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2 1 **Predictability of species diversity by family diversity across global**
3 2 **terrestrial animal taxa**

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5 3 **Running title: Higher taxa diversity surrogacy for animals**

6
7 4 **Abstract**

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9 5 **Aim:** While biodiversity is in sharp decline around the globe, collecting precise
10 information on changes in overall species richness remains extremely
11 challenging. Efficient and reliable proxy methods are therefore needed, with
12 the diversity of higher taxa representing one such potential proxy for
13 species-level diversity. Nonetheless, the stability of using this measure across
14 different regions and animal taxa at the global scale has never been
15 thoroughly investigated.

16 12 **Location:** Global

17 13 **Time period:** Up to 2016

18 14 **Major taxa studied:** Animalia

19 15 **Methods:** We use a large global dataset containing published studies on
20 diversity in the terrestrial Animalia to analyse the relationship between diversity
21 at family, genus and species level across different orders.

22 18 **Results:** Family- and species-diversity are positively correlated, with the
23 strongest correlations in Diptera, Hemiptera and Coleoptera. Correlations are
24 slightly weaker in family-species than genus-species relationships. These
25 differences are stronger in observed richness than in diversity indices. Across
26 all taxa, family-species-correlations of Shannon diversity index values were
27 independent of sample size, and they showed limited variation across biomes
28 for the three orders containing sufficient case studies for this analysis. Based
29 on the Shannon diversity index, the species diversity per site increases linearly
30 with the increase in family diversity, with an average species / family diversity
31 index ratio of 2.5, slightly lower than the ratio of 2.7 for observed species and

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3 28 family richness values.
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29 **Main conclusions:** Our study confirms that recording family-level diversity
30 can be a meaningful proxy to determine species-level diversity patterns in
31 biodiversity studies, while trade-offs between identification costs and retained
32 information content need to be considered when using higher taxon surrogacy.
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Key words

Arthropods, bio-geographical distribution, biodiversity conservation, higher taxa surrogate, meta-analyses, PREDICTS, Shannon diversity

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 (Myers *et al.*, 2000; Kreft & Jetz, 2007; Jenkins *et al.*, 2013). Collecting and recording species diversity information, however, is challenging, since this work requires enormous resources in time, money and expert knowledge, but also because only a fraction of the global species pool is currently known to science, which makes this task extremely difficult (Scheffers *et al.*, 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 *et al.*, 2009).

The application of higher taxa surrogacy for species diversity needs to consider trade-offs between retaining information content and identification

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3 56 costs (Balmford *et al.*, 1996b; Balmford *et al.*, 1996a; Perez-Fuertes *et al.*,
4 57 2016). Identification work at high taxonomic ranks (e.g. order) is easy and fast,
5 58 but resulting information may poorly reflect species diversity (Terlizzi *et al.*,
6 59 2009; Driessen & Kirkpatrick, 2019). The number of lower taxonomic ranks
7 60 (e.g. genera) may strongly indicate underlying species diversity, but
8 61 identification of large numbers of specimens to that level is often
9 62 time-consuming and challenging, particularly in mega-diverse arthropod taxa
10 63 (Balmford *et al.*, 2000; Cardoso *et al.*, 2004; Perez-Fuertes *et al.*, 2016).
11 64 Family-level data in this context might represent a sensible compromise, both
12 65 requiring limited identification effort and still potentially serving as a good proxy
13 66 of species diversity. A further general concern relating to higher taxon
14 67 surrogacy for species diversity is that higher taxa are not natural units, but
15 68 represent rather arbitrary classifications to facilitate the organization of
16 69 taxonomic information (see Gaston, 2000) (Williams & Gaston, 1994;
17 70 Bevilacqua *et al.*, 2012). A key rationale in conserving species diversity across
18 71 taxonomic groups is the maintenance of functionally diverse ecosystems, with
19 72 species diversity often directly linked to the complexity of ecosystem properties
20 73 that in turn affect the strength and resilience of ecological functions (Naeem *et*
21 74 *al.*, 1999; Hooper *et al.*, 2005; Kremen, 2005; Zavaleta *et al.*, 2010). Linkages
22 75 between functional properties and morphological characteristics, meanwhile,
23 76 are already strongly associated with family-level differentiations (Warwick,
24 77 1993), with a high family-level diversity commonly associated with a high
25 78 structural or trait diversity (Terlizzi *et al.*, 2009). While higher taxonomic ranks
26 79 are not as clearly defined as species (Sepkoski, 1992), family level diversity
27 80 cannot therefore be regarded only as an arbitrary functional unit with limited
28 81 ecological meaning. On the contrary, family level diversity in itself provides
29 82 ecologically relevant information (Gaston, 2000).

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52 83 The crucial step for the use of family diversity as a proxy for species diversity
53 84 in biodiversity assessments is to establish the strength of links between
54 85 richness patterns at species level and family level (Gaston & Williams, 1993).
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56 86 In particular, we need to know: i) whether a consistent relationship between
57 87 family diversity and species diversity exists across different geographic

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3 88 regions, and ii) whether the relative species richness per family is stable
4 89 across different geographic regions. The first question has been studied
5 90 already on regional scales for a variety of taxa and geographic regions. For
6 91 example, family richness can be used successfully to predict species richness
7 92 on a regional scale in higher plants (Negi & Gadgil, 2002; Villasenor *et al.*,
8 93 2005), amphibians (Mazaris *et al.*, 2008), birds (Williams & Gaston, 1994;
9 94 Mazaris *et al.*, 2008), mammals (Mazaris *et al.*, 2008) and arthropods
10 95 (Williams & Gaston, 1994; Báldi, 2003; Heino & Soininen, 2007). Nonetheless,
11 96 several studies also reported that species diversity is only poorly predicted by
12 97 family diversity (Prance, 1994; Balmford *et al.*, 2000; Grelle, 2002). All these
13 98 studies have generally focused on one region or a small set of regions, with
14 99 regional or local inventories across the respective taxonomic groups. On their
15 100 own, the results of these individual inventories, however, cannot be used to
16 101 fully guide specific biodiversity studies. This relates to the fact that these
17 102 detailed inventories generally used a much more comprehensive sampling
18 103 effort than 'normal' ecological studies, while higher taxa surrogacy might be
19 104 influenced by sampling effort per se (Larsen & Rahbek, 2005; Vieira *et al.*,
20 105 2012; Neeson *et al.*, 2013). Results from these inventory studies therefore
21 106 represent a compromise between the immense effort required in
22 107 species-specific studies covering a range of families, and the very limited
23 108 regional coverage possible when using such an approach. These studies
24 109 therefore need to balance the spatial and taxonomic resolutions they can
25 110 achieve. To understand the general patterns and links between the richness
26 111 recorded at species levels and that at higher taxonomic levels across taxa and
27 112 regions, it is therefore necessary to combine the existing approaches into a
28 113 common analytical framework.

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31 114 The second question, i.e. are the relative number of species per family across
32 115 different geographic regions similar, to some extent relates to the theory of
33 116 species' bio-geographical distributions. One of the most widely observed
34 117 bio-geographical rules in species distributions is the increase of species
35 118 richness from the poles to the equator (Williams *et al.*, 1997; Willig *et al.*, 2003;
36 119 Hillebrand, 2004). A variety of hypotheses has been proposed to explain the
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3 latitudinal gradients of biodiversity, among which the diversification rate -
4 hypothesis argues generational turnover and speciation rate in low latitude
5 regions is higher than at high latitudes due to the higher temperature and, at
6 least in the case of tropical rainforests, also high levels of humidity (Rohde,
7 1992; Mittelbach *et al.*, 2007; Condamine *et al.*, 2012). These conditions
8 resulted in ample opportunities for isolation, paratactic and sympatric
9 speciation, and genetic drift due to spatial-temporal heterogeneity (Rohde,
10 1992; Mittelbach *et al.*, 2007; Condamine *et al.*, 2012). According to this
11 hypothesis, we can expect that the number of species per higher taxa in
12 random samples increases from the poles to the equator, as well as potentially
13 from mountain tops to mountain bases. Although the diversification rate
14 hypothesis has not been supported by recent studies of ants (Economo *et al.*,
15 2018) and marine fishes (Rabosky *et al.*, 2018), an increasing trend in the
16 species / family ratio from high to low latitude has been observed already for
17 eastern Pacific marine molluscs (Roy *et al.*, 1996). The high heterogeneity of
18 environmental conditions linked for example to mountainous environments and
19 precipitation gradients in many terrestrial systems might limit the strength of
20 this trend in terrestrial taxa (McClain *et al.*, 2007; Rundell & Price, 2009).
21 Nonetheless, establishing existing trends in terrestrial species-family ratios
22 across different geographic regions is seen as important to provide guidance
23 for the use of family-level surrogacy.
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41 Here we examined the relationship between diversity at family and species
42 level across terrestrial animal taxa using data from the PREDICTS database
43 (Projecting Responses of Ecological Diversity in Changing Terrestrial
44 Systems) (Hudson *et al.*, 2017). This database contains site-level terrestrial
45 biodiversity data from hundreds of published studies of over 26,000 study sites
46 around the world. This database can be used to investigate a variety of core
47 ecological and biogeographic questions related to biodiversity and
48 conservation (Newbold *et al.*, 2015; Gray *et al.*, 2016; Newbold *et al.*, 2016;
49 Hudson *et al.*, 2017). We used the PREDICTS database to investigate the
50 following research questions at a global level and across a wide range of taxa:
51 i) What is the predictability of family-level surrogacy for species diversity, i.e.
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3 152 the correlation between the diversity at family and species level? ii) How does
4 153 the predictability of family surrogacy differ from genus-level surrogacy, and
5 154 how does it differ when using diversity indices rather than observed richness?
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7 155 iii) If significant correlations between family and species diversity occur, how
8 156 do these correlations differ between different biomes, and how are they linked
9 157 to sample size? iv) What is the influence of latitude, elevation and sample size
10 158 on the ratio between species number and family number?
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17 159 **Method**
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20 160 *Data selection*
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23 161 The PREDICTS dataset (Hudson *et al.*, 2016), containing more than 3 million
24 162 records, was downloaded in January 2018. Unpublished sources and
25 163 non-English articles were excluded. We selected source studies containing
26 164 orders of both arthropods and vertebrates (Arthropoda and Chordata) with
27 165 abundance recording (presence and absence recordings were excluded),
28 166 which resulted in 215 source articles containing data for 281 studies
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33 167 From these 281 studies, we selected those that have a full coverage within a
34 168 certain order, i.e. excluding source studies that only selected a subset of
35 169 families within an order. This resulted in a total of 160 source articles
36 170 representing 201 studies and 401 order × study data-sets (a study could
37 171 contain multiple orders). In the next step of our analysis, we retained only the
38 172 studies that identified samples to species or morpho-species level with family
39 173 information. For the calculation of genus-level diversity surrogacy, species
40 174 without genus information were excluded. This resulted in 154 source articles
41 175 describing 191 source studies (see Appendix S1 for the flow chart of data
42 176 selection procedure and Appendix S2 for the respective selected study codes
43 177 from the PREDICT data source, with bibliographic references to these studies
44 178 included in list Appendix 1), 366 order × studies, 13183 order × sites, and
45 179 147,003 species records with a recorded abundance >0. Sample sites
46 180 (hereafter referred to as “site”), considered as independent observations with
47 181 coordinate records, for which a list of taxa were sampled using the same
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3 182 method, represent our lowest unit of measurement. In some studies, different
4 183 blocks were distinguished, e.g. according to biome or level of human
5 184 disturbance. We treated such "blocks" as separate studies in the context of
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12 186 *Data Analysis*
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15 187 We calculated the Shannon diversity index for each site for the species, genus
16 188 and family level, respectively. Shannon diversity is the most frequently used
17 189 biodiversity index and has been considered to be a reasonably good measure
18 190 of diversity for taxa that are incompletely sampled (Fiedler & Truxa, 2012).
19 191 Shannon entropy (H , Appendix S3: Equation 1) describes the degree of chaos
20 192 in a species assemblage. Exponentiation of the Shannon entropy results in the
21 193 Shannon diversity (D , Appendix S3: Equation 2), a measure reflecting the
22 194 effective richness (Jost, 2006). In addition, we also calculated Simpson's
23 195 diversity index and the observed richness to check how robust the results
24 196 generated for Shannon's diversity index are in comparison with these
25 197 alternative diversity measures.
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35 198 Pearson correlation coefficients (Pearson's r) between family and species
36 199 diversities, and between genus and species diversities, were calculated for
37 200 each study. Calculations and analysis were performed for each different order,
38 201 respectively. We excluded sites where less than 20 individuals were recorded
39 202 to ensure that diversity index values were robust (Appendix S1). Studies
40 203 reporting from less than 5 sites were also excluded, resulting in a final pool of
41 204 79 source articles, 101 source studies and 232 order \times studies (Appendix S1).
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48 205 A random effect meta-analysis was then conducted using Fisher's z ,
49 206 calculated from Pearson's r (Appendix S3: Equation 3) (Field, 1999) as the
50 207 effect size, based on restricted maximum likelihood (REML) methods to
51 208 estimate the between-study variance, with the study included as a random
52 209 factor (Schwarzer *et al.*, 2015). Funnel plots (for the Shannon diversity index)
53 210 were made of Fisher's z and its standard error (Appendix S3: Equation 4) to
54 211 assess publication bias. Results were converted back to Pearson's r for easier
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3 212 interpretation.

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6 213 To investigate the correlation across different regions, biome-specific
7 correlations (Pearson's r) were calculated according to the Terrestrial
8 Ecoregions of the World dataset (The Nature Conservancy, 2009), as used by
9 PREDICTS (Hudson *et al.*, 2017). Of the 14 biomes represented by the
10 selected source-studies in the PREDICTS dataset, six contained sufficient
11 numbers of studies to allow for comparisons of species-family structures within
12 the same order with other biomes. These six biomes are 'Temperate Broadleaf
13 & Mixed Forests' (TBMF), 'Temperate Grasslands, Savanna & Shrublands'
14 (TGSS), 'Tropical & Subtropical Moist Broadleaf Forests' (TSMBF), 'Tropical &
15 Subtropical Grasslands, Savanna & Shrublands' (TSGSS), 'Montane
16 Grasslands & Shrublands' (MGS) and 'Boreal Forests/Taiga' (BFT).

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19 224 To investigate how sample size affects the correlation between species and
20 family diversity, linear models were used to establish the relationship between
21 Pearson's r (response variable) and sampling effort (explanatory variable),
22 expressed as the median value for the log number of individuals per study. For
23 the modelling analysis exploring the relationship between the response
24 variable and explanatory variable, orders that were presented in the dataset by
25 less than 5 studies (block-studies) were excluded to avoid model over-fit.

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28 231 Linear regression based on Shannon entropy was applied to investigate the
29 relationship between Shannon Entropy at species (H_S) and family level (H_F)
30 (Equation 1):

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

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36 235 where a is the intercept and b is the slope of the model. Coefficients a and b
37 were estimated by meta-analysis (random effects model, REML to estimate
38 between-study variance). Left- and right-hand sides of the above equation are
39 then exponentiated to convert Shannon entropy to Shannon diversity
(Equation 2):

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

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3 241 If the value of $b=1$, the equation represents a linear relationship (without
4 intercept) between the number of species and the number of families. Since
5 this was the case for our data, linear models were used to establish the
6 species / family ratio for the Shannon diversity index (D , Equation 3), allowing
7 a direct comparison between taxa. The model can be expressed as:
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$$D_{S_{m,j}} = \beta * D_{F_{m,j}} + C \quad (3),$$

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16 247 where D_S and D_F are the Shannon diversity indices at species and family level
17 in site j for a study m ; β is the slope, and C is the intercept in the linear model.
18 248 By setting the intercept to 0, the slope (β) therefore corresponds to the number
19 250 of species per family. The mean value of β was estimated by meta-analysis
20 (random effects model, REML to estimate between-study variance). Species /
21 251 family ratios were also calculated for the observed richness in each taxon, in
22 252 addition to the species / genus ratios calculated for both the Shannon diversity
23 253 index and observed richness. All these measures were used to study the
24 254 correlations in diversity patterns between these higher taxonomic levels and
25 255 species diversity in models constructed in the same way as described for the
26 256 Shannon diversity index values in a meta-analysis.
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37 258 Finally, multiple linear regression was used to investigate how the species /
38 family ratio for each study (i.e. β_j) was related to sample size (log transformed
39 number of individuals), latitude (absolute value for UTM system, reflecting
40 kilo-meters from the equator) and elevation (Appendix S3: Equation 5), with
41 elevations obtained from Google Maps based on the coordinates given for
42 each site in the dataset.
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49 264 All analysis and calculations were performed in R (V.3.5.2) (R Core Team,
50 2018). Package “vegan” (Oksanen *et al.*, 2014) was used to calculate diversity
51 indices, “meta” (Schwarzer, 2015) for meta-analysis and “rgbif” (Chamberlain
52 *et al.*, 2015) to obtain elevation information.
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57 268 **Results**
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60 269 The total 401 ‘order x studies’ cases that covered all families within an order

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3 270 included 10 classes (Aves, Amphibia, Arachnida, Mammalia, Insecta,
4 271 Chilopoda, Diplopoda, Reptilia, Malacostraca, Entognatha) and 46 orders.
5 272 Apart from 33 studies out of 132 in Insecta, and 2 out of 36 in Arachnida that
6 273 identified taxa only to family levels, the remaining 366 cases identified taxa to
7 274 (morpho-) species level (Figure 1a). Across Terrestrial Ecoregions of the
8 275 World, most of these 366 cases were located in the biomes Tropical &
9 276 Subtropical Moist Broadleaf Forests (TSMBF, 129), Temperate Broadleaf &
10 277 Mixed Forests (TBMF, 84) and Tropical & Subtropical Grasslands, Savanna &
11 278 Shrublands (TSGSS, 51) (Figure 1b).

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20 279 Valid studies meeting all our selection criteria covered nine orders in 5 classes.
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22 280 The estimated mean correlation coefficients (Pearson's r) were higher than 0.5
23 for all diversity metrics in all orders, and for both, family-species correlation
24 for genus-species correlation (Figure 2). With regards to the performance of
25 the Shannon diversity index in family-level surrogacy, the highest correlations
26 were observed in Diptera (mean, 95% CI and number of samples: 0.88,
27 0.71-0.95, n=6), following by Hemiptera (0.87, 0.75-0.93, n=9) and Coleoptera
28 (0.86, 0.82-0.90, n=33), Passeriformes (0.80, 0.75-0.84, n=61), Hymenoptera
29 (0.73, 0.66-0.79, n=36) and Araneae (0.73, 0.67-0.78, n=45). Weaker
30 correlations were observed in Squamata (0.64, 0.21-0.87, n=4) and Anura
31 (0.60, 0.32-0.78, n=9), while the lowest correlation coefficients were recorded
32 for Lepidoptera (0.57, 0.44-0.68, n=17). The funnel plots indicate an absence
33 of publication bias across all orders (Appendix S4), while scatter plots showing
34 family-level versus species-level Shannon entropy highlight distinct linear
35 relationships (Appendix S5).

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39 295 Comparing different taxonomic ranks, Shannon index correlations were similar
40 for family-level and genus-level surrogacy in Diptera, Hemiptera and
41 Hymenoptera, while correlations were slightly stronger in family-species
42 relationships than genus-species relationship for Coleoptera. In
43 Passeriformes, Araneae, Squamata and Lepidoptera, this trend was reversed
44 (Figure 2a). The patterns for the Simpson diversity index were very similar to
45 results obtained for the Shannon diversity index (Figure 2b). When using

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3 302 observed taxon richness, genus-species correlations generally performed
4 303 better than family-species correlations across all taxa (Figure 2c).
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8 304 Only three orders, Araneae, Coleoptera and Passeriformes, were recorded in
9 305 at least 2 biomes with more than 3 studies in each biome. In these taxa,
10 306 species– family diversity correlations did not differ between biomes with the
11 307 exception of Passeriformes, where assemblages in temperate forests (TBMF
12 308 biome) showed a higher correlation than assemblages in the two tropical
13 309 biomes TSMBF and TSGSS (Figure 3a). Sample size (log-transformed
14 310 number of individuals) did not have a significant influence on Pearson's r for
15 311 any of the orders (Figure 3b).
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23 312 Exponential models (Equation 1) showed that the number of species increases
24 313 linearly with the number of families (b in Equation 1 reaches values ~1 across
25 314 all orders, Figure 4). The species / family ratio based on the Shannon diversity
26 315 index was very similar to the ratio based on species richness. The average
27 316 value of β (Equation 3) was 2.5 for the Shannon diversity indices, in
28 317 comparison to a ratio of 2.7 for species versus family richness. The minimum
29 318 species / family Shannon diversity ratio was 1.6 for Anura (95% CI: 1.4 - 1.8),
30 319 and the maximum was 4.6 in Lepidoptera (3.9 - 5.3, Table 1). In contrast, the
31 320 species / genus ratio was 1.5 and 1.6 based on the Shannon diversity index
32 321 and observed richness, with 7 out of 9 orders showing values ≤ 1.5 . The ratio
33 322 for Lepidoptera based on Shannon diversity index values was only 1.3 (1.20
34 323 – 1.35, Table 1).
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46 324 Species / family Shannon diversity ratios were positively correlated with
47 325 sample size across all taxa, but the increase rate was low, with an average
48 326 increase in the ratio of 0.51 (range: 0.2 to 0.81) for an exponential increase in
49 327 the overall sample size (Table 1). This positive correlation was furthermore
50 328 only significant in Araneae ($\beta=0.72 \pm 0.18$, $P<0.001$), Passeriformes
51 329 ($\beta=0.42 \pm 0.1$, $P<0.001$) and Hymenoptera ($\beta=0.7 \pm 0.27$, $P=0.047$)
52 330 (Table 1, Appendix S6). Effects of elevation and latitude on species / family
53 331 Shannon diversity ratio among taxa differed strongly. For example, elevation
54 332 had a negative relationship with the species / family ratio for Araneae

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3 333 (beta=-0.09 ± 0.03, $P=0.003$), but a positive one for Coleoptera (beta=0.16 ±
4 334 0.08, $P=0.025$); latitude had a significant negative relationship with the species
5 335 / family ratio only in Passeriformes (beta=-0.06 ± 0.03, $P=0.025$), whereas no
6 336 significant links were observed in any of the other taxa (Table 1).
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12 337 **Discussion**
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15 338 Family-species diversity correlation is generally high across a wide range of
16 339 different taxonomic groups, with particularly high correlations observed across
17 340 the majority of arthropod taxa. For other taxa such as mammals, patterns
18 341 remain somewhat inconclusive due to an insufficient number of studies
19 342 available for a robust investigation. While family-level diversity surrogacy was
20 343 weaker than genus-level surrogacy, the cost of using genera as surrogates
21 344 needs to be considered. Genus-species ratios for most orders were less than
22 345 1.5, indicating that limited identification effort has been saved when using
23 346 genus diversity as a surrogate for species diversity. Particularly in some
24 347 mega-diverse arthropod taxa, identification of specimens to genus level might
25 348 already pose significant challenges, resulting in low trade-offs between
26 349 cost-effectiveness and information retention (Cardoso *et al.*, 2004;
27 350 Perez-Fuertes *et al.*, 2016). The weaker trend for family-level surrogacy in
28 351 comparison to genus-level surrogacy was furthermore reversed for Shannon
29 352 diversity index values in Coleoptera, which might reflect the particularly strong
30 353 difficulties in identifying all specimens in this mega-diverse order reliably to
31 354 genus level. In addition, the differences between family-species diversity links
32 355 and genus-species diversity links are stronger in observed richness than for
33 356 diversity indices in many taxa, suggesting that diversity indices represent the
34 357 preferred means when using family-level surrogacy.
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51 358 Our results furthermore showed that sample size had no influence on the
52 359 correlations between Shannon diversity at family- and species-levels
53 360 (Pearson's r). This suggests that the potential requirement to collect very large
54 361 samples can be negated when using higher taxa surrogacy particularly in
55 362 regional investigations and when between-site variance of sample sizes is
56 363 relatively small (Villasenor *et al.*, 2005; Wolters *et al.*, 2006). While species /
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3 364 family ratios were positively correlated with the sample size for all taxa on a
4 365 global scale, the underlying trend (k_1 in Equation 5, Appendix S3) was
5 366 relatively low. Overall, these results suggest that sample size only needs to be
6 367 considered in evaluations of diversity changes at species level based on
7 368 diversity changes at families level in cases where the variance in sample sizes
8 369 within a study is very high (e.g. at exponential scales) (Larsen & Rahbek,
9 370 2005; Terlizzi *et al.*, 2009; Vieira *et al.*, 2012). In addition, it needs to be
10 371 considered that different sample sizes in studies might be related to different
11 372 sampling methods used, while they could also relate to differences in sampling
12 373 effort, such as the number of traps used or of sampling days (Chao *et al.*,
13 374 2014), which may distort family- and species diversity correlations (Vieira *et*
14 375 *al.*, 2012). We were unfortunately unable to comprehensively investigate the
15 376 overall influence of sampling effort in this study, since standardized sampling
16 377 effort information was not available for all studies, and reducing the dataset
17 378 exclusively to studies with available information would have resulted in a
18 379 strong reduction in overall statistical power of the analysis.
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33 380 The consistency of species-family Shannon diversity correlations across
34 381 different biomes, while needing further verification through the inclusion of
35 382 more taxonomic groups, confirms the potential of higher-taxon survey
36 383 approaches for biodiversity assessments. We nonetheless need to
37 384 acknowledge that cross-biome transferability cannot generally be assumed
38 385 across the different taxonomic levels, as shown by a higher family-species
39 386 correlation performance in temperate than tropical regions for Passeriformes.
40 387 Likewise, van Rijn *et al.* (2015) reported, based on both genus- and
41 388 subfamily-level surrogacy, that the performance of higher taxa surrogate
42 389 approaches for bees differed between biomes. Overall, the transferability of
43 390 higher taxa surrogacy across regions requires significant future attention,
44 391 testing and additional research.
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55 392 The mean species / family ratio across our studies is relatively low for both the
56 393 Shannon diversity index (~2.5) and observed richness (~2.7), with all taxa
57 394 showing values on a similar scale and with a low variance. Such low values
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3 395 are in strong contrast to the much greater, and highly variable, number of
4 396 globally described species per family among different taxa, for example
5 397 varying between 40 and 60 for birds (Reddy, 2015), but being about 160 for
6 398 frogs (Pough *et al.*, 2015), about 400 for spiders (World Spider Catalog, 2018)
7 399 and >1400 for Lepidoptera (Capinera, 2008). Nonetheless, this low species /
8 400 family ratio is consistent with previous higher-taxa surrogate studies. For
9 401 example Li *et al.* (2006) reported a linear relationship of about 2 species per
10 402 family in a variety of aquatic plant groups within a grid survey on a 9 X 9 km²
11 403 area in China's northwest arid zone. Williams and Gaston (1994) also
12 404 recorded between 2 and 5 species per family for ferns, butterflies and birds in
13 405 their regional study in Britain, Australia and America when the recorded
14 406 species count is low (i.e. <20 species). This implies that, while species are
15 407 distributed asymmetrically within higher taxa (i.e. some taxa contain many
16 408 species and some contain few) (Gaston, 2000), the species-family ratio is
17 409 relatively low in general ecological studies where spatial resolutions of
18 410 individual study plots are commonly small. Nonetheless, although we found
19 411 the species / family ratio to be similar for many taxa (e.g. 2.7 for Araneae, 2.3
20 412 for Coleoptera and 2.1 for Hemiptera), we suggest a prediction of species
21 413 numbers by observed families should be order-specific, as variance is still
22 414 existent (e.g. 1.6 for Anura and 4.6 for Lepidoptera). In taxa with low ratios, the
23 415 predictability of species diversity by family diversity is greatly enhanced, with a
24 416 high ratio often linked to a high variability due to stochastic factors (Rosser,
25 417 2017; Driessen & Kirkpatrick, 2019). For example, among arthropods,
26 418 Lepidoptera show the highest species-family ratios, but also the lowest
27 419 correlation coefficients between taxonomic levels. Here, we only applied linear
28 420 models to obtain species-family relationship, but considering the relatively low
29 421 observed species in each site for most studies, a linear model usually works
30 422 well (Cardoso *et al.*, 2004). Therefore, we consider the relatively low number of
31 423 species per family that we found to be consistent with previous ecological
32 424 studies, done at much smaller spatial extent than the current global
33 425 meta-analysis.

34 426 In contrast to our expectation, we did not find a uniform decrease in the
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3 427 species / family ratio with higher latitude or elevation across taxa. As local
4 428 species richness is determined not only by speciation, but also by dispersal
5 429 and extinction (Mittelbach *et al.*, 2007; Condamine *et al.*, 2012), inconformity in
6 430 species / family ratios across different taxa may have a number of reasons.
7 431 First, it might be related to the limited statistical power for observing a
8 432 significant geographical trend, due to the relatively low number of species and
9 433 families observed in each study, and the lack of sufficient studies that cover a
10 434 wide range of regions. Second, species might not be randomly distributed
11 435 across their geographical range (McClain *et al.*, 2007). Species diversification
12 436 resulting from ecological processes such as regional and local environmental
13 437 heterogeneity (e.g. isolation) in terrestrial systems may influence their global
14 438 geographical pattern, and such effects might vary between different taxa
15 439 (McClain *et al.*, 2007; Rundell & Price, 2009). Furthermore, separation of
16 440 specimens into species (let alone morpho-species) might be biased due to
17 441 differing ease of separation / identification, and such bias might differ between
18 442 regions and taxa. Overall, species / family ratios in ecological studies are
19 443 therefore ill suited to directly test the latitudinal change of speciation
20 444 hypothesis (Roy *et al.*, 1996).

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30 445 Despite criticism of the higher taxonomic surrogacy approaches raised for
31 446 example suggesting that higher taxa are unlikely to reflect intricate
32 447 species-level responses to environmental disturbances (Bevilacqua *et al.*,
33 448 2012), our results demonstrate that family diversity is generally closely related
34 449 to species-level diversity, which means family-level taxon diversity can provide
35 450 a useful proxies measure for species-level diversity particularly for taxa with
36 451 low species-family ratios in individual samples. Although genus-level diversity
37 452 might perform better in indicating species diversity, family-level proxies are
38 453 applicable much more widely, particularly in studies of mega-diverse
39 454 arthropods, where the trade-off between cost-effectiveness and information
40 455 retained in the recorded data structure is low. However, in studies containing
41 456 data for multiple high-rank taxa (e.g. orders), comparisons between taxa may
42 457 also reflect differences in speciation and taxonomic resolution (Purvis &
43 458 Hector, 2000). Family surrogacy can enrich insights generated by biodiversity-

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and conservation-related studies, offering an additional measure to molecular-based technologies such as DNA barcoding and eDNA (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.

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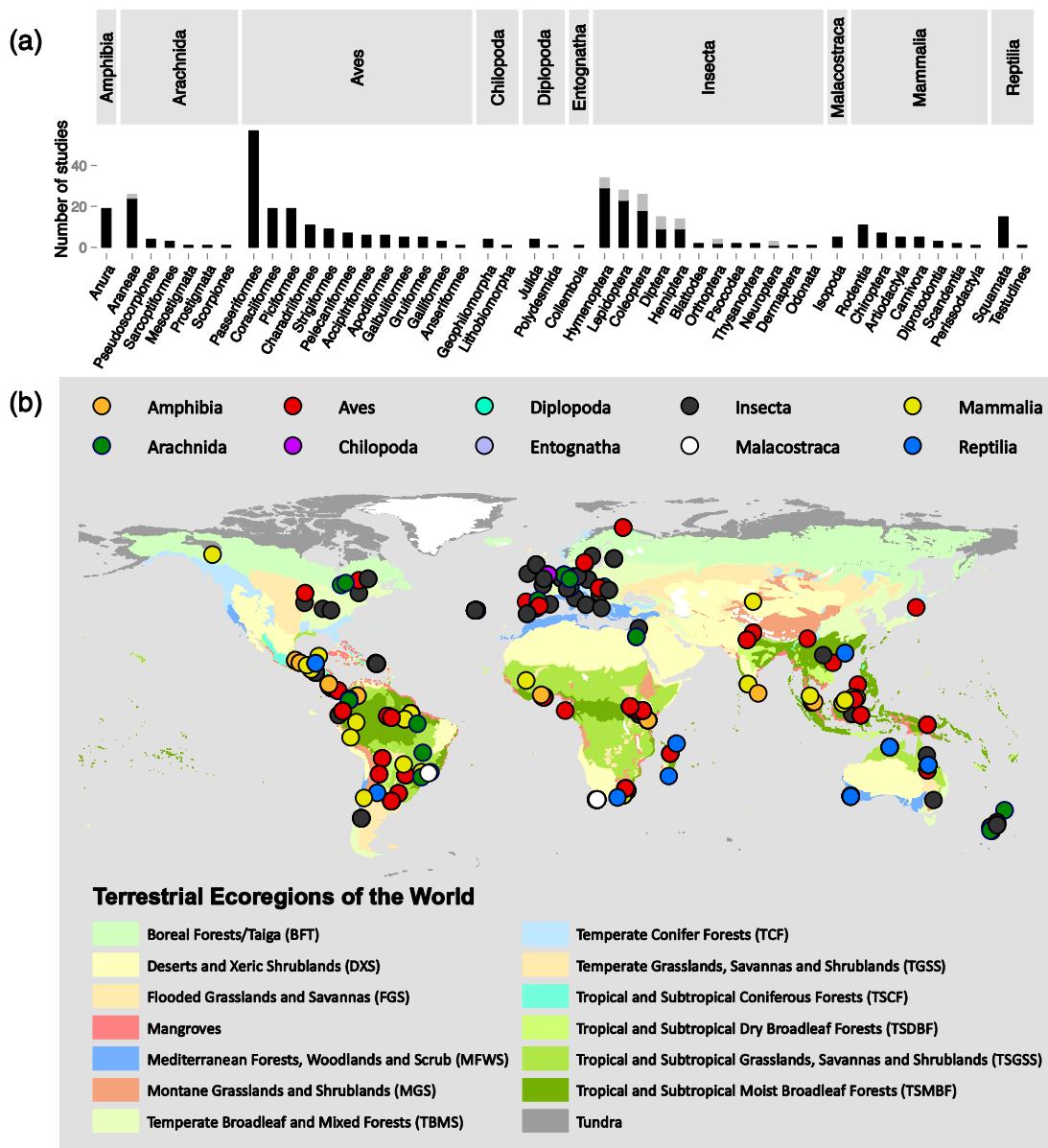
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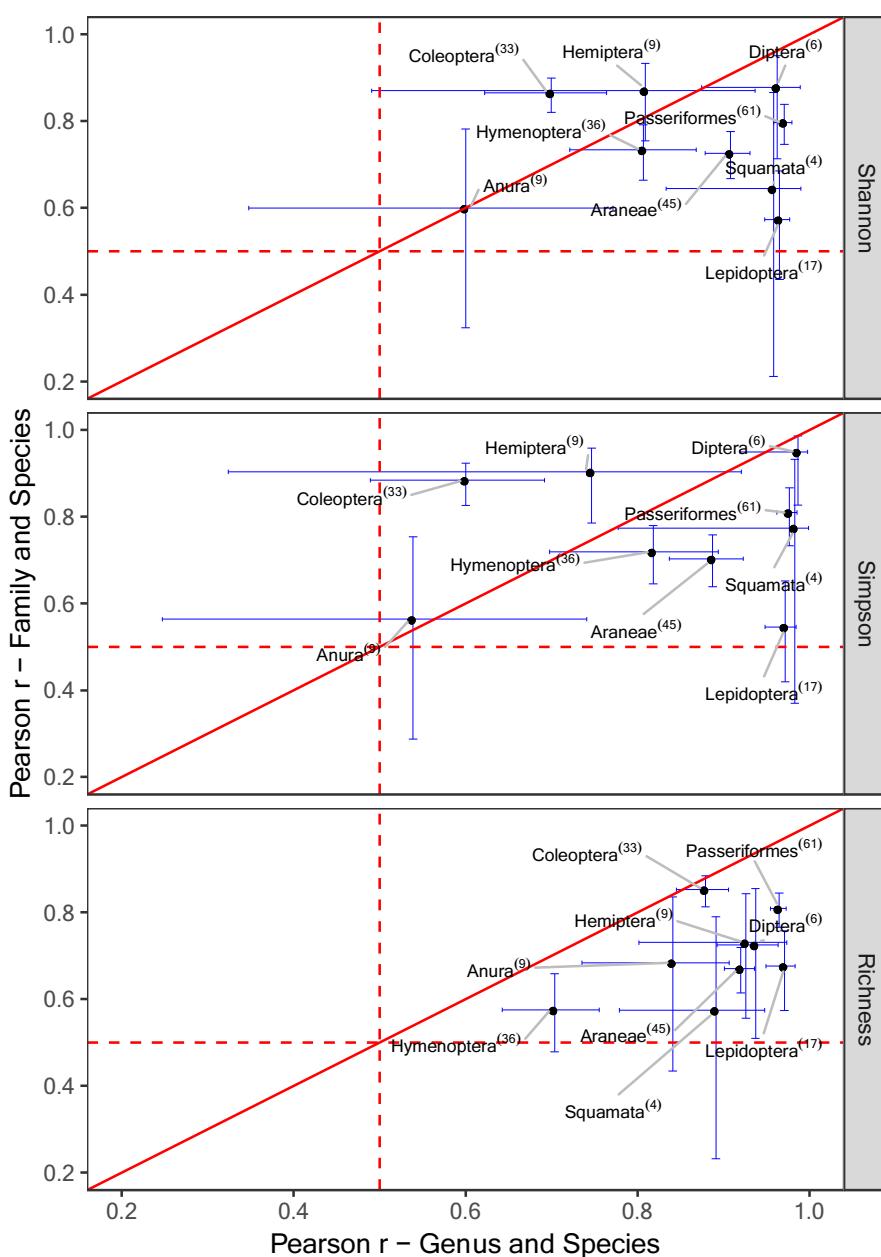
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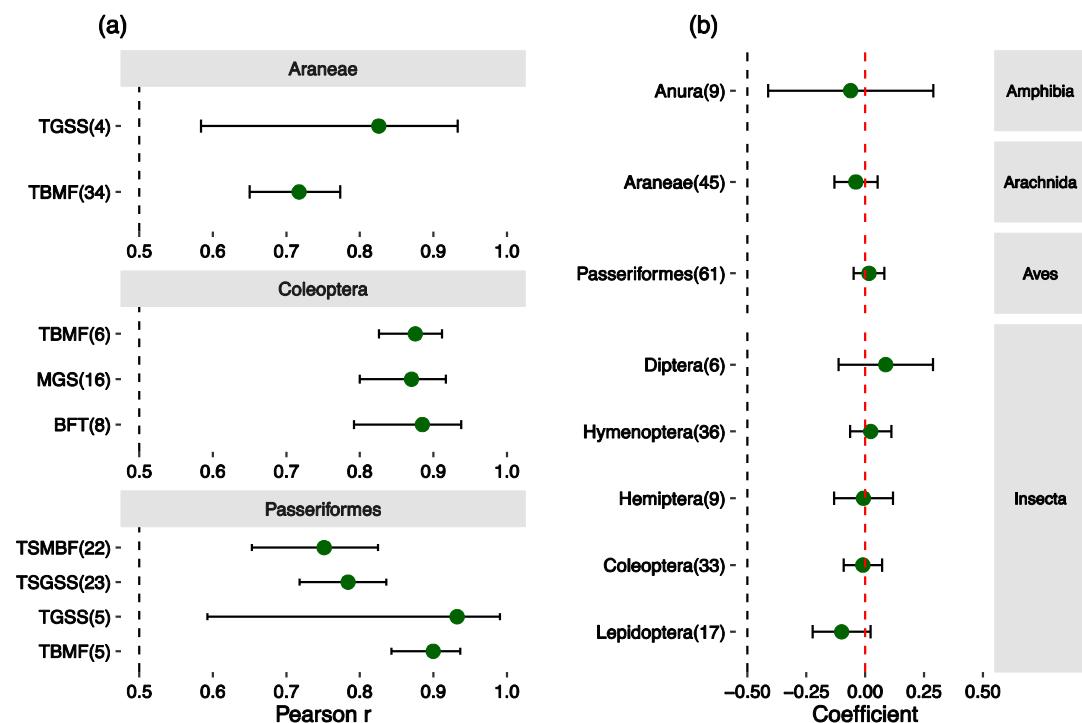
678 **Figures**

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680 Figure 1. World map of biodiversity studies covering all families with an order
681 of terrestrial animals in the PREDICTS database (Hudson et al., 2017). Panel
682 a: grey bars represent studies that identify taxa to family level only, while black
683 bars represent studies that identify taxa in addition to (morpho-)species-level.
684 Panel b: locations of species-level identified studies across the Terrestrial
685 Ecoregions of the World.



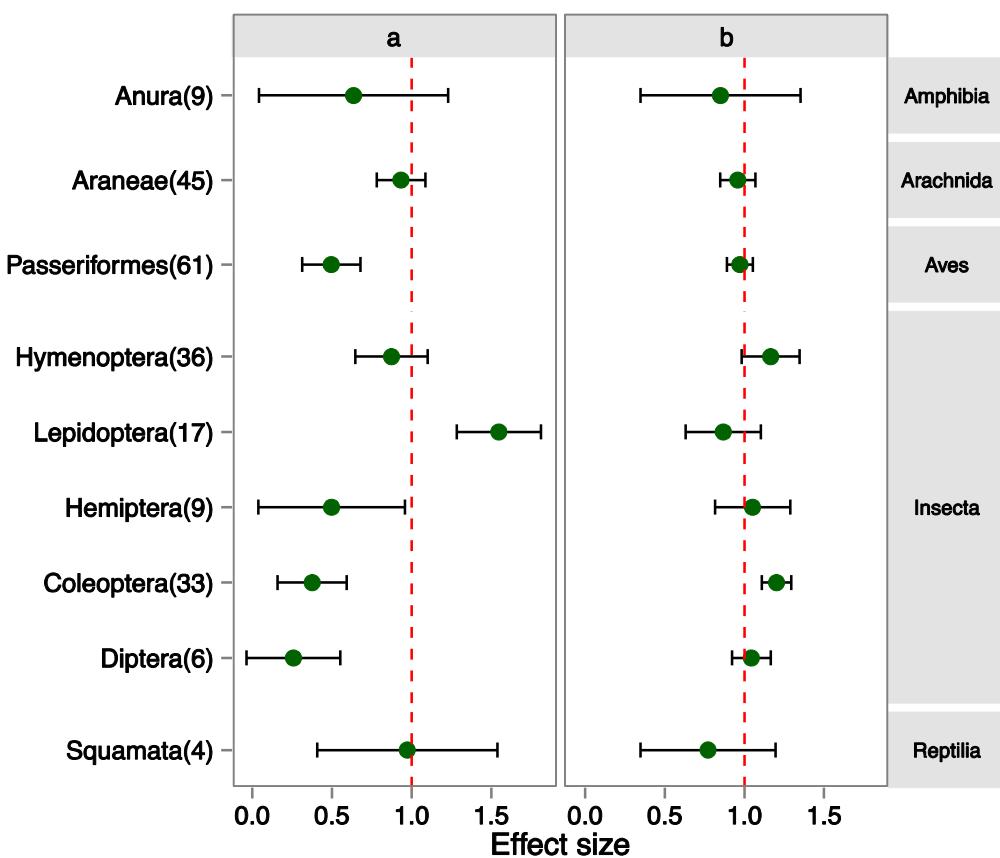
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687 Figure 2. Meta-analysis results from random effects models showing
 688 Pearson's r of family-species relationships and genus-species relationships for
 689 the Shannon diversity index, the Simpson's diversity index and observed
 690 richness in nine different orders of terrestrial animals. Numbers in brackets
 691 refer to the number of studies, and error bars show 95% CI; dashed lines refer
 692 to values of $r = 0.5$; solid lines refer to a 1:1 relationship between x and y axis;
 693 points below the 1:1 diagonal line represent cases where r values for
 694 family-species relationship are lower than for genus-species relationship and
 695 vice versa. Orders represented in less than three studies were not included.



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697 Figure 3 Meta-analysis results (a) for Pearson's r (based on the Shannon
 698 diversity index) in different biomes (only orders that cover at least 2 biomes
 699 with at least 3 studies from each biome were included); TBMF: Temperate
 700 Broadleaf & Mixed Forests, TGSS: Temperate Grasslands, Savannas &
 701 Shrublands, TSMBF: Tropical & Subtropical Moist Broadleaf Forests, TSGSS:
 702 Tropical & Subtropical Grasslands, Savannas & Shrublands, MGS: Montane
 703 Grasslands & Shrublands, BFT: Boreal Forests/Taiga; and slope of the
 704 relationship between Pearson's r and sample size (b), showing the median log
 705 number of individuals per site in each study



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707 Figure 4. Meta-analysis results from random effects models showing the
708 intercept (a) and slope (b) of order-specific regression models of species-level
709 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 <3 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-transformed number of individuals), elevation and latitude for different taxa (Equation 5 in Appendix S4, orders more than six studies were included in the regression); Asterisks show significance levels (*≤0.05; **≤0.01; *<0.001)**

Class	Order	Number of studies	Number of species	Number of families	Species / family	Species / genus	Species / (Shannon)	Species / (Richness)	Regression coefficients		
									genus		Latitude
									Sample Size	Altitude	
Amphibia	Anura	9	9.3	5.0	4.3	1.6 (1.4-1.8)	1.8 (1.6 - 2)	1.5 (1.3 - 1.7)	1.6 (1.5 - 1.8)	0.29 ± 0.17	-0.14 ± 0.25
Arachnida	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)	0.72 ± 0.18	0.19 ± 0.1
Aves	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)	0.42 ± 0.1	-0.11 ± 0.05 *
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)	0.7 ± 0.27 *	0.63 ± 0.2 **
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)	0.2 ± 0.16	0.2 ± 0.11
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)	0.81 ± 0.41	1.23 ± 0.37 **
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)	0.42 ± 0.27	-0.49 ± 0.3
Diptera		6	13.2	10.9	6.5	1.8 (1.2-2.5)	2.6 (1.0 - 4.3)	1.1 (1 - 1.3)	1.3 (1 - 1.6)	/	/
Reptilia	Squamata	4	6.8	6.5	4.1	2.1 (1.2-3.0)	2 (1.3 - 2.7)	1.1 (1 - 1.3)	1.1 (1 - 1.2)	/	/

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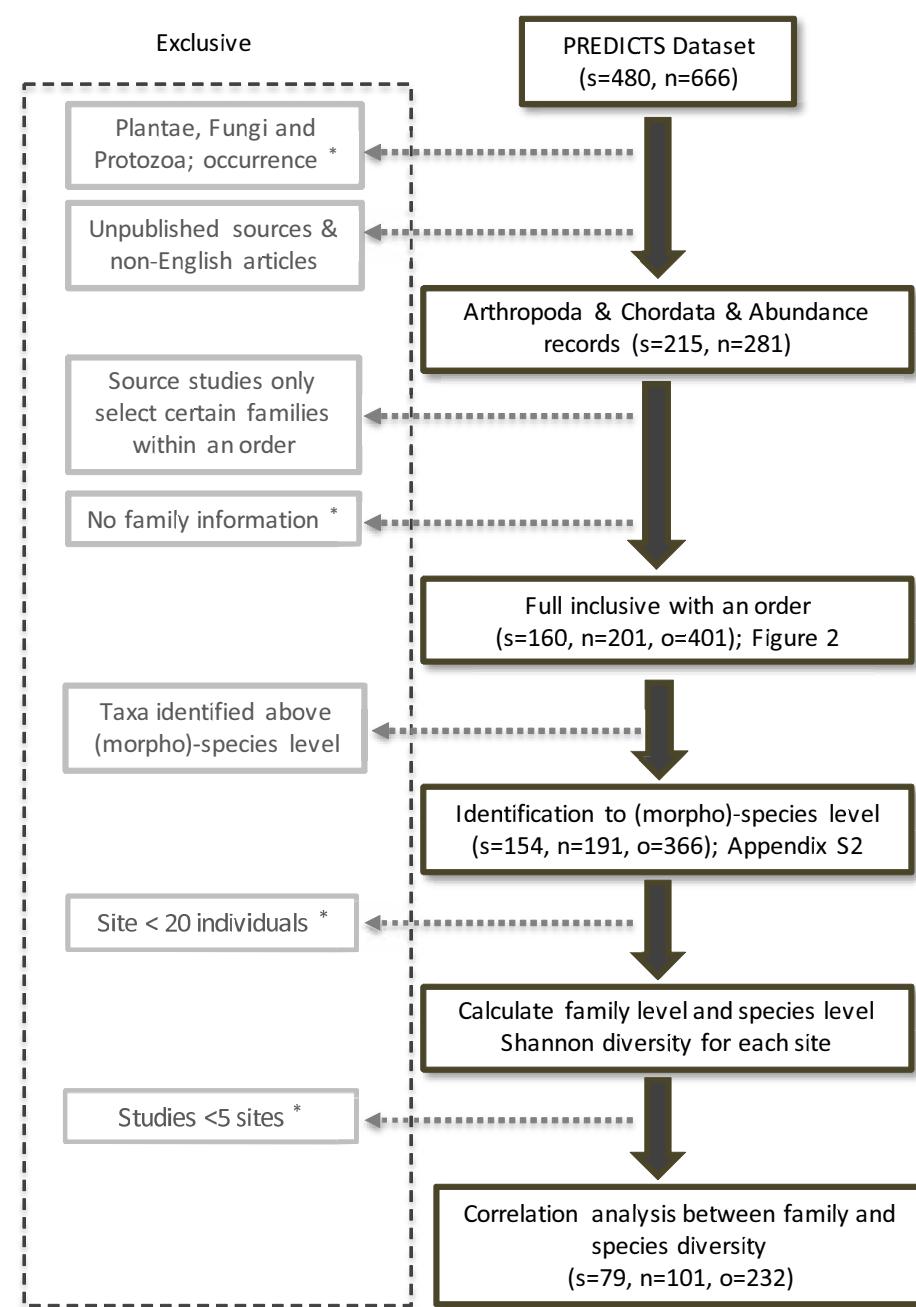
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Electronic Supplementary Materials

Appendix S1. Flow chart of the data selection, s: number of source articles, n: number of studies, o: number of order x studies; * refers to the selection criteria was applied at dataset records



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Appendix S2. List of selected studies from the PREDICTS database (<https://doi.org/10.5519/0066354>) dataset. “Source_ID” and “SS” are indices for the PREDICTS data source, referring to the ID of the Data Source and the code combination of “Source_ID” and “Study_number”.

No.	Source_ID	SS	Class	Order
1	MJ1_2013_Adum	MJ1_2013_Adum 1	Amphibia	Anura
2	SE2_2012_Craig	SE2_2012_Craig 1	Amphibia	Anura
3	SE2_2014a_Craig	SE2_2014a_Craig 1	Amphibia	Anura
4	SE2_2014b_Craig	SE2_2014b_Craig 1	Amphibia	Anura
5	SC1_2008_Eigenbrod	SC1_2008_Eigenbrod 1	Amphibia	Anura
6	DI1_2013_Faruk	DI1_2013_Faruk 1	Amphibia	Anura
7	SE1_2004_Gutierrez	SE1_2004_Gutierrez 1	Amphibia	Anura
8	SE1_2004_Gutierrez	SE1_2004_Gutierrez 2	Amphibia	Anura
9	CM1_2012_Hilje	CM1_2012_Hilje 1	Amphibia	Anura
10	SE1_2011_Isaacs	SE1_2011_Isaacs 1	Amphibia	Anura
11	SC1_2014_Kurz	SC1_2014_Kurz 1	Amphibia	Anura
12	HZ1_2012_Kutt	HZ1_2012_Kutt 1	Amphibia	Anura
13	MJ1_2012_Malonza	MJ1_2012_Malonza 1	Amphibia	Anura
14	DL1_2013_OforiBoateng	DL1_2013_OforiBoateng 1	Amphibia	Anura

1	4	5	KS1_2012_Pethiyagoda	KS1_2012_Pethiyagoda 1	Amphibia	Anura
6	5	15	HP1_2004_Pineda	HP1_2004_Pineda 1	Amphibia	Anura
7	6	16	YP1_2012_Sung	YP1_2012_Sung 1	Amphibia	Anura
8	7	17	SC1_2006_UrbinaCardona	SC1_2006_UrbinaCardona 1	Amphibia	Anura
9	8	18	DL1_2009_Woinarski	DL1_2009_Woinarski 2	Amphibia	Anura
10	9	19	AD1_2008_Billeter	AD1_2008_Billeter 15	Arachnida	Araneae
11	10	20	AD1_2008_Billeter	AD1_2008_Billeter 16	Arachnida	Araneae
12	11	21	AD1_2008_Billeter	AD1_2008_Billeter 17	Arachnida	Araneae
13	12	22	AD1_2008_Billeter	AD1_2008_Billeter 18	Arachnida	Araneae
14	13	23	AD1_2008_Billeter	AD1_2008_Billeter 19	Arachnida	Araneae
15	14	24	AD1_2008_Billeter	AD1_2008_Billeter 20	Arachnida	Araneae
16	15	25	AD1_2008_Billeter	AD1_2008_Billeter 21	Arachnida	Araneae
17	16	26	AD1_2008_Billeter	KS1_2006_Borges 1	Arachnida	Araneae
18	17	27	KS1_2006_Borges	VK1_2008_Buddle 1	Arachnida	Araneae
19	18	28	VK1_2008_Buddle	SE1_2012_Cabra 1	Arachnida	Araneae
20	19	29	SE1_2012_Cabra	SC1_2011_Meijer 1	Arachnida	Araneae
21	20	30	SC1_2011_Meijer	CC1_2004_Clark 1	Arachnida	Araneae
22	21	31	CC1_2004_Clark	GPI_2011_Freire 1	Arachnida	Araneae
23	22	32	GPI_2011_Freire	SE2_2010_Gaigher 1	Arachnida	Araneae
24	23	33	SE2_2010_Gaigher			
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1	4	34	HP1_2008_Kapoor	HP1_2008_Kapoor 1	Arachnida	Araneae
2	5	35	CM1_2008_LoManHung	CM1_2008_LoManHung 1	Arachnida	Araneae
3	6	36	VB1_2011_LoManHung	VB1_2011_LoManHung 1	Arachnida	Araneae
4	7	37	DB1_2010_Magura	DB1_2010_Magura 1	Arachnida	Araneae
5	8	38	CC1_2014_MalumbresOlarte	CC1_2014_MalumbresOlarte 1	Arachnida	Araneae
6	9	39	SH1_2012_Norfolk	SH1_2012_Norfolk 1	Arachnida	Araneae
7	10	40	VK1_2011_Paradis	VK1_2011_Paradis 1	Arachnida	Araneae
8	11	41	SC1_2014_Raub	SC1_2014_Raub 1	Arachnida	Araneae
9	12	42	SC1_2005_Richardson	SC1_2005_Richardson 1	Arachnida	Araneae
10	13	43	VB1_2009_UeharaPrado	VB1_2009_UeharaPrado 1	Arachnida	Araneae
11	14	44	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Arachnida	Mesostigmata
12	15	45	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Arachnida	Prostigmata
13	16	46	SE1_2012_Cabra	SE1_2012_Cabra 1	Arachnida	Pseudoscorpiones
14	17	47	SC1_2011_Meijer	SC1_2011_Meijer 1	Arachnida	Pseudoscorpiones
15	18	48	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Arachnida	Pseudoscorpiones
16	19	49	SC1_2005_Richardson	SC1_2005_Richardson 1	Arachnida	Pseudoscorpiones
17	20	50	MG1_2005_Arroyo	MG1_2005_Arroyo 1	Arachnida	Sarcophiformes
18	21	51	SE1_2012_Cabra	SE1_2012_Cabra 1	Arachnida	Sarcophiformes
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1	4	52	MG1_2006_Zaitsev	MG1_2006_Zaitsev 1	Arachnida	Sarcophiformes
2	5	53	CM1_2008_LoManHung	CM1_2008_LoManHung 1	Arachnida	Scorpiones
3	6	54	DL1_2005_Cockle	DL1_2005_Cockle 1	Aves	Accipitriformes
4	7	55	HP1_2008_Gomes	HP1_2008_Gomes 1	Aves	Accipitriformes
5	8	56	HP1_2010_Lasky	HP1_2010_Lasky 1	Aves	Accipitriformes
6	9	57	HP1_2010_Lasky	HP1_2010_Lasky 2	Aves	Accipitriformes
7	10	58	DI1_2010_Milder	DI1_2010_Milder 2	Aves	Accipitriformes
8	11	59	TN1_2007_ODea	TN1_2007_ODea 1	Aves	Accipitriformes
9	12	60	HW1_2011_Cerezo	HW1_2011_Cerezo 1	Aves	Anseriformes
10	13	61	DL1_2005_Cockle	DL1_2005_Cockle 1	Aves	Apodiformes
11	14	62	HP1_2008_Gomes	HP1_2008_Gomes 1	Aves	Apodiformes
12	15	63	DI1_2010_Milder	DI1_2010_Milder 2	Aves	Apodiformes
13	16	64	TN1_2007_ODea	TN1_2007_ODea 1	Aves	Apodiformes
14	17	65	MH1_2010_Sheldon	MH1_2010_Sheldon 1	Aves	Apodiformes
15	18	66	KS1_2009_SuarezRubio	KS1_2009_SuarezRubio 1	Aves	Apodiformes
16	19	67	DI1_2013_Azhar	DI1_2013_Azhar 1	Aves	Charadriiformes
17	20	68	DL1_2009_Azpiroz	DL1_2009_Azpiroz 1	Aves	Charadriiformes
18	21	69	HW1_2005_Baldi	HW1_2005_Baldi 1	Aves	Charadriiformes
19	22	70	HW1_2011_Cerezo	HW1_2011_Cerezo 1	Aves	Charadriiformes
20	23					
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1	4	5	MJ1_2013_Reynolds	MJ1_2013_Reynolds 1	Aves	Gruiformes
6	5	109	DL1_2008_Aben	DL1_2008_Aben 1	Aves	Passeriformes
7	6	110	DI1_2013_Azhar	DI1_2013_Azhar 1	Aves	Passeriformes
8	7	111	DL1_2009_Azpiroz	DL1_2009_Azpiroz 1	Aves	Passeriformes
9	8	112	HW1_2005_Baldi	HW1_2005_Baldi 1	Aves	Passeriformes
10	9	113	FB1_2007a_Barlow	FB1_2007a_Barlow 1	Aves	Passeriformes
11	10	114	FB1_2007a_Barlow	FB1_2007a_Barlow 2	Aves	Passeriformes
12	11	115	HP1_2007_Borges	HP1_2007_Borges 1	Aves	Passeriformes
13	12	116	SE2_2013_Brandt	SE2_2013_Brandt 1	Aves	Passeriformes
14	13	117	HW1_2011_Cerezo	HW1_2011_Cerezo 1	Aves	Passeriformes
15	14	118	HW1_2007_Chapman	HW1_2007_Chapman 1	Aves	Passeriformes
16	15	119	DL1_2005_Cockle	DL1_2005_Cockle 1	Aves	Passeriformes
17	16	120	DI1_2013_deLima	DI1_2013_deLima 1	Aves	Passeriformes
18	17	121	DB1_2010_Dures	DB1_2010_Dures 1	Aves	Passeriformes
19	18	122	VK1_2011_Edenius	VK1_2011_Edenius 1	Aves	Passeriformes
20	19	123	HP1_2008_Farwig	HP1_2008_Farwig 1	Aves	Passeriformes
21	20	124	HP1_2008_Gomes	HP1_2008_Gomes 1	Aves	Passeriformes
22	21	125	SH1_2012_Ims	SH1_2012_Ims 1	Aves	Passeriformes
23	22	126	HP1_2009_Kessler	HP1_2009_Kessler 5	Aves	Passeriformes
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1	GP1_2007_Kutt	GP1_2007_Kutt 2	Aves	Passeriformes
2	HZ1_2012_Kutt	HZ1_2012_Kutt 1	Aves	Passeriformes
3	HP1_2010_Lasky	HP1_2010_Lasky 1	Aves	Passeriformes
4	HP1_2010_Lasky	HP1_2010_Lasky 2	Aves	Passeriformes
5	HP1_2010_Lasky	MJ1_2009_Lehouck 1	Aves	Passeriformes
6	HZ1_2012_Kutt	MJ1_2009_Lehouck 2	Aves	Passeriformes
7	HP1_2010_Lasky	MJ1_2009_Lehouck 3	Aves	Passeriformes
8	HP1_2010_Lasky	MJ1_2009_Lehouck 4	Aves	Passeriformes
9	HP1_2010_Lasky	MJ1_2009_Lehouck 5	Aves	Passeriformes
10	HP1_2010_Lasky	DG1_2013_Zou 1	Aves	Passeriformes
11	MJ1_2009_Lehouck	DL1_2011_Mallari 1	Aves	Passeriformes
12	MJ1_2009_Lehouck	DL1_2011_Mallari 2	Aves	Passeriformes
13	MJ1_2009_Lehouck	DI1_2010_Milder 2	Aves	Passeriformes
14	MJ1_2009_Lehouck	MJ1_2008_Munyekeny 1	Aves	Passeriformes
15	MJ1_2009_Lehouck	DI1_2004_Naidoo 1	Aves	Passeriformes
16	MJ1_2009_Lehouck	BS1_2012_Naithani 1	Aves	Passeriformes
17	MJ1_2009_Lehouck	MJ1_2013_Ndanganga 1	Aves	Passeriformes
18	MJ1_2009_Lehouck	MJ1_2013_Ndanganga 2	Aves	Passeriformes
19	MJ1_2009_Lehouck	DI1_2011_Neus Schulz 1	Aves	Passeriformes
20	MJ1_2009_Lehouck	TN1_2007_Odea 1	Aves	Passeriformes
21	DG1_2013_Zou			
22	DL1_2011_Mallari			
23	DL1_2011_Mallari			
24	DI1_2010_Milder			
25	DI1_2010_Milder			
26	MJ1_2008_Munyekeny			
27	MJ1_2008_Munyekeny			
28	DI1_2004_Naidoo			
29	BS1_2012_Naithani			
30	BS1_2012_Naithani			
31	MJ1_2013_Ndanganga			
32	MJ1_2013_Ndanganga			
33	MJ1_2013_Ndanganga			
34	DI1_2011_Neus Schulz			
35	DI1_2011_Neus Schulz			
36	TN1_2007_Odea			
37	TN1_2007_Odea			
38	TN1_2007_Odea			
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1	147	TN1_1998_Owiunji 1	Aves	Passeriformes
2	148	MH1_2011_Phalan 1	Aves	Passeriformes
3	149	DL1_2012_Politi 1	Aves	Passeriformes
4	150	KS1_2005_Pons 1	Aves	Passeriformes
5	151	DL1_2010_Proenca 2	Aves	Passeriformes
6	152	DI1_2012_Reid 1	Aves	Passeriformes
7	153	SC1_2010_ReyBenayas 1	Aves	Passeriformes
8	154	MJ1_2013_Reynolds 1	Aves	Passeriformes
9	155	SC1_2014_Sam 1	Aves	Passeriformes
10	156	SC1_2014_Sam 2	Aves	Passeriformes
11	157	SC2_2012_Santana 1	Aves	Passeriformes
12	158	HP1_2007_Shahabuddin 1	Aves	Passeriformes
13	159	MH1_2010_Sheldon 1	Aves	Passeriformes
14	160	VK1_2007_StLaurent 3	Aves	Passeriformes
15	161	SC1_2011_Stouffer 1	Aves	Passeriformes
16	162	KS1_2009_SuarezRubio 1	Aves	Passeriformes
17	163	CC1_2013_Waite 1	Aves	Passeriformes
18	164	DL1_2009_Woinarski 1	Aves	Passeriformes
19	165	HP1_2006_Wunderle 1	Aves	Passeriformes

1	4	5	AD1_2012_Yamaura	AD1_2012_Yamaura 1	Aves	Passeriformes
2	6	7	HW1_2011_Cerezo	HW1_2011_Cerezo 1	Aves	Pelecaniformes
3	8	9	DB1_2010_Dures	DB1_2010_Dures 1	Aves	Pelecaniformes
4	10	11	LK1_2009_Hayward	LK1_2009_Hayward 1	Aves	Pelecaniformes
5	12	13	MJ1_2013_Ndanganga	MJ1_2013_Ndanganga 1	Aves	Pelecaniformes
6	14	15	MJ1_2013_Ndanganga	MJ1_2013_Ndanganga 2	Aves	Pelecaniformes
7	16	17	MJ1_2013_Reynolds	MJ1_2013_Reynolds 1	Aves	Pelecaniformes
8	17	18	DL1_2009_Woinarski	DL1_2009_Woinarski 1	Aves	Pelecaniformes
9	19	20	DL1_2008_Aben	DL1_2008_Aben 1	Aves	Piciformes
10	21	22	DI1_2013_Azhar	DI1_2013_Azhar 1	Aves	Piciformes
11	23	24	FB1_2007a_Barlow	FB1_2007a_Barlow 1	Aves	Piciformes
12	25	26	HP1_2007_Borges	HP1_2007_Borges 1	Aves	Piciformes
13	27	28	DL1_2005_Cockle	DL1_2005_Cockle 1	Aves	Piciformes
14	29	30	HP1_2008_Farwig	HP1_2008_Farwig 1	Aves	Piciformes
15	31	32	HP1_2008_Gomes	HP1_2008_Gomes 1	Aves	Piciformes
16	33	34	MJ1_2009_Lehouck	MJ1_2009_Lehouck 1	Aves	Piciformes
17	35	36	MJ1_2009_Lehouck	MJ1_2009_Lehouck 4	Aves	Piciformes
18	37	38	DI1_2010_Milder	DI1_2010_Milder 2	Aves	Piciformes
19	39	40	MJ1_2008_Munyekenyе	MJ1_2008_Munyekenyе 1	Aves	Piciformes

1	4	5	BS1_2012_Naithani	BS1_2012_Naithani 1	Aves	Piciformes
2	6	7	DI1_2011_Neuschulz	DI1_2011_Neuschulz 1	Aves	Piciformes
3	8	9	TN1_2007_ODea	TN1_2007_ODea 1	Aves	Piciformes
4	10	11	TN1_1998_Owiunji	TN1_1998_Owiunji 1	Aves	Piciformes
5	12	13	MH1_2011_Phalan	MH1_2011_Phalan 1	Aves	Piciformes
6	14	15	DL1_2012_Politi	DL1_2012_Politi 1	Aves	Piciformes
7	16	17	DI1_2012_Reid	DI1_2012_Reid 1	Aves	Piciformes
8	18	19	MH1_2010_Sheldon	MH1_2010_Sheldon 1	Aves	Piciformes
9	20	21	DI1_2013_Azhar	DI1_2013_Azhar 1	Aves	Strigiformes
10	22	23	DL1_2009_Azpiroz	DL1_2009_Azpiroz 1	Aves	Strigiformes
11	24	25	DL1_2005_Cockle	DL1_2005_Cockle 1	Aves	Strigiformes
12	26	27	HP1_2009_Kessler	HP1_2009_Kessler 5	Aves	Strigiformes
13	28	29	GP1_2007_Kutt	GP1_2007_Kutt 2	Aves	Strigiformes
14	30	31	HZ1_2012_Kutt	HZ1_2012_Kutt 1	Aves	Strigiformes
15	32	33	DI1_2010_Milder	DI1_2010_Milder 2	Aves	Strigiformes
16	34	35	TN1_2007_ODea	TN1_2007_ODea 1	Aves	Strigiformes
17	36	37	DL1_2009_Woinarski	DL1_2009_Woinarski 1	Aves	Strigiformes
18	38	39	KS1_2006_Borges	KS1_2006_Borges 1	Chilopoda	Geophilomorpha
19	40	41	SC1_2011_Meijer	SC1_2011_Meijer 1	Chilopoda	Geophilomorpha

1	VB1_2008_Smith	Chilopoda	Geophilomorpha
2	VB1_2008a_Smith	Chilopoda	Geophilomorpha
3	SE2_2010_Gaigher 1	Chilopoda	Lithobiomorpha
4	KS1_2006_Borges 1	Diplopoda	Julida
5	SC1_2011_Meijer 1	Diplopoda	Julida
6	VB1_2008_Smith 1	Diplopoda	Julida
7	VB1_2008a_Smith 1	Diplopoda	Julida
8	SE2_2010_Gaigher 1	Diplopoda	Julida
9	KS1_2006_Borges 1	Diplopoda	Polydesmida
10	SC1_2011_Meijer 1	Diplopoda	Polydesmida
11	VB1_2008a_Smith 1	Diplopoda	Polydesmida
12	VB1_2008_Smith 1	Diplopoda	Polydesmida
13	SC1_2011_Meijer 1	Diplopoda	Polydesmida
14	SC1_2011_Meijer 1	Entognatha	Collembola
15	SC1_2005_Richardson	Insecta	Blattodea
16	SC1_2005_Richardson	Insecta	Blattodea
17	SC1_2011_Meijer 1	Insecta	Coleoptera
18	SC1_2011_Meijer 1	Insecta	Coleoptera
19	SC1_2011_Meijer 1	Insecta	Coleoptera
20	SC1_2011_Meijer 1	Insecta	Coleoptera
21	SE2_2010_Gaigher 1	Insecta	Coleoptera
22	KS1_2006_Borges	Insecta	Coleoptera
23	SC1_2011_Meijer 1	Insecta	Coleoptera
24	VB1_2012_Carpenter 5	Insecta	Coleoptera
25	CC1_2007_Ewers 1	Insecta	Coleoptera
26	SE2_2010_Gaigher 1	Insecta	Coleoptera
27	AD1_2013_Grass 1	Insecta	Coleoptera
28	HW1_2012_Jonsell 1	Insecta	Coleoptera
29	HP1_2009_Kessler 3	Insecta	Coleoptera
30	VB1_2008_Smith 1	Chilopoda	Geophilomorpha
31	VB1_2008a_Smith 1	Chilopoda	Geophilomorpha
32	SE2_2010_Gaigher 1	Chilopoda	Lithobiomorpha
33	KS1_2006_Borges 1	Diplopoda	Julida
34	SC1_2011_Meijer 1	Diplopoda	Julida
35	VB1_2008_Smith 1	Diplopoda	Julida
36	VB1_2008a_Smith 1	Diplopoda	Julida
37	SE2_2010_Gaigher 1	Diplopoda	Julida

1	4	223	VK1_2011_Legare	VK1_2011_Legare 1	Insecta	Coleoptera
2	5	224	VK1_2011_Legare	VK1_2011_Legare 2	Insecta	Coleoptera
3	6	225	CC1_2013_Litchwark	CC1_2013_Litchwark 1	Insecta	Coleoptera
4	7	226	HP1_2013_Mico	HP1_2013_Mico 1	Insecta	Coleoptera
5	8	227	DI1_2012_Muchane	DI1_2012_Muchane 1	Insecta	Coleoptera
6	9	228	SH1_2012_Norfolk	SH1_2012_Norfolk 1	Insecta	Coleoptera
7	10	229	MG1_2008_Paritsis	MG1_2008_Paritsis 1	Insecta	Coleoptera
8	11	230	AD1_2010_Quintero	AD1_2010_Quintero 1	Insecta	Coleoptera
9	12	231	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Coleoptera
10	13	232	AD1_2011_Schuepp	AD1_2011_Schuepp 1	Insecta	Coleoptera
11	14	233	SC1_2011_Meijer	SC1_2011_Meijer 1	Insecta	Dermoptera
12	15	234	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Insecta	Diptera
13	16	235	AD1_2013_Grass	AD1_2013_Grass 1	Insecta	Diptera
14	17	236	CC1_2013_Litchwark	CC1_2013_Litchwark 1	Insecta	Diptera
15	18	237	AD1_2010_Quintero	AD1_2010_Quintero 1	Insecta	Diptera
16	19	238	CC1_2014_Rader	CC1_2014_Rader 1	Insecta	Diptera
17	20	239	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Diptera
18	21	240	HW1_2011_Savage	HW1_2011_Savage 1	Insecta	Diptera
19	22	241	AD1_2011_Schuepp	AD1_2011_Schuepp 1	Insecta	Diptera
20	23					
21	24					
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1	4	242	AD1_2009_Vergara	AD1_2009_Vergara 1	Insecta	Diptera
2	5	243	KS1_2006_Borges	KS1_2006_Borges 1	Insecta	Hemiptera
3	6	244	SC1_2011_Meijer	SC1_2011_Meijer 1	Insecta	Hemiptera
4	7	245	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Insecta	Hemiptera
5	8	246	DB1_2004_Helden	DB1_2004_Helden 1	Insecta	Hemiptera
6	9	247	DB1_2004_Helden	DB1_2004_Helden 2	Insecta	Hemiptera
7	10	248	MG1_2012_Littlewood	MG1_2012_Littlewood 1	Insecta	Hemiptera
8	11	249	MG1_2012_Littlewood	MG1_2012_Littlewood 2	Insecta	Hemiptera
9	12	250	SE2_2005_Moir	SE2_2005_Moir 1	Insecta	Hemiptera
10	13	251	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Hemiptera
11	14	252	AD1_2011_Bates	AD1_2011_Bates 1	Insecta	Hymenoptera
12	15	253	AD1_2008_Billeter	AD1_2008_Billeter 1	Insecta	Hymenoptera
13	16	254	AD1_2008_Billeter	AD1_2008_Billeter 2	Insecta	Hymenoptera
14	17	255	AD1_2008_Billeter	AD1_2008_Billeter 3	Insecta	Hymenoptera
15	18	256	AD1_2008_Billeter	AD1_2008_Billeter 4	Insecta	Hymenoptera
16	19	257	AD1_2008_Billeter	AD1_2008_Billeter 5	Insecta	Hymenoptera
17	20	258	AD1_2008_Billeter	AD1_2008_Billeter 6	Insecta	Hymenoptera
18	21	259	AD1_2008_Billeter	AD1_2008_Billeter 8	Insecta	Hymenoptera
19	22	260	AD1_2008_Billeter	AD1_2008_Billeter 9	Insecta	Hymenoptera

1	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45																																																				
261	AD1_2008_Billeter	AD1_2008_Billeter 10	Insecta	Hymenoptera	262	AD1_2008_Billeter	AD1_2008_Billeter 11	Insecta	Hymenoptera	263	AD1_2008_Billeter	AD1_2008_Billeter 12	Insecta	Hymenoptera	264	AD1_2008_Billeter	AD1_2008_Billeter 13	Insecta	Hymenoptera	265	AD1_2008_Billeter	AD1_2008_Billeter 14	Insecta	Hymenoptera	266	AD1_2006_Blanche	AD1_2006_Blanche 1	Insecta	Hymenoptera	267	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Insecta	Hymenoptera	268	AD1_2013_Grass	AD1_2013_Grass 1	Insecta	Hymenoptera	269	AD1_2012_Lentini	AD1_2012_Lentini 1	Insecta	Hymenoptera	270	CC1_2013_Litchwark	CC1_2013_Litchwark 1	Insecta	Hymenoptera	271	AD1_2007_Meyer	AD1_2007_Meyer 1	Insecta	Hymenoptera	272	AD1_2007_Meyer	AD1_2007_Meyer 2	Insecta	Hymenoptera	273	AD1_2012_MudriStojnic	AD1_2012_MudriStojnic 1	Insecta	Hymenoptera	274	AD1_2004_Quaranta	AD1_2004_Quaranta 1	Insecta	Hymenoptera	275	AD1_2010_Quintero	AD1_2010_Quintero 1	Insecta	Hymenoptera	276	CC1_2014_Rader	CC1_2014_Rader 1	Insecta	Hymenoptera	277	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Hymenoptera	278	AD1_2011_Schuepp	AD1_2011_Schuepp 1	Insecta	Hymenoptera	279	DI1_2005_Tylianakis	DI1_2005_Tylianakis 1	Insecta	Hymenoptera

280	AD1_2009_Vergara	AD1_2009_Vergara 1	Insecta
281	MG1_2006_Baur	MG1_2006_Baur 2	Insecta
282	MG1_2006_Baur	MG1_2006_Baur 3	Insecta
283	KS1_2006_Borges	KS1_2006_Borges 1	Insecta
284	SC1_2011_Meijer	SC1_2011_Meijer 1	Insecta
285	HP1_2004_Cleary	HP1_2004_Cleary 1	Insecta
286	SC2_2011_DAniello	SC2_2011_DAniello 1	Insecta
287	CC1_2012_deSassi	CC1_2012_deSassi 1	Insecta
288	AD1_2013_Grass	AD1_2013_Grass 1	Insecta
289	SC2_2012_Kati	SC2_2012_Kati 1	Insecta
290	HP1_2010_Krauss	HP1_2010_Krauss 3	Insecta
291	CC1_2013_Litchward	CC1_2013_Litchward 1	Insecta
292	LH1_2008_Littlewood	LH1_2008_Littlewood 1	Insecta
293	DI1_2010_Milder	DI1_2010_Milder 3	Insecta
294	AD1_2011_Peer	AD1_2011_Peer 1	Insecta
295	AD1_2011_Power	AD1_2011_Power 1	Insecta
296	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta
297	CM1_2011_Safian	CM1_2011_Safian 1	Insecta
298	HW1_2011_Summerville	HW1_2011_Summerville 1	Insecta

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37																																																										
299	SC1_2002_Summerville	SC1_2002_Summerville 1	Insecta	Lepidoptera	300	HW1_2006_Summerville	HW1_2006_Summerville 1	Insecta	Lepidoptera	301	SC2_2012_Verdasca	SC2_2012_Verdasca 1	Insecta	Lepidoptera	302	HB1_2009_Vu	HB1_2009_Vu 1	Insecta	Lepidoptera	303	AD1_2008_Franzen	AD1_2008_Franzen 1	Insecta	Lepidoptera	304	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Neuroptera	305	HP1_2004_Cleary	HP1_2004_Cleary 1	Insecta	Odonata	306	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Insecta	Orthoptera	307	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Orthoptera	308	KS1_2006_Borges	KS1_2006_Borges 1	Insecta	Psocidea	309	SC1_2011_Meijer	SC1_2011_Meijer 1	Insecta	Psocidea	310	KS1_2006_Borges	KS1_2006_Borges 1	Insecta	Thysanoptera	311	SC1_2011_Meijer	SC1_2011_Meijer 1	Insecta	Thysanoptera	312	SE2_2010_Gaigher	SE2_2010_Gaigher 1	Insecta	Malacostraca	313	VB1_2011_Magnini	VB1_2011_Magnini 1	Insecta	Malacostraca	314	SC1_2005_Richardson	SC1_2005_Richardson 1	Insecta	Malacostraca	315	VB1_2008_Smith	VB1_2008_Smith 1	Insecta	Malacostraca	316	VB1_2008a_Smith	VB1_2008a_Smith 1	Insecta	Malacostraca	317	HZ1_2013_Garmendia	HZ1_2013_Garmendia 1	Mammalia	Artiodactyla

1	4	318	LK1_2009_Hayward	LK1_2009_Hayward 1	Mammalia	Artiodactyla
2	5	319	HZ1_2009_McShea	HZ1_2009_McShea 1	Mammalia	Artiodactyla
3	6	320	DI1_2008_Sridhar	DI1_2008_Sridhar 1	Mammalia	Artiodactyla
4	7	321	DL1_2009_Woinarski	DL1_2009_Woinarski 2	Mammalia	Artiodactyla
5	8	322	HZ1_2013_Garmenda	HZ1_2013_Garmenda 1	Mammalia	Carnivora
6	9	323	LK1_2009_Hayward	LK1_2009_Hayward 1	Mammalia	Carnivora
7	10	324	SE2_2010_McCarthy	SE2_2010_McCarthy 1	Mammalia	Carnivora
8	11	325	HZ1_2009_McShea	HZ1_2009_McShea 1	Mammalia	Carnivora
9	12	326	DI1_2008_Sridhar	DI1_2008_Sridhar 1	Mammalia	Carnivora
10	13	327	HP1_2007c_Barlow	HP1_2007c_Barlow 1	Mammalia	Chiroptera
11	14	328	TN1_2007_CastroLuna	TN1_2007_CastroLuna 1	Mammalia	Chiroptera
12	15	329	HP1_2007_MacSwiney	HP1_2007_MacSwiney 1	Mammalia	Chiroptera
13	16	330	HP1_2008_Presley	HP1_2008_Presley 1	Mammalia	Chiroptera
14	17	331	LH1_2011_Shafie	LH1_2011_Shafie 1	Mammalia	Chiroptera
15	18	332	HP1_2007_Willig	HP1_2007_Willig 1	Mammalia	Chiroptera
16	19	333	DL1_2009_Woinarski	DL1_2009_Woinarski 2	Mammalia	Chiroptera
17	20	334	SE2_2012_Craig	SE2_2012_Craig 1	Mammalia	Diprotodontia
18	21	335	HZ1_2012_Kutt	HZ1_2012_Kutt 1	Mammalia	Diprotodontia
19	22	336	DL1_2009_Woinarski	DL1_2009_Woinarski 2	Mammalia	Diprotodontia
20	23					
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356	TN1_2003_Fabricius	TN1_2003_Fabricius 1	Reptilia	Squamata
357	SC1_2014_Kurz	SC1_2014_Kurz 1	Reptilia	Squamata
358	GP1_2007_Kutt	GP1_2007_Kutt 1	Reptilia	Squamata
359	HZ1_2012_Kutt	HZ1_2012_Kutt 1	Reptilia	Squamata
360	TN1_2008_Luja	TN1_2008_Luja 1	Reptilia	Squamata
361	HW1_2012_Pelegrin	HW1_2012_Pelegrin 1	Reptilia	Squamata
362	YP1_2012_Sung	YP1_2012_Sung 1	Reptilia	Squamata
363	SC1_2006_UrbinaCardona	SC1_2006_UrbinaCardona 1	Reptilia	Squamata
364	DL1_2009_Woinarski	DL1_2009_Woinarski 2	Reptilia	Squamata
365	DI1_2006_Scott	DI1_2006_Scott 1	Reptilia	Squamata
366	TN1_2008_Luja	TN1_2008_Luja 1	Reptilia	Testudines

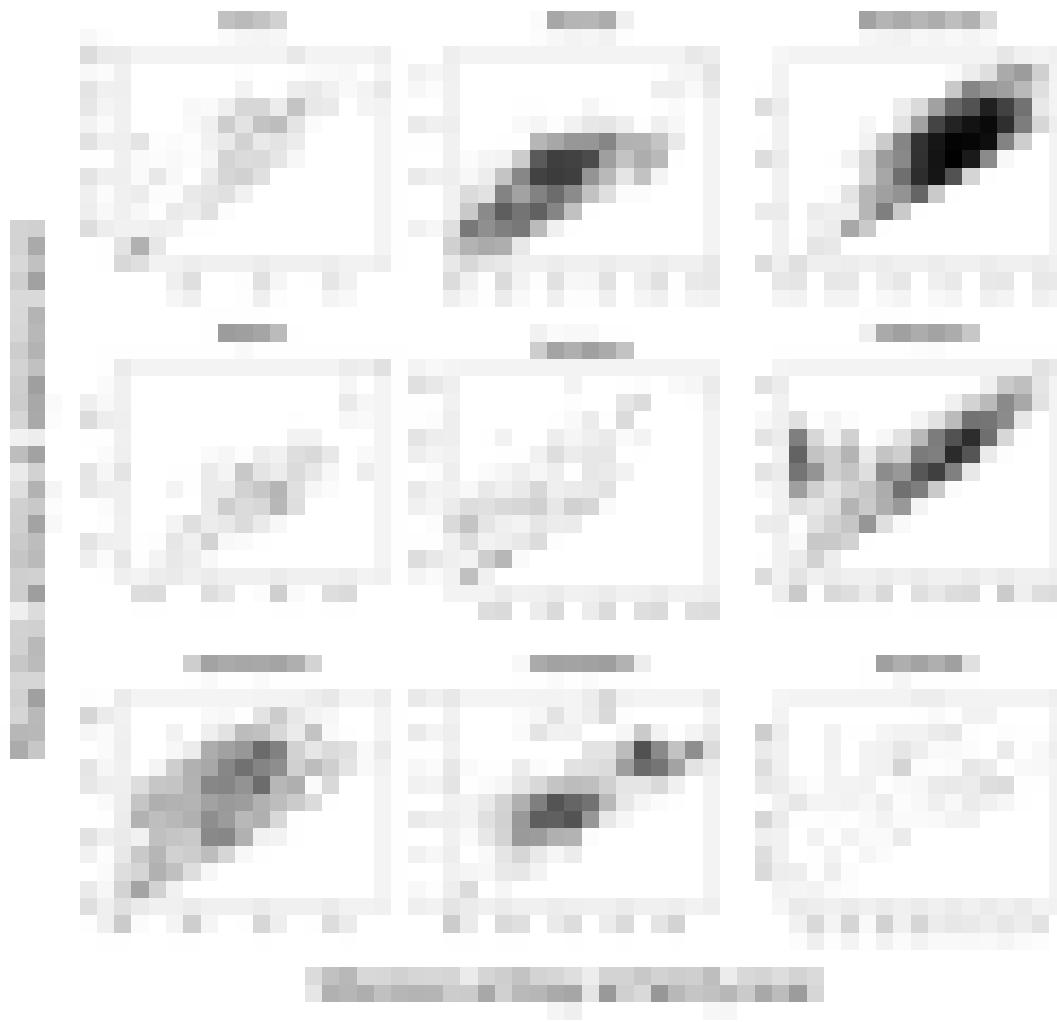
Appendix S3. Equations used in our analysis

Equation No.	Equation Name	Equation Expression	Explanation
1	Shannon entropy	$H_{m,j} = - \sum_{i=1}^{S_{m,j}} P_i \ln P_i$	For site j in study m , H is the Shannon entropy, D is the Shannon diversity, and S represents the number of species, while P_i is the relative abundance (proportion) of species i in the sample from the respective study site.
2	Shannon diversity	$D_{m,j} = \exp(H_{m,j})$	
3	Fisher's z	$z = 0.5 * \ln\left(\frac{1+r}{1-r}\right)$	" r " refers to the Pearson correlation coefficient and n represents the sample size.
4	Standard Error of Fisher's z	$SE_z = \sqrt{\frac{1}{n-3}}$	
5	Multiple linear regression	$\beta_j = k_1 * \log_e(N_j) + k_2 * Lat_{je} + k_3 * Alt_j + T$	Multiple linear regression reflects the species / family ratio for each study (β_j) in relation to the sample size, latitude and elevation. N_j , Lat_j and Alt_j are mean values for the number of individuals, latitude and elevation for the j^{th} study; $k1$, $k2$ and $k3$ are estimated coefficients, and T is the intercept.

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3 **Appendix S4.** Funnel plots showing the relationship between Fisher's z
4 (based on the correlation between Species and Family Shannon entropy index
5 values) and its's standard error for different orders.
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Appendix S5. Relationship between species- and family-level Shannon
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5 entropy indices for different orders.
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3 1 **Appendix S6.** Influence of sample size (number of individuals) on the species
4 / family ratio for Araneae, Passeriformes and Lepidoptera; lines and shadings
5 refer to mean and SE of the estimates. Models estimated using Equation 5 in
6
7
8 4 **Appendix S3.**

