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Global Ecology and Biogeography

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<https://doi.org/10.1111/geb.13043>

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Predictability of species diversity by family diversity across global terrestrial animal taxa

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Funding information

Jiangsu Science and Technology Department, Grant/Award Number: BK20181191; National Natural Science Foundation of China, Grant/Award Number: 31700363 and 41871186; National Key R&D Program of China, Grant/Award Number: 2018YFC05072

Editor: Anne Bjorkman

Abstract

Aim: Although biodiversity is in sharp decline around the globe, collecting precise information on changes in overall species richness remains extremely challenging. Efficient and reliable proxy methods are therefore needed, with the diversity of higher taxa representing one such potential proxy for species-level diversity. Nonetheless, the stability of using this measure across different regions and animal taxa at the global scale has never been investigated thoroughly.

Location: Global.

Time period: Up to 2016.

Major taxa studied: Animalia.

Methods: We used a large global dataset containing published studies on diversity in the terrestrial Animalia to analyse the relationship between diversity at the family, genus and species level across different orders.

Results: Family and species diversity were positively correlated, with the strongest correlations in Diptera, Hemiptera and Coleoptera. Correlations were slightly weaker in family-species than in genus-species relationships, whereas differences were stronger in observed richness than in diversity indices. Across all taxa, family-species correlations of Shannon diversity index values were independent of sample size, and they showed limited variation across biomes for the three orders containing sufficient case studies for this analysis. Based on the Shannon diversity index, the species diversity per site increased linearly with the increase in family diversity, with an average species : family diversity index ratio of 2.5, slightly lower than the ratio of 2.7 for observed species and family richness values.

Main conclusions: Our study confirmed that recording family-level diversity can be a meaningful proxy for determining species-level diversity patterns in biodiversity studies, and trade-offs between identification costs and retained information content need to be considered when using higher taxon surrogacy.

KEYWORDS

arthropods, biodiversity conservation, biogeographical distribution, higher taxa surrogate, meta-analyses, PREDICTS database, Shannon diversity

1 | INTRODUCTION

The decrease in biodiversity has led to dramatic declines in the provision of ecosystem services (Díaz et al., 2015). To address these declines and devise effective conservation measures, we need a thorough understanding of the specific quantitative changes in biodiversity, with species diversity representing the most commonly used currency (Jenkins, Pimm, & Joppa, 2013; Kreft & Jetz, 2007; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). However, collecting and recording species diversity information is challenging, for the following reasons: (a) this work requires enormous resources in terms of time, money and expert knowledge; and (b) only a fraction of the global species pool is currently known to science (Scheffers, Joppa, Pimm, & Laurance, 2012; Stork, 2018). A potential alternative approach in biodiversity assessments is to focus on the diversity patterns at higher taxonomic levels. The relative ease of identification at higher taxonomic levels makes working on this scale significantly cheaper and quicker, and it also allows for the efficient training of staff and volunteers with limited taxonomic knowledge to contribute towards biodiversity assessments (Lovell, Hamer, Slotow, & Herbert, 2009).

The application of higher taxa surrogacy for species diversity needs to consider trade-offs between retaining information content and identification costs (Balmford, Green, & Murray, 1996; Balmford, Jayasuriya, & Green, 1996; Perez-Fuertes et al., 2016). Identification work at high taxonomic ranks (e.g., order) is easy and fast, but the resulting information may provide a poor reflection of species diversity (Driessen & Kirkpatrick, 2019; Terlizzi et al., 2009). The number of lower taxonomic ranks (e.g., genera) may provide a strong indication of underlying species diversity, but identification of large numbers of specimens to that level is often time-consuming and challenging, particularly in mega-diverse arthropod taxa (Balmford, Lyon, & Lang, 2000; Cardoso, Silva, de Oliveira, & Serrano, 2004; Perez-Fuertes et al., 2016). Family-level data in this context might represent a sensible compromise, both requiring limited identification effort and still potentially serving as a good proxy of species diversity. A further general concern relating to higher taxon surrogacy for species diversity is that higher taxa are not natural units, but instead represent rather arbitrary classifications to facilitate the organization of taxonomic information (Bevilacqua, Terlizzi, Claudet, Frascchetti, & Boero, 2012; Gaston, 2000; Williams & Gaston, 1994).

A key rationale in conserving species diversity across taxonomic groups is the maintenance of functionally diverse ecosystems, with species diversity often being directly linked to the complexity of ecosystem properties, which, in turn, affect the strength and resilience of ecological functions (Hooper et al., 2005; Kremen, 2005; Naeem et al., 1999; Zavaleta, Pasari, Hulvey, & Tilman, 2010). Linkages between functional properties and morphological characteristics, meanwhile, are already strongly associated with family-level differentiations (Warwick, 1993), with a high family-level diversity commonly being associated with a high structural or trait diversity (Terlizzi et al., 2009). Although higher taxonomic ranks are not as clearly defined as species (Sepkoski, 1992), family-level

diversity cannot therefore be regarded only as an arbitrary functional unit with limited ecological meaning. On the contrary, family-level diversity in itself provides ecologically relevant information (Gaston, 2000).

The crucial step for the use of family-level diversity as a proxy for species-level diversity in biodiversity assessments is to establish the strength of links between richness patterns at the species level and the family level (Gaston & Williams, 1993). In particular, we need to know: (a) whether a consistent relationship between family diversity and species diversity exists across different geographical regions; and (b) whether the relative species richness per family is stable across different geographical regions.

The first question has been studied on regional scales for a variety of taxa and geographical regions. For example, family richness can be used successfully to predict species richness on a regional scale in higher plants (Negi & Gadgil, 2002; Villaseñor, Ibarra-Manríquez, Meave, & Ortiz, 2005), amphibians (Mazaris, Kallimanis, Sgardelis, & Pantis, 2008), birds (Mazaris et al., 2008; Williams & Gaston, 1994), mammals (Mazaris et al., 2008) and arthropods (Báldi, 2003; Heino & Soininen, 2007; Williams & Gaston, 1994). Nonetheless, several studies have also reported that species diversity is only poorly predicted by family diversity (Balmford et al., 2000; Grelle, 2002; Prance, 1994). All these studies have generally focused on one region or a small set of regions, with regional or local inventories across the respective taxonomic groups. On their own, the results of these individual inventories cannot be used to guide specific biodiversity studies. This relates to the fact that these detailed inventories generally used a much more comprehensive sampling effort than 'normal' ecological studies, whereas higher taxa surrogacy might be influenced by sampling effort per se (Larsen & Rahbek, 2005; Neeson, Rijn, & Mandelik, 2013; Vieira, Oliveira, Brewster, & Gayubo, 2012). Accordingly, results from these inventory studies represent a compromise between the immense effort required in species-specific studies covering a range of families and the very limited regional coverage possible when using such an approach. These studies therefore need to balance the spatial and taxonomic resolutions they can achieve. To understand the general patterns and links between the richness recorded at the species level and that at higher taxonomic levels across taxa and regions, it is necessary to combine the existing approaches into a common analytical framework.

The second question (i.e., are the relative number of species per family across different geographical regions similar?) relates to some extent to the theory of species biogeographical distributions. One of the most widely observed biogeographical rules in species distributions is the increase of species richness from the poles to the equator (Hillebrand, 2004; Williams, Gaston, & Humphries, 1997; Willig, Kaufman, & Stevens, 2003). A variety of hypotheses have been proposed to explain the latitudinal gradients of biodiversity, among which the diversification rate hypothesis argues that generational turnover and speciation rate in low-latitude regions is higher than at high latitudes owing to the higher temperature and, at least in the case of tropical rain forests, also high levels of humidity (Condamine,

Sperling, Wahlberg, Rasplus, & Kergoat, 2012; Mittelbach et al., 2007; Rohde, 1992). These conditions resulted in ample opportunities for isolation, paratactic and sympatric speciation and genetic drift owing to spatio-temporal heterogeneity (Condamine et al., 2012; Mittelbach et al., 2007; Rohde, 1992). According to this hypothesis, we can expect the number of species per higher taxon in random samples to increase from the poles to the equator and, potentially, from mountain tops to mountain bases. Although the diversification rate hypothesis has not been supported by recent studies of ants (Economio, Narula, Friedman, Weiser, & Guénard, 2018) and marine fishes (Rabosky et al., 2018), an increasing trend in the species : family ratio from high to low latitude has been observed for eastern Pacific marine molluscs (Roy, Jablonski, & Valentine, 1996). The high heterogeneity of environmental conditions linked, for example, to mountainous environments and precipitation gradients in many terrestrial systems might limit the strength of this trend in terrestrial taxa (McClain, White, & Hurlbert, 2007; Rundell & Price, 2009). Nonetheless, establishing the existing trends in terrestrial species : family ratios across different geographical regions is seen as important to provide guidance for the use of family-level surrogacy.

Here, we examine the relationship between diversity at family and species levels across terrestrial animal taxa using data from the PREDICTS database (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems; Hudson et al., 2017). This database contains site-level terrestrial biodiversity data from hundreds of published studies of > 26,000 study sites around the world. This database can be used to investigate a variety of core ecological and biogeographical questions related to biodiversity and conservation (Gray et al., 2016; Hudson et al., 2017; Newbold et al., 2016, 2015). We used the PREDICTS database to investigate the following research questions at a global level and across a wide range of taxa.

1. What is the predictability of family-level surrogacy for species diversity (i.e., the correlation between the diversity at family and species levels)?
2. How does the predictability of family surrogacy differ from genus-level surrogacy, and how does it differ when using diversity indices rather than observed richness?
3. If significant correlations between family and species diversity occur, how do these correlations differ between different biomes, and how are they linked to sample size?
4. What is the influence of latitude, elevation and sample size on the ratio between the number of species and the number of families?

2 | METHODS

2.1 | Data selection

The PREDICTS dataset (Hudson et al., 2017), containing > 3 million records, was downloaded in January 2018. Unpublished sources and non-English articles were excluded. We selected source studies containing orders of both arthropods and vertebrates (Arthropoda and

Chordata) with abundance recording (presence and absence recordings were excluded), which resulted in 215 source articles containing data for 281 studies.

From these 281 studies, we selected those that had a full coverage within a certain order (i.e., excluding source studies that selected only a subset of families within an order). This resulted in a total of 160 source articles, representing 201 studies and 401 order × study datasets (a study could contain multiple orders). In the next step of our analysis, we retained only the studies that identified samples to species or morpho-species level with family information. For the calculation of genus-level diversity surrogacy, species without genus information were excluded. This resulted in 154 source articles describing 191 source studies (see Supporting Information Appendix S1 for the flow chart of the data selection procedure and Supporting Information Appendix S2 for the respective selected study codes from the PREDICT data source, with bibliographic references to these studies included in list Appendix 1), 366 order × studies, 13,183 order × sites, and 147,003 species records with a recorded abundance greater than zero. Sample sites (hereafter referred to as “site”), considered as independent observations with coordinate records, for which a list of taxa were sampled using the same method, represent our lowest unit of measurement. In some studies, different blocks were distinguished (e.g., according to biome or level of human disturbance). We treated such “blocks” as separate studies in the context of this analysis.

2.2 | Data analysis

We calculated the Shannon diversity index for each site for the species, genus and family level, respectively. Shannon diversity is the most frequently used biodiversity index and has been considered to be a reasonably good measure of diversity for taxa that are incompletely sampled (Fiedler & Truxa, 2012). Shannon entropy (H ; Supporting Information Appendix S3: Equation 1) describes the degree of chaos in a species assemblage. Exponentiation of the Shannon entropy results in the Shannon diversity (D ; Supporting Information Appendix S3: Equation 2), a measure reflecting the effective richness (Jost, 2006). In addition, we also calculated Simpson's diversity index and the observed richness to check how robust the results generated for Shannon's diversity index were in comparison with these alternative diversity measures.

Pearson correlation coefficients (Pearson's r) between family and species diversities and between genus and species diversities were calculated for each study. Calculations and analysis were performed for each different order. We excluded sites where < 20 individuals were recorded to ensure that diversity index values were robust (Supporting Information Appendix S1). Studies reporting from fewer than five sites were also excluded, resulting in a final pool of 79 source articles, 101 source studies and 232 order × studies (Supporting Information Appendix S1).

A random effect meta-analysis was then conducted using Fisher's z , calculated from Pearson's r (Supporting Information Appendix S3:

Equation 3) (Field, 1999) as the effect size, based on restricted maximum likelihood (REML) methods to estimate the between-study variance, with the study included as a random factor (Schwarzer, Carpenter, & Rucker, 2015). Funnel plots (for the Shannon diversity index) were made of Fisher's z and its standard error (Supporting Information Appendix S3: Equation 4) to assess publication bias. Results were converted back to Pearson's r for easier interpretation.

To investigate the correlation across different regions, biome-specific correlations (Pearson's r) were calculated according to the Terrestrial Ecoregions of the World dataset (The Nature Conservancy, 2009), as used by PREDICTS (Hudson et al., 2017). Of the 14 biomes represented by the selected source studies in the PREDICTS dataset, six contained sufficient numbers of studies to allow for comparisons of species-family structures within the same order with other biomes. These six biomes are as follows: temperate broadleaf and mixed forests (TBMF), temperate grasslands, savanna and shrublands (TGSS), tropical and subtropical moist broadleaf forests (TSMBF), tropical and subtropical grasslands, savanna and shrublands (TSGSS), montane grasslands and shrublands (MGS) and boreal forests/taiga (BFT).

To investigate how sample size affects the correlation between species and family diversity, linear models were used to establish the relationship between Pearson's r (response variable) and sampling effort (explanatory variable), expressed as the median value for the logarithm of the number of individuals per study. For the modelling analysis exploring the relationship between the response variable and explanatory variable, orders that were presented in the dataset by fewer than five studies (block studies) were excluded to avoid model over-fitting.

Linear regression based on Shannon entropy was applied to investigate the relationship between Shannon entropy at species (H_S) and family level (H_F) (Equation (1)):

$$H_{S_{mj}} = b * H_{F_{mj}} + a, \quad (1)$$

where a is the intercept and b is the slope of the model. Coefficients a and b were estimated by meta-analysis (random effects model, REML to estimate between-study variance). Left- and right-hand sides of the above equation are then exponentiated to convert Shannon entropy to Shannon diversity (Equation (2)):

$$D_{S_{mj}} = \exp(a) * D_{F_{mj}}^b. \quad (2)$$

If the value of $b = 1$, the equation represents a linear relationship (without intercept) between the number of species and the number of families. Given that this was the case for our data, linear models were used to establish the species : family ratio for the Shannon diversity index (D ; Equation (3)), allowing a direct comparison between taxa. The model can be expressed as:

$$D_{S_{mj}} = \beta * D_{F_{mj}} + C, \quad (3)$$

where D_S and D_F are the Shannon diversity indices at species and family level in site j for a study m ; β is the slope, and C is the intercept in the linear model. By setting the intercept to zero, the slope (β)

therefore corresponds to the number of species per family. The mean value of β was estimated by meta-analysis (random effects model, REML to estimate between-study variance). Species : family ratios were also calculated for the observed richness in each taxon, in addition to the species : genus ratios calculated for both the Shannon diversity index and observed richness. All these measures were used to study the correlations in diversity patterns between these higher taxonomic levels and species diversity in models constructed in the same way as described for the Shannon diversity index values in a meta-analysis.

Finally, multiple linear regression was used to investigate how the species : family ratio for each study (i.e., β_j) was related to sample size ($\log_{10}$ -transformed number of individuals), latitude (absolute value for Universal Transverse Mercator system, reflecting kilometres from the Equator) and elevation (Supporting Information Appendix S3: Equation 5), with elevations obtained from Google Maps based on the coordinates given for each site in the dataset.

All analyses and calculations were performed in R (v.3.5.2; R Core Team, 2018). The package "vegan" (Oksanen et al., 2014) was used to calculate diversity indices, "meta" (Schwarzer, 2015) for meta-analysis and "rgl" (Chamberlain, Ram, Barve, & McGlinn, 2015) to obtain information about elevation.

3 | RESULTS

The total 401 order $\times$ studies cases that covered all families within an order included 10 classes (Aves, Amphibia, Arachnida, Mammalia, Insecta, Chilopoda, Diplopoda, Reptilia, Malacostraca and Entognatha) and 46 orders. Apart from 33 studies out of 132 in Insecta and two out of 36 in Arachnida that identified taxa only to family levels, the remaining 366 cases identified taxa to (morpho-) species level (Figure 1a). Across terrestrial ecoregions of the world, most of these 366 cases were located in the biomes TSMBF (129), TBMF (84) and TSGSS (51) (Figure 1b).

Valid studies meeting all our selection criteria covered nine orders in five classes. The estimated mean correlation coefficients (Pearson's r) were $> .5$ for all diversity metrics in all orders, and for both family-species correlation and genus-species correlation (Figure 2). With regard to the performance of the Shannon diversity index in family-level surrogacy, the highest correlations were observed in Diptera [mean, 95% confidence interval (CI) and number of samples: .88, .71-.95, $n = 6$], followed by Hemiptera (.87, .75-.93, $n = 9$) and Coleoptera (.86, .82-.90, $n = 33$), Passeriformes (.80, .75-.84, $n = 61$), Hymenoptera (.73, .66-.79, $n = 36$) and Araneae (.73, .67-.78, $n = 45$). Weaker correlations were observed in Squamata (.64, .21-.87, $n = 4$) and Anura (.60, .32-.78, $n = 9$), and the lowest correlation coefficients were recorded for Lepidoptera (.57, .44-.68, $n = 17$). Funnel plots indicate an absence of publication bias across all orders (Supporting Information Appendix S4), and scatter plots showing family-level versus species-level Shannon entropy highlight distinct linear relationships (Supporting Information Appendix S5).

FIGURE 1 World map of biodiversity studies covering all families with an order of terrestrial animals in the PREDICTS database (Hudson et al., 2017). (a) Grey bars represent studies that identify taxa to family level only, and black bars represent studies that identify taxa in addition to (morpho-)species level. (b) Locations of species-level identified studies across the terrestrial ecoregions of the world

Comparing different taxonomic ranks, Shannon index correlations were similar for family-level and genus-level surrogacy in Diptera, Hemiptera and Hymenoptera, while correlations were slightly stronger for family–species relationships than for genus–species relationship for Coleoptera. In Passeriformes, Araneae, Squamata and Lepidoptera,

this trend was reversed (Figure 2a). The patterns for the Simpson diversity index were very similar to results obtained for the Shannon diversity index (Figure 2b). When using observed taxon richness, genus–species correlations generally performed better than family–species correlations across all taxa (Figure 2c).

FIGURE 2 Meta-analysis results from random effects models showing Pearson's r of family-species relationships and genus-species relationships for the Shannon diversity index, Simpson's diversity index and observed richness in nine different orders of terrestrial animals. Numbers in parentheses refer to the number of studies, and error bars show the 95% confidence interval; dashed lines indicate values of $r = .5$; continuous diagonal lines indicate a 1:1 relationship between the x and y axes; points below the diagonal line represent cases where r values for the family-species relationship are lower than for the genus-species relationship and vice versa. Orders represented in fewer than three studies were not included

Only three orders, Araneae, Coleoptera and Passeriformes, were recorded in at least two biomes with more than three studies in each biome. In these taxa, species-family diversity correlations did not differ between biomes, with the exception of Passeriformes, where assemblages in temperate forests (TBMF biome) showed a higher correlation than assemblages in the two tropical biomes, TSMBF and TSGSS (Figure 3a). Sample size ($\log_{10}$ -transformed number of individuals) did not have a significant influence on Pearson's r for any of the orders (Figure 3b).

Exponential models (Equation 1) showed that the number of species increases linearly with the number of families (b in Equation 1 reaches values of approximately one across all orders; Figure 4). The species : family ratio based on the Shannon diversity index was very similar to the ratio based on species richness. The average value of β (Equation 3) was 2.5 for the Shannon diversity indices, in comparison to a ratio of 2.7 for species versus family richness. The minimum

species : family Shannon diversity ratio was 1.6 for Anura (95% CI: 1.4–1.8), and the maximum was 4.6 in Lepidoptera (95% CI: 3.9–5.3; Table 1). In contrast, the species : genus ratio was 1.5 and 1.6 based on the Shannon diversity index and observed richness, with seven out of nine orders showing values ≤ 1.5 . The ratio for Lepidoptera based on Shannon diversity index values was only 1.3 (95% CI: 1.20–1.35; Table 1).

Species : family Shannon diversity ratios were positively correlated with sample size across all taxa, but the rate of increase was low, with an average increase in the ratio of .51 (range: .2–.81) for an exponential increase in the overall sample size (Table 1). Furthermore, this positive correlation was significant in only Araneae ($\beta = .72 \pm .18, p < .001$), Passeriformes ($\beta = .42 \pm .1, p < .001$) and Hymenoptera ($\beta = .7 \pm .27, p = .047$) (Table 1; Supporting Information Appendix S6). The effects of elevation and latitude on species : family Shannon diversity ratio among taxa differed greatly. For example,

FIGURE 3 Meta-analysis results: (a) for Pearson's r (based on the Shannon diversity index) in different biomes (only orders that cover at least two biomes with at least three studies from each biome were included); and (b) slope of the relationship between Pearson's r and sample size, showing the median logarithm of the number of individuals per site in each study. Abbreviations: BFT, boreal forests/taiga; MGS, montane grasslands and shrublands; TBMF, temperate broadleaf and mixed forests; TGSS, temperate grasslands, savannas and shrublands; TSGSS, tropical and subtropical grasslands, savannas and shrublands; TSMBF, tropical and subtropical moist broadleaf forests

FIGURE 4 Meta-analysis results from random effects models showing: (a) the intercept and (b) the slope of order-specific regression models of species-level versus family-level values for Shannon entropy (H)

TABLE 1 Median value of the number of species, genera and families per site, meta-analysis results from random effects models showing estimated species : family and species : genus ratios based on Shannon diversity and observed richness (orders represented by fewer than three studies were excluded) and coefficients of the species : family ratio based on the Shannon diversity index, in response to the change of sample size ($\log_{10}$ -transformed number of individuals), elevation and latitude for different taxa (Equation 5) in Supporting Information Appendix S4; orders in more than six studies were included in the regression)

Class	Order	Number of studies	Number of species	Number of genera	Number of families	Regression coefficient			
						Species : family (Shannon)	Species : family (richness)	Species : genus (Shannon)	Species : genus (richness)
Amphibia	Anura	9	9.3	5.0	4.3	1.6 (1.4–1.8)	1.8 (1.6–2.0)	1.5 (1.3–1.7)	1.6 (1.5–1.8)
	Araneae	45	18.1	13.7	6.0	2.7 (2.4–3.0)	2.7 (2.4–2.9)	1.3 (1.2–1.3)	1.3 (1.3–1.4)
	Passeriformes	61	11.3	10.7	7.5	1.7 (1.6–1.9)	1.7 (1.5–1.8)	1.1 (1.08–1.14)	1.1 (1.08–1.13)
Insecta	Hymenoptera	36	11.4	4.8	3.3	3.1 (2.7–3.6)	3.7 (3.1–4.3)	2.4 (2.1–2.7)	2.5 (2.2–2.8)
	Coleoptera	33	34.7	12.1	15.9	2.3 (2.1–2.5)	2.4 (2.2–2.5)	2.1 (1.8–2.5)	2.7 (2.3–3.1)
	Lepidoptera	17	55.8	43.1	5.8	4.6 (3.9–5.3)	5.3 (3.8–6.8)	1.3 (1.20–1.35)	1.3 (1.2–1.4)
Hemiptera	Hemiptera	9	6.8	5.9	4.1	2.2 (1.5–2.9)	2.2 (1.6–2.9)	1.4 (1.1–1.6)	1.6 (1.2–2.0)
	Diptera	6	13.2	10.9	6.5	1.8 (1.2–2.5)	2.6 (1.0–4.3)	1.1 (1.0–1.3)	1.3 (1–1.6)
	Squamata	4	6.8	6.5	4.1	2.1 (1.2–3.0)	2.0 (1.3–2.7)	1.1 (1.0–1.3)	1.1 (1–1.2)
Reptilia									

Note: Asterisks indicate significance levels (* $\leq .05$; ** $\leq .01$; *** $\leq .001$).

elevation had a negative relationship with the species : family ratio for Araneae ($\beta = -.09 \pm .03$, $p = .003$), but a positive one for Coleoptera ($\beta = .16 \pm .08$, $p = .025$); and latitude had a significant negative relationship with the species : family ratio only in Passeriformes ($\beta = -.06 \pm .03$, $p = .025$), whereas no significant links were observed in any of the other taxa (Table 1).

4 | DISCUSSION

The family–species diversity correlation is generally high across a wide range of different taxonomic groups, with particularly high correlations being observed across the majority of arthropod taxa. For other taxa, such as mammals, the patterns remain somewhat inconclusive owing to an insufficient number of studies being available for a robust investigation. Although family-level diversity surrogacy was weaker than genus-level surrogacy, the cost of using genera as surrogates needs to be considered. Genus : species ratios for most orders were < 1.5 , indicating that limited identification effort has been saved when using genus diversity as a surrogate for species diversity. Particularly in some mega-diverse arthropod taxa, the identification of specimens to genus level might already pose significant challenges, resulting in low trade-offs between cost-effectiveness and information retainment (Cardoso et al., 2004; Perez-Fuertes et al., 2016). Furthermore, the weaker trend for family-level surrogacy in comparison to genus-level surrogacy was reversed for Shannon diversity index values in Coleoptera, which might reflect the particularly great difficulties in identifying all specimens in this mega-diverse order reliably to genus level. In addition, the differences between family–species diversity links and genus–species diversity links are stronger for observed richness than for diversity indices in many taxa, suggesting that diversity indices represent the preferred means when using family-level surrogacy.

Furthermore, our results showed that sample size had no influence on the correlations between Shannon diversity at family and species levels (Pearson's r). This suggests that the potential requirement to collect very large samples can be negated when using higher taxa surrogacy, particularly in regional investigations and when between-site variance of sample sizes is relatively small (Villasenor et al., 2005; Wolters, Bengtsson, & Zaitsev, 2006). Although species : family ratios were positively correlated with the sample size for all taxa on a global scale, the underlying trend (k_1 in Equation 5) in the Supporting Information Appendix S3) was relatively low. Overall, these results suggest that sample size only needs to be considered in evaluations of diversity changes at species level based on changes in diversity at family level in cases where the variance in sample sizes within a study is very high (e.g., at exponential scales) (Larsen & Rahbek, 2005; Terlizzi et al., 2009; Vieira et al., 2012). In addition, it needs to be considered that different sample sizes in studies might be related to different sampling methods used, although they could also be related to differences in sampling effort, such as the number of traps used or of sampling days (Chao et al., 2014), which might distort family and species diversity correlations (Vieira et al., 2012).

Unfortunately, we were unable to investigate the overall influence of sampling effort comprehensively in this study, because standardized sampling effort information was not available for all studies, and reducing the dataset exclusively to studies with available information would have resulted in a large reduction in the overall statistical power of the analysis.

The consistency of species–family Shannon diversity correlations across different biomes, although requiring further verification through the inclusion of more taxonomic groups, confirms the potential of higher-taxon survey approaches for biodiversity assessments. Nonetheless, we need to acknowledge that cross-biome transferability cannot be assumed generally across the different taxonomic levels, as shown by a higher family–species correlation performance in temperate than in tropical regions for Passeriformes. Likewise, van Rijn, Neeson, and Mandelik (2015) reported, based on both genus- and subfamily-level surrogacy, that the performance of higher taxa surrogate approaches for bees differed between biomes. Overall, the transferability of higher taxa surrogacy across regions requires significant future attention, testing and additional research.

The mean species : family ratio across our studies is relatively low for both the Shannon diversity index (~2.5) and observed richness (~2.7), with all taxa showing values on a similar scale and with a low variance. Such low values are in strong contrast to the much greater, and highly variable, number of globally described species per family among different taxa, for example varying between 40 and 60 for birds (Reddy, 2015), but being c. 160 for frogs (Pough et al., 2015), c. 400 for spiders (World Spider Catalog, 2018) and > 1,400 for Leiodoptera (Capinera, 2008). Nonetheless, this low species : family ratio is consistent with previous higher taxa surrogate studies. For example Li, Yu, Xiong, Wang, and Tu (2006) reported a linear relationship of about two species per family in a variety of aquatic plant groups within a grid survey on a 9 km × 9 km area in the northwest arid zone of China. Williams and Gaston (1994) also recorded between two and five species per family for ferns, butterflies and birds in their regional study in Britain, Australia and America when the recorded species count was low (i.e., < 20 species). This implies that, although species are distributed asymmetrically within higher taxa (i.e., some taxa contain many species and some contain few) (Gaston, 2000), the species : family ratio is relatively low in general ecological studies where spatial resolutions of individual study plots are commonly small. Nonetheless, although we found the species : family ratio to be similar for many taxa (e.g., 2.7 for Araneae, 2.3 for Coleoptera and 2.1 for Hemiptera), we suggest that a prediction of species numbers by observed families should be order specific, owing to variance among orders (e.g., 1.6 for Anura and 4.6 for Lepidoptera). In taxa with low ratios, the predictability of species diversity by family diversity is greatly enhanced, with a high ratio often linked to a high variability owing to stochastic factors (Driessen & Kirkpatrick, 2019; Rosser, 2017). For example, among arthropods, Lepidoptera show the highest species : family ratios, but also the lowest correlation coefficients between taxonomic levels. Here, we applied linear models only to obtain the species–family

relationship, but considering the relatively low number of observed species in each site for most studies, a linear model usually works well (Cardoso et al., 2004). Therefore, we consider the relatively low number of species per family that we found to be consistent with previous ecological studies carried out at much smaller spatial extents than the current global meta-analysis.

In contrast to our expectation, we did not find a uniform decrease in the species : family ratio with higher latitude or elevation across taxa. Given that local species richness is determined not only by speciation, but also by dispersal and extinction (Condamine et al., 2012; Mittelbach et al., 2007), inconformity in species : family ratios across different taxa might have a number of reasons. First, it might be related to the limited statistical power for observing a significant geographical trend, owing to the relatively low number of species and families observed in each study and the lack of sufficient studies that cover a wide range of regions. Second, species might not be distributed randomly across their geographical range (McClain et al., 2007). Species diversification resulting from ecological processes such as regional and local environmental heterogeneity (e.g., isolation) in terrestrial systems may influence their global geographical pattern, and such effects might vary between different taxa (McClain et al., 2007; Rundell & Price, 2009). Furthermore, separation of specimens into species (let alone morpho-species) might be biased owing to differing ease of separation/identification, and such bias might differ between regions and taxa. Overall, species : family ratios in ecological studies are therefore ill suited to test the latitudinal change of speciation hypothesis directly (Roy et al., 1996).

Despite criticism of the higher taxonomic surrogacy approaches raised, for example suggesting that higher taxa are unlikely to reflect intricate species-level responses to environmental disturbances (Bevilacqua et al., 2012), our results demonstrate that family diversity generally exhibits a close relationship to species-level diversity, which means that family-level taxon diversity can provide a useful proxy measure for species-level diversity, particularly for taxa with low species : family ratios in individual samples. Although genus-level diversity might perform better in indicating species diversity, family-level proxies are applicable much more widely, particularly in studies of mega-diverse arthropods, where the trade-off between cost-effectiveness and information retained in the recorded data structure is low. However, in studies containing data for multiple high-rank taxa (e.g., orders), comparisons between taxa may also reflect differences in speciation and taxonomic resolution (Purvis & Hector, 2000). Family surrogacy can enrich insights generated by biodiversity- and conservation-related studies, offering an additional measure to molecular-based technologies, such as DNA barcoding and environmental DNA (Bush et al., 2017; Lopes et al., 2017), and provide complementary information to the current well-established measures that focus on vertebrates and plants. The use of family diversity proxies could address the problems associated with the current focus in biodiversity conservation on a minute fraction of the global species pool, facilitating much-needed rapid biodiversity assessments to inform conservation-related evaluation and planning.

ACKNOWLEDGMENTS

We are thankful to all data contributors and to all members of the PREDICTS team for collation and curation of data. We thank Tim Newbold for advice on the dataset and Shahid Naeem for discussing the manuscript. We also thank Johannes Knops for providing comments and editorial help with the manuscript draft. This study was financially supported by the National Natural Science Foundation of P.R. China (31700363 and 41871186), Jiangsu Science and Technology Department (BK20181191) and National Key R&D Program of China (No. 2018YFC05072).

AUTHOR CONTRIBUTIONS

Y.Z., Y.L. and J.C.A. conceived the idea. Y.Z. and W.W. undertook the analysis. Y.Z. and J.C.A. wrote the paper, with significant contributions from all authors.

DATA AVAILABILITY STATEMENT

Data used in this study are publicly accessible from the PREDICTS database: <https://doi.org/10.5519/0066354> (Hudson et al., 2016). Selected references to PREDICTS data are provided in Appendix 1. Indices we used for selecting the datasets from the PREDICTS database are provided in the Supporting Information (Appendix S1).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zou Y, van der Werf W, Liu Y, Axmacher JC. Predictability of species diversity by family diversity across global terrestrial animal taxa. *Global Ecol Biogeogr*. 2020;00:1–16. <https://doi.org/10.1111/geb.13043>

APPENDIX 1: LIST OF SELECTED REFERENCES TO PREDICTS DATA USED

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