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Seasonal patterns of dietary partitioning in vertebrates

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Abstract

Dietary partitioning plays a central role in biological communities, yet the extent of partitioning often varies dramatically over time. Food availability may drive temporal variation in dietary partitioning, but alternative paradigms offer contrasting predictions about its effect. We compiled estimates of dietary overlap between co-occurring vertebrates to test whether partitioning is greater during periods of high or low food abundance. We found that dietary partitioning was generally greatest when food abundance was low, suggesting that competition for limited food drives partitioning. The extent of dietary partitioning in birds and mammals was also related to seasonality in primary productivity. As seasonality increased, partitioning increased during the nonbreeding season for birds and the breeding season for mammals. Although some hypotheses invoke changes in dietary breadth to explain temporal variation in dietary partitioning, we found no association between dietary breadth and partitioning. These results have important implications for the evolution of dietary divergence.

KEYWORDS
diet overlap, niche breadth, niche partitioning, Pianka's overlap index, resource competition

INTRODUCTION

Niche partitioning plays a key role in shaping biodiversity because it promotes adaptive divergence (Axelrod et al., 2018), reproductive isolation (Sobel & Streisfeld, 2015) and stable coexistence (Chesson, 2000; Ellner et al., 2019; Letten et al., 2017). For many organisms, the dietary niche is the primary axis partitioned (Donadio & Buskirk, 2006; Grant & Grant, 2006; Martin & Wainwright, 2013) and has thus been particularly well-studied. However, the extent of dietary partitioning between co-occurring species often varies tremendously over short timescales (e.g. across seasons; Smith et al., 1978, Hasui et al., 2009, Correa & Winemiller, 2014). Although many studies find seasonal variation in the extent of dietary partitioning, the factors causing this variation are poorly understood.

One factor thought to influence seasonal variation in dietary partitioning is resource abundance, but alternative paradigms offer contrasting predictions about its effect. Classic optimal foraging theory (i.e. prey model) predicts that species specialise on narrow subsets of alternative resources and are thus strongly partitioned during seasons of high resource abundance (hereafter 'fat seasons', sensu Schoener, 1982; Perry & Pianka, 1997). According to the prey model, diets of co-occurring species expand and thus overlap more in response to prey depletion by competitors during resource-poor seasons (hereafter 'lean seasons', sensu Schoener, 1982; Perry & Pianka, 1997). Conversely, niche-based models (Schoener, 1982) and some foraging models (e.g. Robinson & Wilson, 1998) predict that differential food depletion by competitors during lean seasons favours partitioning, whereas food depletion by competitors is inconsequential when resources are abundant, making high diet overlap more likely.

The relative support for these models is unclear. Smith et al. (1978) and Schoener (1982) found that partitioning was greatest during lean seasons and diets overlapped during fat seasons in 27 of 30 systems surveyed. However, the results of subsequent studies seemingly vary widely. Some studies find that interspecific partitioning is

greatest during lean seasons and diets overlap during fat seasons (e.g. Benkman, 1987; Grant & Grant, 2014; Smith, 1990), while others find the opposite (e.g. Ashrafi et al., 2011; Dostine & Franklin, 2002; Petrov et al., 2016). Furthermore, some systems exhibit seasonally stable levels of partitioning (e.g. Martin & Genner, 2009). Without a contemporary analysis of interspecific dietary partitioning studies, it is unclear whether there is a consistent seasonal pattern of partitioning, and if so, what it is.

Furthermore, resource abundance is only one determinant of how available resources are to consumers (Hutto, 1990). Many variables such as handling time and competitor density relative to resource abundance jointly determine resource availability (Stephens & Krebs, 1986). Such parameters have not been estimated for most systems. Nonetheless, one key determinant of resource availability can be estimated across systems: seasonality in primary productivity. If productivity is stable across seasons, populations can numerically track resources and continuously reside near carrying capacities (Sherry et al., 2020). This results in elevated competition and low resource availability throughout the year (Ashmole, 1961, 1963; Ricklefs, 1980). Conversely, in more seasonal environments with an unproductive lean season followed by a productive fat season, populations experience variation in the intensity of competition and per capita resource availability. Low per capita resource availability during the lean season results in intense competition and high mortality (Brittingham & Temple, 1988; Danner et al., 2013). Lean season mortality reduces consumer densities which, combined with increased resource abundance, increases per capita resource availability during the fat season (Ricklefs, 1980). Such seasonal variation can explain much of the geographical variation in avian clutch size (Lunblad & Conway, 2021; Ricklefs, 1980) and mammalian litter size (Battistella et al., 2019; Lord, 1960), where clutch and litter sizes increase with increasing seasonality because of greater per capita resource availability in the breeding season. However, the effect of seasonality on interspecific dietary partitioning has received little study (but see Rabenold, 1978, 1979, Rusterholz, 1981).

Here, we compiled estimates of dietary overlap (the inverse of dietary partitioning) between co-occurring species during fat and lean seasons to test the effect of resource abundance on interspecific dietary partitioning. We searched the literature for studies that quantified interspecific dietary overlap across seasons in amphibians, birds, fish, mammals and reptiles. We also compared dietary partitioning across breeding and nonbreeding periods. While the breeding season often coincides with the fat season, some reproductive strategies decouple the fat and breeding seasons (Jönsson, 1997; Willliams et al., 2017). Thus, comparing breeding versus nonbreeding seasons and fat versus lean seasons allows us to explore how variation in reproductive strategies affects dietary partitioning. Because seasonality in primary productivity affects per capita resource availability (Lunblad & Conway, 2021) and may thus affect dietary partitioning, we also collected primary productivity data from the locations of dietary studies. Finally, optimal foraging and niche-based models posit that species' diets expand or contract in response to fluctuating food abundance, which affects interspecific dietary partitioning (e.g. Stephens & Krebs, 1986). To test whether dietary breadth changes with seasonal changes in food abundance, we also collected data on dietary breadth across seasons.

METHODS

Literature survey

We searched for studies that quantified pairwise dietary overlap between two or more sympatric species across seasons by searching for "seasonal*" AND "diet*" AND "overlap*" using the Web of Science (Thomson ISI) and Google Scholar. Although we use the term 'species' throughout this paper, our sample includes sympatric morphs and ecotypes that are not distinct species (e.g. Schluter & McPhail, 1992; Smith, 1990). These searches yielded 766 and 1000 articles on 28 August 2019 and 31 August 2019 respectively. We only collected data from species that are native to study locations and only included studies with sufficient information to calculate effect sizes (see Calculating effect sizes). We also searched for relevant citations within each article to collect additional data on the focal system or other systems.

Data collection

Dietary overlap

Within each article, we searched for raw diet data (e.g. percentage of diet composed by different prey species) or pairwise estimates of Pianka's (1974) overlap index:

$$O_{jk} = \frac{\sum_i^n \hat{p}_{ij}\hat{p}_{ik}}{\sqrt{\sum_i^n \hat{p}_{ij}^2 \sum_i^n \hat{p}_{ik}^2}}$$

where O_{jk} is the overlap between species j and k, $\hat{p}$ represents the proportion of resource i consumed by species j or k and n represents the total number of resource categories. Values of this index range from 0 to 1, where 1 represents total overlap and 0 represents no overlap.

Raw data were used to calculate Pianka's (1974) overlap index with the ra3 algorithm in the R package EcoSimR (Gotelli et al., 2015). If data were only available from figures, we used WebPlotDigitizer v4 (Rohatgi, 2019) to extract data. We only included studies that used direct observations of diet such as behavioural observations or stomach content analyses.

We did not use stable isotope data because they can be integrated over long periods of time and thus not capture the temporal variation needed for our study (Post, 2002). Moreover, stable isotopes may not provide reliable estimates of species-level diet composition, given that there are often many possible prey combinations that can produce a given isotope value (Post, 2002). We also did not use DNA barcoding data, as these do not usually include data on abundance. When data from multiple years and/or locations were available within a study, we averaged across them. Because we were interested in absolute overlap during each season, we did not factor in the relative abundance of different resources in the environment into estimates of overlap. For example, if high overlap is due to consumption of a few abundant and easily accessible prey taxa, this represents an inability to partition resources given the prey distribution (Kent & Sherry, 2020).

Dietary breadth

We calculated Levin's unstandardised niche breadth (Hurlbert, 1978) for each species from each season to estimate seasonal differences in dietary breadth:

$$B = \frac{1}{\sum_i^n \hat{p}_i^2}$$

where B is the dietary breadth of a species and $\hat{p}$ represents the relative proportion of resource i in the total diet. Unstandardised niche breadth (B) was subsequently standardised by the following equation:

$$B_S = \frac{B - 1}{n - 1}$$

where n denotes the number of possible resources (Krebs, 1999). Values of this index range from 0 to 1, where 0 represents consumption of a single resource and 1 represents equal consumption of all resources (Krebs, 1999).

Resource abundance and timing of breeding

We searched for information on seasonal variation in resource abundance and the timing of breeding in each article. We categorised seasons as fat or lean based on estimates of resources by the authors of each study. If information on the timing of breeding was unavailable in the article or its citations, we searched online and other references (e.g. field guides). Because the timing of breeding can vary geographically, we searched for information as close as possible to the location where dietary data were collected. If information on the breeding season and seasonal food abundance were unavailable for a particular species, we excluded that species from our analyses.

Our focus on dietary overlap and breadth in fat and lean seasons excludes species that do not feed in lean seasons (e.g. species that hibernate). Similarly, our focus on nonbreeding and breeding seasons excludes continuous breeders (e.g. some primates) from these analyses. However, in the latter case, such species are not necessarily excluded from fat versus lean season analyses. Finally, we note that we only included studies with data on the same population(s) across seasons. Thus, our literature survey excluded studies on long-distance migrants in, for example, distinct summering and wintering ranges because no such studies in our literature survey had information on population identity across seasons. It is also unclear whether seasonality in productivity on the summer or winter range should most affect resource availability for migratory species (Lunblad & Conway, 2021).

Calculating effect sizes

We used the raw mean difference D as the measure of effect size because all estimates of dietary overlap and breadth were converted to the same scale (i.e. Pianka's overlap index or Levin's standardised niche breadth; Borenstein et al., 2009). Because some studies estimated dietary overlap between more than two species, there were sometimes multiple effect sizes per study. The non-independence arising from multiple effect sizes per study is controlled for in the statistical analyses (see Statistical analyses). For dietary partitioning analyses, the effect size represents dietary overlap between a pair of species in the fat or breeding season minus that in the lean or nonbreeding season. Thus, positive values reflect greater dietary overlap in the fat or breeding season and negative values reflect the opposite. For dietary breadth analyses, the effect size represents dietary breadth for a single species in the fat or breeding season minus that in the lean or nonbreeding season. Thus, positive values reflect greater dietary breadth in the fat or breeding season and negative values reflect the opposite. Larger values of D represent a greater difference in partitioning or breadth across seasons, and an effect size of zero indicates no difference in partitioning or breadth across seasons. The associated variance for all analyses was calculated as $(n_1 + n_2)/(n_1 n_2) + D^2/2(n_1 + n_2)$, where n_1 is the total number of animals sampled in one season and n_2 is the total number of animals sampled in the other season (Borenstein et al., 2009).

Phylogenetic tree

To control for non-independence of effect sizes due to phylogenetic relationships (Koricheva et al., 2013), we created a phylogeny of the species included in our dataset. Given the diversity of species included in our study, no single phylogeny included all species. We therefore

constructed a phylogenetic supertree using the Open Tree of Life (OTL) database (Hinchliff et al., 2015). Because accurate branch length data are unavailable for these trees, all branch lengths were set to one and made ultrametric (Grafen, 1989) using the R package ape v5.4 (Paradis et al., 2004). In cases where the OTL database produced a polytomy, we searched for published phylogenies that could resolve them. If we could not find a published phylogeny to resolve polytomies, we consulted the OneZoom Tree of Life (OneZoom Core Team 2021) which randomly splits polytomies into bifurcations. The final ultrametric tree is available in the supplementary material (Figure S1).

Predictors of dietary partitioning and breadth

Clade

Seasonal patterns of dietary partitioning and breadth could vary among clades. Therefore, we included clade (amphibian, bird, fish, mammal or reptile) as a categorical predictor variable in analyses. The relationship between predictor variables and the relative degree of dietary partitioning and breadth in different seasons may also vary among clades. Therefore, we also conducted clade-specific analyses for well-sampled groups (birds, fish and mammals).

Primary productivity

Seasonality in primary productivity influences resource availability (Ricklefs, 1980) and thus may affect seasonal patterns of dietary partitioning and/or breadth. To quantify seasonality in primary productivity, we extracted enhanced vegetation index (EVI) data from each study location using the MOD13A1 v6 product in Google Earth Engine. We extracted monthly EVI at each location from 2010 to 2019 and averaged EVI across years for each month. Ideally, our EVI sampling would focus on the time of data collection for each study. However, because many studies took place prior to the development of Google Earth Engine's satellite imagery, we sampled EVI over a standardised 10-year window. A limitation of this approach is that primary productivity in different biomes may respond differently to climate change (Ritter et al., 2020). Thus, our measurements of EVI may not reflect patterns of primary productivity at the time of dietary data collection in all regions equally well, which could limit our ability to detect an effect of primary productivity. Nonetheless, there was no obvious temporal bias in our sampling of regions with different climates or seasonal patterns of primary productivity (Figure S2), which should minimise this issue. Our estimate of annual EVI seasonality at each site was the average of the 4 months with the maximum EVI minus the average of the 4 months with the minimum EVI (Somveille et al., 2015). In cases where EVI

seasonality was associated with the relative degree of dietary partitioning across seasons, we tested if minimum or maximum EVI drove this pattern through its effects on dietary partitioning in both seasons.

Mammalian body size and trophic level

Our analyses revealed that EVI seasonality affects dietary partitioning in birds and mammals (see Results). Interestingly, while our results in birds align with prior studies (Rabenold, 1978, 1979; Rusterholz, 1981), we found a different pattern in mammals. One possibility is that the tremendous variation in body size and trophic level in our mammalian sample could affect the response to seasonal variation in primary productivity. For example, herbivores might experience a greater degree of seasonality in food availability compared to carnivores, which might be more 'buffered' from fluctuations in productivity. Likewise, larger species might be more buffered from fluctuations in productivity than smaller species, given the potential of the former to store internal energetic reserves (Humphries et al., 2004). To test these hypotheses, we collected body size and trophic level data of the mammalian species in our sample and included them as predictors in mammal-specific models. We collected data on body mass and trophic level primarily from two large comparative studies (Smith et al., 2003; Tucker & Rogers, 2014). Other sources, primarily field guides, were consulted for species lacking data in these references.

Statistical analyses

Comparing dietary partitioning and breadth across seasons

Statistical analyses were performed using R v4.0.5 (R development Core Team 2021). Meta-analyses were performed using the package Metafor v3.0–2 (Viechtbauer, 2010). To determine the mean effect size for each comparison, we ran multilevel random-effects models using the rma.mv function, with study, pair of species and phylogeny as random effects (Nakagawa & Santos, 2012). Phylogeny was incorporated into the model using a variance–covariance matrix, assuming a Brownian motion model of trait evolution. The raw mean difference D was used as the effect size in all models. These overall models were run separately for comparisons of dietary partitioning and breadth in fat versus lean seasons and breeding versus nonbreeding seasons.

Heterogeneity of effect sizes

We used I^2 as a measure of effect size heterogeneity (Higgins et al., 2003). I^2 values of 25, 50 and 75% are

considered low, moderate and high respectively (Higgins et al., 2003). We calculated I^2 across all effect sizes and partitioned at different levels of the model using the method of Nakagawa and Santos (2012). This allowed us to quantify the amount of variation in effect size attributed to differences in study, species pair and phylogeny.

Predictors of effect sizes

To test the effect of predictors we ran meta-regression models that were identical to the above models except for the inclusion of categorical (clade) or continuous (EVI seasonality) fixed effects using three approaches. First, we ran a separate model for each fixed effect. Second, we ran a full model including all fixed effects and their interaction. Third, we ran separate analyses for each clade when evaluating the relationships between dietary overlap/breadth and EVI. We evaluated whether a predictor significantly influenced the mean effect size by examining the Q_M statistic, which performs a global test of model coefficients. We used the method of Nakagawa and Schielzeth (2013) to calculate marginal R^2 values for each fixed effect. To estimate the average effect size for each level of clade, we ran meta-regressions including a single fixed effect but excluding the model intercept (Dougherty, 2021).

RESULTS

Sample sizes and their geographical distribution

For fat-lean and breeding-nonbreeding season comparisons of dietary partitioning, we obtained 479 pairwise estimates for 251 species from 94 studies and 311 pairwise estimates for 161 species from 63 studies respectively. For fat-lean and breeding-nonbreeding season comparisons of dietary breadth, we obtained 271 estimates for 236 species from 89 studies and 173 estimates for 154 species from 60 studies respectively. Our samples were globally distributed (Figures 1a,c, 2a,c). Amphibians and reptiles were underrepresented compared to other clades (Figures 1b,d, 2b,d).

Dietary partitioning in fat versus lean seasons

Overall comparison

Overall, the average effect size was significantly positive (Figure 3a; mean effect size = 0.130, 95% CI = 0.085–0.174), indicating greater partitioning in the lean season. There was high heterogeneity across effect sizes (Total I^2 = 82.83%), with 32.82% attributable to between-study differences, 50.00% to between-species pair differences and <0.001% to phylogeny.

Clade comparisons

The mean estimated effect sizes were positive (greater dietary partitioning in the lean relative to fat season) for all clades (Figure 3a) and did not differ among them (Table S1). Effect sizes were significant for birds (mean = 0.241, 95% CI = 0.144–0.338), fish (mean = 0.117, 95% CI = 0.047–0.188) and mammals (mean = 0.093, 95% CI = 0.019–0.166).

EVI seasonality

Overall, differences in dietary partitioning between fat and lean seasons were unaffected by EVI seasonality (Table S1). However, dietary partitioning in the lean season increased relative to that in the fat season as EVI seasonality increased in birds (mean = 0.278, 95% CI = 0.043–0.512) in a model that included an interaction between EVI seasonality and clade as a fixed effect. Clade-specific meta-regression gave a similar result for birds (Figure 4a; marginal R^2 = 0.212, mean = 0.494, 95% CI = 0.030–0.959). This result was driven by a tendency for greater dietary partitioning in the lean season as EVI seasonality increased (marginal R^2 = 0.122, mean = −0.442, 95% CI = −1.047–0.163). Neither minimum or maximum EVI alone were associated with the extent of dietary partitioning (Table S2 and S3), and partitioning in the fat season was unaffected by EVI seasonality in birds (Table S4).

Clade-specific meta-regression also revealed that the difference in dietary partitioning between seasons decreased in mammals as EVI seasonality increased, contra the results in birds (Figure 4b; marginal R^2 = 0.091, mean = −0.259, 95% CI = −0.493 to −0.025). This result is driven by greater dietary partitioning in the fat season as EVI seasonality increased (Figure 5a; marginal R^2 = 0.070, mean = −0.291, 95% CI = −0.587 - 0.005). Variation in body size and trophic level did not influence these results (Table S5 and S6). Neither minimum or maximum EVI alone was associated with the extent of dietary partitioning (Table S7 and S8), and partitioning in the lean season was unaffected by EVI seasonality in mammals (Table S9).

Dietary partitioning in breeding versus nonbreeding seasons

Overall comparison

Overall, the average effect size was significantly positive (Figure 3b; mean = 0.102, 95% CI = 0.047–0.158), indicating greater partitioning in the nonbreeding season. There was high heterogeneity across effect sizes (Total I^2 = 81.57%), with 27.72% attributable to between-study differences, 53.85% to between-species pair differences and <0.001% to phylogeny.
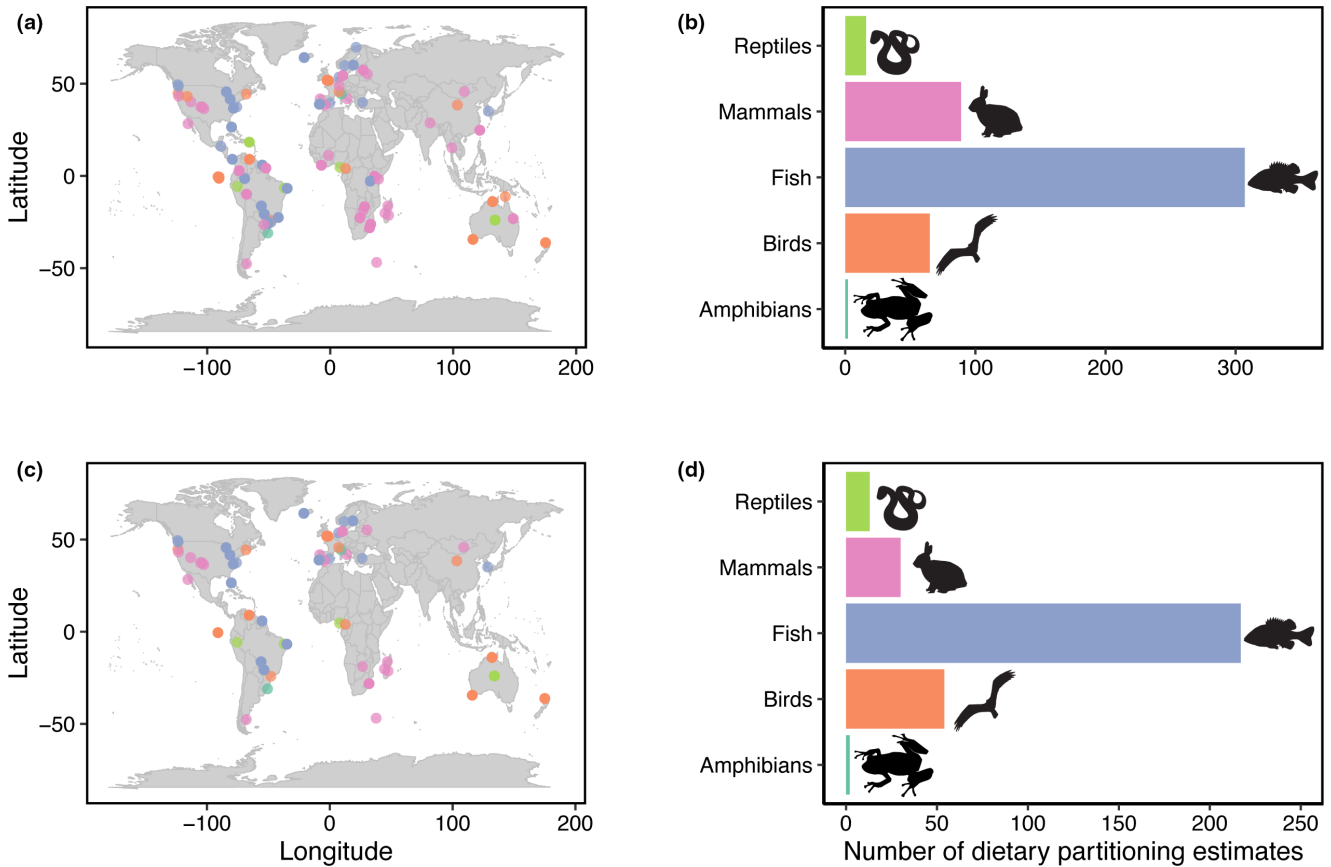
FIGURE 1 (a) The geographical distribution of dietary partitioning studies across fat and lean seasons ($n = 94$) and (b) the taxonomic distribution of dietary partitioning estimates across fat and lean seasons ($n = 479$) included in our meta-analysis. (c) Depicts the geographic distribution of dietary partitioning studies across breeding and nonbreeding seasons ($n = 63$) and (d) illustrates the taxonomic distribution of dietary partitioning estimates across breeding and nonbreeding seasons ($n = 311$).

Clade comparisons

Mean estimated effect sizes were positive (greater dietary partitioning in nonbreeding than breeding season) for all clades (Figure 3b) and did not differ among them (Table S1). However, effect sizes were significant only for birds (mean effect size = 0.245, 95% CI = 0.139–0.350).

EVI seasonality

Overall, differences in dietary partitioning between breeding and nonbreeding seasons were unaffected by EVI seasonality (Table S1). However, dietary partitioning in the nonbreeding season increased relative to that in the breeding season as EVI seasonality increased in birds (mean = 0.463, 95% CI = 0.219–0.707) in a model that included an interaction between EVI seasonality and clade as a fixed effect. Clade-specific meta-regression gave a similar result for birds (Figure 4c; marginal $R^2 = 0.261$, mean = 0.452, 95% CI = 0.082–0.821). This result was driven by greater dietary partitioning in the nonbreeding season as EVI seasonality increased (Figure 5b;

marginal $R^2 = 0.300$, mean = −0.669, 95% CI = −1.293 to −0.045). Neither minimum or maximum EVI alone was associated with the extent of nonbreeding dietary partitioning (Table S10 and S11), and partitioning in the breeding season was unaffected by EVI seasonality in birds (Table S12).

Dietary breadth

Dietary breadth did not consistently differ between lean and fat seasons or nonbreeding and breeding seasons (Figure 6a: mean = −0.032, 95% CI = −0.5808–0.5171; Figure 6b: mean = −0.024, 95% CI = −0.718–0.669). Relative dietary breadth in both comparisons was unrelated to clade, EVI seasonality, or their interaction (Table S13). There was high heterogeneity across effect sizes in the fat-lean season data (Total $I^2 = 95.08\%$), with 92.10% attributable to between-study differences and 2.97% to phylogeny. There was similarly high heterogeneity across effect sizes in the breeding-nonbreeding season data (Total $I^2 = 98.03\%$), with 95.25% attributable to between-study differences and 2.78% to phylogeny.
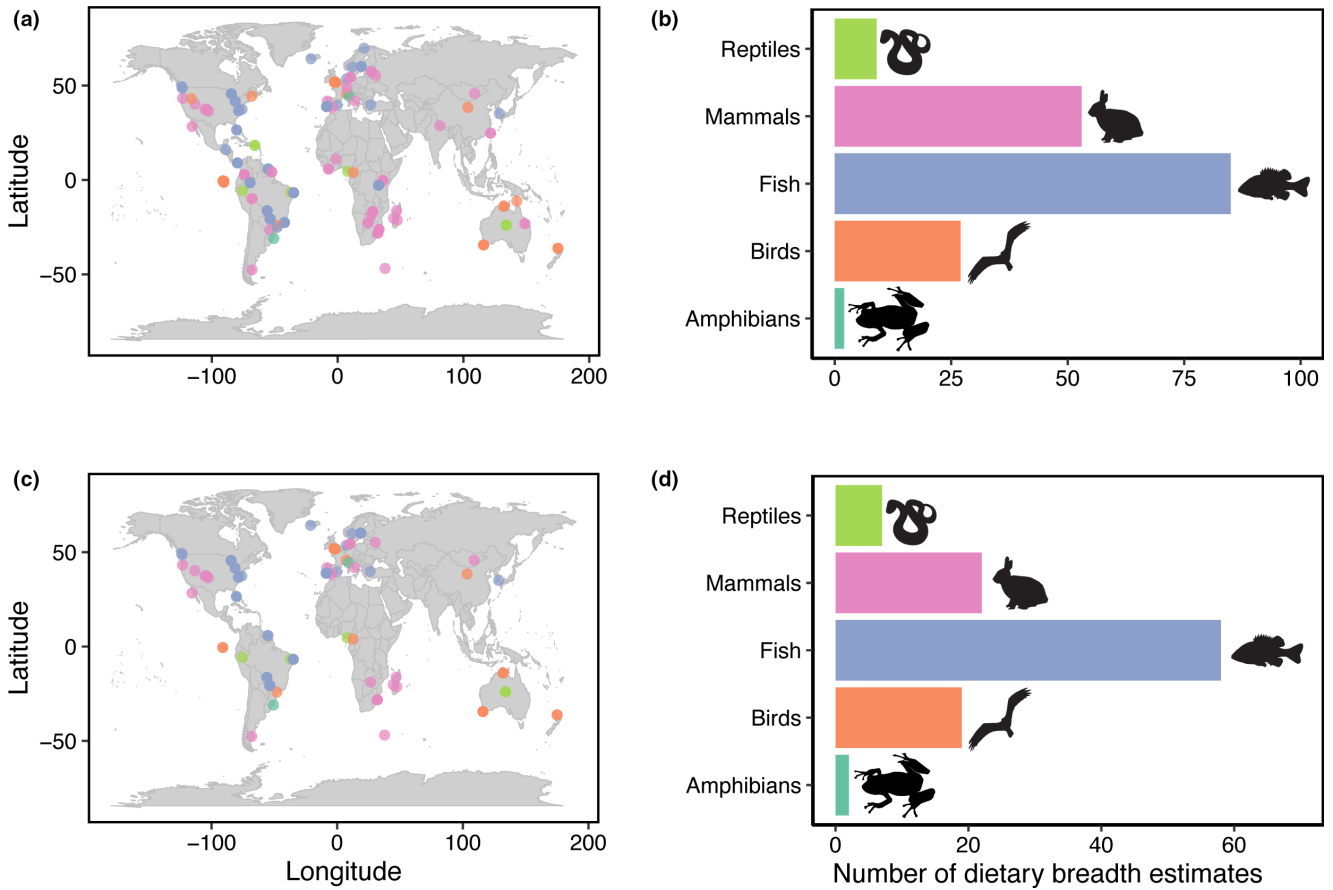
FIGURE 2 (a) The geographical distribution of dietary breadth studies across fat and lean seasons ($n = 89$) and (b) the taxonomic distribution of dietary breadth estimates across fat and lean seasons ($n = 271$) included in our meta-analysis. (c) Depicts the geographical distribution of dietary breadth studies across breeding and nonbreeding seasons ($n = 60$) and (d) illustrates the taxonomic distribution of dietary breadth estimates across breeding and nonbreeding seasons ($n = 173$).
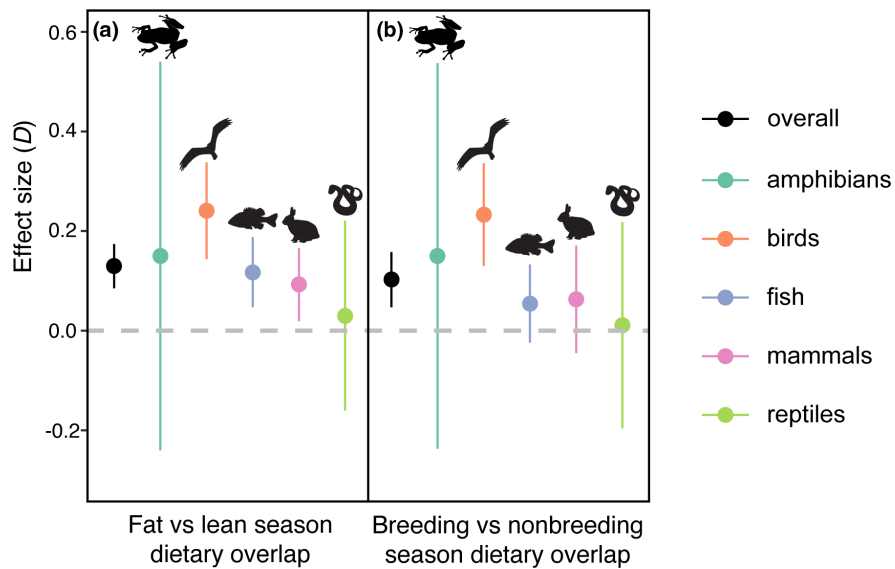
FIGURE 3 Average effect sizes (D with 95% confidence intervals) from meta-analytic models comparing the differences in dietary partitioning between (a) fat (resource-abundant) and lean (resource-poor) seasons and (b) breeding and nonbreeding seasons. Positive effect sizes indicate greater dietary partitioning in the lean and nonbreeding seasons than in the fat and breeding seasons respectively. The dashed grey line indicates equal dietary partitioning across seasons (i.e. $D = 0$).
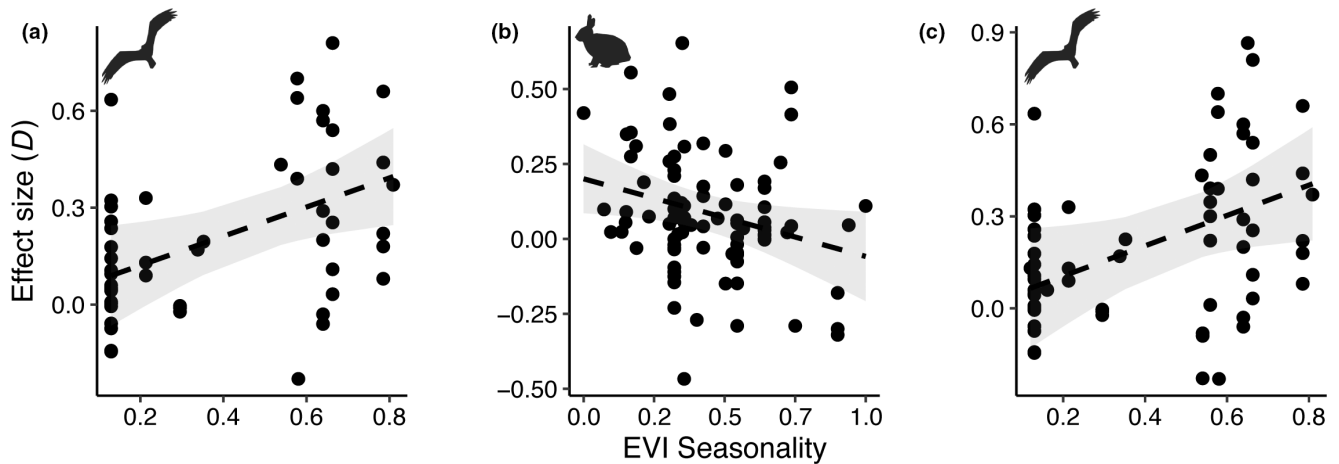
FIGURE 4 As seasonality in enhanced vegetation index (EVI) increases, dietary partitioning in the lean relative to that in the fat season increases in birds (a; marginal $R^2 = 0.212$) but decreases in mammals (b; marginal $R^2 = 0.091$). In birds, dietary partitioning in the nonbreeding season increases relative to that in the breeding season as seasonality in EVI increases (c; marginal $R^2 = 0.261$). Meta-analytic model predictions are plotted with dashed lines and shaded 95% confidence intervals while values from individual studies are plotted as points.
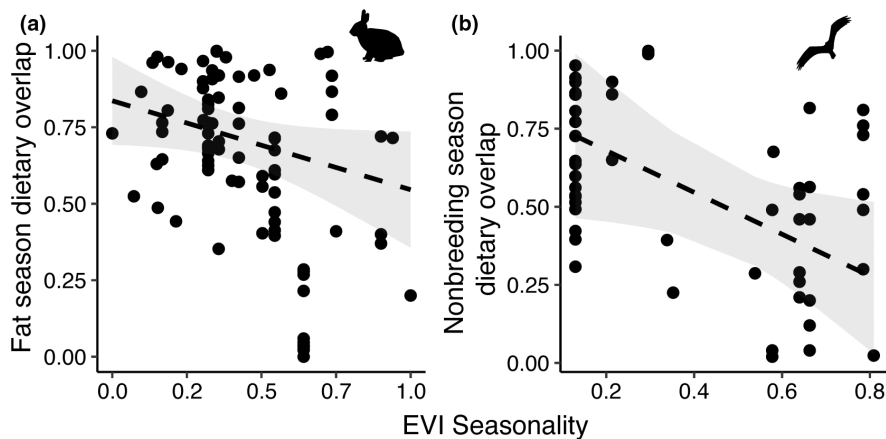
FIGURE 5 Seasonality in enhanced vegetation index (EVI) is negatively associated with a) the extent of dietary overlap in the fat season in mammals (marginal $R^2 = 0.070$) and (b) the extent of dietary overlap in the nonbreeding season in birds (marginal $R^2 = 0.300$). Meta-analytic model predictions are plotted with dashed lines and shaded 95% confidence intervals while values from individual studies are plotted as points.

DISCUSSION

Our results reveal that dietary partitioning is greater during seasons of food scarcity (generally the nonbreeding season) than during seasons of food abundance. Conversely, dietary breadth does not consistently change in relation to seasonal variation in food abundance or the occurrence of breeding. Thus, changes in dietary partitioning are not due to changes in dietary breadth. Instead, there are multiple 'routes' to greater dietary partitioning in the lean season and less dietary partitioning in the fat season. For example, diets may contract in the lean season as species specialise on private resources unavailable to competitors (Smith et al., 1978) or diets may expand to include private resources (Smith, 1990). In both scenarios, dietary partitioning increases during lean seasons, but in the former diet breadth decreases while in the latter it increases. Likewise, diets may

contract in fat seasons as species converge on a few profitable food items (Golcher-Benavides & Wagner, 2019) or diets may expand to include many shared food items (Overdorff, 1993). In both scenarios, dietary partitioning decreases during fat seasons, but neither scenario is more common. While classic optimal foraging theory is often used to infer consistent relationships between dietary breadth and partitioning, recent theory predicts complex relationships that depend on many variables (e.g. variation in ranked preferences among competitors; Araújo et al., 2011), consistent with our findings. More empirical work is necessary to determine which factors influence the relationship between dietary breadth and partitioning.

While dietary partitioning was typically greatest in lean and nonbreeding seasons, not all systems conformed to this pattern. Some variation might be related to a decoupling between the breeding and fat seasons in 18% of species in our sample (Appendix S1). This likely reflects
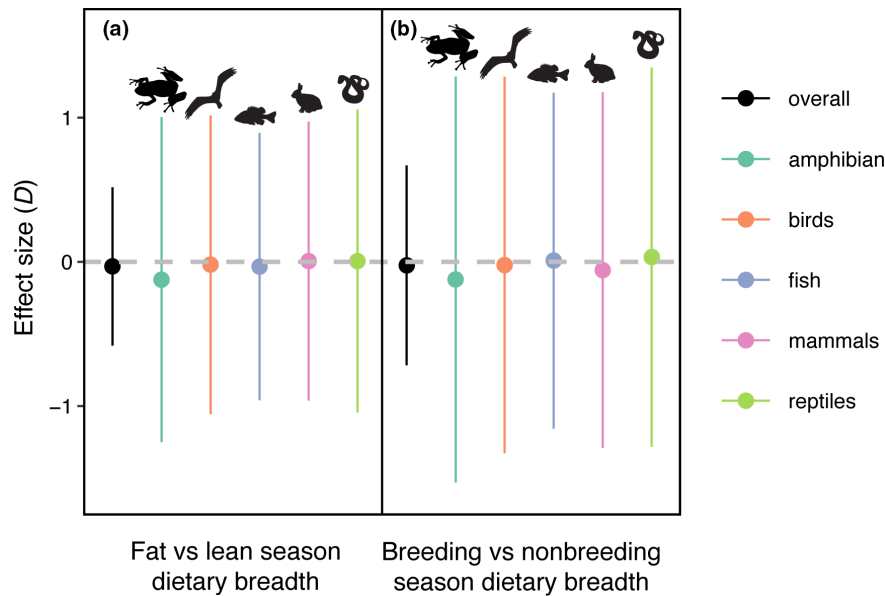
FIGURE 6 Average effect sizes (D with 95% confidence intervals) from meta-analytic models comparing the differences in dietary breadth between (a) fat (resource-abundant) and lean (resource-poor) seasons and (b) breeding and nonbreeding seasons. Positive effect sizes indicate greater dietary breadth in the lean and nonbreeding seasons than in the fat and breeding seasons respectively. The dashed grey line indicates equal dietary breadth across seasons (i.e. $D = 0$).

the presence of capital breeders (i.e. species that rely on stored reserves to fuel reproduction) in our data. Capital breeders might, for example, accumulate resources for reproduction in the fat season but breed at another time (Jönsson, 1997), thus decoupling periods of peak resource abundance from the timing of breeding. Effect sizes were more likely to be significant for fat-lean season comparisons than for breeding-nonbreeding season comparisons (Figure 3), consistent with resource abundance affecting dietary partitioning more than breeding. It is also worth noting that our sample size for fat-lean season comparisons was larger than for breeding-nonbreeding comparisons, which could affect the relative statistical power of these analyses.

Another factor that could cause deviations from the general pattern is the lack of standardised food availability estimates. Consider, for example, the two Darwin's ground finch (*Geospiza spp.*) datasets in our analysis (De León et al., 2014; Smith et al., 1978). Smith et al. (1978) compared *Geospiza* diets across wet (fat) and dry (lean) seasons, whereas De León et al. (2014) made comparisons across wet seasons that differed less in food abundance. Although both studies found that dietary partitioning was generally greatest when resources were relatively scarce, De León et al. (2014) documented more deviations from this pattern than Smith et al. (1978). This highlights the coarseness of our fat versus lean season distinction and suggests that, in some studies, food abundance does not differ enough across seasons to cause a shift in the extent of dietary partitioning. Furthermore, our fat versus lean season distinction is based only on differences in food abundance. However, the extent to which this reflects differences in per capita

food availability (energy per unit time foraging) will be influenced by numerous factors (e.g. handling times of different resources; Hutto, 1990) that could add additional noise to our data.

Indeed, we found that one factor influencing food availability (seasonality in primary productivity) is related to dietary partitioning in birds and mammals (Figures 4 and 5). In birds, greater seasonality in primary productivity is associated with greater dietary partitioning in the lean (nonbreeding) season relative to the fat (breeding) season (Figures 4a,c, 5b). We hypothesise that this pattern emerges because high seasonality in primary productivity enhances food availability in the fat season and exacerbates food limitation in the lean season. Bird populations are often limited by nonbreeding food availability (Brittingham & Temple, 1988; Danner et al., 2013; Dunning Jr. & Brown, 1982). Consequently, the leaner the nonbreeding season, the fewer individuals survive to reach the breeding season. The amount of resources available in the breeding season to individuals that survive the lean nonbreeding season increases as seasonality increases (Ashmole, 1961, 1963; Ricklefs, 1980). Consistent with this scenario and our results, previous studies have found that higher seasonality permits greater dietary overlap among bird species during the breeding season (Rabenold, 1978, 1979; Rusterholz, 1981). Increased per capita resource availability during breeding with increasing seasonality can explain why clutch size and seasonality are positively correlated (Lunblad & Conway, 2021; Ricklefs, 1980). Moreover, larger clutches in highly seasonal environments combined with enhanced parent and offspring survival under conditions of high food availability

(Martin, 1987) leads to larger consumer populations with greater energetic demands (Wiens & Innis, 1974) following the breeding season. This should result in greater competition as resources decline, further depressing food availability during the nonbreeding season in highly seasonal environments and favouring stronger dietary partitioning as we found. Interestingly, recent evidence suggests that bill shape diversification occurs most rapidly at higher latitudes (Freeman et al., 2022). This finding is consistent with the scenario we describe above and our results, given that diversification in bill morphology is a common evolutionary response to resource competition and dietary partitioning (Anderson & Weir, 2021; Grant & Grant, 2014).

Seasonality in productivity also affects dietary partitioning in mammals, but the effect is different than in birds. In mammals, dietary partitioning in the fat season increases (Figure 5a) and converges on that in the lean season as seasonality increases (Figure 4b). Thus, in highly seasonal environments, dietary partitioning is elevated year-round, whereas in less seasonal environments, partitioning is elevated in the lean season but weaker in the fat season. These results are consistent across a wide range of body sizes and trophic levels (Table S5 and S6). A possible explanation for these results is that mammals in highly seasonal environments incur an energetic deficit in the lean season that is replenished in the fat season. Mammals that are active year-round in highly seasonal environments must often survive extended periods in the lean season with little to no food intake from foraging (Lindstedt & Boyce, 1985). Indeed, many species rely on fat, muscle, and/or external caches accumulated in the fat season to survive lean season conditions (Humphries et al., 2004). Therefore, at the onset of the fat season, mammals in highly seasonal environments may have large energetic deficits that require intense foraging to replenish lost reserves (Long et al., 2014). In addition, males and females have high demands of reproduction (Frisch, 1984; Gittleman & Thompson, 1988) and need to accumulate energy reserves relied on during the ensuing lean season (Merems et al., 2020). In highly seasonal environments, the fat season is generally brief, further exacerbating individual demands and increasing the likelihood that physiological effects from the lean season 'carry over' to influence foraging throughout the fat season (Harrison et al., 2010). Thus, mammals' energetic demands in highly seasonal environments may be particularly high during the fat season (Merems et al., 2020; Stawski & Rojas, 2016), leading to intense competition that favours strong dietary partitioning. This scenario is speculative, but we note that food availability relative to energetic demands is a key determinant of competitive interactions (Auer et al. 2020).

Collectively, our results point to the importance of interspecific competition for scarce resources as a major cause of dietary partitioning, consistent with niche-based foraging models (Schoener, 1982). Importantly,

optimal foraging models that incorporate realistic assumptions about rank preferences of resources also predict dietary partitioning in response to competition for scarce resources (Robinson & Wilson, 1998). Robinson and Wilson's model predicts that high abundance of widely preferred resources leads to high dietary overlap among species with minimal competitive effects. Such resources are preferred by multiple species, even those with divergent trophic phenotypes, because they are energetically rich and do not require specific adaptations to process (e.g. juvenile clupeids fed on by multiple cichlid ecomorphs; Golcher-Benavides & Wagner, 2019). Interestingly, some work suggests that even when species differ in their ability to process a resource, such resources may be profitable to multiple species if they are sufficiently abundant (Poisot et al., 2011; Porter & Benkman, 2022). Regardless, as preferred resources are depleted, scarce and difficult-to-access resources (i.e. 'fallback foods'; Marshall & Wrangham, 2007) are all that remain available to consumers. The combination of low resource abundance and strong performance tradeoffs is predicted to favour a subtle shift towards greater partitioning (Robinson & Wilson, 1998), consistent with the magnitude of effect sizes in our analyses (Figure 3). Importantly, Robinson and Wilson's model shows that even subtle differences in the extent of partitioning can have profound ecological and evolutionary consequences (Robinson & Wilson, 1998).

When viewed through the lens of Robinson and Wilson's model, our results have myriad implications for ecology and evolution, especially competition's role in phenotypic diversification. For example, fat season diets may be relatively inconsequential for adaptive divergence between species. Therefore, inferences about mechanisms underlying diversification based on fat season diets may be misleading. Indeed, there is no evidence for selection on bill morphology in Darwin's ground finches (*Geospiza spp.*) during fat seasons when species' diets overlap, yet selection can be intense during the lean season when competition and partitioning are pronounced (Grant & Grant, 2014). Similarly, there is often little relationship between phenotypic and dietary variation during fat seasons, given that species with divergent phenotypes overlap greatly in their diets at this time (Dumont, 1995; Lambert et al., 2004; Nummi & Väänänen, 2001; Sæther, 1982; Török, 1993; Weeks et al., 2020). Historically, this has led some to suggest that the roles of competition, dietary partitioning and character displacement in phenotypic diversification have been exaggerated (e.g. Fryer & Iles, 1972, Wiens and Rotenberry 1979, Liem, 1990). Recent comparative studies that did not differentiate between lean and fat season diets reached similar conclusions and proposed mechanisms of diversification that do not emphasise competition (McEntee et al., 2018; Navalón et al., 2019). We suggest that future work would benefit from considering lean season diets, especially in seasonal environments,

as our results combined with others indicate that this is when dietary partitioning is most pronounced and evolutionarily consequential.

CONFLICT OF INTEREST
The authors have no competing interests to declare.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.