LETTER

Species interactions have predictable impacts on diversification

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Abstract

A fundamental goal of ecology is to reveal generalities in the myriad types of interactions among species, such as competition, mutualism and predation. Another goal is to explain the enormous differences in species richness among groups of organisms. Here, we show how these two goals are intertwined: we find that different types of species interactions have predictable impacts on rates of species diversification, which underlie richness patterns. On the basis of a systematic review, we show that interactions with positive fitness effects for individuals of a clade (e.g. insect pollination for plants) generally increase that clade's diversification rates. Conversely, we find that interactions with negative fitness effects (e.g. predation for prey, competition) generally decrease diversification rates. The sampled clades incorporate all animals and land plants, encompassing 90% of all described species across life. Overall, we show that different types of local-scale species interactions can predictably impact large-scale patterns of diversification and richness.

Keywords

Competition, diversification, macroevolution, mutualism, parasitism, phylogeny, predation, species interactions.

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INTRODUCTION

Species interactions are unquestionably widespread and important across the Tree of Life. Most animals depend on other animals and/or plants for their food. Many plant species depend on animals for reproduction (*c*. 88% of angiosperms; Ollerton *et al*., 2011) and dispersal (*c*. 48% of angiosperms; Hernández-Hernández and Wiens, 2020). Thousands (or millions) of species of bacteria, fungi and protists live as symbionts inside plants and animals (Larsen *et al*., 2017). Some of these symbionts can cause deadly diseases, whereas others are essential for host survival (e.g. McFall-Ngai *et al*., 2013).

An intriguing possibility is that these species interactions themselves have helped shape global biodiversity patterns and the Tree of Life (e.g. Dobzhansky, 1950; Simpson, 1953; Rensch, 1960; Stanley, 1975; Vermeij, 1978; Thompson, 2005; Jablonski, 2008). Differences in diversification rates among clades are important drivers of species richness patterns across living organisms (Scholl and Wiens, 2016). The diversification rate of a clade is the rate at which it accumulates species over time, or the speciation rate minus the extinction rate (Morlon, 2014). Thus, clades with high diversification rates can have many species despite being relatively young. Many studies have shown that diverse types of species interactions have impacted diversification rates in various clades. For example, herbivory may accelerate diversification in some insects and crustaceans (Futuyma and Agrawal, 2009; Wiens *et al*., 2015; Poore *et al*., 2017), whereas insect pollination may help explain the rapid diversification of angiosperms relative to other land plants (Raven, 1977; Stebbins, 1981; Hernández-Hernández and Wiens, 2020).

These case studies raise the question: are there general patterns in how species interactions influence diversification rates? For example, do interactions with negative fitness effects for individuals of one clade (e.g. predation, parasitism) decrease that clade's diversification rates? Conversely, do interactions with positive fitness effects for individuals of one (or both) clades increase that clade's diversification rates? The idea that interactions with positive/beneficial fitness effects on individuals might increase clade-level diversification rates is intuitively appealing, as is the idea that negative/harmful effects decrease diversification (e.g. Ricklefs, 2010). For example, positive fitness effects might facilitate species-level and clade-level range expansion, whereas negative fitness effects might increase species-level extinction rates (see Discussion). However, the idea that individual-level fitness effects of species interactions predictably impact clade-level diversification rates has not been tested quantitatively across organisms.

Several studies have reviewed the general topic of species interactions and macroevolution (e.g. Weber *et al*., 2017; Hembry and Weber, 2020), but little consensus has emerged about the effect of different interaction types on diversification. For example, Jablonski (2008) reviewed paleontological and neontological studies, and showed that negative interactions at the organismal level (e.g. competition, predation) can increase or decrease speciation rates, and positive interactions (e.g. mutualisms) can increase or decrease extinction rates. Hembry *et al*. (2014) reviewed competitive, antagonistic and mutualistic coevolution and showed that the impact of coevolution on diversification may depend on the type of interaction and the scale of the study. For example, competition is often invoked as a process that dampens clade-level diversification (e.g. Simpson, 1953; Schluter, 2000; Gillespie and Baldwin, 2009; Bennett and O'Grady, 2013; Hembry *et al*., 2014), although it may also be important in driving speciation (e.g. Schluter, 1994, 2000; Dieckmann and Doebeli, 1999; Hembry *et al*., 2014). Recently, Chomicki *et al*. (2019) described how mutualisms could increase or decrease diversification rates.

However, what is lacking is a systematic review and quantitative analysis of how different types of interactions influence diversification rates, utilising the dozens of empirical studies that examined the correlates of diversification.

Here, we test if different types of species interactions impact diversification rates in predictable ways. We first conduct a systematic review of studies that examined the impacts of species interactions on diversification rates in one of the interacting clades. We then classify these interactions as being predominantly positive/beneficial or negative/costly in their fitness effects on individuals of each clade, and test whether positive-effect interactions tend to increase diversification rates and negative-effect interactions decrease diversification rates. We perform both count-based analyses (e.g. how many studies of positive-effect interactions show significantly increased vs. decreased diversification rates?) and analyses of effect sizes (e.g. by how much do positive-effect interactions increase rates?). Our results generally support the idea that positive-effect interactions tend to increase diversification rates, whereas negative-effect interactions decrease diversification rates.

MATERIALS AND METHODS

Search methods and criteria

We conducted 11 systematic searches for research papers using the Web of Science Core Collection on September 25, 2019. Each search used one of 11 pairs of keywords, with one word from each of two groups (connected with "AND"). The first group was related to species interactions, including "amensalism", "commensalism", "competition", "herbivory", "mutualism", "neutralism", "parasitism", "pollination" and "predation", and the more general terms "symbiosis OR ectosymbiosis OR endosymbiosis" and "species interaction." The second group of keywords was related to diversification (i.e. "diversification OR macroevolution"). The document type was restricted to "Article". These searches yielded 4,162 papers. We reduced this pool to 403 after removing papers that were duplicates, outside biology and clearly irrelevant based on their titles.

We further screened these 403 studies using three criteria, which reduced the total number to 28. The first was the need for a clear empirical, statistical test of how species interactions were related to diversification rates. However, we also included statistical sister-clade comparisons (and similar methods; Joy, 2013), since these should also capture diversification-rate differences between clades.

The second criterion was that the paper needed to provide some ecological evidence for species interactions. Thus, we did not include paleontological studies, since all paleontological studies we found had limited ecological evidence for species interactions. Furthermore, some paleontological studies did not separate speciation from immigration or extinction from emigration (potentially confounding dispersal and diversification). We did include papers that analysed the presence/absence of traits with functions previously shown to be tightly linked to species interactions, including aposematic coloration (Przeczek et al., 2008), venom glands (Liu et al., 2018) and extrafloral nectaries (Weber and Agrawal, 2014).

Among neontological studies, those invoking competition often lacked ecological evidence. Therefore, we only included studies with evidence for competition from previous ecological studies (Miraldo and Hanski, 2014) or with data on species co-occurrence (Price et al., 2014; Machac et al., 2018). We excluded studies that merely showed diversification slowdowns over time, unless those studies provided evidence that competition between species actually caused these slowdowns (given the other possible explanations for apparent slowdowns; Moen and Morlon, 2014).

Our third criterion was based on an interaction grid (Bronstein, 1994, 2015), which describes whether interactions have positive (beneficial), neutral or negative (harmful) net effects (+/0/-) on individuals of a given species or clade. We focused primarily on studies in which an interaction varied in its presence and absence among species. We excluded studies that compared different versions of interactions that were of the same sign (+/0/-) and similar in nature. Examples included studies that examined shifts in diets, shifts in pollinators and antagonistic vs. mutualistic interactions (with both types positive for the focal taxon). In these cases, it is unclear which state is more beneficial (or harmful) for individuals of the focal clade. Similarly, it is unclear whether we should predict an increase or decrease in diversification rates associated with such shifts, since both new and old interactions are of the same type (e.g. positive for the focal clade). Generally, we only included studies that compared diversification rates in species with a given interaction type to those without.

Nevertheless, we did consider studies that varied in the apparent effects of a single interaction type. For example, we assumed that the negative net effect of competition weakens when competitive release occurs (Miraldo and Hanski, 2014) and intensifies with greater niche filling (Price et al., 2014) and increased co-occurrence between species (Machac et al., 2018). Similarly, we assumed that defensive traits against predation and herbivory decrease negative effects of these interactions (Farrell et al., 1991; Ge et al., 2010; Arbuckle and Speed, 2015; Liu et al., 2018). In these cases, the predicted effects on diversification are relatively straightforward, given the potential benefits to individuals of the focal clade gained by reducing predation or competition. This is very different from (for example) changing the species of prey or pollinator.

We also included a study that was published after our searches (Hernández-Hernández and Wiens, 2020). This brought the total number to 29. We did not include studies that treated within-species units as equivalent to species (e.g. Sachs et al., 2014), since within-species splits may not represent speciation.

Count-based hypothesis testing

We tested the hypothesis that species interactions that have predominantly positive (beneficial) net effects on individuals of the focal clade will increase diversification rates of lineages having that interaction type within the clade, relative to those lineages lacking that interaction. 'Lineage' can refer to both species and clades. Conversely, we tested whether interactions with predominantly negative (harmful) net effects on individuals of the focal clade will decrease diversification rates of

lineages having that interaction type. We used an interaction grid (see above) to assign interactions as being positive or negative for individuals having that interaction type. Thus, when the interaction had positive net effects on individuals of the focal clade, we predicted that diversification rates in the focal clade would be higher when the interaction was present (vs. absent) or when the net effect of the interaction was stronger (vs. weaker). Conversely, for negative net effects, we predicted lower diversification rates when the interaction was present or the interaction effect was stronger. The alternative hypotheses include: (1) interactions with negative effects on individuals of the focal clade increase diversification rates in that clade, (2) interactions with positive effects decrease diversification rates and (3) positive/negative interaction types have no consistent effect on diversification rates.

We generally refer to 'fitness' effects when we describe interaction types as being positive or negative for individuals of the focal clade. However, we acknowledge that the fitness effects of each interaction type have been quantified in relatively few species. Furthermore, authors do not always refer directly to fitness when characterising interactions as having overall positive or negative effects on individuals (e.g. Bronstein, 2015). Nevertheless, we think that it is clear that being eaten has negative fitness impacts on individuals being eaten (e.g. predation, parasitism), whereas food offers positive fitness benefits for the individual doing the eating (e.g. predation, parasitism, many forms of mutualism), even without quantification of fitness costs and benefits. Similarly, shelter (e.g. many symbioses), facilitating reproduction (e.g. pollination) and offspring dispersal (e.g. seed dispersal) can positively impact individual fitness, whereas competing for finite resources can negatively impact individual fitness.

We recognise that species interactions can be variable and context-dependent within species in their fitness effects (Chamberlain et al., 2014). We assumed that the original studies scored each included species correctly, and that our overall characterisation of interactions as positive or negative applied to most species in the relevant clades (even if not to every species). We see mischaracterisations as a source of random error that would prevent us from finding consistent, significant effects of different interaction types on diversification.

The units for our analyses were previous studies that tested for effects of species interactions on diversification rates within specific clades. In one study, analyses were performed separately for different interaction types on the same phylogeny. Bruun-Lund et al. (2018) examined both hemi-epiphytism (commensalism) and biotic pollination (mutualism) in figs. These were treated as two units. Therefore, we included 30 units in the analyses, from 29 papers (Table 1). However, we refer to each unit as a 'study' for convenience.

We classified all studies based on the effect of the interaction on individuals of the focal clade (positive/beneficial or negative/harmful) and based on the inferred effect of that interaction on diversification rates in that clade in the original study (significantly positive, significantly negative, or no significant effect). Using a two-tailed Fisher's exact test (McDonald, 2009), we then tested whether interactions that were positive for individuals of the focal clade showed a significantly higher proportion of positive effects of these

interactions on diversification rates across studies, whereas species interactions with negative effects for individuals showed a higher proportion of negative effects on diversification across studies. All statistical analyses were performed using the R package *stats* (R Core Team, 2018). We performed analyses both including and excluding five studies that showed no significant effect of the interaction on diversification. All focal clades were either plants or animals. We also performed separate analyses of plants and animals.

We did not correct for phylogeny, for several reasons. First, a phylogenetic test assumes that species share traits because of common ancestry: this is the phylogenetic non-independence that phylogenetic tests correct for. But this is only relevant if the trait is homologous among species. However, the main traits tested here are clearly not homologous (i.e. a negative fitness effect from competition is not homologous with that from predators; a positive effect from anti-herbivory defence is not homologous with biotic pollination). Thus, a phylogenetic test could be positively misleading. Moreover, all studies involved associations between interactions and diversification rates in which both variables varied among species within the clade being studied. Furthermore, most smaller clades were phylogenetically isolated from each other. These two factors also make it very unlikely that the effects of interactions on diversification are shared across clades due to common ancestry. Finally, many taxa are overlapping or redundant between studies, even though different traits are involved in different studies. For example, some studies span all animals, whereas others involve subgroups of animals. We are unaware of a way to accommodate this with existing phylogenetic methods. In summary, we did not perform a phylogenetic correction, but this seems unlikely to be problematic here.

Nevertheless, there was initially some overlap between traits and taxa among studies. We performed our initial analyses including all studies, and then we corrected for potential non-independence as follows. Arbuckle and Speed (2015) and Przeczek et al. (2008) both focused on anti-predator defence in amphibians. However, Przeczek et al. (2008) also included arthropods, and excluding amphibians does not change their conclusions. Therefore, we included both studies. Marazzi and Sanderson (2010) and Weber and Agrawal (2014) both addressed plant-defence mutualism with ants (in *Senna* [Fabaceae] and vascular plants). Both showed a positive effect on diversification, so we treated them as one unit. Bolinder et al. (2016), Bruun-Lund et al. (2018) and Hernández-Hernández and Wiens (2020) all examined effects of biotic pollination on diversification (in *Ephedra,* figs and land plants). We performed analyses excluding either the large-scale study (Hernández-Hernández and Wiens, 2020) or both smaller-scale studies. Weinstein and Kuris (2016) and Jezkova and Wiens (2017) analysed parasitism across animals, but disagreed in their conclusions (Table 1). We excluded each one in alternative analyses. Medina and Langmore (2015) and Krüger et al. (2009) both examined brood parasitism in birds, one across multiple bird clades and one in cuckoos alone. We used the former given its broader coverage. Overall, we performed a series of analyses (Table 2) in which either all studies were included or with various studies excluded to account for potential overlap. We then performed a sequential

Table 1 Summary of studies of species interactions and diversification rates analysed

Study	Type of interaction	Interacting taxa	Higher taxonomic group for focal clade	Presumed fitness effect	Effect of interaction on diversification
Miraldo and Hanski (2014)	Competition	**dung beetles** and competitors	Arthropods	Negative	Decreased
Machac *et al.* (2018)	Competition	**mammals** and mammalian competitors	Mammals/vertebrates	Negative	Decreased
Price *et al.* (2014)	Competition	**birds** and bird competitors	Birds/Vertebrates	Negative	Decreased
Farrell *et al.* (1991)	Herbivory	**plants** and herbivores/ pathogens	Plants	Negative	Decreased
Arbuckle and Speed (2015)	Predation	**amphibians** and predators	Amphibians/vertebrates	Negative	Increased
Ge *et al.* (2010)	Predation	**flea beetles** and predators	Arthropods	Negative	Decreased
Liu *et al.* (2018)	Predation	*Meiacanthus* and predators	Actinopterygians/vertebrates	Negative	Decreased
Przeczek *et al.* (2008)	Predation	**amphibians, insects, spiders** and predators	Vertebrates & Arthropods	Negative	Decreased
Roalson and Roberts (2016)	Commensalism/ Epiphytism	**Gesneriaceae** and epiphytic host	Angiosperms	Positive	Increased
Li *et al.* (2016)	Commensalism	**Galeommatoidea** and hosts	Molluscs	Positive	Decreased
Bruun-Lund *et al.* (2018)	Commensalism/ Epiphytism	**figs** and host plants (hemi-epiphytes)	Angiosperms	Positive	Increased
Freudenstein and Chase (2015)	Commensalism/ Epiphytism	**epidendroids** and hosts	Angiosperms	Positive	Increased
Givnish *et al.* (2014)	Commensalism/ Epiphytism	**Bromeliaceae** and hosts	Angiosperms	Positive	Increased
Givnish *et al.* (2015)	Commensalism/ Epiphytism	**orchids** and hosts	Angiosperms	Positive	Increased
Davis *et al.* (2018)	Commensalism– Parasitism	**caridean shrimps** and symbiotic partners	Arthropods	Positive	Decreased
Lengyel *et al.* (2009)	Mutualism/Plant –disperser	**angiosperms** and ants	Angiosperms	Positive	Increased
Marazzi and Sanderson (2010)	Mutualism/Plant –defender	*Senna* and ants	Angiosperms	Positive	Increased
Weber and Agrawal (2014)	Mutualism/Plant –defender	**vascular plants** and defenders	Vascular plants	Positive	Increased
Larson-Johnson (2016)	Mutualism/Plant –disperser	**Fagales** and seed dispersers	Angiosperms	Positive	Increased
Bolinder *et al.* (2016)	Mutualism/Plant –pollinator	*Ephedra* and insect pollinators	Gnetophytes/ plants	Positive	Decreased
Bruun-Lund *et al.* (2018)	Mutualism/Plant –pollinator	**figs** and pollinators	Angiosperms	Positive	Increased
Hernández-Hernández and Wiens (2020)	Mutualism/Plant –pollinator	**land plants** and pollinators	Land plants	Positive	Increased
Afkhami *et al.* (2018)	Mutualism	**legumes** and root-nodulating bacteria	Angiosperms	Positive	Neither
Lorion *et al.* (2013)	Mutualism	**mussels** and symbionts	Molluscs	Positive	Neither
Litsios *et al.* (2012)	Mutualism	**clownfish** and sea anemones	Vertebrates	Positive	Increased
Weinstein and Kuris (2016)	Parasitism	**animals** and hosts	Animals	Positive	Neither
Medina and Langmore (2015)	Parasitism	**birds (brood parasites)** and hosts	Birds	Positive	Neither
Jezkova and Wiens (2017)	Parasitism	**animals** and hosts	Animals	Positive	Increased
Joy (2013)	Parasitism	**galler insects** and hosts	Insects/arthropods	Positive	Increased
Krüger *et al.* (2009)	Parasitism	**cuckoos** and hosts	Birds/vertebrates	Positive	Decreased

The focal clades (ones in which diversification rates were estimated) are shown in boldface. The presumed fitness effect refers to individuals of the focal clade. The last column indicates whether the interaction significantly increased or decreased diversification rates in the focal clade, based on the results of the original study. In some studies, there was no consistent significant effect of the interaction on diversification rates, and 'Neither' is listed instead. Studies are listed based on presumed fitness effect first (negative/harmful vs. positive/beneficial) and then by interaction type.

Bonferroni correction (Holm, 1979; Rice, 1989) on *P*-values from this table.

Analysis of effect sizes

We quantified the magnitude of the effects of different inter-action types on diversification rates. First, we extracted an effect size from each study, when possible. We calculated effect size as the binary log-response ratio (Rosenberg *et al.*,

2013) of diversification rates, $\log_2(R)$, where R is the ratio of the two diversification rates (i.e. with the interaction present vs. absent or stronger vs. weaker). The sampled studies used various measures of diversification. The binary log-ratio of diversification rates was used when rates were directly esti-mated using BAMM (Rabosky, 2014), BiSSE (Maddison *et al.*, 2007), MEDUSA (Alfaro *et al.*, 2009), the method of Bokma (2003) and the maximum-likelihood and method-of-moments estimators (Magallón and Sanderson, 2001). We give

Table 2 Count-based analyses

Analysis	Overlapping studies excluded	Individual-level effects						Fisher's exact test results	
		Positive			Negative				
		Inferred effects on diversification						"Neither" studies included	"Neither" studies excluded
		Increase	Decrease	Neither	Increase	Decrease	Neither		
A	None	14	4	4	1	7	0	$P = 0.0026$, $n = 30$	$P = 0.0033$, $n = 26$
B	Marazzi and Sanderson (2010), Krüger *et al.* (2009), Weinstein and Kuris (2016), and Hernández-Hernández and Wiens (2020)	12 (2)	3 (1)	3 (1)	1	7	0	$P = 0.0035$, $n = 26$	$P = 0.0059$, $n = 23$
C	Same as B, but including Hernández-Hernández and Wiens (2020) and excluding Bolinder *et al.* (2016), and Bruun-Lund *et al.* (2018).	12 (2)	2 (2)	3 (1)	1	7	0	$P = 0.0009$, $n = 25$	$P = 0.0015$, $n = 22$
D	Marazzi and Sanderson (2010), Krüger *et al.* (2009), Jezkova and Wiens (2017), and Hernández-Hernández and Wiens (2020)	11 (3)	3 (1)	4	1	7	0	$P = 0.0044$, $n = 26$	$P = 0.0062$, $n = 22$
E	Same as D, but including Hernández-Hernández and Wiens (2020) and excluding Bolinder *et al.* (2016), and Bruun-Lund *et al.* (2018).	11 (3)	2 (2)	4	1	7	0	$P = 0.0007$, $n = 25$	$P = 0.0022$, $n = 21$

These analyses test whether species interactions with positive/beneficial fitness effects on individuals of the focal clade tend to significantly increase diversification rates (vs. decrease them) and whether negative/harmful effects significantly decrease diversification rates (vs. increase them), based on the frequency of these results among studies. A series of analyses (A–E) were conducted to account for potential overlap in interaction types and traits among focal studies. Numbers of studies excluded because of overlap are shown in parentheses. For each analysis, Fisher's exact tests were conducted both including and excluding those studies that found no significant increase or decrease in diversification rates associated with the species interaction in the focal clade (indicated as 'Neither'). Note that a sequential Bonferroni correction does not impact which results are considered significant, and all results are significant in this table. Separate analyses for plants and animals are shown in Table S1.

details of how we obtained rate estimates for each study in Appendix S1, including sister-clade comparisons. However, we were unable to extract comparable rates from the gamma statistic (Pybus and Harvey, 2000), and two case studies (Price *et al.*, 2014; Machac *et al.*, 2018) were therefore excluded from this analysis. We combined effect sizes (log-ratios) from individual studies of the same interaction type (all studies with interactions positive or negative for individuals of the focal taxa, and subsequently all studies with predation, or mutualism, etc.). We obtained usable effect sizes from 23 studies.

Again, some studies overlapped. We again excluded the amphibian data from Przeczek *et al.* (2008). In other cases, we chose large-scale studies instead of small-scale ones. For parasitism, we used Jezkova and Wiens (2017) because it directly estimated diversification rates. We excluded five studies overall, including 18 (see Table S2).

A Shapiro–Wilk's test of effect sizes failed to reject normality, allowing us to combine and analyse effect sizes across studies. To test whether a type of species interaction (i.e. negative, positive) had effect sizes significantly greater or less than zero, we calculated the grand mean and constructed a 95% confidence interval for each mean, assuming a t-distribution (Rosenberg, 2013), using *stats*. We concluded that the

effect size was significantly greater or less than zero when the confidence interval did not overlap with zero.

RESULTS

Interactions that were positive/beneficial for individuals of the focal clade included cases of mutualism, commensalism, parasitism, pollination, epiphytism, plant–disperser interactions and plant–defender interactions (Fig. 1a; Table 1). Interactions that were negative/harmful for focal-clade individuals included predation, competition and herbivory.

A two-tailed Fisher's exact test including all three possible outcomes of inferred effects on diversification rates (increase, decrease, neither) showed that individual-level positive/negative effects significantly impacted clade-level diversification rates (Table 2: $P = 0.0026$, $n = 30$, all studies included, Analysis A; $P = 0.0007$–0.0044, $n = 25$–26; overlapping studies excluded, Analyses B–E). We then excluded studies showing no significant impacts of interactions on diversification rates. We found that among studies of interactions with positive/beneficial fitness effects for focal-clade individuals, there were proportionally more studies in which these interactions increased diversification rates than among studies of negative/
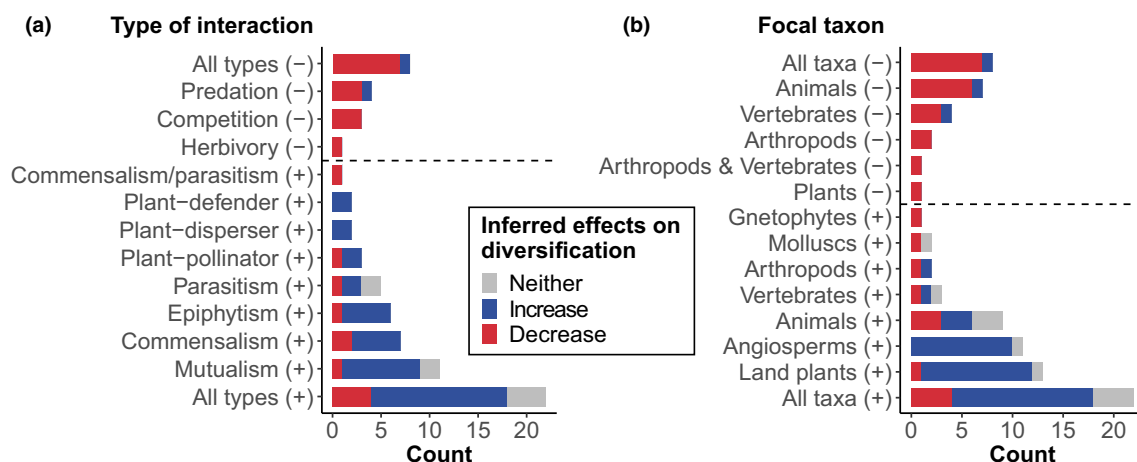
Figure 1 Summary of effects of species interactions on diversification rates (all studies included). Studies are sorted by type of interaction (a) and taxon (b). A '+' and '−' indicate whether species interactions have positive or negative fitness effects on individuals of the focal clade (the one in which diversification rates were measured). Colours indicate whether the studies supported a significant positive impact of the interaction on diversification (blue: increase), a significant negative impact (red: decrease), or neither (grey; no significant effect). Some interaction types are shown as two participants joined by a hyphen to indicate the focal taxon, with the focal taxon placed before the hyphen (Table 1). We predict that interactions with negative fitness effects for individuals of the focal clade (−) decrease diversification rates (red), whereas those with positive fitness effects (+) increase diversification rates (blue). The dashed line demarcates studies of interactions with negative fitness effects from those with positive fitness effects.

harmful interactions (Table 2: $P = 0.0033$, $n = 26$, all studies included; $P = 0.0015$–0.0062, $n = 21$–23, overlapping studies excluded). Conversely, among studies of negative/harmful interactions, there was a significantly higher proportion of studies in which these interactions decreased diversification rates than among positive-interaction studies (same test).

Separate count-based analyses of plants and animals showed similar patterns, but not as strongly. The effect of interaction types on diversification rates was not significant (including non-significant studies), although a test in animals approached significance (Table S1: animals: $P = 0.0536$–0.1362, $n = 14$–16; plants: $P = 0.1352$–0.2500, $n = 11$–14). For animals, 50–60% of positive-interaction studies showed significant increases in diversification rates (vs. 40–50% with significant decreases). Among negative-interaction animal studies, 86% showed significant decreases in diversification (14% with significant increases). For plants, 90–100% of positive-interaction studies showed significant increases in diversification rates (0–10% showed decreases), whereas 100% ($n = 1$) of negative-interaction studies showed significant decreases. Analyses excluding studies that found no significant effects on diversification rates also gave non-significant results (Table S1). Overall, neither group was significant when analysed alone, presumably because animals included some positive-interaction studies with patterns opposite to those predicted, whereas plants included too few negative-interaction studies.

We also estimated effect sizes on diversification rates and compared these based on types of species interactions (Fig. 2; Tables S2–S3). In this sample ($n = 18$), all studies of positive interactions involved presence/absence ($n = 12$), and studies of negative interactions involved stronger/weaker effects of the interaction ($n = 6$). Grand means of log-response ratios were positive for beneficial/positive interactions and negative for harmful/negative interactions (Fig. 2; Table S4). Effects sizes
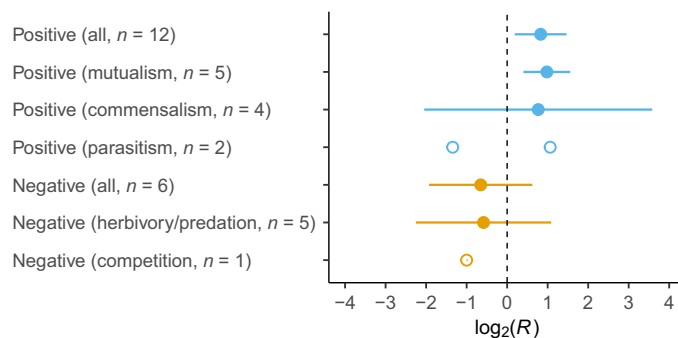

Figure 2 Analyses of effect sizes of different types of species interactions on diversification rates. Grand means (filled circles) and 95% confidence intervals (coloured lines) are shown. Results are considered significant when the confidence interval does not overlap with zero (dashed vertical line). R is the ratio of logarithmic diversification rates (when an interaction is present vs. absent or strong vs. weak). In this sample of studies, studies of positive/beneficial interactions for the focal clade all involve the presence/absence of the interaction, whereas studies of the negative/harmful interactions all involve the strength of the interaction. Interaction types with sample sizes too small for calculating intervals ($n < 3$) are shown as single data points (open circles). Details on obtaining effect sizes for each study are given in Appendix S1 and Tables S2–S4.

were significantly greater than zero for all positive interactions combined, and for mutualisms (Fig. 2; Table S4). Effect sizes were not significantly greater or less than zero for all negative interactions combined, commensalisms and predation/herbivory, likely due to smaller sample sizes for these latter categories (Fig. 2; Table S4). On average (Fig. 2), lineages with positive interactions diversified 1.77 times faster than those without ($n = 12$), whereas lineages with stronger negative species interactions diversified 1.56 times slower ($n = 6$).

DISCUSSION

In this study, we test the idea that species interactions with positive effects at the individual level increase diversification rates in lineages in which they are present, whereas those with negative impacts decrease diversification rates. We take advantage of the dozens of phylogenetic studies that have examined the relationship between species interactions and diversification rates. Our results suggest that there are general patterns across plants and animals, despite considerable uncertainty in the literature about how species interactions might impact diversification (e.g. Jablonski, 2008; Ricklefs, 2010; Weber *et al.*, 2017; Chomicki *et al.*, 2019; Hembry and Weber, 2020). Below we discuss the potential causes of these patterns, and their broader implications.

How do species interactions affect diversification rates?

We find that species interactions with positive individual-level effects generally increase diversification rates and that negative-effect interactions decrease diversification. At some level, these results make intuitive sense. After all, an interaction that has negative fitness effects on individuals might be expected to increase species-level extinctions over longer timescales. Similarly, traits that increase an individual's fitness might buffer a clade from extinction and thereby promote its long-term persistence and proliferation. Yet, it is less obvious how increases in individual fitness will necessarily increase speciation rates. One potential mechanism is that larger population sizes might lead to species-level range expansion (e.g. Ricklefs, 2010), which can then lead to larger clade-level ranges (e.g. spreading to new regions), which can increase diversification rates (e.g. Gómez and Verdú, 2012; Hernández-Hernández and Wiens, 2020).

Chomicki *et al.* (2019) discussed other mechanisms by which positive interactions (specifically mutualisms) might increase diversification rates, which seem generally relevant here. In addition to increased range size, they also discussed divergent selection, ecological opportunity and reduced extinction. We discuss these in turn below. One example of how divergent selection might increase diversification involves animal pollination in land plants (especially angiosperms), a trait that is significantly related to increased diversification rates across plants (Hernández-Hernández and Wiens, 2020). This increase may have occurred through increased reproductive isolation and speciation among plant species, mediated by divergent selection associated with shifts in pollinator species and flower morphology (e.g. Whitehead and Peakall, 2014). The effects of different pollinators on speciation might be particularly important in combination with other isolating factors (reviewed in Kay and Sargent, 2009). Partner switching in general might be an important driver of diversification in clades with mutualisms (Chomicki *et al.*, 2019) and with antagonisms (e.g. parasites).

Ecological opportunity is thought to fuel adaptive radiation and thus rapid diversification (e.g. Yoder *et al.*, 2010), potentially through utilisation of new resources and freedom from the constraints of competition and limited resources. Ecological opportunity might underlie both positive impacts of mutualism on diversification, and positive impacts of antagonistic interactions for the focal clade.

Clade-level diversification rates might also be increased by decreasing species-level extinction rates, through increased survival of individuals involved in the mutualism. For example, one mutualistic trait considered here involves extra-floral nectaries (Weber and Agrawal, 2014). These nectaries provide nectar for insects that then defend the plants against herbivores, and are associated with higher diversification rates in the plants (Weber and Agrawal, 2014). These insect defenders might reduce the extinction risk of these plant species (although not explicitly tested by Weber and Agrawal, 2014).

Chomicki *et al.* (2019) also described mechanisms by which mutualisms might decrease diversification rates instead, including stabilising selection associated with co-evolution, reduced genetic diversity of symbionts and increased extinction risk associated with reduced niche breadth or high fitness costs of partner loss. These mechanisms might apply to some of our results that were opposite to the predicted patterns, especially the positive-effect interactions that decreased diversification rates in some animal clades.

At some level, our results might seem contrary to the simulation study by Yoder and Nuismer (2010). They concluded that the impact of co-evolutionary interactions on diversification depends on the type of interaction, with competition and host–parasite antagonism potentially increasing diversification (when there is a cost to matching phenotypes between interactors), and mutualisms restricting diversification. However, in that study, 'diversification' referred to variation in a single phenotypic trait among two interacting species. Thus, those results may not generalise to rates of speciation and extinction among dozens to thousands of species over timescales of tens of millions of years (our focus here). We suggest that new theory is needed, building on Yoder and Nuismer (2010), to address the impact of different types of species interactions on speciation and extinction rates over macroevolutionary timescales.

There is also a body of empirical and theoretical work that suggests that competition drives speciation (e.g. Schluter, 1994, 2000; Dieckmann and Doebeli, 1999), which seems counter to our finding that competition decreases diversification. However, there are also many studies suggesting that competition impedes diversification, especially studies proposing that adaptive radiations occur when there is ecological opportunity associated with competitive release (e.g. Yoder *et al.*, 2010). The effects of competition may be scale specific, with intraspecific competition driving ecological speciation within populations over shorter timescales, and interspecific competition decreasing diversification over longer timescales (Hembry *et al.*, 2014). Our results, showing the importance of interspecific competition in decreasing diversification rates over macroevolutionary timescales, are consistent with this idea. Importantly, our results do not rule out the possibility that competition can also help drive speciation, especially at shallower timescales.

Overall, the specific mechanisms by which species interactions increase or decrease diversification may depend on the interaction and taxa. Yet, some mechanisms may be general, such as links between fitness, population size, range sizes,

extinction and speciation, and the potential for partner-switching to drive diversification.

Potential caveats

We acknowledge several potential caveats regarding our analyses. First, our analyses are merely correlative. Therefore, it is possible that in some cases, an apparent effect of a species inter-action on diversification rates was actually caused by some other factor instead. However, it seems unlikely that this explains the overall pattern across these diverse interactions and groups of organisms. Similarly, it is possible that increases in diversification rates might somehow influence the evolution of species interactions in some cases, instead of vice versa (as we postulate here). We know of few plausible mechanisms by which this would happen. For example, any trait (including a species inter-action) is more likely to evolve in a more-species rich clade by chance, all else being equal. Yet, most methods for testing trait-diversification associations should not yield a significant result under these circumstances (e.g. if the interaction originates randomly within a large clade and is therefore present in only some species having accelerated diversification rates). Again, these sorts of false positives seem possible in a few cases, but much less so across many studies. Furthermore, our main result is not simply that species interactions influence diversification rates, but rather that positive-effect interactions increase them and negative-effect interactions decrease them. This more complex pattern makes chance associations between interactions and diversification rates seem even less likely to explain our overall results.

Second, our sampling is based on relevant studies available in the literature, not systematic sampling of all clades and/or interactions. This latter type of sampling is simply not possible at this point in time. Nevertheless, the literature did contain many relevant studies across taxa and interaction types (Table 1). We acknowledge that some patterns might change as more studies are published. We suggest that our summary here can still guide future empirical and theoretical studies going forward.

Third, methods for estimating diversification rates and linking them to traits can be controversial (e.g. Morlon, 2014). For example, state-dependent speciation-extinction models (like BiSSE) can potentially infer trait-dependent diversification when no dependency is present (e.g. Maddison and FitzJohn, 2015). However, if a method routinely inferred trait-dependent diversification when it was absent, this should make it harder to infer that positive-effect interactions increase diversification and negative-effect interactions decrease diversification. Other methods may underestimate variation in diversification rates among clades (e.g. Rabosky, 2014; Meyer and Wiens, 2018), making it more difficult to find significant relationships with traits. Overall, it seems unlikely that our results are an artifact of methods for estimating diversification rates, because problems in these methods should make it harder to find significant patterns.

Non-significant results may have been underrepresented in our analysis due to publication bias. However, the direction of effects (i.e. positive vs. negative effects on diversification rates) should be insensitive to this bias. Furthermore, there is little evidence that effect sizes are generally greater in published than unpublished studies (e.g. Koricheva, 2003; Møller et al., 2005). Another bias ("research bias"; Koricheva et al., 2013), may arise if researchers focus on unevenness in richness across a phylogeny. Again, this should not affect the direction of the effects on diversification. Importantly, our study is testing how different interaction types impact diversification, and not how often species interactions affect diversification.

Finally, we acknowledge that our sample size of studies is limited. However, dismissing significant results because of low sample sizes is statistically nonsensical (since lower sample sizes reduce power). Furthermore, some of our single data points include all animals and also all land plants (together encompassing approximately 90% of all described species on Earth; Scholl and Wiens, 2016). We also included multiple studies (>10) within both of these groups. Future studies will doubtless find some exceptions to these general patterns (as did we), but our results do suggest that a broad overall pattern may exist.

CONCLUSIONS

We find broad macroevolutionary patterns in the myriad species interactions across the Tree of Life, with interactions that are positive for individuals of the focal clade generally increasing diversification rates and negative-effect interactions generally decreasing them. Understanding the common mechanisms behind these shared patterns across diverse organisms should be an exciting area for future empirical and theoretical studies. Our results highlight that species interactions between clades can help explain the diversity of some of the most species-rich clades across the Tree of Life (e.g. angiosperms, insects). These results offer a surprising contrast to the widespread idea in ecology that species interactions are primarily important to diversity patterns at only smaller spatial and temporal scales.

AUTHORSHIP

YZ and JJW designed the study, collected data and wrote the paper. YZ performed analyses.

DATA AVAILABILITY STATEMENT

All data are included with this submission as Supporting Information. In addition, these data are archived in an appropriate public repository (Dryad; https://doi.org/10.5061/dryad.m63xsj40j).

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