

24 **Abstract**

25 Predicting the outcome and strength of species interactions is a central goal of community
26 ecology. Researchers have proposed that outcomes of species interactions (competitive exclusion
27 and coexistence) are a function of both phylogenetic relatedness and functional similarity.
28 Studies relating phylogenetic distance to competition strength have shown conflicting results.
29 Work investigating the role of phylogenetic relatedness and functional similarity in driving
30 competitive outcomes has been limited in terms of the breadth of taxa and ecological contexts
31 examined, which makes the generality of these studies unclear. Consequently, we gathered 1,748
32 pairwise competition effect sizes from 269 species and 424 unique species pairs with divergence
33 times ranging from 1.14 to 1,275 million years and used meta-regression and model selection
34 approaches to investigate the importance of phylogenetic relatedness and functional similarity to
35 competition across ecological contexts. We revealed that functional similarity, but not
36 phylogenetic relatedness, predicted the relative strength of interspecific competition (defined as
37 the strength of interspecific competition relative to intraspecific competition). Further, we found
38 that the presence of predators, certain habitats, increasing density of competitors, and decreasing
39 spatial grain of experiments were all associated with more intense interspecific competition
40 relative to intraspecific competition. Our results demonstrate that functional similarity, not
41 phylogenetic relatedness, may explain patterns of competition-associated community assembly,
42 highlighting the value of trait-based approaches in clarifying biotic assembly dynamics.

43 **Keywords**

44 Interspecific competition, intraspecific competition, competitive response, meta-analysis,
45 functional similarity, phylogenetic relatedness, coexistence theory

46

47 Introduction

48 Predicting the outcomes of species interactions and community assembly and
49 disassembly processes have long been the foci of community ecologists¹. A core prediction of
50 community ecology, originally described by Darwin², is that closely related species will compete
51 more strongly with each other than distantly related species, referred to as the “competition-
52 relatedness hypothesis”³. Due in part to advances in genetics, molecular biology, and
53 phylogenetic tools in the last 25 years, Darwin’s hypothesis has undergone repeated empirical
54 tests. However, the generality of the relationship between phylogenetic relatedness and
55 competition strength remains uncertain, as studies show conflicting results^{3–12}.

56 Conflicting empirical patterns between phylogeny and competition may suggest that the
57 assumptions underlying Darwin’s hypothesis may be flawed⁷. Darwin’s hypothesis assumes that
58 phylogenetically related species are more ecologically similar than distantly related species (i.e.,
59 phylogenetic niche conservatism)^{2–4,13,14}. While some support exists for phylogenetic niche
60 conservatism^{4,15–17}, niches can evolve convergently or randomly^{18–20}, suggesting that
61 phylogenetically similar species may not be ecologically similar²¹. Darwin’s hypothesis also
62 assumes that ecologically similar species compete more strongly than less similar species,
63 because they share similar niches^{2–4,13,14}. However, niche differences (i.e., degree of niche
64 overlap) alone may not predict competition strength; rather, competitive ability differences (i.e.,
65 differences in species’ abilities to utilize shared limiting resources) may drive patterns of
66 competitive exclusion, while niche overlap may determine whether species pairs can coexist^{22–24}.
67 This suggests that ecologically similar species may not inherently compete more strongly than
68 ecologically dissimilar species. Specifically, coexistence theory predicts competitive exclusion
69 when species with overlapping niches differ in their competitive abilities, and coexistence when

70 strong niche differentiation overcomes differences in competitive ability between species^{22–24}.
71 Thus, without information on both the niche and competitive ability of interacting species,
72 successfully predicting the strength of competition remains challenging.

73 Experimental efforts to quantify factors that influence competition strength have been
74 limited by the breadth of focal taxa²⁵ and/or the experimental and ecological contexts of
75 observations^{26,27}. For instance, competition strength has been shown to be higher in certain
76 taxonomic groups and habitat types^{25,28}. Additionally, certain experimental conditions may
77 intensify competition between species; specifically, studies have shown that competition is
78 stronger when predators are present^{26,29}, under resource limitation^{30,31}, or when experiments are
79 conducted in mesocosms rather than natural field settings^{27,32}. Thus, certain experimental
80 conditions might obscure patterns among phylogenetic relatedness, functional similarity, and
81 competition strength.

82 We propose to address a central goal in ecology by resolving the uncertainty regarding
83 the influences of phylogenetic relatedness and functional similarity on competition. Resolving
84 this uncertainty will improve predictions concerning the outcome of species interactions and
85 increase understanding of biotic mechanisms involved in the assembly and structuring of
86 communities^{33–37}. Here, we use a meta-analysis of 1,748 effect sizes of pairwise competitive
87 interactions across a range of taxa and ecological contexts to assess whether the strength of
88 interspecific competition relative to the strength of intraspecific competition (referred to here as
89 competitive response^{38,39}) is better predicted by phylogenetic relatedness or functional similarity
90 of competing species. Competitive response represents the ability of a species to tolerate
91 competition from other species³⁸ and translates to the long-term winners and losers of
92 competition (i.e., a species that experiences low interspecific competition relative to intraspecific

93 competition will eventually competitively exclude a competing species that is less tolerant of
94 interspecific competition)³⁹. Our objectives are to: 1) investigate the relationships among
95 phylogenetic distance (time since divergence), functional similarity (body size of focal species
96 relative to body size of competing species), and competitive response across taxonomic groups
97 and 2) determine the ecological and experimental contexts that may influence the response to
98 competition. Per Darwin's competition-relatedness hypothesis², we predict that competitive
99 response is negatively related to phylogenetic distance (e.g., stronger relative interspecific
100 competition in closely related species pairs) and, per coexistence theory²³, we predict that
101 competitive response is positively related to functional similarity (e.g., stronger relative
102 interspecific competition when the focal species is smaller than the competing species; size-
103 asymmetric competition⁴⁰). Further, we hypothesize that certain ecological and experimental
104 contexts will influence a species' response to competition. For instance, we predict that 1)
105 resource limitation, 2) relatively high densities of the competing species, 3) the presence of
106 predators, and 4) interactions in closed experimental systems compared to those in open, field
107 systems will increase interspecific competition relative to intraspecific competition.

108 **METHODS**

109 We used Web of Science to search eight ecology journals (*American Naturalist*,
110 *Ecological Monographs*, *Ecology*, *Journal of Animal Ecology*, *Journal of Ecology*, *Journal of*
111 *Experimental Marine Biology and Ecology*, *Oecologia*, and *Oikos*) from 1988-2008 for the
112 keywords 'interspecific competition' on 20 June 2008, which yielded 1,039 studies. A second
113 search for the same keywords within the same subset of ecological journals from 2008-2020 was
114 conducted on 3 March 2021, which yielded an additional 399 studies. In total, our searches
115 yielded 1,438 studies. After studies were collected, they were examined to determine if they met

116 seven criteria for inclusion in our meta-analyses: 1) the study species had phylogenetic
117 information (at the species or genus level) deposited in the TimeTree database^{41,42}, an online
118 comprehensive list of estimated divergence times across all the major taxonomic groups, 2) the
119 density of at least one of the study species was manipulated experimentally, 3) the experimental
120 design used appropriate controls (e.g., non-manipulated groups of individuals), 4) the means,
121 variance, and sample sizes were reported or displayed (data from figures were extracted using
122 the imageJ software⁴³) or data were available, allowing us to calculate effect sizes (studies with
123 single replicates were excluded from the analyses, because effect sizes could not be reliably
124 calculated from these data), 5) clear pair-wise interactions were present in the study (e.g., species
125 A and species B were grown together and species A was grown separately), 6) the endpoint
126 measured was broadly applicable across different taxonomic groups (e.g., a measure of biomass,
127 density, or survival, as opposed to a taxon-specific variable such as time to metamorphosis), and
128 7) the species studied had published information on mean size at maturity available from the
129 study itself, the USDA Plants Database (www.plants.usda.gov), or Animal Diversity Web
130 (<https://animaldiversity.org/>). In total, 96 studies with 1,748 effect sizes met our inclusion
131 criteria.

132 Once studies were determined to meet the criteria for inclusion, we collected data on
133 means, variances, sample sizes, the number of individuals of the species pairs, habitat (aquatic or
134 terrestrial), whether the experiment also manipulated predator (or herbivore) presence and/or
135 resource levels, the experimental venue (field or mesocosm), the spatial grain of the experiment
136 (area or volume of study; m² or liters), and the length of experiment (days). A mesocosm venue
137 was defined as any lab, greenhouse, or outdoor experiment conducted in a bounded and partially
138 enclosed venue (e.g., beaker in the lab, pots in a greenhouse, outdoor aquatic tanks), and a field

139 venue was defined as any experiment conducted in a natural setting outside of an enclosed venue
140 (e.g., managed field system, streams, forests). We calculated relative spatial grain as the log10
141 transformation of spatial grain divided by body size of the focal species (species A).
142 Phylogenetic relatedness was calculated as the log10 transformation of time since the divergence
143 (mya) of the competing species (median value from TimeTree^{41,42} recorded on 20 March 2021).
144 We calculated relative density as the log10 transformation of ratio of the number of individuals
145 of the focal species (species A) to the number of individuals of the competing species (species
146 B). Functional similarity was estimated as the log10 transformation of the ratio of body size (cm)
147 at maturity of the focal species (species A) to the body size of the competing species (species B;
148 relative body size).

149 **Effect sizes**

150 We calculated the effect sizes for the outcome of species interactions using the Delta-
151 method-adjusted LRR (LRR^Δ; equation (1)), as log response ratio (LRR) can be biased when
152 estimating the outcome of studies with small sample sizes⁴⁴.

$$153 \quad LRR^{\Delta} = \ln \left(\frac{X_T}{X_C} \right) + \frac{1}{2} \left[\frac{(SD_T)^2}{N_T X_T^2} - \frac{(SD_C)^2}{N_C X_C^2} \right] \quad (1)$$

154 Where X_T is the mean of the treatment group (focal species grown with heterospecifics), X_C is the
155 mean of the control group (focal species grown with conspecifics), and SD and N are the within-
156 study standard deviations and sample sizes, respectively, of the treatment and control groups.
157 Effective sample sizes (N) were calculated as the number of replicates multiplied by the number
158 of individuals per replicate. Here, LRR^Δ is the ratio between interspecific and intraspecific
159 effects and can be interpreted as the competitive response of a species (ability of a species to
160 avoid being suppressed; *sensu* refs^{38,39}). Specifically, when LRR^Δ is negative, the focal species is
161 more responsive to interspecific effects than intraspecific effects, indicating that the species is

162 sensitive to interspecific competition and long-term competitive exclusion of the focal species
 163 can occur³⁹. Conversely, when LRR^{Δ} is zero or positive, interspecific effects are equal to or less
 164 than intraspecific effects, indicating that the species is not sensitive to interspecific competition
 165 and the focal species may, in the long-term, competitively exclude the competing species³⁹. As
 166 some effect sizes within studies were calculated using the same control group and their
 167 observations were therefore non-independent (equation (2)), we calculated variance-covariance
 168 matrices for observations (**A** and **B** below) within studies that shared control groups using the
 169 ‘covariance_commonControl’ function in the ‘metagear’ R package⁴⁵ and adjusted per the Delta-
 170 method⁴⁴.

$$171 \quad V^{Xc}(LRR^{\Delta}) = \begin{bmatrix} \frac{(SD_C)^2}{N_C X_C^2} + \frac{(SD_T^A)^2}{N_T^A (X_T^A)^2} + \frac{1}{2} \left[\frac{(SD_T)^4}{N_T X_T^4} + \frac{(SD_C)^4}{N_C X_C^4} \right] & \frac{(SD_C)^2}{N_C X_C^2} + \frac{1}{2} \left[\frac{(SD_C)^4}{N_C X_C^4} \right] \\ \frac{(SD_C)^2}{N_C X_C^2} + \frac{1}{2} \left[\frac{(SD_C)^4}{N_C X_C^4} \right] & \frac{(SD_C)^2}{N_C X_C^2} + \frac{(SD_T^B)^2}{N_T^B (X_T^B)^2} + \frac{1}{2} \left[\frac{(SD_T)^4}{N_T X_T^4} + \frac{(SD_C)^4}{N_C X_C^4} \right] \end{bmatrix} \quad (2)$$

172 Statistical analyses

173 All analyses were conducted using R 4.0.3⁴⁶. We used the package ‘metafor’⁴⁷ and the
 174 ‘rma.mv’ function to generate mixed effects meta-regression models, described with equation
 175 (3).

$$176 \quad y_i \sim \beta_1 m_i + \beta_2 f_i + \beta_3 d_i + \beta_4 g_i + \beta_5 s_i + \beta_6 l_i + \beta_7 h_i + \beta_8 p_i + \beta_9 r_i + \beta_{10} V_i + \dots + \gamma_1 e_i + \\ 177 \quad \gamma_2 b_i + v_i \quad (3)$$

178 Where y_i denotes the Delta-adjusted LRR and v_i denotes the Delta-adjusted LRR
 179 variance for the i th effect size. Our effect sizes have a hierarchical structure; multiple effect sizes
 180 exist within single experiments. To minimize the risk of Type I error associated with the
 181 nonindependence among effect sizes that were not explained by sampling error alone^{48,49}, we
 182 accounted for this nonindependence by 1) including a random effects component for effect sizes
 183 within studies (e) and between studies (b) and 2) estimating sampling covariance among effect

184 sizes that have shared control groups (equation (2); v). We did not assess potential publication
185 bias, because the nonindependence among effect sizes within a study and the resulting variance-
186 covariance matrix invalidates these tests^{48,50}.

187 Moderators in the mixed effects meta-analytic models included log₁₀ phylogenetic
188 distance (m), log₁₀ relative body size (f), log₁₀ relative density (d), log₁₀ relative spatial grain
189 (g), study endpoint (density/growth/survival; s), log₁₀ length of experiment (days; l) habitat
190 (terrestrial/aquatic; h), predators (present/absent; p), resource level (low/ambient/high; r), venue
191 (field/mesocosm; V), and all possible two-way interactions (... in equation (3); interactions
192 between both resource and study endpoint and any other categorical moderator as well as
193 between venue and habitat were not possible due to missing cells or highly unbalanced
194 replication across cells). To evaluate the importance of these moderators, we performed model
195 selection based on AIC in which we fit all possible combinations of main effects and two-way
196 interactions as moderators using the ‘dredge’ function in the ‘MuMIn’ R package⁵¹. To prevent
197 overfitting of models, we limited models to 8 moderators (main and interactive effects). Model
198 weights (AIC_w) and relative importance values (sum of AIC_w across models in which the focal
199 moderator appears) for each moderator were calculated from models with a $\Delta AIC \leq 4$ (see Supp.
200 Table S1 and Supp. Fig. S1 for model weights and moderator importance values)⁵². To test
201 whether continuous moderators were different from 0, we used z-tests. Similarly, to test whether
202 categorical moderators were different from 0, we used z-tests and pairwise differences among
203 groups within categorical moderators were evaluated with t-test contrasts. To estimate and plot
204 marginal effects of moderators, we calculated estimated marginal means; continuous covariate
205 moderators were held at their median values and categorical covariate moderators were averaged

206 over the proportions of the groups. Summary statistics, p-values, and figures were generated
207 from the model with the lowest AIC.

208 Following the primary analyses described above, we examined the effect of resource
209 limitation on endpoints for species grown with conspecific and heterospecific neighbors, by
210 selecting the 14 studies in our database that manipulated resources (e.g., ambient and high,
211 ambient and low, or low and high resources). In each study, for all species that were grown with
212 both conspecific and heterospecific neighbors, we calculated the Delta-method-adjusted LRR
213 (LRR^{Δ} ; equation (1)) with “treatment” set as resource limitation and “control” set as higher
214 resource conditions for each species-neighbor combination, which resulted in 150 effect sizes.
215 As with the primary analyses, we calculated a variance-covariance matrix from equation (2) and
216 used the ‘rma.mv’ function to generate a mixed effects meta-analysis model with random effects
217 components for effect sizes within studies and between studies. To test whether resource
218 limitation differentially affected inter- and intra-specific competition, we included a single
219 moderator: the identity of the neighbor(s) of the focal species (conspecific/heterospecific).

220 **RESULTS**

221 We collected 1,748 effect sizes from 96 studies (involving 269 different species and 424
222 species pairs) that met our inclusion criteria. The divergence times of the species obtained from
223 the TimeTree database ranged from 1.14 million years ago (MYA) to 1,275 MYA, with a median
224 divergence time of 121 MYA. Species belonged to various taxonomic groups (49.3%
225 angiosperms, 17.2% amphibians, 11.8% arthropods, 8.1% fish, 4.1% mollusks, and 3.2%
226 mammals, with the remainder from bryophytes, echinoderms, gymnosperms, reptiles, and
227 rotifers), and data represent different measures of competition (88.7% growth, 8.9 % survival,
228 and 2.4% density). Effect sizes were distributed among various ecological contexts (Fig. 1) and

229 were not different among broad taxonomic groupings of focal species (Supp. Fig. S2) or among
230 study endpoints (Supp. Fig. S3).

231 When controlling for within- and among-study variance, model selection indicated that
232 competitive response was negatively related to relative body size of the focal species ($z = 3.944$,
233 $p < 0.001$; Table 1, Fig. 2A, Supp. Fig. S4). Specifically, when the focal species was smaller than
234 the competing species, interspecific competition was greater than intraspecific competition, but
235 interspecific competition was less than intraspecific competition when individuals of the focal
236 species were larger than the competing species. The magnitude of this effect increased when
237 predators were present ($z = 2.682$, $p = 0.007$; Table 1, Fig. 2A, Supp. Fig. S4).

238 The presence of predators also interacted with several ecological moderators to affect the
239 competitive response of species (Table 1). Specifically, there was an interaction between relative
240 spatial grain of the study and the presence of predators, such that when predators were absent,
241 there was a weak positive relationship between relative spatial grain and competitive response
242 ($\beta: 0.017$; Table 1, Fig. 2B, Supp. Fig. S5), but when predators were present, competitive
243 response was negatively related to relative spatial grain ($\beta: -0.191$; Table 1, Fig. 2B, Supp. Fig.
244 S5). Further, predator presence interacted with habitat to affect the competitive response of
245 species ($z = -3.459$, $p = <0.001$). In terrestrial habitats, the presence of predators increased
246 competitive response (marginal $\ln RR^\Delta = -0.78 \pm 0.53$ 95% CI) relative to when predators were
247 absent (marginal $\ln RR^\Delta = -0.23 \pm 0.17$ 95% CI; pairwise comparison, $t = 1.966$, $p = 0.049$; Fig.
248 3). Conversely, in aquatic systems, the presence of predators reduced competitive response
249 (marginal $\ln RR^\Delta = 0.91 \pm 0.56$ 95% CI) relative to when predators were absent (marginal $\ln RR^\Delta$
250 $= -0.25 \pm 0.21$ 95% CI; pairwise comparison, $t = -3.799$, $p < 0.001$; Fig. 3).

251 Finally, model selection also indicated that the relative density of the focal species to the
252 competing species was negatively related to competitive response ($z = 3.510$, $p < 0.001$; Table 1,
253 Fig. 4, Supp. Fig. S6). Specifically, when densities of the focal species were less than the
254 densities of the competing species, interspecific competition was greater than intraspecific
255 competition, whereas the opposite was true when the densities of the focal species were greater
256 than the densities of the competing species. Despite functional similarity and phylogenetic
257 relatedness being positively correlated (simple linear regression: $F_{1,422} = 11.59$, $p < 0.001$, $R^2 =$
258 0.03 ; Supp. Fig. S7), we found no evidence that phylogenetic distance alone or when controlling
259 for functional distance was a significant predictor of competitive response (Supp. Tables S1, S2;
260 Supp. Fig. S1). Additionally, analysis of effect sizes comparing resource limitation on inter- and
261 intraspecific competition indicated that resource limitation consistently intensifies competition,
262 regardless of whether focal species were with hetero- or conspecifics (effect of resource
263 limitation on intra- vs. inter-specific competition, $Z = -0.01$, $p = 0.88$; Supp. Fig. S8). Thus,
264 resource limitation does not appear to alter the ratio of inter- to intraspecific competition
265 (competitive response; our measure of competition strength). Rather, on average, it seems to
266 equally intensify inter- and intraspecific competition. Finally, we found little evidence for study
267 endpoint, study duration, or venue influencing competitive response (Supp. Table S1, Supp. Fig.
268 S1).

269 **DISCUSSION**

270 Predicting the outcome of competition, and thus, the mechanisms underlying species
271 coexistence patterns and biotic assembly processes within communities, is a core tenet of
272 community ecology¹. A long held assumption was that the strength of interspecific competition
273 is driven by phylogenetic relatedness, with closely related species competing more strongly than

274 distantly related species²⁻⁴. Previous investigations of phylogenetic relatedness and functional
275 similarity effects on competition strength have been limited by the breadth of focal taxa
276 examined^{3,7,25} and/or the experimental and ecological contexts in which observations
277 occurred^{26,27}. Using a meta-analysis of 1,748 effect sizes across a range of taxa and ecological
278 contexts, we evaluated whether phylogenetic relatedness and/or functional similarity explained
279 species' competitive responses and whether specific ecological contexts influenced the
280 competitive response of species. Our results suggest that functional similarity, and not
281 phylogenetic relatedness, predicts the competitive response of species (i.e., strength of
282 interspecific competition relative to strength of intraspecific competition). Further, we found that
283 certain ecological and experimental contexts, such as habitat, the presence of predators, relative
284 spatial grain, and relative densities of competing species, can directly alter a species' competitive
285 response.

286 Our findings add to an increasing number of studies that do not support Darwin's
287 hypothesis that phylogenetic relatedness drives competition strength^{4,5,7,53-55}, suggesting that one
288 or both underlying assumptions of this hypothesis are invalid⁷. Examples of phylogenetic niche
289 conservatism exist^{4,15-17}, but niches can evolve convergently or randomly¹⁸⁻²⁰, suggesting that
290 phylogenetic and ecological relatedness may not always be correlated. Regardless of whether
291 niche overlap between species pairs is related to their phylogenetic relatedness, the degree of
292 niche overlap might not exclusively drive competition; rather, competitive ability differences
293 (i.e., differences in species' abilities to utilize shared limiting resources) in addition to niche
294 overlap are thought to influence the outcome of species interactions²²⁻²⁴. While there was some
295 evidence for a phylogenetic signal in the functional similarity of species, phylogenetic
296 relatedness was never a predictor of competition strength in our analyses. Therefore, our

297 findings, in conjunction with previous research⁶, suggest that phylogeny is not an effective
298 predictor of the outcome of species interactions.

299 Our meta-analysis indicated that a species' competitive response is driven by functional
300 similarity, which may be correlated with differences in competitive ability between species
301 pairs^{53,56-58}. Thus, we can infer that a species' competitive response (sensitivity to interspecific
302 competition) is likely driven by that species' relative functional ability (e.g., the height of a plant
303 species relative to its competitor), lending further credence to modern coexistence theory²²⁻²⁴,
304 which, in contrast to Darwin's competition-relatedness hypothesis, posits that functional
305 similarity drives competitive exclusion when species pairs have overlapping niches, while niche
306 differences facilitate coexistence. While we did not explicitly test for niche differences between
307 competing species²³, species pairs within our meta-analysis were those that were likely to
308 compete (i.e., researchers would not select species that do not compete with one another if they
309 were interested in studying competition) and, as such, likely have some niche overlap. Therefore,
310 to thoroughly test modern coexistence theory²²⁻²⁴, future research should explicitly test
311 competitive response in an assortment of taxa across a range of both competitive ability and
312 niche differences³².

313 While previous research suggests that certain ecological contexts can influence the
314 effects of phylogenetic relatedness and functional similarity on competition strength^{3,4,6,9}, we
315 found that only the presence of predators altered the relationship between functional similarity
316 and competitive response. Specifically, the presence of predators intensified asymmetrical
317 competition⁴⁰, such that the relative strength of interspecific competition was more responsive to
318 the relative size differences between competing species when predators were present than when
319 predators were absent. Aside from predators, no other ecological or experimental factors

320 influenced the relationship between functional similarity and competitive response. Nonetheless,
321 we found evidence that certain ecological and experimental contexts may directly alter the
322 competitive response of species.

323 Lending support to previous research showing effects of predation on competition^{26,29},
324 we found evidence that the presence of predators, interacting with habitat, can influence
325 competition strength. The interaction between predators and habitat observed here might be
326 related to habitat productivity. Specifically, predators are hypothesized to increase competition in
327 low productivity systems, because 1) predators reduce the range of conditions that allow for
328 coexistence, 2) species that are well-defended from predation are likely poor at attaining
329 resources and are likely to be outcompeted, and/or 3) traits that increase competitive ability may
330 simultaneously increase vulnerability to predation, and, thus, these traits may be less pronounced
331 in low productivity systems relative to high productivity systems^{29,59}. Consistent with our results,
332 predation pressures in terrestrial systems, which may be less productive than aquatic systems^{60,61},
333 may increase interspecific competition strength, whereas predation pressures in aquatic systems
334 may reduce or not affect the strength of interspecific competition^{29,59}.

335 Further, we found an interaction between predators and relative spatial grain. When
336 predators were present, but not when they were absent, competitive response was negatively
337 related to relative spatial grain (i.e., interspecific competition was stronger than intraspecific
338 competition in experiments with relatively larger spatial grain), suggesting that spatial refugia
339 are a more limiting resource for the competing species when predators are present than absent²⁹.
340 The predator-mediated reduction of space likely increases interactions between competing
341 species⁶², which, in turn, likely leads to increased interspecific competition^{26,29} because species
342 pairs were likely to have some degree of niche overlap.

343 As predicted, we found a relationship between competitive response and the relative
344 density of the focal species, providing support for density-dependent competition^{32,63}.
345 Interspecific competition was greater than intraspecific competition across all taxa when the
346 focal and competing species were at the same densities, suggesting that per capita interspecific
347 competition (e.g., α_{ij} in Lotka-Volterra competition models) is generally greater than per capita
348 intraspecific competition (e.g., α_{ii} in Lotka-Volterra competition models), in contrast to results
349 found within plant communities³². Differences between our results and previous research³² may
350 be a product of our inclusion of animal, plant, and cross-kingdom species pairs, as opposed to
351 only plant species pairs, and/or not explicitly estimating the Lotka-Volterra competition
352 coefficients for these competing species³². These results also imply that total intraspecific
353 competition pressures may be relatively strong at higher conspecific densities, providing further
354 evidence that the density-dependent mortality observed with Janzen-Connell effects (i.e., greater
355 mortality when conspecifics are aggregated in close proximity) may be, in part, the result of
356 strong intraspecific competition, not just from natural enemies^{32,64,65}. To robustly test Janzen-
357 Connell effects, future research should attribute density-dependent mortality to both enemies and
358 intraspecific competition⁶⁴. As we found that certain experimental and ecological factors alter the
359 relative strengths of inter- and intra-specific competition, some discrepancies across studies
360 investigating phylogenetic relatedness and functional similarity controls on competition might be
361 the result of differences in predator presence, habitat, relative size of the experimental venue, and
362 relative densities of competing species. Therefore, future research must account for the influence
363 of these experimental and ecological factors on species' competitive responses.

364 While previous research has highlighted the importance of resource availability in driving
365 competition strength³⁰, we found no evidence that resource availability affected species'

366 competitive responses. Rather, we found that resource limitation consistently negatively affected
367 species endpoints, regardless of whether their competitors were hetero- or conspecifics. This
368 result may suggest that resource limitation increases both inter- and intra-specific competition
369 similarly, supporting previous research showing that competition strength increases as resources
370 become limited^{30,31}. Alternatively, this result may indicate that resource limitation reduces
371 species performance, but because resource limitation did not affect the ratio between inter- and
372 intraspecific competition, competition strength may be independent of resource availability^{66,67}.
373 To clarify the effects of resource availability on competition intensity, future research should
374 explicitly test the strength of inter- and intraspecific competition across a range of taxa and
375 resource levels.

376 The ability for phylogeny to predict the outcomes of species interactions and biotic
377 assembly processes has been highly debated, with recent evidence suggesting that phylogenetic
378 relatedness alone cannot predict patterns of species coexistence^{1,6,7,21,37}. Here, using a meta-
379 analysis of competitive responses across taxa and ecological contexts, we found that functional
380 similarity, a proxy for differences in competitive ability, but not phylogenetic relatedness, was
381 key to predicting species responses to competition, lending support for coexistence theory^{22,23}.
382 The lack of a phylogenetic signal in competitive response across broad taxonomic and ecological
383 contexts found here, in conjunction with previous studies^{3,6,7,9}, provides considerable evidence
384 against Darwin's competition-relatedness hypothesis and, thus, against the hypothesis that
385 phylogeny predicts the outcome of species interactions. Our results demonstrate that functional
386 similarity may explain patterns of competition-associated community assembly, thereby
387 highlighting the value of trait-based approaches in clarifying biotic assembly dynamics.

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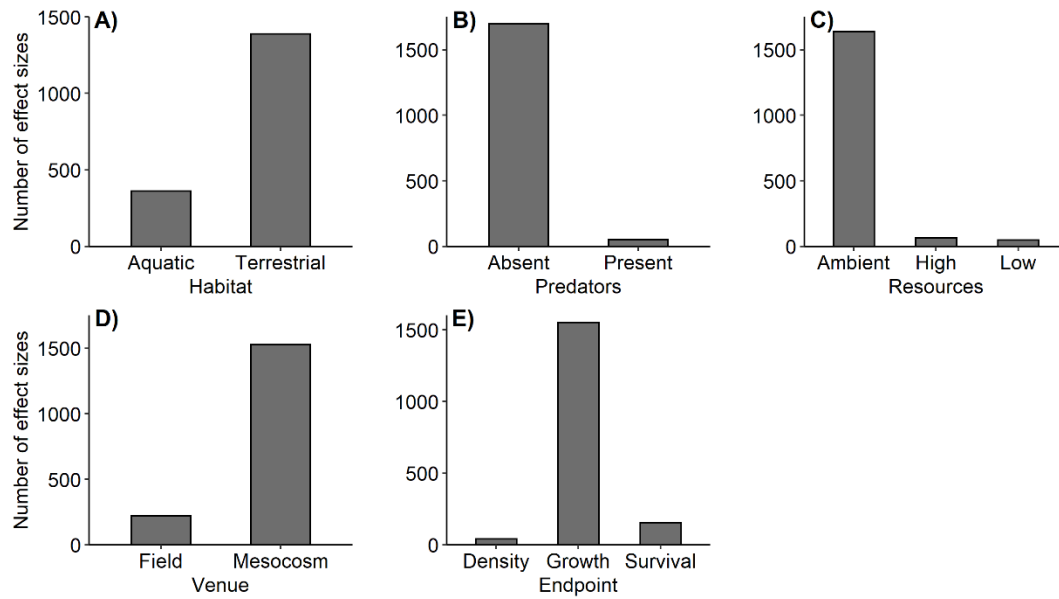
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540 Table 1: Results of a mixed-effects meta-regression model from the model selection indicated
 541 best model (lowest AIC) relating competition strength to factors including the relative size of the
 542 focal species, relative density of the focal species, presence of predators, and habitat. Variance
 543 estimates of the within and across study random effects are 0.390 and 0.257, respectively.

Moderators	Coefficient	95% CI	Z-value	P-value
Grand Mean	-0.239	0.18	-2.607	0.009
Relative Body Size (log10) †	0.224	0.11	3.944	<0.001
Relative Density (log10) †	0.234	0.13	3.510	<0.001
Relative Spatial Grain (log10) †	0.017	0.06	0.512	0.609
Predators Present	0.983	0.44	4.387	<0.001
Predators Present * Relative Body Size	1.062	0.78	2.682	0.007
Predators Present * Relative Spatial Grain	-0.208	0.15	-2.656	0.008
Terrestrial Habitat	0.024	0.26	0.181	0.856
Predators Present * Terrestrial Habitat	-1.715	0.72	-4.687	<0.001

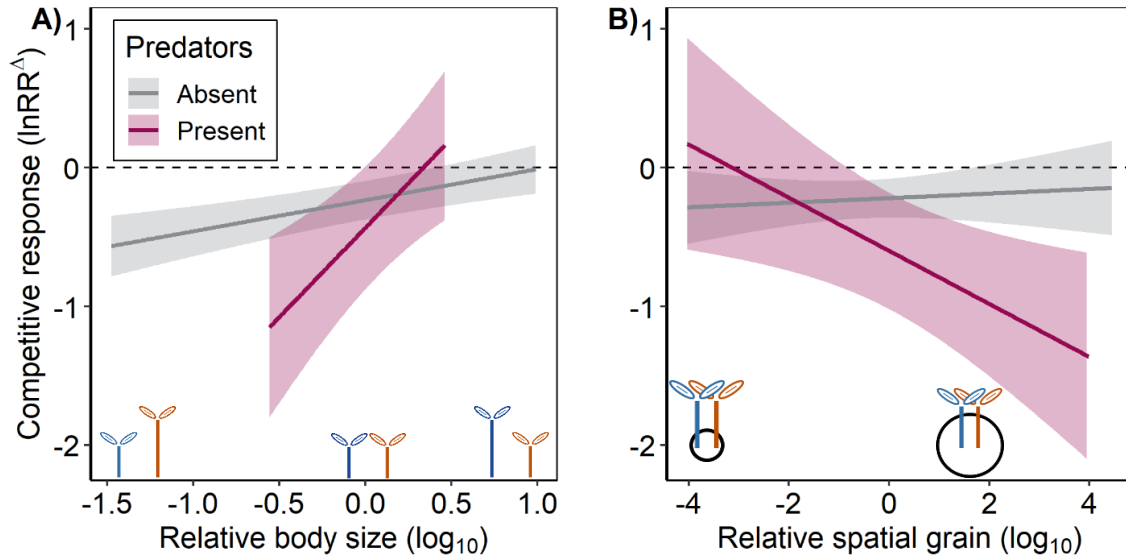
544 Notes: The average outcome of competition is indicated by the grand mean, as the coefficient
 545 represents the pooled outcome of competition. For continuous moderators (†), bolded p-values
 546 indicate a slope that deviates significantly from zero and the sign of the coefficient indicates the
 547 direction of the effect. For categorical moderators, bolded p-values indicate a significant
 548 difference from the grand mean with the coefficient indicating the direction and the estimated
 549 mean of the category. For interactions between categorical and continuous moderators, bolded p-
 550 values indicate a slope that deviates significantly from the continuous moderator and the sign of
 551 the coefficient indicates the direction of the effect.
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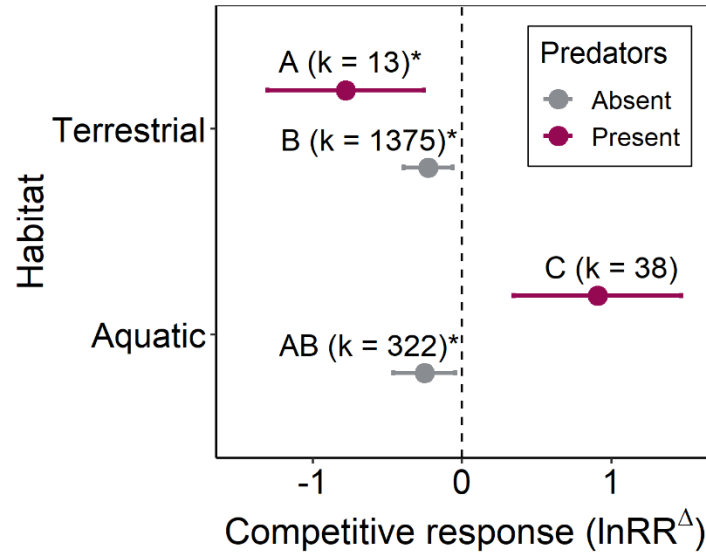
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554 Figure 1. Representation of effect size data for different ecological contexts. Shown are a) habitat
555 (aquatic or terrestrial), b) whether the experiment manipulated the predator presence, c) whether
556 the experiment manipulated resource levels, d) the experimental venue (field or mesocosm), and
557 e) the endpoint measured.

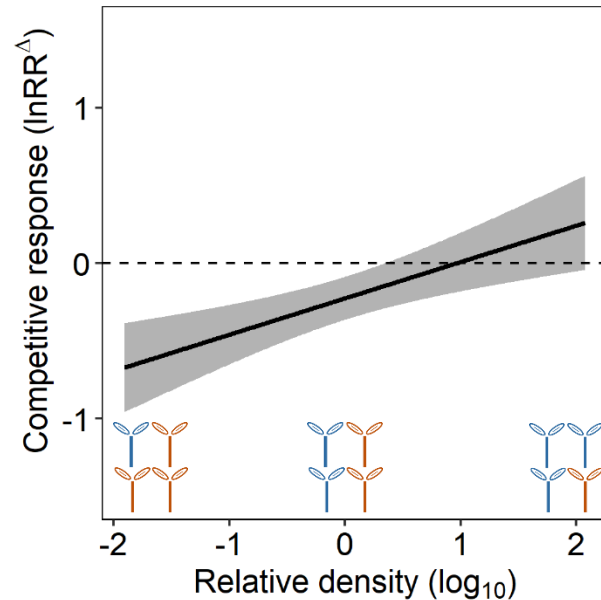
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559 Figure 2. Marginal effects plot showing the interactive effects of predation and (A) relative body
560 size (size of focal species (blue) / size of competing species (orange); functional similarity) and
561 (B) relative spatial grain (spatial grain / size of focal species; size of black circle relative to blue
562 individual) on the outcome of species interactions (lnRR^Δ), respectively. In (A), competition
563 strength decreases as the focal species (Sp1, blue) increased in size relative to the competing
564 species (Sp2, orange), suggesting that relative functional differences drive competition strength.
565 The magnitude of this effect is increased in the presence of predators. In (B), the presence of
566 predators increases competition strength with relative spatial grain is high, but not when relative
567 spatial grain is low, suggesting that the presence of predators may alter spatial resource use by
568 competing species (increased aggregation) in experiments with relatively large spatial grain.
569 Lines represent marginal effects of (A) relative body size and (B) relative spatial grain included
570 in the mixed-effects meta-regression model and shading shows associated 95% credible bands.
571 To estimate these marginal effects, categorical covariates from the mixed-effects meta-regression
572 model were held at their proportional values and continuous covariates were held at their median
573 value. Model-predicted regression lines and credible bands are shown with data points in Fig. S4
574 and S5 in the supplement.



575 Figure 3. Interaction plot showing the marginal interactive effect of habitat (aquatic or terrestrial)
576 and predators (absent or present) on competitive response. Pooled effects and errorbars (95% CI)
577 were generated from the mixed-effects meta-regression model (see Table 1). The coloration of
578 points and errorbars corresponds with predators (grey are predators absent and purple is
579 predators present). Factor combinations sharing the same letter are not different from each other
580 in pairwise comparisons. Asterisks represent factor combination estimates that are significantly
581 different from 0. Above each estimate are counts of effect sizes for each factor combination.
582 There are no differences in competition strength between aquatic and terrestrial habitats when
583 predators are absent. When predators are present, competition strength increases in terrestrial
584 habitats, but decreases in aquatic habitats. To estimate these pooled effects, continuous
585 covariates from the mixed-effects meta-regression model were held at their median values.
586



587 Figure 4. Marginal effects plot showing the effects of relative density (density of focal species
588 (blue)/ density of competing species (orange)) on the outcome of species interactions ($\ln RR^\Delta$).
589 Competition strength decreases as the focal species (Sp1, blue) increased in density relative to
590 the competing species (Sp2, orange), suggesting that relative densities of competing species can
591 influence the outcome of the interaction and, thus, potentially obscure generalities from
592 individual competition studies. Lines represent marginal effects of relative density included in
593 the mixed-effects meta-regression model and shading shows associated 95% credible bands. To
594 estimate these marginal effects, categorical covariates from the mixed-effects meta-regression
595 model were held at their proportional values and continuous covariates were held at their median
596 value. Model-predicted regression line and credible band are shown with data points in Fig. S6 in
597 the supplement.