysis showed that the relationship of sampling situation for both the test group and the actual group (equivalent to the distribution of worldwide Buprestidae) (Figure 1), the taxa diversity was converted by log10 to better display the test data discretely. Four curves which represented the collection of test genus ($y = 0.57 + 0.88 * x - 0.16 * x^2$; Quadratic $R^2 = 0.909$), test species ($y = 1.04 + 0.96 * x - 0.19 * x^2$; Quadratic $R^2 = 0.911$), worldwide genus ($y = 0.87 + 1.35 * x - 0.24 * x^2$; Quadratic $R^2 = 0.933$) and worldwide species ($y = 2.27 + 0.98 * x - 0.18 * x^2$; Quadratic $R^2 = 0.793$) fitted well with the test data. Based on a Mann-Whitney U test no significant difference was found between the global and sampling dataset not only in the genus-level test ($P = 0.873$, which well above the standard of 0.05) but also in the species-level test ($P = 0.749$, which well above the standard of 0.05).

Table 1. Sampling ratio of genus/species of test and worldwide dataset.

Test groups	Sampling ratio of test genus	Sampling ratio of test species	Sampling ratio of worldwide genus	Sampling ratio of worldwide species
Polycestinae	0.13714	0.11439	0.15830	0.08523
Chrysochroinae	0.20571	0.28865	0.21622	0.18623
Buprestinae	0.20571	0.24307	0.22008	0.22453
Agrilinae	0.41143	0.27971	0.39189	0.48873
Julodinae	0.03429	0.07328	0.01158	0.00958
Galbellinae	0.00571	0.00089	0.00193	0.00570

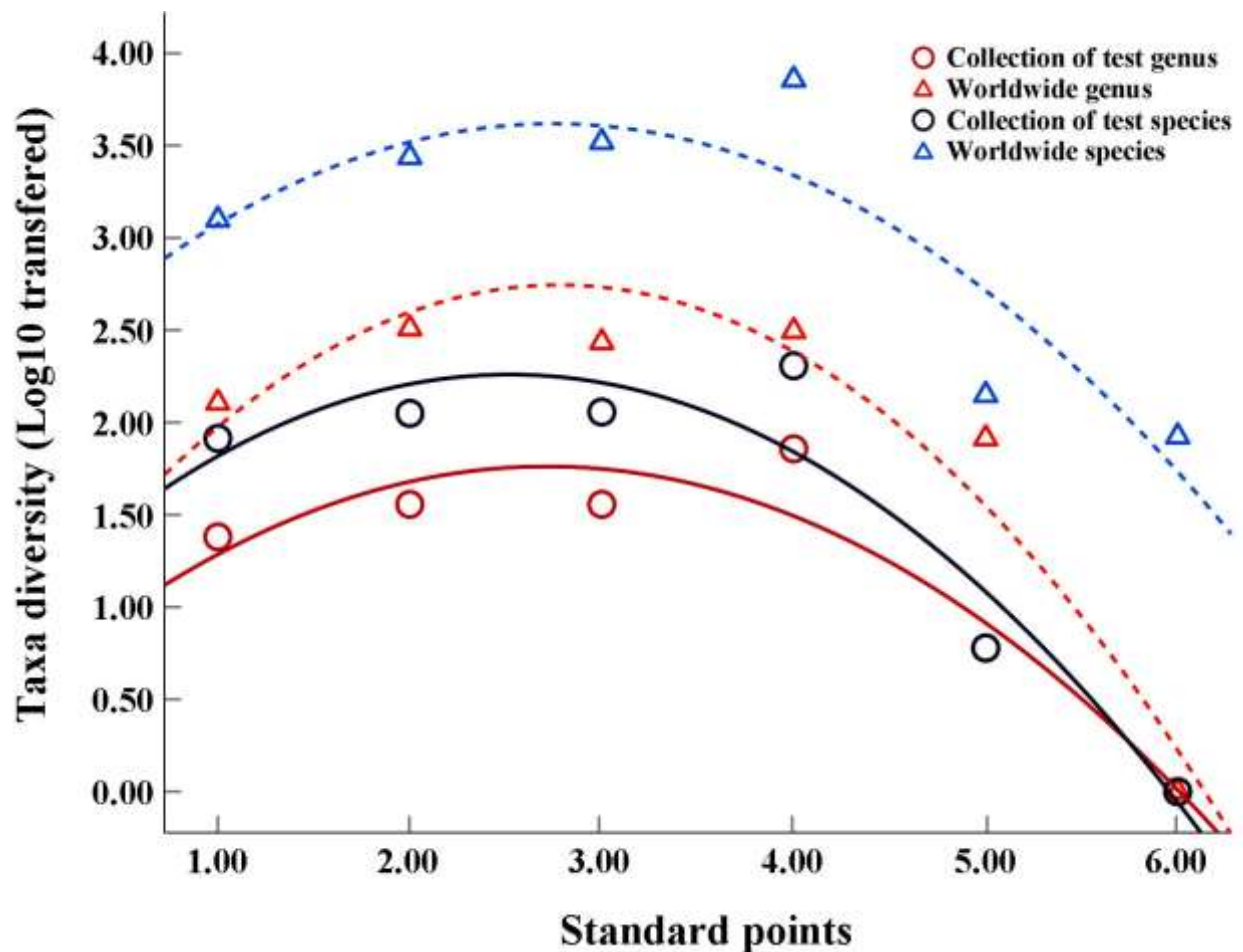


Figure 1. Distribution of taxa diversity in each test and worldwide groups. The taxa diversity was converted by \log_{10} .

3.2. Species/Genus Richness among Test Groups

Species/genus richness values from the 6 taxonomic groups are illustrated in Figure 2 (see also Table S2). In the family category, for our sample Agrilinae and Chrysochroinae both exhibited very high species richness (313/323) and genus richness (72/36) values. Buprestinae has the same genus richness as Chrysochroinae, yet its number of test species was nearly 1/5 smaller than the latter (272). The taxa richness of Polycestinae showed a downward trend: it got a lower test genus richness (24) and species richness (128), and this pattern was also found in the statistical work of Julodinae (the genus richness and species richness was 82 and 6, respectively). In addition, the Galbellinae was found to exhibit the lowest species richness value (1) with only one genus included in the test sample.

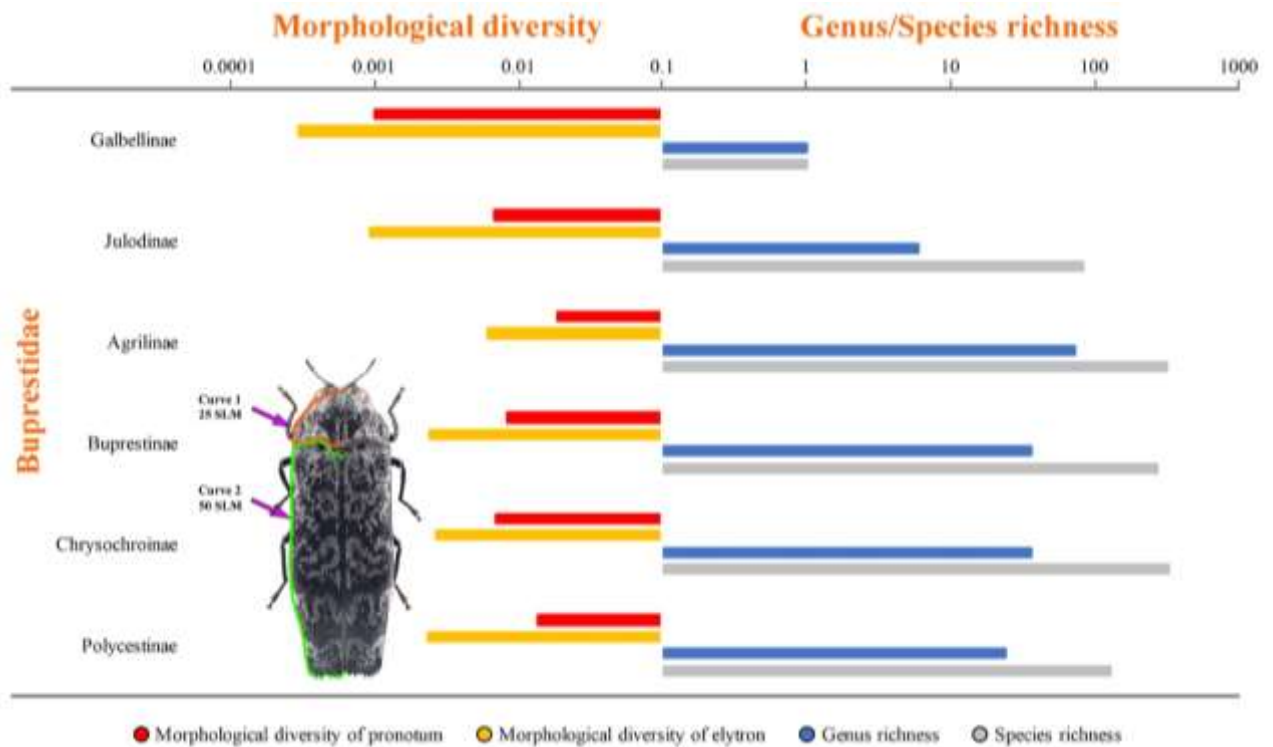


Figure 2. Species/genus richness and morphological diversity among groups. The curves on the pronotum and elytron of the beetles (*Coraebus spathatus*) demonstrated the morphological representation used in geometric morphometric analysis. Curve 1 (orange) was resampled in 25 semi-landmarks (SLM); Curve 2 (green) was resampled in 50 semi-landmarks (SLM).

3.3. Morphological Variation of the Pronotum and Elytron

The first three principal components (PCs) of the pronotum and elytron from 1119 species accounted for 86.255% and 90.4%, of observed shape variation respectively (Figure 3). Shape models were calculated at equally spaced intervals along these PC axes to document the deformation of test characters.

Along the positive direction of the first PC axis, the left contour of the pronotum became stretched longitudinally and diminished horizontally with the posterior angle shrinking inwardly horizontally and the anterior angle extending outwards, the entire pronotum becoming markedly more quadrate. Along the positive direction of the second PC axis, pronotum shape changed from an inverted trapezoidal to trapezoidal outline with the producing posterior angle, and retracting posterior margin, making it sharper; while the anterior angle diminished and became less distinct. Along the third PC axis, the entire half pronotum contour tended towards a triangle with the anterior angle diminishing and becoming less distinct and the posterior angle extending outward horizontally.

Along positive direction of its first PC axis, the left half contour of test elytron became larger and the posterior margin protrudes, the anterior margin stretched horizontally. The shrinking smaller scutellum causes the anterior margin to become shorter with the lateral margin, that protruded outward originally, contracting inward. Along the positive direction of the second elytron PC axis, the overall morphology of the elytron became narrow and long. This pattern was contrary to the previous one: the posterior border of elytron expanded laterally, while the anterior angle broadened outward. The expansion of the scutellum edge led to a more inward change trend of the anterior margin of elytron. Along the positive direction of third elytron PC axis, the smaller scutellum flattened the front margin and at the same time the posterior border of elytron contracted inward leading the overall morphology of elytron became to an inverted triangle.

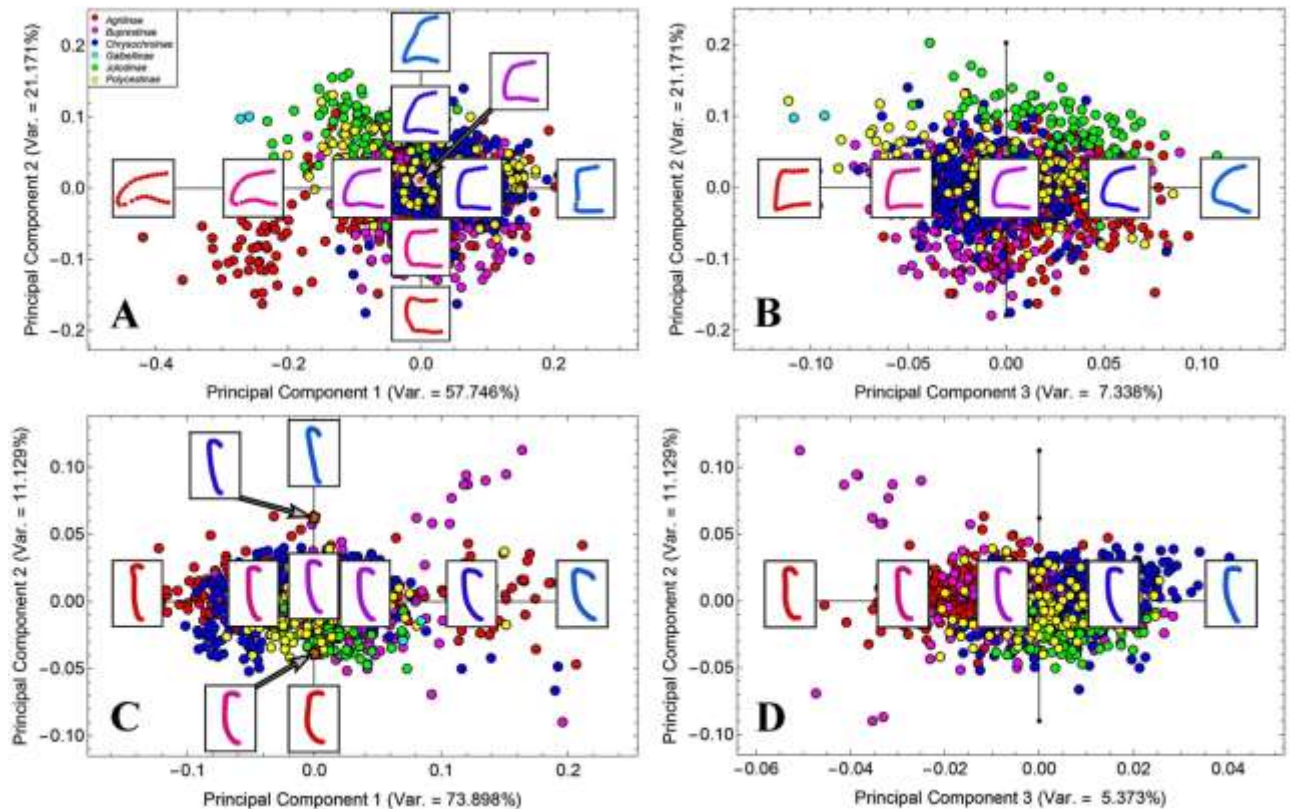


Figure 3. Morphological variation of the pronotum and elytron in Buprestidae. 86.255%/90.4% of observed shape variation was represented by first three PCs in pronotum and elytron test, respectively. **A:** Variations of PC1 and PC2 in pronotum test. **B:** Variations of PC2 and PC3 in pronotum test. **C:** Variations of PC1 and PC2 in elytron test. **D:** Variations of PC2 and PC3 in elytron test. Each shape model of variation was calculated at equally spaced intervals along PC axes with coordinates for individual shape model calculations indicated by marks and numbers in the two-dimensional PC shape spaces.

3.4. Morphological Diversity among Groups

The Agrilinae exhibited both the highest pronotum diversity (Procrustes variance, $r = 0.01868813$) and elytron diversity (0.00623315), with the highest genus richness and fairly high species richness (Figure 2, see also Table S2 and Table S3). Similar pronotum diversity and elytron diversity were found in the test of Buprestinae (0.00855479/0.0024758) and Chrysochroinae (0.00701155/0.00269789) which hold the same test genus richness. The Galbellinae, a small group for which only 1 test species were included in this study, was found to have the lowest morphological diversity (0.00103251/0.00030453). However, the relation between morphological diversity and species richness was not always consistent. Polycestinae was found to have a very high pronotum diversity (0.013702) with a comparatively small number of test species (128) and only 24 test genera, its elytron diversity (0.00236388) was also relatively high as it is in the test of Buprestinae. Similar to the test of Polycestinae, the Julodinae was found to have a high pronotum diversity while its genus and species richness were very low.

In addition, morphological diversity was also found to vary with the tested traits. The changing trends of characters and species richness values were not always highly associated: elytron diversity of the Polycestinae was relative low compared with Buprestinae and Chrysochroinae despite its very high pronotum diversity; the Julodinae was found to exhibit a high pronotum diversity, but a fairly low elytron diversity.

3.5. Relationship between Morphological Diversity and Species Richness

Application of the Spearman correlation coefficient to our test parameters revealed the correlation between test morphological diversity and species richness, and the variation in both groups and traits. Four best-fit lines used through ordinary least squares (OLS) regression analysis showed the relationship between parameters and are shown in Figure 4.

Three different types of relationships were revealed by the correlation test in this study. Firstly, the correlation between morphological diversity and species richness among test subfamilies was found to be always consistent ($P = 0.05/0/0.005$ in pronotum-genus/elytron-genus/elytron-species test, respectively), with one exception: the species-level test of pronotum ($P = 0.208$), the correlation test result of which was non-significant correlation. Secondly, the correlation of pronotum test was found weaker than it in elytron test: the coefficient value was 0.812 in pronotum genus test and became 0.986 in elytron genus test, it was 0.60 in pronotum species test while 0.943 in elytron species test. Thirdly, the degree of correlation between parameters was found to be closer in the higher taxonomic category (Spearman correlation coefficient $r = 0.986/0.812$ in genus-level test; $r = 0.943/0.6$ in species-level test).

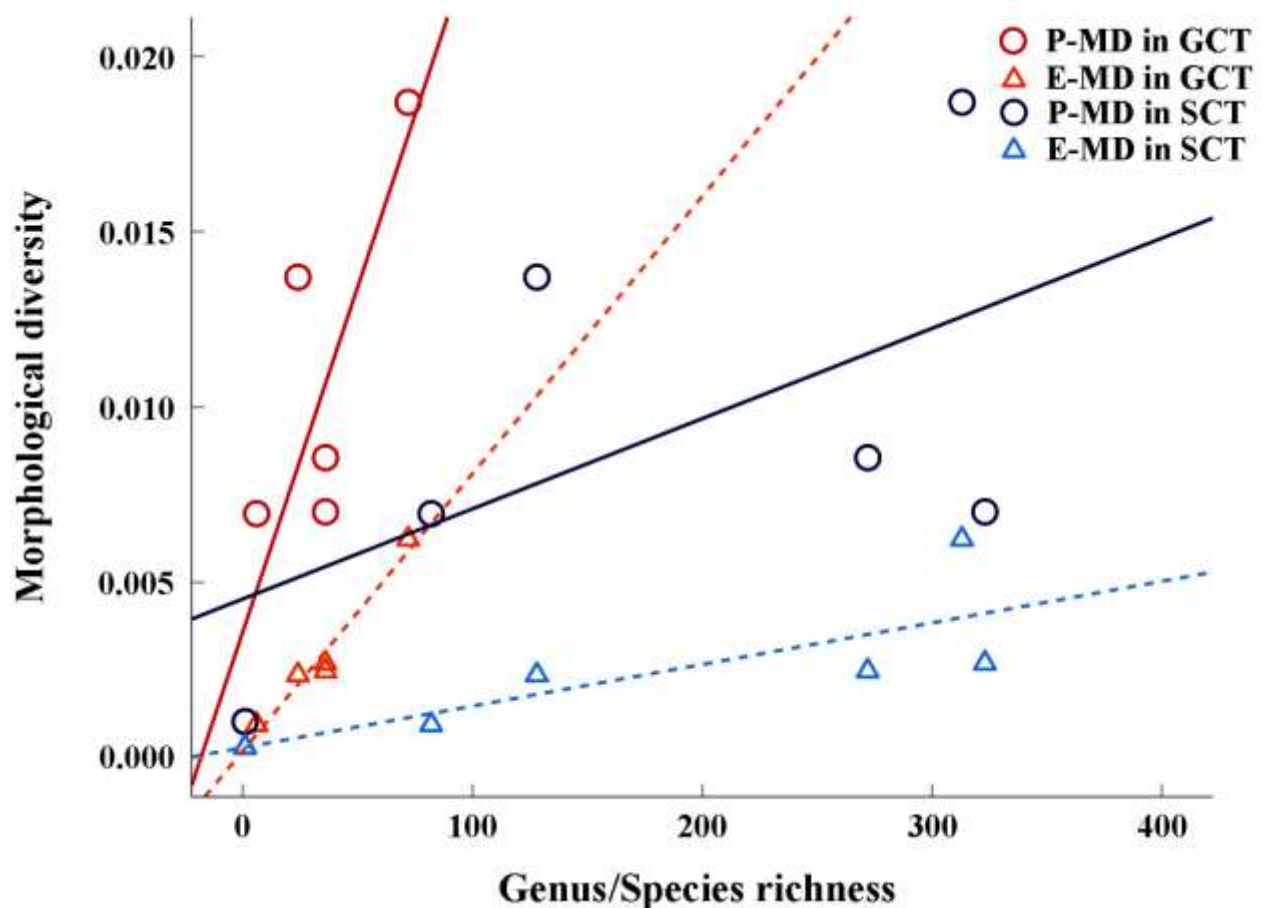


Figure 4. Relationships between morphological diversity of contour of pronotum/elytron and category richness. P-MD = morphological diversity of pronotum, E-MD = morphological diversity of elytron, GCT = genus category test, SCT = species category test.

4. Discussion

Different morphologies are associated with diverse functional aspects of niches [49,50] and both the evolution and development of taxa, and these also account for the variable morphological characteristics of jewel beetles [51-55]. In this study, complex and irregular relationships were found

among different groups in the subfamily categories along with their diverse habits and quite different coevolutionary modes. The Agrilinae which is widely distributed in the world, has a large species diversity, more than 3,000 species of *Agrilus* are recorded in this group alone [25,56,57]. Most adults and larvae feed on a particular species of host plant, in fact, within this group, there are some very pronounced coevolutionary trends apparent with entire species-groups utilizing only one genus of host plant [56]. The extensive distribution area and diverse feeding habits lead to a huge variation of members' niches in this group [58,59], which resulted in a high degree of deformation of their outer morphology, that is represented in the variation of test traits' contours in this study. A total of 84 species in Galbellinae have been recorded worldwide and this subfamily was found to have the lowest morphological diversity in this study. Most members of this group are relatively flat in shape, almost all of them have enlarged tibiae and are able to contract well under their bodies. A single genus in this subfamily and specialized characters determined that this group was relatively conservative [25,56], leading to its very low external morphological diversity. Julodinae are nearly cylindrical, tapering towards the posterior end. The results for this subfamily were that they have high pronotum diversity while its genus and species richness were very low. This result is perhaps caused by the wide distribution of the members in this community: many species are distributed from the southern Palaearctic and Oriental regions to the Cape region of South Africa. The largest two genera, *Julodis* and *Sternocera*, are recorded from the west part of Pakistan to Southeast Asia [56]. There are not many species of Polycestinae, only 82 genera and more than 1,000 species distributed worldwide (only 128/24 test species/genera in this study). However, we find that the test trait of this group has a high degree of morphological variation, which is inseparable with the biological characteristics of this group. Although there are few species in the world, the members of this group are widely distributed in seven major geographic regions and most species also follow the host-plant specialization of Buprestidae.

Biological diversity can be quantified in terms of species richness and morphological diversity [60], both of which are dependent on ecological variability and species interactions [61,62]. As a result of selection-based feedback due to the variability of ecological factors, new forms emerge as a result of biological evolution [63]. Since the pronotum is not restricted by flight machinery, its higher possibility of variation is influenced by the function of buprestid foreleg [64], as well as the buprestid feeding behavior and the movement mode of head due to the association of dorsal source cervical muscle and cervical sclerite muscle between the head and prothorax. Usually the adults feed on foliage of the larval host plant or of other plants and/or visit flowers to feed on pollen and nectar, except a unique feeding strategy employed by one species, *Xyroscelis crocata* [65] (Polycestinae: Xyroscelidini) in Australia which is reported to feed on the sap of the host plant [66]. The functional diversity of the pronotum decreases with the fixed feeding habit and the deflected and resting head on the prosternum, while the external morphology is highly convergent. In our study, morphological variation of the pronotum contour was found not to be a major factor affecting the buprestid species richness. This phenomenon can be explained by the inconsistent changing trend between parameters of some test groups as well: Chrysochroinae, Buprestinae and Polucestinae. On the other hand, we found the morphological diversity of the test pronotum part was correlated with the test groups' genus richness, this appearance was also found in the test of elytron: the correlation between morphological diversity and test genus richness was higher than that between species category. In addition, our sampling dataset in Buprestidae was found to exhibit a very high correlation of morphological diversity with both genus richness and species richness, but relative low pronotum-correlation. As the function of the elytra is to mainly protecting the beetles' abdomen, it is under more direct selection pressure from diverse environmental and ecological factors, presumably as a consequence of playing an important role the structuring of the muscle systems responsible for hind leg locomotion. As mentioned above, the morphology of pronotum converged because of the buprestid fairly specialized biology, and so its requirement for environmentally mediated shape adjustment is far less pronounced than the elytron.

5. Conclusions

We tested the diversity of different categories and traits from a large number of samples from around the world, and revealed some of the buprestid ecological characteristics. In this study, genus/species richness proportions between the worldwide dataset and test dataset was found consistent based on Mann-Whitney U test, this suggested our analysis represented the correlation between species/genus richness and morphological diversity relative objectively. Then we compared the genus/species richness in the context of morphological diversity in the pronotum and elytron of 1119 buprestid species quantitatively through geometric morphometrics and Spearman correlation coefficient. Results suggested that morphological diversity of test elytron's contour was consistent with test taxa diversity (also described as genus/species richness in this study), on the contrary, this situation of correlation in the pronotum species category test was refuted.

Nonetheless, there also remain some limitations in our results. Firstly, our experiment only tested a certain number of samples from each group by proportion, with almost one sample per species. Secondly, as our study only considered the contours of pronotum and elytron, the investigation of more test species and characters should improve the chances to get a better understanding of the relationship between morphological diversity and species richness in the future.

Supplementary Materials: Table S1: List of test samples, Table S2: Information of worldwide categories parameters, Table S3: Information of test parameters.

Author Contributions: MB designed the study. YT and HY collected the data. YT analyzed the data and wrote the manuscript. MB and XY revised the manuscript and provided funding. All of the authors contributed critically to the drafts and gave final approval for publication.

Funding: This research was supported by the National Natural Science Foundation of China (No. 31672345, 31961143002, 61872348), GDAS Special Project of Science and Technology Development (No. 2020GDASYL-20200102021, 2020GDASYL-20200301003), the Biological Resources Program, Chinese Academy of Sciences (KFJ-BRP-017-26).

Acknowledgments: We thank the Group of Morphology and Evolution of Beetles of IZCAS for providing the platform of this research. We extend our sincere appreciation to our colleague Prof. Dr. Norman MacLeod for his detailed comments and fruitful suggestions. We are also grateful to thank Prof. Rongfei Zhu for his helps in the use of statistical software.

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

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