# Abstract

1. Classic evolutionary theory suggests that sexual dimorphism evolves primarily via sexual and fecundity selection. However, theory and evidence is beginning to accumulate suggesting that resource competition can drive the evolution of sexual dimorphism, via ecological character displacement between sexes. A key prediction of this hypothesis is that the extent of ecological divergence between sexes will be associated with the extent of sexual dimorphism.
2. As the stable isotope ratios of animal tissues provide a quantitative measure of various aspects of ecology, we carried out a meta-analysis examining associations between the extent of isotopic divergence between sexes and the extent of body size dimorphism. Our models demonstrate that large amounts of between-study variation in isotopic (ecological) divergence between sexes is due to systematic heterogeneity, which may be associated with the traits of study subjects. We then completed meta-regressions to examine whether the extent of isotopic divergence between sexes is associated with the extent of sexual size dimorphism.
3. We found a modest but significantly positive association between size dimorphism and sex differences in trophic level. Furthermore, the strength of this positive association varied between ecological contexts, increasing in species whose diets provide the greatest scope for trophic variation and in those for which body size is of greater relevance to feeding.
4. Our results therefore provide further evidence that ecologically mediated selection, unrelated to reproduction, can contribute to the evolution of sexual dimorphism.

## Keywords:

disruptive selection, ecological character displacement, evolution, resource competition, sexual dimorphism, sexual selection

# Introduction

## Evolutionary Theory

Classic evolutionary theory posits that anisogamy, or variation between males and females in gametic investment, causes sex differences in optimum life history and reproductive strategy (Andersson 1994; Lehtonen et al. 2016). Evolution towards these sex specific optima ultimately produces phenotypic differences between males and females, known as sexual dimorphism (Parker and Pizzari 2015). One frequently observed sex difference is sexual size dimorphism, in which the mean body size of one sex exceeds that of the other (Fairbairn et al. 2007). Size dimorphism is typically predicted to arise via sexual selection when the reproductive success of one sex is limited by mating opportunities, and large size allows individuals of that sex to increase their matings. For example, the biggest male southern elephant seals (*Mirounga angustirostris*) are best able to monopolize females at breeding colonies (Le Boeuf et al. 2019). Alternatively, or additionally, size dimorphism may be favored by fecundity selection, when one sex’s reproductive success is limited by gamete production and gamete production relates to body size, such as in emydid turtles (Emydidae), in which larger females produce more eggs and are therefore more fecund (Stephens and Wiens 2009). It is this traditional view, that size dimorphism is primarily attributable to reproductive differences, which is best evidenced and dominates scientific literature and consensus (Blanckenhorn 2005).

However, as far back as Darwin’s discussions of their “habits of life” (Darwin 1871, p.254), authors have noted that sexual dimorphisms can relate not only to each sex’s reproductive success, but also to their respective ecologies (Temeles 2000; Shine and Goiran 2021; Wasiljew et al. 2021). Divergence of the sexes along various biotic and abiotic niche axes (e.g., temperature, diet, habitat) should facilitate intersex niche partitioning, which may covary with sexual dimorphism in traits relevant to ecology (Herrel et al. 1999; Butler et al. 2007). For example, in the seabird *Sula nebouxii,* larger females dive deeper and feed on larger prey than their male counterparts (Zavalaga et al. 2007). Theoretical work suggests that such ecological sexual dimorphisms can arise solely from ecologically mediated natural selection, if frequency dependent competition for a resource produces disruptive selection. Under these circumstances, the sexes could evolve towards distinct phenotypes, which maximize resource acquisition, by facilitating divergence along niche axes (Slatkin 1984). This process of ecological character displacement between sexes is analogous to that between nascent species and offers an alternative evolutionary outcome to frequency-dependent resource competition (Bolnick and Doebeli 2003).

The ecological character displacement hypothesis for sexual dimorphism is perhaps best evidenced by a series of experiments by de Lisle and Rowe (2015), in which male and female salamanders (*Notophthalmus viridescens*) were placed in semi-natural mesocosms, at various competitor densities. In this species, sexual dimorphism in body size and feeding morphology corresponds to sex differences in diet and microhabitat. In de Lisle and Rowe’s study, growth rates, a fitness proxy, were lower in high density mesocosms. Furthermore, growth rates were found to change in response to sex ratio; whereby females grew faster in mesocosms with a male-biased sex ratio. This suggests that resource competition impacts fitness and that this impact is sex specific and alleviated, to some extent, by sexual dimorphism. Given such evidence, it is conceivable that ecologically mediated selection can play a role in the evolution of ecological sexual dimorphisms.

One issue with theoretical models of ecological character displacement, however, is the lack of an *a priori* justification for character displacement between sexes, as opposed to random subsets of populations (Bolnick and Doebeli 2003). As a result, an integrated view of reproductive competition and ecological character displacement provides the best model for the evolution of ecological sexual dimorphisms (de Lisle 2019; de Lisle et al. 2021). From this perspective, initial phenotypic divergence and/ or differing ecological optima between the sexes may usually arise due to anisogamy and reproductive differences (Maklakov et al. 2008; Schärer et al. 2012). For instance, reproductive differences may create sex differences in nutritional optima, leading to divergent foraging decisions and resource allocation (Morehouse et al. 2009; Raubenheimer and Simpson 2018). These initial differences may then be acted upon by disruptive natural selection, such that the observed differences between sexes emerge through both sexual and ecologically mediated selection. For example, intra-specific reversals in the direction of python (*Morelia spilota*) size dimorphism track inter-population differences in mating system, but the degree of size dimorphism relates to available prey sizes (Pearson et al. 2002).

An outstanding and unresolved question concerns the importance of ecologically mediated selection for creating diversity in sexual dimorphisms. Here we address this question by investigating general associations across species between size dimorphism and ecological divergence in trophic level and basal carbon resources. A central tenet of the ecological character displacement hypothesis is that the degree of dimorphism should scale positively with the degree of ecological divergence between sexes (de Lisle and Rowe 2015). It therefore follows that more sexually dimorphic species should generally show greater ecological divergence than less dimorphic species. Associations between sexual dimorphism and ecological divergence between sexes would suggest a greater role for ecology in the evolution of sexual dimorphism than previously appreciated. Ecological divergence related to size dimorphism could be exhibited by sex differences in ecological mean; for example, the larger sex may have access to larger prey and so feed on average at a higher trophic level (Mills et al. 2021). Furthermore, sexual size dimorphism could lead to sex differences in ecological variation, via numerous mechanisms. For example, the larger sex may be more variable if large size confers access to a greater range of resources (Voigt et al. 2018), or the smaller sex more variable if they are competitively subordinate (Wan et al. 2013). We therefore examine associations between size dimorphism and ecological differences between males and females, measured using stable isotope analysis. Stable isotope analysis is a common technique for analyzing foraging ecology and we outline our rationale for why it is appropriate for quantifying sex differences in feeding below. Our investigation uses a meta-analytic approach, synthesizing previously published stable isotope data on vertebrates, with a global geographical scope.

## Stable Isotope Ecology

Over recent decades, stable isotope analysis has become an effective tool used for investigating animal ecology (Hobson and Welch 1992; Hobson 1999; Swan et al. 2020). Because the ratios of naturally occurring stable isotopes vary in the foods animals consume, and these ratios are incorporated into animal tissues during formation, much can be revealed about an animal’s ecology by analyzing stable isotope ratios in its different tissues (Ponsard and Arditi 2000). Different isotopic systems provide alternative information about the animal from which they are sampled (Newton 2016), such that ratios of nitrogen stable isotopes (15N, see methods for explanation of notation) vary with trophic level (Caut et al. 2009) and ratios of carbon stable isotopes (13C) vary with food chain basal resource (Farquhar et al.1989; Yoneyama et al. 2010). For example, relative 15N enrichment of polar bears compared to seals indicate polar bears occupy a higher trophic level (Hobson et al. 2002). Combined stable isotope ratios of animal tissues thus allow inferences about individual niche, meaning ecological differences can be quantified at various levels, including niche differences between males and females, with greater difference in stable isotope ratios taken to indicate more ecological divergence (Foote et al. 2012, Lehmann et al. 2015).

Because stable isotope data tend to be reported reasonably consistently, the considerable stable isotope ecology literature provides an opportunity to investigate cross-species associations between sexual dimorphism and ecological (isotopic) sex differences. Of course, associations between dimorphism and isotopic sex differences would not necessarily indicate causation but would be consistent with predicted outcomes of ecological character displacement working in isolation, or reproductive differences creating the *opportunity* for disruptive ecologically mediated selection. Regardless of which evolutionary mechanism is true in any individual species, the strength of cross-species associations between dimorphism and isotopic sex differences can indicate the general importance of ecologically mediated selection to the evolution of sexual dimorphism.

Our study achieves three main aims. Firstly, using meta-analytic models, we quantify between-study variation in isotopic sex differences in the stable isotope literature and the fraction of this variation due to systematic heterogeneity. In the context of meta-analysis, heterogeneity describes the amount of between-study variation in effect size that may be explained by predictor variables, such as the traits of study subjects. We next investigate how much heterogeneity in isotopic sex differences can be explained by size dimorphism. We use meta-regression models including size dimorphism as a predictor variable, to examine associations with isotopic sex differences, and interpret the strength of associations as an indicator of the amount of heterogeneity in ecological sex differences that is explained by sexual dimorphism.

We use size dimorphism as a predictor variable in our analyses despite our interest in its response to certain ecological contexts. Our choice is primarily pragmatic: the diversity of the stable isotope literature means we can readily compute effect sizes using means, errors and sample sizes for isotopic data of both sexes in many species. In contrast body size data are most commonly available as mean values, and therefore more suitable as a predictor variable.

Finally, we examine the possibility that the influence of size dimorphism on feeding depends on ecological context. We first test whether species dietary class and/ or mean species size modify relationships between size dimorphism and isotopic sex differences. Dietary class may modify the impact of size dimorphism on isotopic sex differences because species consuming different diets differ in their trophic flexibility. For example, omnivores by definition feed at more trophic levels than herbivores, which should create more opportunity for size dimorphism to exert an influence on the trophic level of each sex. Mean species size (defined here as the mean of males and females) may influence the effects of size dimorphism by causing between-species differences in resource access, which may then impact the effects of size dimorphism on resource use within-species. For example, if size affects the maximum prey size available to each sex, size dimorphism may have a greater impact in smaller species that are already more limited concerning the size of their prey. Conversely, the greater absolute size of larger species may mean proportional size differences between males and females are more impactful on their respective interactions with other food web members. For example, one sex being 10% larger may have a greater impact on sex differences in prey access in bigger species, as a 10% size change in smaller species may not be a large enough absolute change for prey accessibility to differ between sexes. We quantify the potential influence of species dietary class and mean size by including them as additional predictor variables, alongside size dimorphism, in meta-regression models.

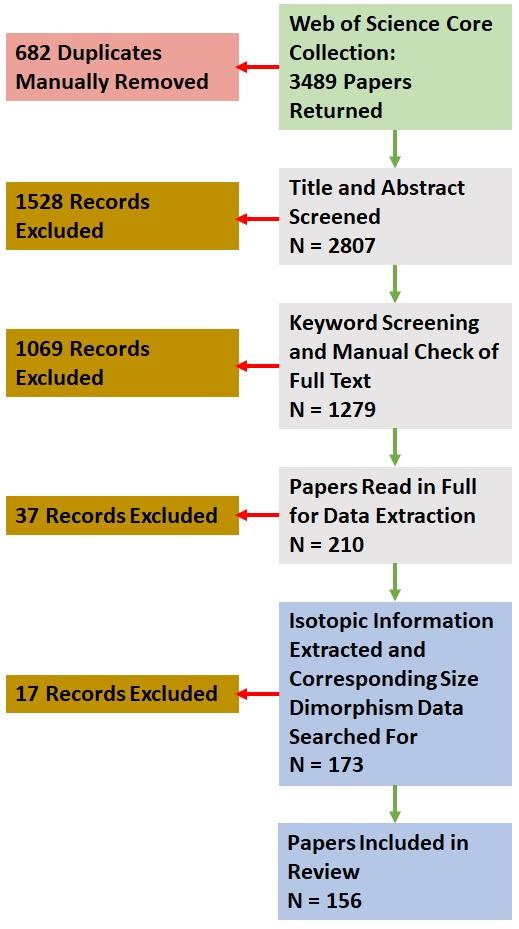
Another possibility is that size dimorphism has the greatest ecological impact in carnivores that are gape-limited, meaning they can only consume prey smaller than themselves (Shine 1991; Shine et al. 2003). For example, in an aquatic food chain formed of gape-limited fish, each species can consume all species smaller than itself, but no species the same size or larger. Trophic level should therefore closely track body size, with the largest fish at the highest trophic level. If a fish species in such a food chain were size dimorphic, the larger sex would have greater access to larger, higher trophic level prey, than the smaller sex, resulting in a difference between males and females in maximum possible trophic level. As optimal foraging theory predicts that predators often feed preferentially on larger prey, due to greater energetic returns per prey item (Stephens and Krebs 1986; Dodrill et al. 2021), the larger sex in a dimorphic gape-limited fish would be predicted to feed at a higher trophic level. Conversely, non-gape-limited predators and scavengers, such as cats, can consume prey orders of magnitude larger than themselves, which may minimise any impact of size dimorphism on the trophic levels of each sex. Therefore, we investigate whether gape-limitation strengthens associations between size dimorphism and isotopic sex differences. We do this by completing a meta-regression using a dataset constrained to fish and snake species, which are presumed to be able to feed solely by swallowing whole prey and thus considered gape-limited. The predictions from this model are then be compared to those from a model containing all other carnivores in our dataset, to assess whether the effect of size dimorphism on trophic sex differences is greater in gape-limited carnivores.

# Methods

Our meta-analytic approach and reporting was completed with reference to the guidelines laid out by O’Dea et al. (2021).

## Data Collection

We collated peer-reviewed literature available in the Web of Science Core Collection. The stable isotope literature is large, with the search term “stable isotope” returning ~76 500 studies at the time of writing. To constrain the search, we combined the following specific terms, using the default publication year range of 1900-2020, on 10/11/2020: Isotop\* Nich*;* Isotop Nich\* Male; Isotop\* Nich\* Female; Isotop\* Nich\* Male Female; Isotop\* Nich\* Sex Diff\*; Isotop Nich\* Dimorph; Isotop Dimorph\*.



**Figure 1.** Our sequence of study collation, screening, and data extraction, alongside the number of studies excluded at each stage and included in the final analysis.

Our searches returned 3489 studies, which we placed into a spreadsheet to highlight duplicates for manual removal. Removing duplicates resulted in 2807 studies for title and abstract screening. At this stage, we made the decision to constrain our analysis to the nitrogen and carbon stable isotope systems, due to the relatively small number of studies using other systems that were returned by our search terms. We also rejected studies during title and abstract screening if they did not use bulk stable isotope analysis, used samples of human, museum, archeological or palaeontological origin, were review, comment, or method papers, or if the animals sampled were not wild, not adults, not vertebrates or if data were not available for both sexes. We then searched the remaining 1279 studies using the ctrl+F search function and, separately, the terms “sex”, “male” and “female”, excluding studies if they contained none of these terms, under the assumption that they did not contain stable isotope ratios for each sex and, if at least one term was present, checking for the presence of the required data. Additional reasons for exclusion were if the full text was inaccessible without purchase or contacting authors, presented incomplete data (mean, error or sample size missing), was not in English or was a paper correction. We then attempted to extract data from the remaining 210 studies. Additional reasons for exclusion at this stage were if raw data was presented as images with >50 rows, if data were from an earlier study already included or if data extraction from figures was not possible. We extracted data from figures using a mouse pointer to individually select data points from an image of the figure, with the image calibrated to the axis values from the original figure; therefore, too much point overlap made this process inaccurate, because not all points could be selected for inclusion. The entire process provided 173 studies in which mean, standard deviation and sample sizes for each sex were presented in the manuscript, or could be calculated from raw data, or could be taken from model outputs, or extracted from figures. We collected data for any vertebrate species, from any global location and, if stable isotope ratios for each sex were presented for more than one tissue type, we entered each tissue as a separate row in our database.

## Effect Size Choice and Calculation

All the stable isotope data we collected were presented in permil units (‰). Permil units describe enrichment or depletion in heavy isotopes, relative to international standards, which exist for nitrogen, carbon, and all other commonly used systems in stable isotope analysis. For example, the standard for nitrogen stable isotope ratios is atmospheric nitrogen (air). The relative enrichment or depletion is expressed using delta () notation, such that:

where Rsample equals the isotope ratio of the sample and Rstandard equals the isotope ratio of the standard (McKinney et al. 1950) where R = heavy isotope/light isotope, e.g. 15N/14N. Thus, a positive ẟ value indicates enrichment in the heavier isotope (in this case 15N) and a negative value indicates isotopic depletion of the sample, relative to the international standard. When comparing two sampling units, such as sex, a more positive (or less negative) value for one sex indicates enrichment in the heavy isotope relative to both the standard and the other sex. It is this difference between sexes in isotopic enrichment that we have used to calculate the effect sizes in our meta-analysis.

In ecology and evolution, it is common to use standardized effect sizes (Nakagawa and Santos 2012). However, as all studies from which we extracted data already expressed stable isotope data in permil units, further standardization was not necessary (Nakagawa and Cuthill 2007). Therefore, we have calculated mean differences between male and female stable isotope ratios as the raw mean difference between isotopic means of each sex, as found in each study. We calculated these with a positive mean difference indicating that males were 15N or 13C enriched compared to females and a negative mean difference indicating females were isotopically enriched compared to males. For example, a positive ẟ15N mean difference indicates that males feed, on average, at a higher trophic level.

Regarding meta-analyses of variation, two effect size measures are often recommended in ecology and evolution, which are the log Variability Ratio (lnVR) and the log Coefficient of Variation Ratio (lnCVR) (Senior et al. 2020). lnCVR has the advantage of allowing for mean-variance relationships in effect sizes (i.e., an increase in variance with mean value) (Senior et al. 2016): our data did not show any evidence of such relationships (Appendix 1). In addition, because lnCVR accounts for variation in mean value by expressing absolute variation as a proportion of group mean, sex differences in isotopic variation could actually be misrepresented through this standardisation. For example, if one sex is twice as enriched relative to the international standard as the other and shows twice as much variation, lnCVR would express this as equal variation. Conversely, as lnVR is calculated using the raw variation values for each group, with no accounting for mean values, the more enriched sex would also be shown to be twice as variable, more accurately representing each sex’s ecology. We therefore selected lnVR as our effect size metric for sex differences in variation.

Finally, we selected mass dimorphism (Kg) as our measure of size dimorphism, as this measure was most readily available for the highest number of vertebrates, allowing the taxonomic scope of our analysis to be as high as possible. Body masses for each sex were established using web searches, prioritizing data from peer-reviewed scientific studies, followed by published books and, if necessary, taxon-specific websites. As reliable body mass data could not be obtained for all species, the number of studies in the analysis was reduced to 156. A list of data sources used in our meta-analyses are provided in the Data Sources section.

## Model Choice and Structure

All models used complete case analysis, meaning rows containing missing data for predictor variables or effect sizes (dependent variables) were removed from the analysis. We used multilevel meta-analytic models to quantify the amount of between-study variation that exists for each isotope and effect size and how much of this variation is due to systematic heterogeneity, as opposed to random sampling variation. We then used multilevel meta-regression models to investigate whether the systematic heterogeneity found could be explained by our predictor variables. To investigate the possibility that ecological character displacement between sexes could be a strong selective force on body size, we examined the strength of associations between size dimorphism and sex differences in isotopic mean and variance, for carbon and nitrogen.

To examine whether ecological context can modify the potential for ecological character displacement, we ran meta-regressions using sex differences in mean nitrogen isotope as the response variable, with additional predictor variables, dietary class and mean species size, included alongside size dimorphism. Dietary class constituted a categorical variable with three levels: carnivore, omnivore, herbivore. Mean size was a continuous variable, calculated by averaging the male and female mass data used for calculating size dimorphism. We ran models including dietary class and mean size separately and together, with and without all combinations of two- and three-way interactions. Three-way interactions were theoretically justified because, if mean species size could modify the effect of size dimorphism on trophic level, this modification may be more apparent in species with more inherent trophic flexibility, such as omnivores, than those with less, such as herbivores. In addition, sample size was large enough that the number of parameters to be estimated with three-way interactions did not prevent models converging. The best models were identified using AICc scores, with lower scores taken to indicate better models (Arnold et al. 2010). As a final test of whether ecological context may influence the strength of ecological character displacement, we quantified the effect of gape-limitation by running two meta-regressions including only size dimorphism as a predictor variable and limiting the datasets to gape-limited and non-gape-limited carnivores, in which size dimorphism may have differing impacts on sex differences in trophic level.

Residuals of all models were approximately normally distributed; thus, no data transformations were used.

## Random Effects

In all the above multilevel models we included study identity and species as random factors, to account for random sampling variation at both of these levels and to adequately account for pseudoreplication, since we potentially considered measures for several tissue samples from the same specimens.

## Publication Bias and Sensitivity Analysis

Scientific literature may be subject to publication bias, whereby favorable results are preferentially published, thus skewing the results of meta-analyses. Funnel plots may be used to identify such biases, by visualizing the distribution of published effect sizes and whether this distribution is skewed towards particular results. We therefore produced funnel plots to visualize the distribution of published effect sizes for isotopic sex differences. In addition, biases may arise when research builds upon influential results from poor quality or low power studies, leading to reduced effect sizes through time, as the true effect is quantified with repetition or higher quality studies. To test for such publication bias in isotopic sex differences, we ran meta-regressions using sex differences in isotopic mean and variance, for carbon and nitrogen, as the dependent variable and publication year as the only predictor variable.

The results of meta-analyses may also be sensitive to decisions about the weights assigned to individual studies, as well as to high influence data points (Koricheva et al. 2013). Meta-analytic models usually account for both within-study variance and between-study variance when assigning weights to individual study results. However, when between-study variance is high, within-study variance can be masked when weighting studies, potentially impacting model results. We therefore ran additional models using only the inverse of within-study variance to assign study weights, to determine the influence of our choice of weighting parameter. Finally, to analyze the sensitivity of our models to high influence data points, we completed leave-one-out analysis, to calculate Cook’s distances for each data point and ran additional models with high influence data points removed. The results of our tests of publication bias, alternate study weighting and sensitivity analysis, alongside justifications for final data inclusion and model choices can be found in Appendix 1.

## Software

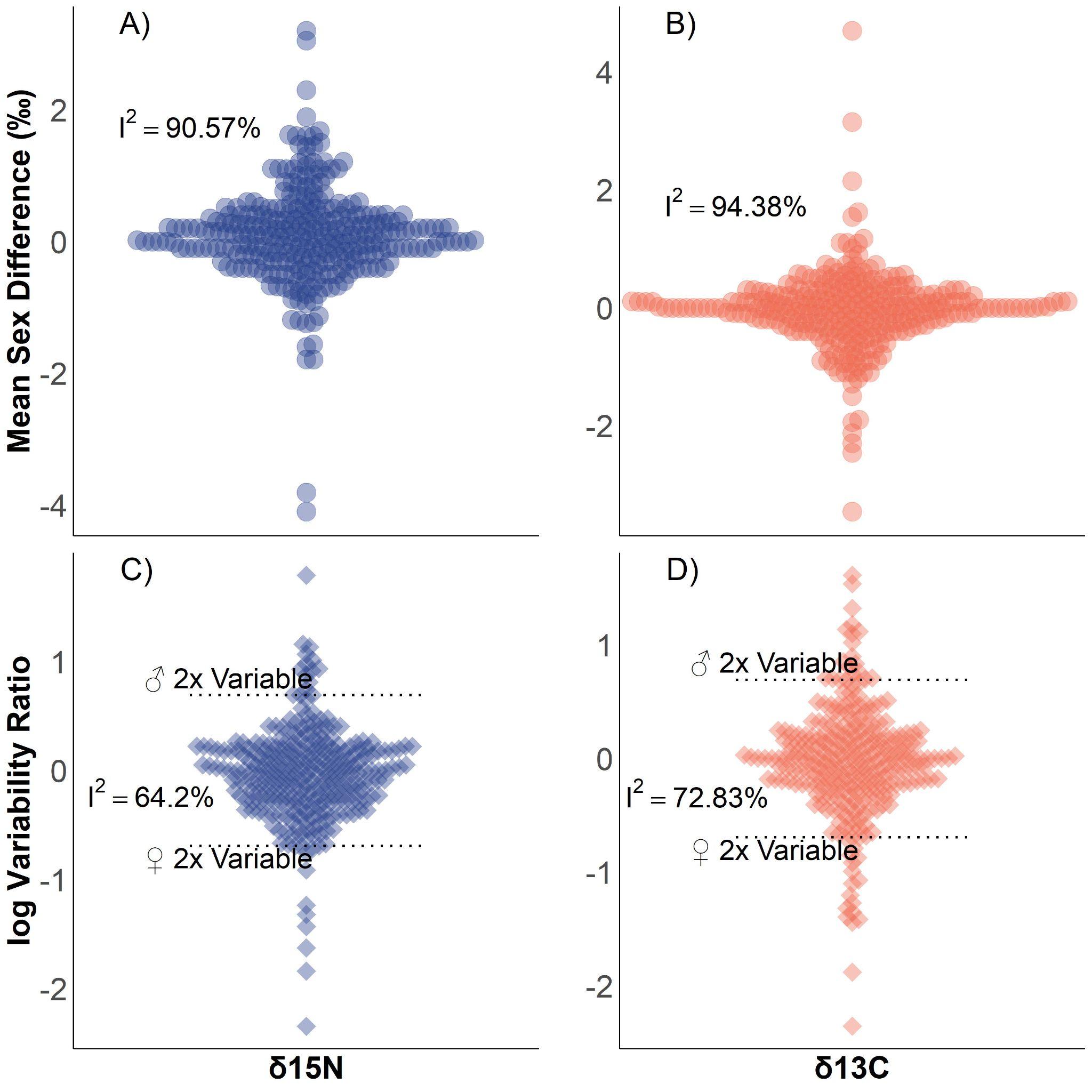
All data processing, analyses and plotting were completed using R v4.0.2. We used the R package ‘metaDigitise’ v1.0.1 (Pick, Nakagawa & Noble, 2019) for all data extraction from figures and the package ‘metafor’ v.2.4-0 (Viechtbauer 2020) to calculate all effect sizes and to run all meta-analytic and meta-regression models. We created all plots using the R package ‘ggplot2’ v3.3.3 (Wickham et al. 2020).

# Results

## Dataset

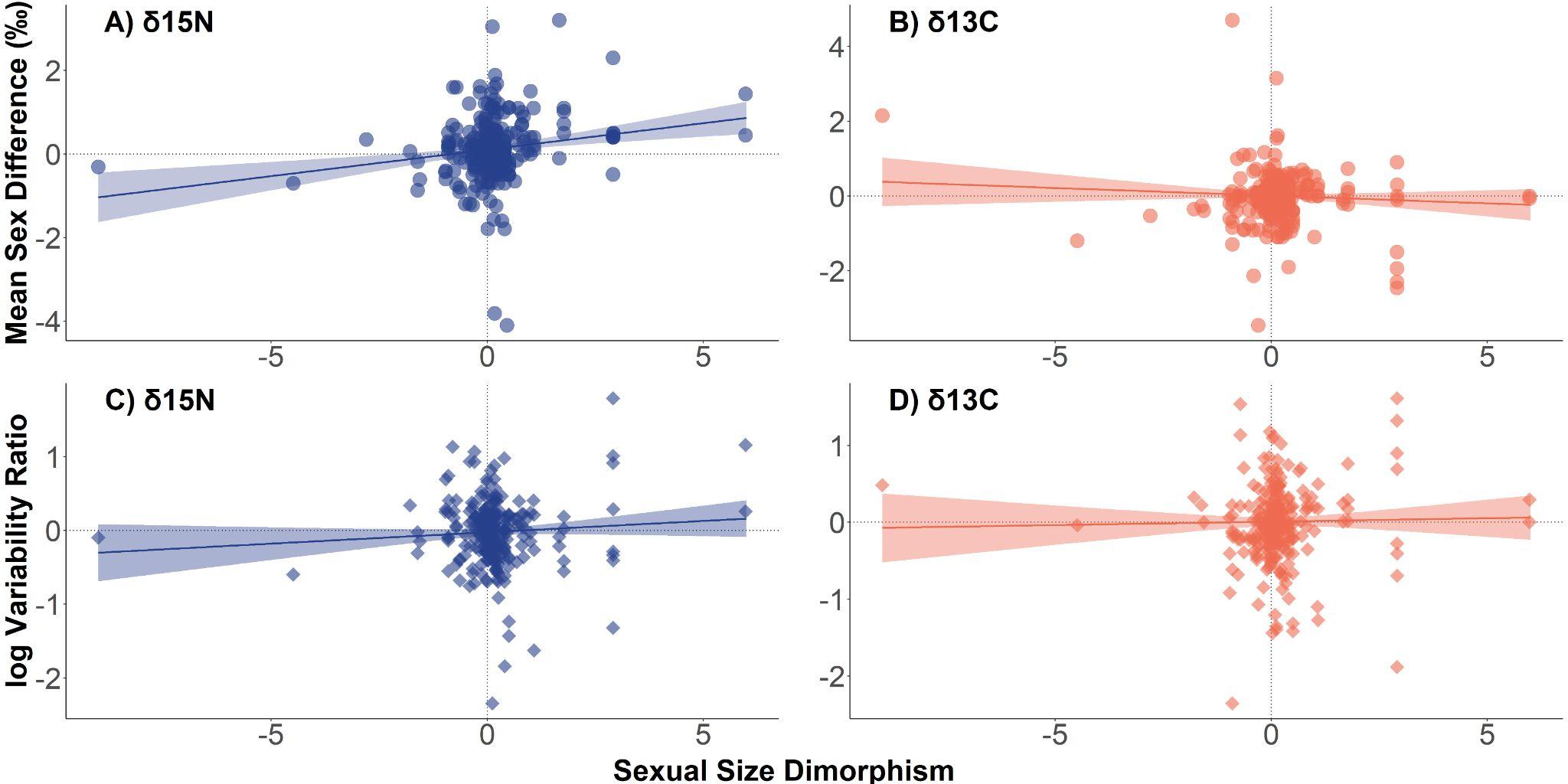
Our final database contained isotopic information from 156 studies, covering 166 species. Mammals were the most common subphylum (n = 70), followed by birds (n = 60), fish (n = 19), reptiles (n = 17) and a single amphibian. The most dimorphic species were the turtle *Graptemys geographica*, in which females are 10x the mass of males and elephant seals (*Mirounga leonina*), with males seven times larger than females. The number of effect sizes used in the analyses was highest for 15N mean sex differences (n = 282), followed by 13C mean differences (n = 276), 15N lnVR (n = 272) and 13C lnVR (n = 266).

### 1) Quantifying Heterogeneity in Between-Sex Isotopic Differences

Heterogeneity was found for sex differences in mean 15N (trophic level) and 13C (food chain basal carbon resource) and sex differences in 15N and 13C variation (Figure 2). The amount of heterogeneity due to systematic variation (I2), as opposed to random error was 90.57% and 94.38% for 15N and 13C mean sex differences, respectively. Such high systematic heterogeneity indicates that almost all between-study variation in effect size can be explained by predictor variables. Regarding sex differences in isotopic variation, I2 was 64.2% and 72.83% for 15N and 13C, respectively, indicating that the majority of heterogeneity in between-sex differences in isotopic variation may also be explained by predictor variables. In the case of nitrogen, one sex was at least twice as variable as the other in 8.5% cases and for carbon, in 13.1% cases(Figure 2). 

**Figure 2.** Published stable isotope ratio sex differences for nitrogen mean (A), carbon mean (B), nitrogen variation (C) and carbon variation (D). In (A) and (B) each point represents the raw difference between male and female mean stable isotope ratio, of one tissue of one species. Positive values indicate higher values in males, negative values indicate higher values in females. In (C) and (D) each point represents the log male:female variability ratio of one tissue, of one species. Positive values indicate males showed more isotopic variation and those above the dotted line indicate that males were more than twice as variable as females. Negative values indicate females showed more isotopic variation and those below the dotted line indicate that females were more than twice as variable as males. X axes constitute one category, with a jitter added to best display the data.

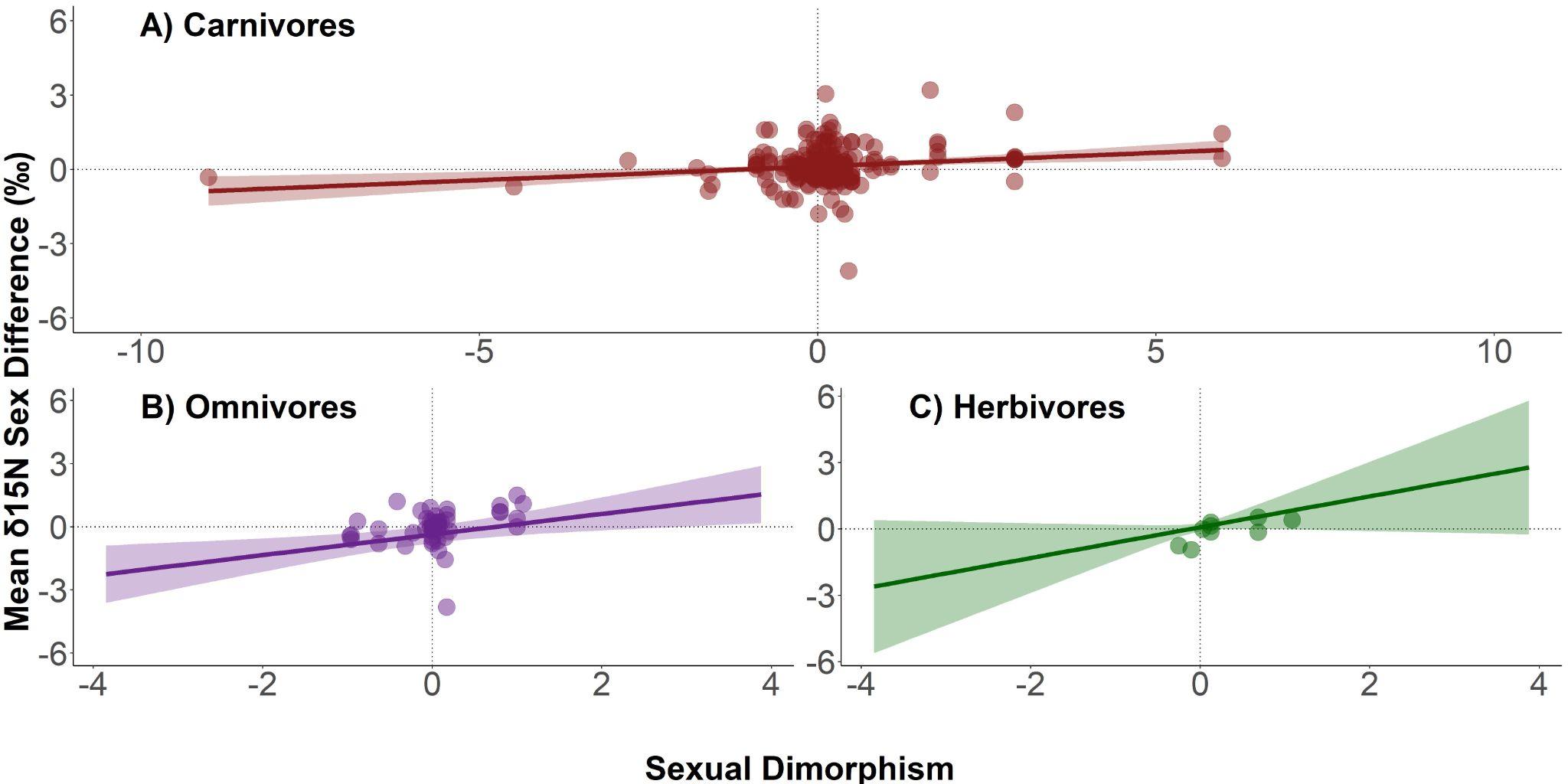
### 2) Associations Between Isotopic Sex Difference and Size Dimorphism

To examine the possibility that the evolution of size dimorphism relates to ecology, we carried out meta-regressions containing size dimorphism as the sole predictor variable and found modest or non-existent associations with isotopic sex differences. The estimated effect size of size dimorphism on 15N mean difference was positive, but modest when compared to the variation in isotopic sex differences in our dataset [mean = 0.127, 95% CI: 0.06 - 0.19, *p*=< 0.001]. Models of relationships between size dimorphism and 13C mean differences, 15N variation and 13C variation produced estimate confidence bands that overlapped zero, indicating no significant associations between size dimorphism and these measures of isotopic sex differences. The predictions from these models, alongside their underlying raw data, are visualized in Figure 3.

**Figure 3.** The relationship between sexual size dimorphism and stable isotope sex differences in nitrogen mean (A), carbon mean (B), nitrogen variation (C) and carbon variation (D). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains isotopic sex differences.

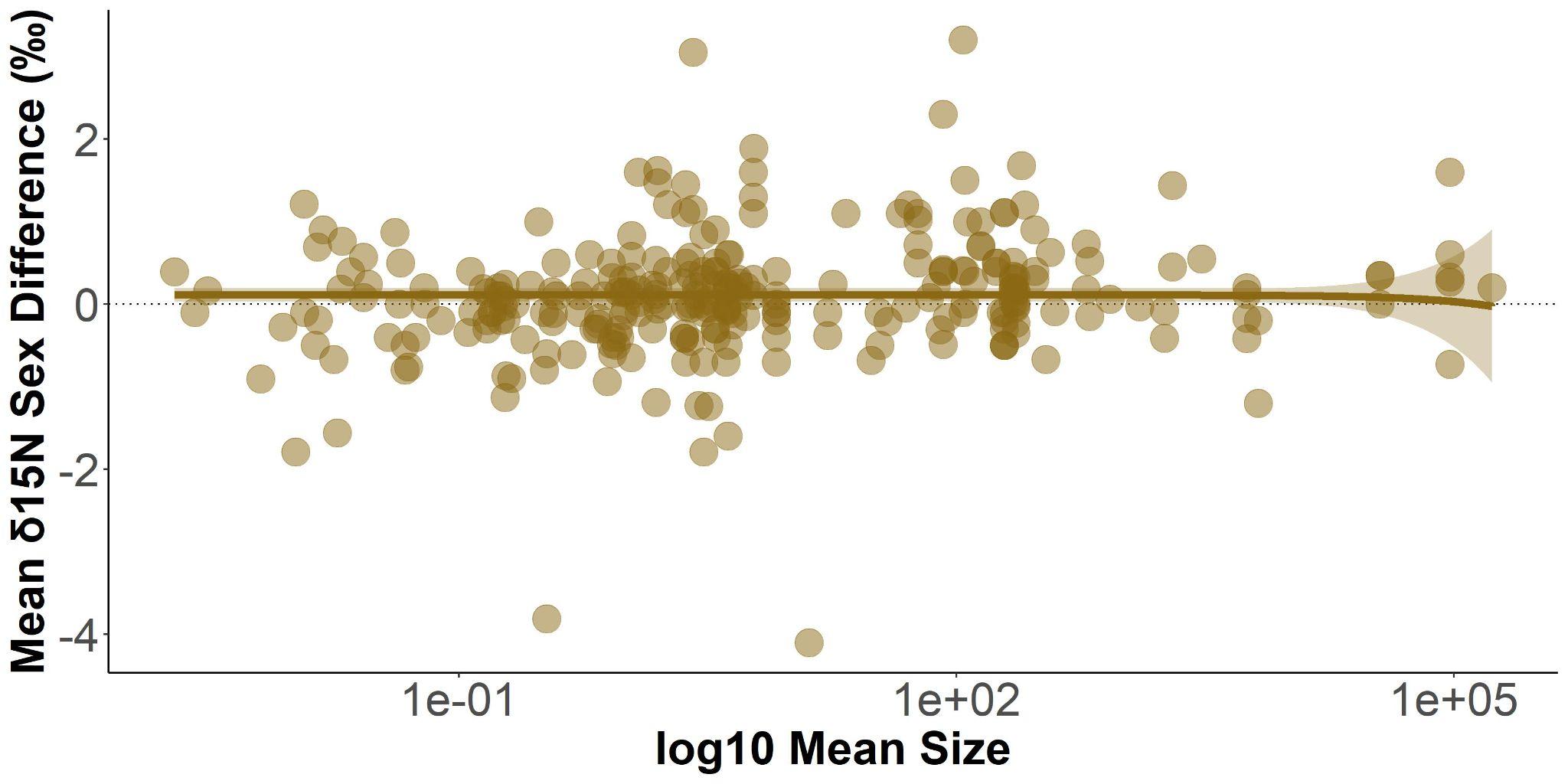
### 3) Quantifying the Effects of Ecological Context

To test the possibility that associations between size dimorphism and feeding vary in strength among ecological contexts, we used meta-regressions to test whether dietary class, mean size or gape-limitation modified the effect of size dimorphism on sex differences in trophic level. Model selection using AICc scores indicated that a model containing species mean size and dietary class as predictors of 15N sex differences, with an interaction between size dimorphism and dietary class, improved model fit (AICc = 511), compared to the size dimorphism only model above (AICc = 517). However, when we fitted predictions using this model, we found the effect of dietary class to confound that of mean size, inversing the predicted effect of mean size on sex differences in nitrogen mean, compared to the model summary. We therefore selected the two best models containing dietary class and mean size separately (which did not change our qualitative conclusions). The best model containing dietary class alongside size dimorphism (AICc = 513), contained an interaction between predictors, such that the association between size dimorphism and sex differences in nitrogen mean was absent in herbivores, moderate in carnivores [0.111, 95% CI: 0.0466-0.175, *p* <0.001] and strongest in omnivores [0.379, 95% CI: 0.0361-0.721, *p* = 0.03] (Figure 4).



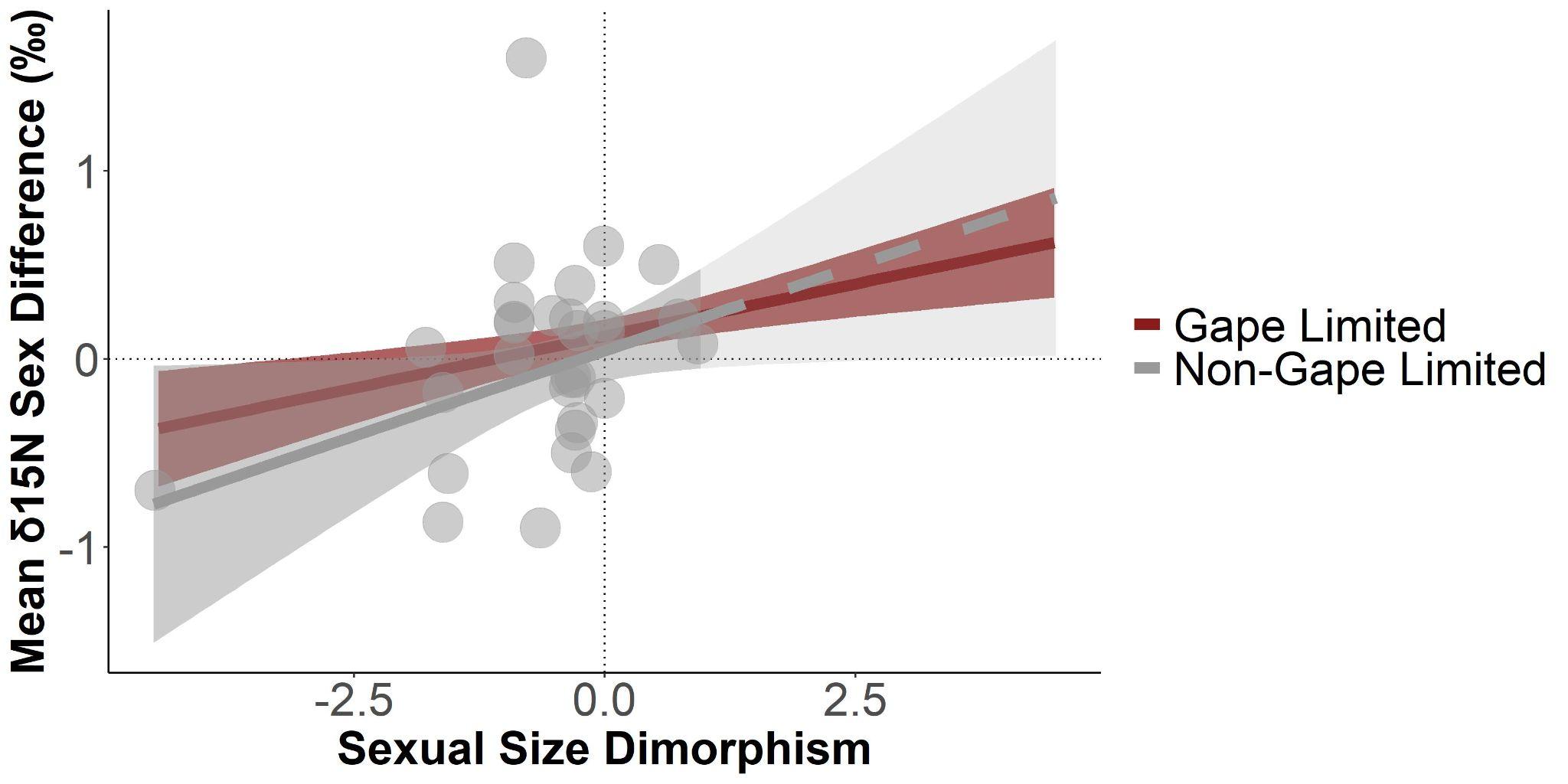
**Figure 4.** The relationship between sexual size dimorphism and mean nitrogen stable isotope ratio sex differences in carnivores (A), omnivores (B) and herbivores (C). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains trophic sex differences in each dietary class.

The best model containing mean size alongside size dimorphism (AICc = 513) contained an interaction, with a moderate effect of size dimorphism on sex differences in nitrogen mean [0.151, 95% CI: 0.0863-0.216, *p* <0.001], that decreased modestly as species mean size increased [-0.00000799, 95% CI: -0.0000155 - -0.000000449, *p* <0.05]. Mean size had no effect on sex differences in nitrogen mean independent of size dimorphism (Figure 5).



**Figure 5.** The relationship between species mean size and mean nitrogen stable isotope ratio sex differences (D). Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data, overlaid to visually assess how well size dimorphism explains trophic sex differences in each dietary class.

Limiting the dataset to only gape-limited predators, in which trophic level is predicted to relate more closely to body size, resulted in a 92% increase in the estimated effect of size dimorphism on 15N mean difference [0.18, 95% CI: 0.0095-0.35, *p*<0.05], relative to non-gape-limited [0.094, 95% CI: 0.023-0.17, *p*=0.01] (Figure 6).



**Figure 6.** The relationship between sexual size dimorphism and mean nitrogen stable isotope ratio sex difference in gape-limited and non-gape-limited carnivores. Lines and 95% confidence intervals are based on meta-regression predictions. Data points are raw data for gape-limited carnivores, overlaid to assess how well size dimorphism explains trophic sex differences in gape-limited carnivores. Predictions based on gape-limited species are shown in grey (prediction line is dashed outside the raw data range) and for the non-gape-limited carnivores in red.

# Discussion

Using meta-analytical methods, we examined cross species relationships between sexual size dimorphism and ecological divergence between sexes, measured using stable isotopes. We found that, across 166 globally distributed species, size dimorphism was weakly associated with sex differences in mean 15N (trophic level), but not mean 13C (food chain basal carbon resource), or variation in either isotope. The relationship between size dimorphism and mean 15N was influenced by ecological context, however, being unrelated to species mean size and absent in herbivores, but present in carnivores and strongest in omnivores. Sex differences in trophic level were also more strongly associated with size dimorphism in gape-limited than in non-gape-limited carnivores, as predicted by theory.

### 1) Between-study heterogeneity exists in isotopic sex differences.

We found systematic between-study heterogeneity for between-sex differences in isotopic mean and variance, for nitrogen and carbon isotopes. Heterogeneity for sex differences in mean 15N and 13C indicates systematic between-study variation in the extent to which males and females feed at different trophic levels and in different food chains, respectively. The heterogeneity found for sex differences in 15N and 13C variation is suggestive of systematic between-study variation in the extent to which individuals exhibit trophic and food chain variability. Our meta-analytic models therefore indicated that large amounts of between-study variation in ecological sex differences may be explained by study-level variables. Though we found that sex differences in trophic level was related to size dimorphism, which we discuss presently, our analyses also highlight that large amounts of the ecological sex differences documented by the stable isotope literature remain open to explanation by further analyses, some suggestions for which we will also outline below. We hope our database provides a useful starting point for further investigations of sexual dimorphism and ecological differences between males and females.

### 2) Size dimorphism is associated with sex differences in trophic level, but not food chain basal carbon resources or ecological variability.

We found evidence that sexual size dimorphism does, in some instances, scale positively with ecological sex differences. Size dimorphism exhibited a moderate positive association with sex differences in mean 15N and thus explained some variation in trophic level differences between males and females. Previous cross-species investigations of the relationship between size dimorphism and 15N sex differences have often found inconsistencies, with size dimorphism sometimes relating to trophic differences and sometimes not (Phillips et al. 2011; Mancini et al. 2013). These inconsistencies are likely because the effect is probably modest and may be modified by a wide range of factors, as evidenced by the amount of unexplained variation in our dataset. Thus, the size and scope of our analysis is likely the factor that has allowed us to find a clear but moderate effect of size dimorphism on trophic level differences between sexes. No relationships existed between size dimorphism and variation in 13C mean sex differences, or sex differences in variation in either isotope. Size dimorphism thus does not appear to have a systematic cross-species influence on sex differences in food chain basal carbon resources or trophic variability. These results conflict somewhat with the conclusions of studies on individual species (Voigt et al. 2018; Calado et al. 2020). It may therefore be the case that size dimorphism is related to sex differences in basal carbon resources and trophic variability in particular species or populations but does not provide a general explanation for these ecological sex differences across species.

### 3) Associations between size dimorphism and trophic sex differences are modified by dietary class and gape-limitation, but not mean size.

We found that ecological context influenced associations between size dimorphism and trophic sex differences. Dietary class modified the effect of size dimorphism on trophic differences between males and females, with no effect of dimorphism in herbivores, a moderate effect in carnivores and the strongest effect in omnivores . These results corroborate our prediction, that inherent differences in trophic flexibility would alter the impact of size dimorphism on trophic sex differences, and make sense given the respective feeding niches of the three dietary classes. As herbivores would be expected to feed exclusively on plants, they should only occupy the trophic position of primary consumer, leaving little scope for size dimorphism to influence trophic level. Carnivores may occupy any position from secondary consumer upwards, meaning each sex could take prey from one or multiple trophic levels. There is thus some opportunity in carnivores for trophic differences between the sexes to be influenced by size dimorphism, hence the moderate positive effect in our model. In contrast to the other two groups, omnivores would be expected to consume foods from a minimum of two trophic levels, leading to a greater probability of trophic differences between sexes and the largest opportunity for size dimorphism to influence this difference. This is likely why size dimorphism was most strongly associated with trophic sex differences in omnivores in our dataset. Together, these results suggest that the impact of size dimorphism on trophic level differences between males and females is dependent on the ecological opportunity for feeding differences between sexes.

An independent effect of species mean size was absent in our model. There was an interaction between mean size and size dimorphism, with the effect of size dimorphism falling slightly as mean size increased. However, this effect was multiple orders of magnitude lower than the analytical reproducibility of nitrogen stable isotope analysis. Thus, even though the model estimate was technically negative, we conclude that absolute species size has no modifying effect on the association between size dimorphism and trophic level differences between sexes.

The effect of size dimorphism on intersex trophic level differences is predicted to be greater in gape-limited species (Shine 1991; Shine 2000; Shine et al. 2003) and when we limited our analysis to gape-limited predators, the mean estimated effect of size dimorphism on trophic differences between sexes increased by 92%, relative to non-gape-limited carnivores, though the confidence intervals overlapped (Figure 4). There is substantial evidence available that larger gape increases maximum ingestible prey size and trophic level in fish and snakes (Web and Shine 1993; Persson et al. 1996; Nilsson and Bronmark 2003; Barnes and Beaudreau 2021). We thus interpret our results as evidence that size dimorphism has a greater impact on trophic level difference between males and females in gape-limited species. When size dimorphism more directly impacts access to resources, it is more strongly associated with ecological differences between sexes.

In summary, we found the extent of size dimorphism to relate to the extent of trophic sex differences, an association that increased in strength when ecological opportunity for trophic variation was greatest and when size dimorphism was more ecologically relevant. These cross-species associations between size dimorphism and ecological sex differences are consistent with predictions from ecological character displacement theory (Shine 1989; de Lisle 2019; Introduction). Past comparative analyses of the sought we have conducted have used such directional cross-species associations to infer causation when investigating the evolutionary drivers of size dimorphism (Székely et al. 2004). We therefore believe that our results provide evidence linking size dimorphism to ecological sex differences, and that that link is causative, supporting earlier conclusions that sexual dimorphism evolves partly via ecological character displacement between sexes (Shine 1989; de Lisle and Rowe 2015; de Lisle 2019). However, the weakness of the associations we found also supports the predictions of other authors that the role of ecological character displacement is relatively minor (Fairbairn 1997; de Lisle and Rowe 2015).

Given this conclusion, and the remaining unexplained variation in our dataset, several questions arise from our meta-analysis that should form the subjects of future work. Firstly, if ecological character displacement plays only a minor role in the evolution of sexual dimorphism, what is its strength as a selective force, relative to other forms of disruptive selection on male and female traits? A weak role for ecologically mediated selection implies that sexual and fecundity selection are the main drivers of sexual dimorphism. However, a recent analysis found that size dimorphism was only weakly associated with sexual selection across species, leading the authors to suggest that “alternative mechanisms such as ecological character displacement may be crucial to understand the full diversity of (size dimorphism) in animals” (Janicke and Fromonteil 2021). Considering our own results, alongside their conclusion, we suggest that a future priority should be the incorporation of sexual, fecundity and ecologically mediated selection into single cross-species analyses, to quantify their relative importance to the evolution of size dimorphism.

Secondly, why would ecological character displacement be weaker than other drivers of sexual dimorphism? One possibility is that the frequency-dependent nature of resource competition means that the strength of competition falls as the sexes phenotypically diverge (de Lisle and Rowe 2015). Alternatively, divergence from the species mean phenotype, whilst alleviating resource competition, may itself entail fitness costs that eventually exceed those of competition for resources (Slatkin 1984; Bolnick and Doebeli 2003). Either possible scenario may place an upper limit on the extent to which ecologically mediated selection can drive character displacement between sexes. Therefore establishing the mechanistic limitations on ecological character displacement between sexes should also become the focus of future investigations, most likely via modelling and experiment.

A final question is what additional variables could be included in future analyses, to explain variation in ecological sex differences? Our analyses have highlighted that high amounts of between-study variation in our data remains unexplained, providing opportunities to use our database to investigate additional explanations of ecological differences between males and females. Importantly, isotopic values for an animal’s tissues may be affected by many factors, such as body size, body condition, diet quality and ontogenetic growth (Wolf et al. 2009; Carleton and Martinez de Rio 2010; Lecompte et al. 2011). Sex differences in any of these variables could potentially influence sex differences in isotopic signal and influence cross-species isotopic comparisons. However, their impact is often species-specific, so a comparative synthesis of the sort we have conducted would require species-level data to become widely available across many taxa. In relation to questioning why ecological sex differences evolve, nutritional requirements are one potential avenue of investigation. Males and females may target distinct sets of resources in order to meet sex specific nutritional needs, such as lactation or sexually selected signals (Thompson 2013; Harrison et al. 2017). These differences may influence foraging and other aspects of behavioral ecology (Morehouse et al. 2018). As stable isotopes in animal tissues vary with the foods animals consume, the sex differences in isotope ratio we have observed may be an illustration of males and females targeting distinct resources, to fulfill their own sex-specific nutritional requirements. Future investigations could therefore seek to quantify the strength of associations between-sex differences in nutritional requirements and stable isotopes values, which could contribute greatly to our understanding of why ecological differences arise between males and females.

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# Data Availability Statement

All raw data supporting our analyses, as well as modelling and plotting scripts, will be made available on dryad: Dryad doi: XX.XXXX/dryad.XXXXX

# Competing Interests

The authors declare no competing interests.

# Author Contributions

Conception, design, data acquisition, analysis and interpretation: JB, LB, KA, IJ, JN, DL.

Article drafting and revision: JB, LB, KA, IJ, JN, DL.

Final manuscript approval: JB, LB, KA, IJ, JN, DL.

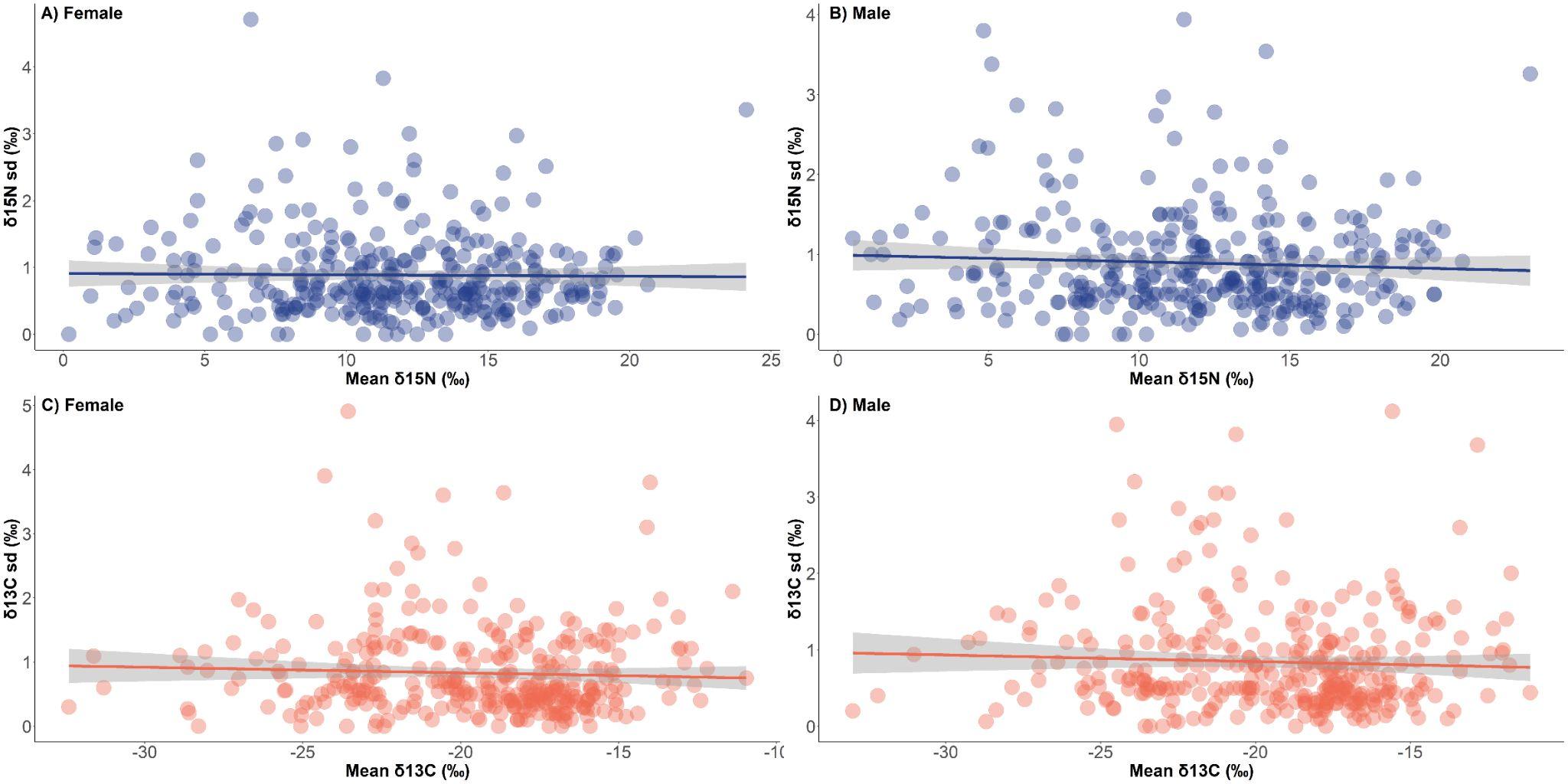
# Acknowledgements

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# Appendix 1

## Mean-Variance Relationships

Calculating effect sizes that quantify variation differences between groups, such as sex, may be impacted by mean-variance relationships. These describe an increase in variance with an increase in mean and may adversely influence the outcome of meta-analyses. We therefore plotted the relationship between raw isotopic mean and standard deviation, alongside linear regressions, to investigate the presence of mean-variance relationships in our data. We found no evidence for mean-variance relationships in female nitrogen (Figure 7a), male nitrogen (Figure 7b), female carbon (Figure 7c) or male carbon (Figure 7d).



**Figure 7.** Mean-variance relationships in female nitrogen(A), male nitrogen (B), female carbon (C) and male carbon (D).

**Publication Bias**

**Publication Year**

As one possible identifier of publication bias is a reduction of effect sizes through time, we completed meta-regressions with publication year as the sole predictor variable. We found no effect of publication year on the magnitude of published sex differences in isotopic mean or variation, for either nitrogen or carbon isotopes (Table 1).

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Effect of Publication Year** | | | | | | |
| **Isotope** | **Measure** | **Effect of**  **Publication Year** | **Standard**  **Error** | **ci lb** | **ci ub** | ***p*** |
| Nitrogen | Mean Difference | -0.0004 | 0.0107 | -0.0213 | 0.0205 | 0.9728 |
| Nitrogen | Variation | -0.0044 | 0.0064 | -0.0169 | 0.0081 | 0.4933 |
| Carbon | Mean Difference | 0.0060 | 0.0082 | -0.0100 | 0.0220 | 0.4594 |
| Carbon | Variation | -0.0092 | 0.0073 | -0.0235 | 0.0052 | 0.2121 |

**Table 1.** Effect of publication year on sex difference in mean and variation, for nitrogen and carbon.

**Funnel Plots**

Funnel plots can be used to investigate possible publication bias by illustrating asymmetries in published effect sizes, which would suggest particular results are favorably published. Such biases in published literature would influence the outcome of meta-analyses, by skewing summary effect size estimates towards the favored outcome. We therefore produced funnel plots displaying published effect sizes for sex differences in nitrogen mean (Figure 8), nitrogen variation (Figure 9), carbon mean (Figure 10) and carbon variation (Figure 11). In all four cases, our plots displayed a fairly even distribution in study outcomes, suggesting that publication bias is not prominent in the literature we have examined.Chart, scatter chart

Description automatically generated

**Figure 8.** Distribution of published sex differences in nitrogen isotope mean.

Chart, scatter chart

Description automatically generated

**Figure 9.** Distribution of published sex differences in nitrogen isotope variation.

Chart, scatter chart

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**Figure 10.** Distribution of published sex differences in carbon isotope mean.

Chart, scatter chart

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**Figure 11.** Distribution of published sex differences in carbon isotope variation.

**Effect of Study Weighting Method**

The weight given to individual effect sizes can alter the outcome of meta-analyses. As our analysis consisted of meta-regressions, including the random factors ‘paper number’ and ‘species’, each effect size used as a response in our analysis was weighted accounting for within-study variance, heterogeneity between studies and species and covariance between those two random factors. Thus, our models assumed differences between studies and species in the true isotopic difference between sexes. However, high heterogeneity, which was present in our data, can mask within-study variance. It is therefore recommended to also conduct models weighting studies solely by the inverse of within-study variance, to examine the impact of weighting method on model predictions and, therefore, the conclusions of the meta-analysis.

Regarding the relationship between sex differences in nitrogen mean (trophic level) and size dimorphism, our results were not robust to changing the weighting method, as the confidence interval for the estimated effect of size dimorphism on trophic sex differences overlapped zero (Table 2). Our qualitative conclusion would therefore have changed with the alternate weighting, to state that size dimorphism is unrelated to trophic differences between sexes. However, as this weighting method does not account for between-study and between-species heterogeneity in trophic sex differences, we believe it to be inappropriate. The diversity of species investigated by the studies we have meta-analysed, and the consequent diversity of our analysis, mean assuming a universal difference in sex differences in trophic level is clearly erroneous. We are therefore skeptical of the conclusion this weighting method produces and are more confident in the original model included in the main text.

When weighting by the inverse of within study variance in model examining the effect of size dimorphism on sex difference in nitrogen variation (Table 3), carbon mean (Table 4) and carbon variation (Table 5), our qualitative conclusions remained the same.

When including dietary class and mean size alongside size dimorphism, as predictors of sex differences in nitrogen mean, the effect of mean size (which was effectively zero) remained, but, as for the size dimorphism only model, the effect of size dimorphism was absent in all dietary classes, when weighting by the inverse of within study variance (Table 6). Our results in models examining gape-limited (Table 7) and non-gape-limited carnivores (Table 8) were also not robust to alternate weighting. However, for the same reasons as the size dimorphism only model, we are more confident in the original models included in the main text.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.046 | 0.091 | 0.507 | 0.612 | −0.132 | 0.223 |
| SSD | summary | 0.102 | 0.062 | 1.630 | 0.103 | −0.021 | 0.224 |

**Table 2.** Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, weighting studies only by the inverse of within-study variance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Variation Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | −0.007 | 0.032 | −0.223 | 0.823 | −0.069 | 0.055 |
| SSD | summary | 0.039 | 0.027 | 1.420 | 0.155 | −0.015 | 0.092 |

**Table 3.** Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen variation, weighting studies only by the inverse of within-study variance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Carbon Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | −0.051 | 0.104 | −0.490 | 0.624 | −0.256 | 0.154 |
| SSD | summary | 0.144 | 0.078 | 1.843 | 0.065 | −0.009 | 0.298 |

**Table 4.** Output of fixed effects model examining the effect of size dimorphism on sex differences in carbon mean, weighting studies only by the inverse of within-study variance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Carbon Variation Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.044 | 0.039 | 1.134 | 0.257 | −0.032 | 0.120 |
| SSD | summary | 0.030 | 0.033 | 0.912 | 0.362 | −0.035 | 0.095 |

**Table 5.** Output of fixed effects model examining the effect of size dimorphism on sex differences in carbon variation, weighting studies only by the inverse of within-study variance***.***

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism \* Dietary Class + Mean Size** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.209 | 0.075 | 2.766 | 0.006 | 0.061 | 0.357 |
| Size Dimorphism | summary | 0.059 | 0.060 | 0.994 | 0.320 | −0.058 | 0.177 |
| Herbivore | summary | −0.705 | 0.296 | −2.381 | 0.017 | −1.286 | −0.125 |
| Omnivore | summary | −0.529 | 0.280 | −1.889 | 0.059 | −1.078 | 0.020 |
| Size | summary | 0.000 | 0.000 | 0.368 | 0.713 | 0.000 | 0.000 |
| Size Dimorphism: Herbivore | summary | 0.651 | 0.548 | 1.189 | 0.234 | −0.422 | 1.725 |
| Size Dimorphism: Omnivore | summary | 0.380 | 0.265 | 1.434 | 0.152 | −0.139 | 0.900 |

**Table 6.** Output of fixed effects model examining the effect of size dimorphism, dietary class and species mean size on sex differences in nitrogen mean, weighting studies only by the inverse of within-study variance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Gape Limited Carnivores: Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.109 | 0.107 | 1.019 | 0.308 | −0.100 | 0.318 |
| Size Dimorphism | summary | 0.113 | 0.124 | 0.913 | 0.361 | −0.130 | 0.357 |

**Table 7.** Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, in gape-limited carnivores, weighting studies only by the inverse of within-study variance.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Non-Gape Limited Carnivores: Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.226 | 0.087 | 2.601 | 0.009 | 0.056 | 0.397 |
| Size Dimorphism | summary | 0.054 | 0.066 | 0.821 | 0.412 | −0.075 | 0.182 |

**Table 8.** Output of fixed effects model examining the effect of size dimorphism on sex differences in nitrogen mean, in non-gape-limited carnivores, weighting studies only by the inverse of within-study variance.

**High Leverage Data Points**

The outcome of meta-analyses may also be adversely impacted by outliers/ high leverage data points that skew model estimates. We therefore used Cook’s leave-one-out analysis to identify high leverage data points that may have an unduly large effect on our models. Several approaches are possible for identifying data points as high leverage based on Cook’s scores, and we chose to assign those with a Cook’s score over three times the mean score, for data points in a given model, as potentially high leverage. We found this approach to be the most conservative, by identifying the highest number of points as possibly high leverage. We then removed these data from the models for which they may be high leverage and re-ran each model.

In models examining only the effect of size dimorphism on sex differences in nitrogen mean (Table 9), nitrogen variation (Table 10), carbon mean (Table 11) and carbon variation (Table 12), removing high leverage data points did alter estimated effect sizes, but did not change the qualitative conclusions we could draw from the models. When including dietary class as a predictor, alongside size dimorphism, the effect size changed (Table 13), but our qualitative conclusions did not. When including species mean size as an additional predictor, removal of high leverage data points resulted in the confidence intervals of the interaction between size dimorphism and mean size overlapping zero, in contrast to the original model (Table 14). However, as we had already concluded the effect of this interaction to have little meaning, removing high leverage data points in this model did not change our qualitative conclusions. In models analyzing the impact of size dimorphism on sex differences in nitrogen mean in gape-limited (Table 15) and non-gape-limited carnivores (Table 16), removing high leverage data points also did not change our qualitative conclusions.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.077 | 0.039 | 1.980 | 0.048 | 0.001 | 0.153 |
| Size Dimorphism | summary | 0.192 | 0.053 | 3.638 | <0.001 | 0.089 | 0.296 |

**Table 10.** Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Variation Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.001 | 0.020 | 0.034 | 0.972 | −0.039 | 0.041 |
| Size Dimorphism | summary | 0.000 | 0.032 | 0.001 | 0.999 | −0.063 | 0.063 |

**Table 11.** Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen variation, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Carbon Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.022 | 0.030 | 0.722 | 0.470 | −0.037 | 0.080 |
| Size Dimorphism | summary | 0.064 | 0.039 | 1.655 | 0.098 | −0.012 | 0.140 |

**Table 12.** Output of meta-regression model examining the effect of size dimorphism on sex differences in carbon mean, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Carbon Variation Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | −0.003 | 0.027 | −0.107 | 0.915 | −0.055 | 0.049 |
| Size Dimorphism | summary | 0.031 | 0.028 | 1.117 | 0.264 | −0.024 | 0.086 |

**Table 13.** Output of meta-regression model examining the effect of size dimorphism on sex differences in carbon variation, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism \* Dietary Class** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| intercept | summary | 0.114 | 0.042 | 2.677 | 0.007 | 0.030 | 0.197 |
| Size Dimorphism | summary | 0.159 | 0.054 | 2.933 | 0.003 | 0.053 | 0.265 |
| Herbivore | summary | 0.021 | 0.448 | 0.047 | 0.963 | −0.857 | 0.899 |
| Omnivore | summary | −0.147 | 0.108 | −1.359 | 0.174 | −0.359 | 0.065 |
| Size Dimorphism:Herbivore | summary | 0.170 | 0.617 | 0.276 | 0.782 | −1.039 | 1.380 |
| Size Dimorphism:Omnivore | summary | 0.464 | 0.221 | 2.102 | 0.036 | 0.031 | 0.897 |

**Table 14.** Output of meta-regression model examining the effect of size dimorphism and dietary class on sex differences in nitrogen mean, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism \* Mean Size** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.072 | 0.040 | 1.791 | 0.073 | −0.007 | 0.151 |
| Size Dimorphism | summary | 0.232 | 0.052 | 4.464 | 0.000 | 0.130 | 0.334 |
| Mean Size | summary | 0.000 | 0.000 | −0.063 | 0.950 | 0.000 | 0.000 |
| Size Dimorphism: Size | summary | 0.000 | 0.000 | −0.688 | 0.492 | 0.000 | 0.000 |

**Table 15.** Output of meta-regression model examining the effect of size dimorphism and species mean size on sex differences in nitrogen mean, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci ub** |
| Intercept | summary | 0.095 | 0.041 | 2.304 | 0.021 | 0.014 | 0.177 |
| Size Dimorphism | summary | 0.114 | 0.034 | 3.328 | 0.001 | 0.047 | 0.181 |

**Table 16.** Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, in gape-limited carnivores, with high leverage data points removed.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Nitrogen Mean Difference ~ Size Dimorphism** | | | | | | | |
| **Term** | **Type** | **Estimate** | **Standard**  **Error** | **Statistic** | ***p*** | **ci lb** | **ci lb** |
| Intercept | summary | 0.087 | 0.069 | 1.267 | 0.205 | −0.047 | 0.221 |
| Size Dimorphism | summary | 0.160 | 0.076 | 2.119 | 0.034 | 0.012 | 0.309 |

**Table 17.** Output of meta-regression model examining the effect of size dimorphism on sex differences in nitrogen mean, in non-gape-limited carnivores, with high leverage data points removed.