nature communications

Article

https://doi.org/10.1038/s41467-025-65639-6

Revisiting competitive outcomes through a trait lens: a global meta-analysis across species provenance

Received: 6 October 2024

Accepted: 20 October 2025

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Biological invasions change the landscape of competition within communities and can have major consequences for biodiversity by driving competitive exclusion. However, the effects of competition on trait distributions are less understood, especially in how it depends on the native or nonnative provenance of the species involved. Here, we synthesize global data across plants and animals to investigate how competition alters trait distributions within species. We find that competition consistently reduces trait means and increases trait variation, following a directional-disruptive pattern. These effects depend on species provenance. Native competitors have limited influence on trait distributions within nonnatives, while nonnatives exert stronger impacts on natives. Morphological and life-history traits are especially responsive, whereas chemical and physiological traits show weak overall effects. However, nonnatives disproportionately affect the distribution of chemical and physiological traits. Intraspecific competition exerts a greater influence on trait distribution than interspecific competition, particularly in nonnatives. We discuss how these patterns align with key hypotheses on the evolution and ecology of species invasions. Our work provides insight into how competition shapes trait distributions and provides a trait-based null model for future tests of species interactions in the Anthropocene.

Competitive interactions shape the distributions of ecological traits, defined as characteristics of organisms that influence their survival, growth, and reproduction. In the context of biological invasion, competition plays a pivotal role in determining the success and impact of nonnative species[1]. While numerous studies have examined how competition affects trait expression at the levels of individuals, populations and species[2,3], their outcomes remain inconsistent across taxa and trait types. This underscores the need for a synthetic understanding of how trait distributions within species respond to competition, especially across species of different provenance. Nonnative species often differ from natives in key ecological traits, such as higher competitive ability, broader environmental tolerance, more efficient resource acquisition, or reduced susceptibility to natural enemies[4,5], which may alter the nature and magnitude of competitive interactions. The effects of competition on traits can be assessed through changes in trait distributions within populations, typically expressed as shifts in mean values and in variation, two complementary dimensions of functional diversity[6,7]. Trait mean reflects the average characteristics expressed by individuals in a population, offering insight into the typical strategy used for survival, growth, and reproduction. In contrast, trait variation captures how much individuals differ from one another, revealing the diversity of strategies and potential for niche

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differentiation within populations. Yet, most invasion studies have focused on either trait means or trait variation in isolation[8–10], limiting our ability to fully capture the trait dynamics shaped by competitive interactions.

Competition can occur between co-occurring species, regardless of provenance—whether both are native[11–13] (historically established in their native range), both nonnative[14,15] (introduced beyond their native range), or one native and one nonnative[16,17]. However, there are reasons to expect that the effects of competition will depend on the species provenance. For example, due to founder effects and demographic bottlenecks during introduction[18], nonnative species often differ from natives in baseline trait variability and competitive ability[19,20]. These differences may give rise to asymmetric competitive responses and impacts on trait distributions[21,22]. Nonnatives may exert greater impacts[23,24] and experience weaker trait responses to competition than natives[25]. These patterns align with the Evolution of Increased Competitive Ability (EICA) hypothesis[19], which posits that nonnatives may evolve enhanced competitive ability in the introduced environments. Therefore, species provenance may influence not only how species compete, but also how they adjust their traits in response[26]. Such responses can manifest as directional (shifts in means), disruptive or stabilizing (changes in variation), or a combination thereof, all of which have empirical support across ecological contexts (Supplementary Table S1). Yet, a synthetic understanding of how provenance modulates these trait responses remains elusive. Here, we conduct a global meta-analysis to test whether species provenance consistently shapes how competition alters trait distributions and to identify generalizable patterns that can serve as a null model for future research on competition and invasion.

How competition involving different provenances influences trait distributions can be shaped by multiple factors, such as organism type, trait type, and the nature of competitive interactions. Species vary in their ecological roles and trait repertoires, which mediate how they respond to competition. Traits commonly examined in this context span morphological, life-history, and chemical/physiological dimensions. Chemical/physiological traits are particularly relevant to biological invasion, as nonnative species often exhibit novel biochemical or physiological mechanisms that native species have not previously encountered and therefore may not effectively defend against, an idea central to the Novel Weapons hypothesis[27,28]. The nature of competition also influences trait dynamics: intraspecific competition, which involves individuals of the same species, is generally stronger than interspecific competition due to greater niche overlap. By accounting for these moderators, our analysis captures the complexity of trait responses to competition and provides a framework for uncovering generalizable patterns across diverse ecological contexts.

In this study, we present a quantitative synthesis of how competition influences trait distributions across species of different provenance. We compile effect sizes reflecting changes in trait means and variation in response to competitive interactions and categorize them into four provenance scenarios based on whether the focal and competing species are native or nonnative. The focal species are those with measured traits, while competing species are background species exerting competitive pressure. We begin with an examination of trait change patterns in response to competition across four provenance scenarios and then test the extent to which these responses are consistent across organismal lineages (plants and animals), trait types (morphological, life-history, and chemical/physiological traits), and competition types (intraspecific and interspecific competition). Together, these analyses address two central questions. First, how do competitive interactions between species of different provenance influence trait distributions? Second, which ecological factors modulate shifts in trait means and variation?

Results

By integrating 3779 observations (K) from 346 studies (N) conducted over three decades and spanning diverse geographic regions across plants and animals (Fig. 1 and Supplementary Data 1; Supplementary Figs. S1 and S2), we synthesized experiments and field studies where focal organisms were exposed to replicated control and competition conditions. Competitive environments were established through manipulations of competitor presence or abundance or through observational gradients, with low-abundance scenarios serving as controls. We quantified responses as changes in trait means (log-response ratio, lnRR) and trait variation (log-coefficient of variation ratio, lnCVR)[28,29] under competition relative to control conditions. From these data, our global meta-analysis revealed that competition reduced trait means while increasing trait variation within species (lnRR, $P < 0.001$; lnCVR, $P < 0.001$; Fig. 2 and Supplementary Fig. S3 and see Supplementary Data 2 for statistical details), indicating a directional-disruptive response. Native species followed this pattern, regardless of whether they competed with other natives (native on native; lnRR, $P < 0.001$, lnCVR, $P < 0.001$) or nonnatives (nonnative on native; lnRR, $P < 0.001$, lnCVR, $P = 0.004$). By contrast, nonnative species showed no significant trait changes when competing with natives (native on nonnative; lnRR, $P = 0.09$, lnCVR, $P = 0.21$), suggesting a competitive asymmetry. However, when nonnatives competed with each other, they exhibited directional-disruptive responses (nonnative on nonnative; lnRR, $P < 0.001$, lnCVR, $P = 0.007$).

Trait shifts in plants vs. animals

Plant studies dominated the dataset (86%, $K = 3261$), with animals comprising 14% ($K = 518$). Both groups exhibited overall reductions in trait means and increases in trait variation within species under competition (Fig. 3 and Supplementary Fig. S4). For plants, the directional-disruptive response was broadly observed across provenance combinations, except when nonnatives competed with natives (native on nonnative; lnRR, $P = 0.07$, lnCVR, $P = 0.99$). For animals, the directional-disruptive response was only observed when natives competed with each other (native on native; lnRR, $P = 0.004$, lnCVR, $P = 0.009$); all other provenance scenarios showed no strong effect.

Trait type influences competitive response

Morphological traits accounted for 66% ($K = 2510$) of the observations, followed by life-history (18%, $K = 659$) and chemical/physiological traits (16%, $K = 610$). Both morphological and life-history traits exhibited directional-disruptive responses to competition (Fig. 4 and Supplementary Fig. S5). In contrast, chemical/physiological traits showed no overall response, except in the nonnative on native scenario, where competition reduced trait mean. The nonnative on nonnative scenario was excluded due to the small sample size ($K = 3$). Across provenance combinations, morphological traits broadly followed the directional-disruptive pattern, while life-history traits showed nuanced responses, with stronger shifts observed in the native on native and nonnative on nonnative scenarios.

Competition type modulates trait shifts

Our analysis included data from intraspecific (30%, $K = 1141$) and interspecific (70%, $K = 2638$). Trait responses varied by competition type (Fig. 5 and Supplementary Fig. S6). Under intraspecific competition, both native and nonnative species exhibited directional-disruptive responses. In contrast, under interspecific competition, only native species exhibited significant directional-disruptive responses, regardless of the provenance of their competitors; nonnative species showed no strong responses. Notably, intraspecific competition drove stronger trait shifts than interspecific competition. In the native on native scenario, intraspecific competition led to a 1.8-fold greater reduction in trait means ($P < 0.001$) and a comparable increase in trait variation. In the nonnative on nonnative scenario,

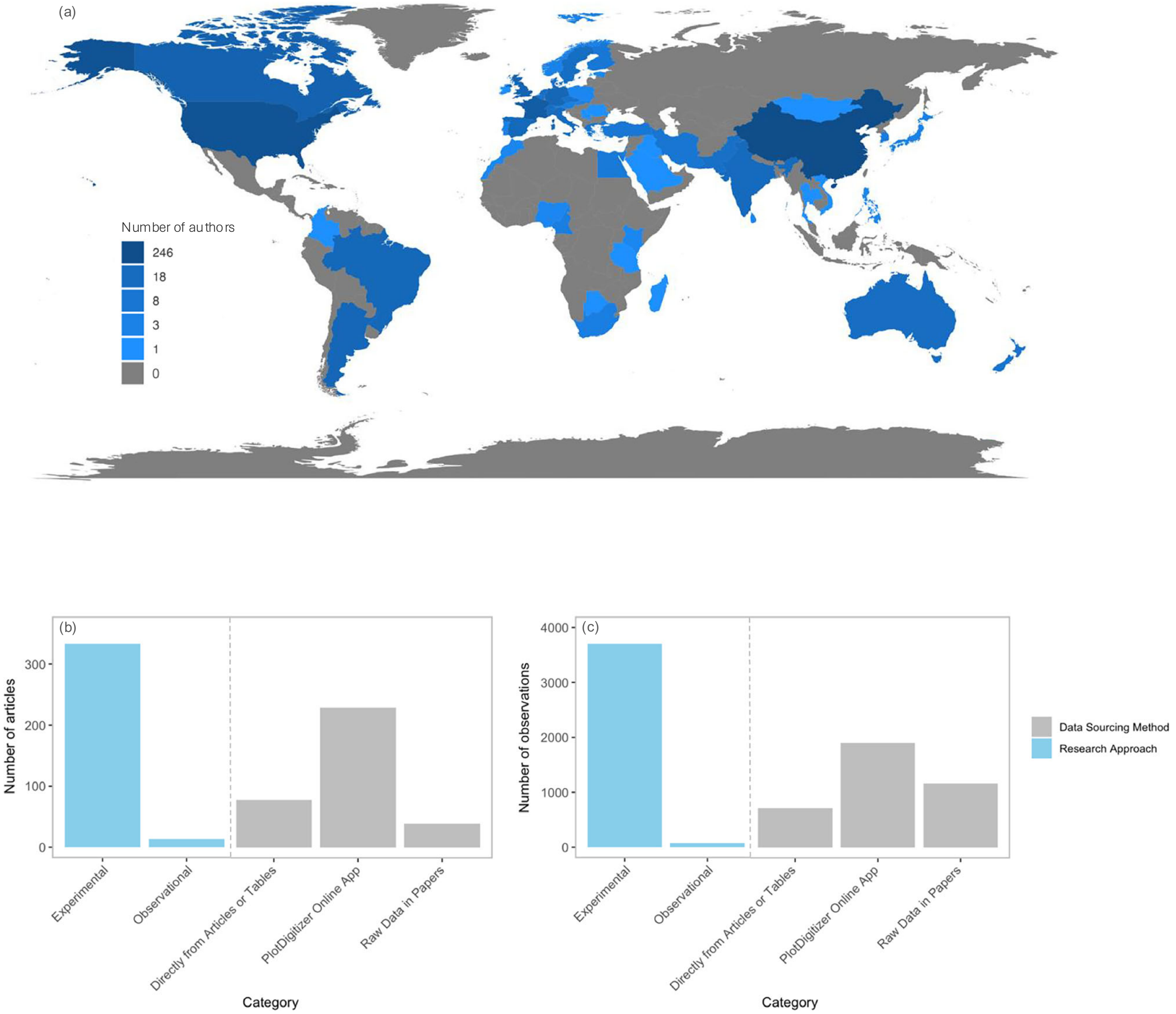

Fig. 1 | Distribution of studies included in the meta-analysis ($N = 346$). **a** Geographic distribution of authors, with color indicating the cumulative number of authors in each country; countries in gray had no data; studies with coauthors from multiple countries are counted multiple times. **b** The number of studies (N) by research approach (experimental or observational, blue) and data source (gray). **c** Number of individual observations (K) contributed by each category defined in (**b**).

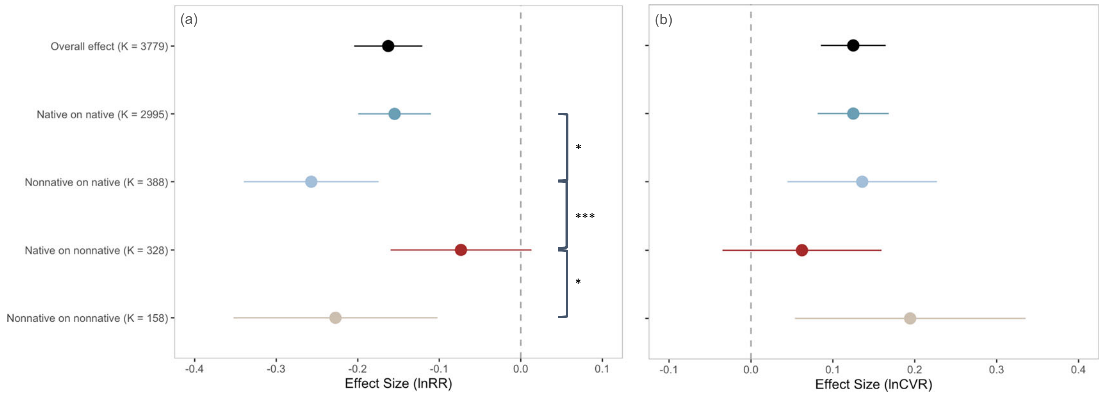

Fig. 2 | Forest plots of overall effect sizes. **a** Trait means, expressed as log-response ratios (lnRR) between competition and control groups. **b** Trait variation, expressed as log-coefficients of variation ratio (lnCVR). Effect sizes are shown as mean ± 95% confidence intervals (CIs). K denotes the number of effect-size estimates. Statistical significance was assessed using a random-effects meta-regression model and two-sided Tukey post hoc post hoc comparisons. Statistical details are provided in Supplementary Data 2. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

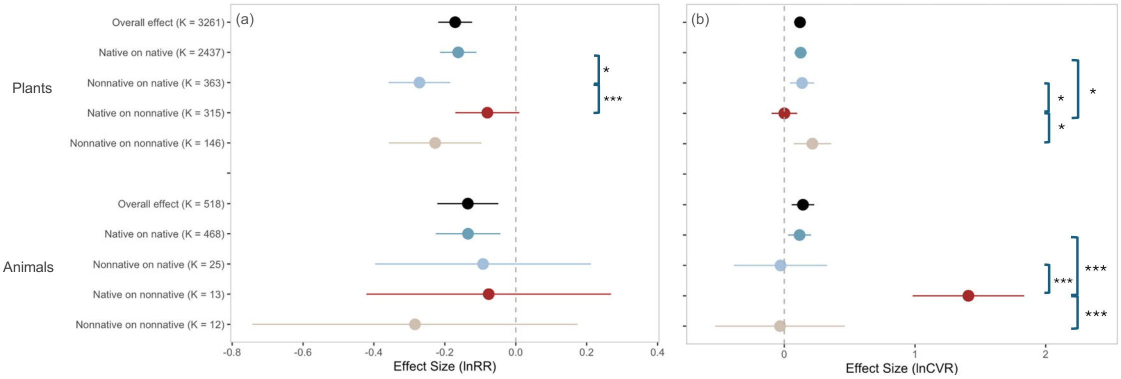

Fig. 3 | Forest plots of effect sizes for traits of different organism types under four species provenance scenarios. a Trait means, expressed as log-response ratios (lnRR) between competition and control groups. **b** Trait variation, expressed as log-coefficients of variation ratio (lnCVR). Effect sizes are shown as mean ± 95% confidence intervals (CIs). K denotes the number of effect-size estimates derived from $N = 346$ studies (see Supplementary Data 1) and two-sided Tukey post hoc comparisons. Statistical details are provided in Supplementary Data 2. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

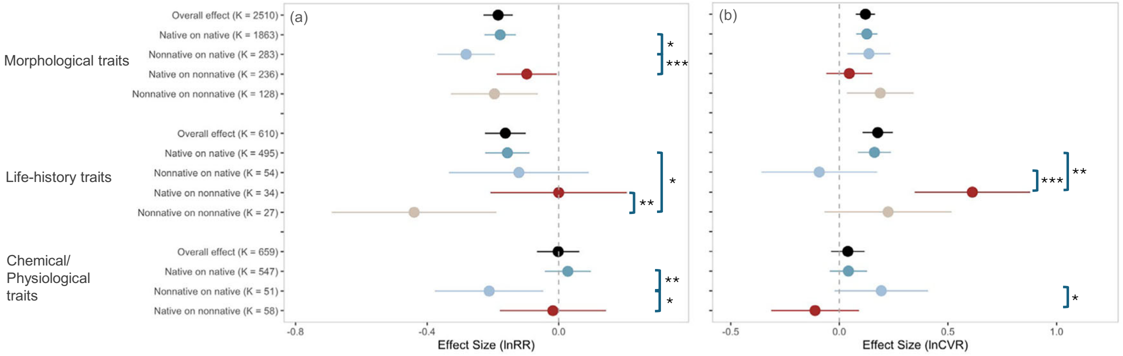

Fig. 4 | Forest plots of effect sizes for different trait types under four species provenance scenarios. a Trait means, expressed as log-response ratios (lnRR) between competition and control groups. **b** Trait variation, expressed as log-coefficients of variation ratio (lnCVR). The nonnative on nonnative scenario for chemical/physiological traits was excluded due to insufficient observations ($K = 3$). Effect sizes are shown as mean values ± 95% confidence intervals (CIs). K denotes the number of effect-size estimates derived from $N = 346$ studies (see Supplementary Data 1) and two-sided Tukey post hoc comparisons. Statistical details are provided in Supplementary Data 2. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

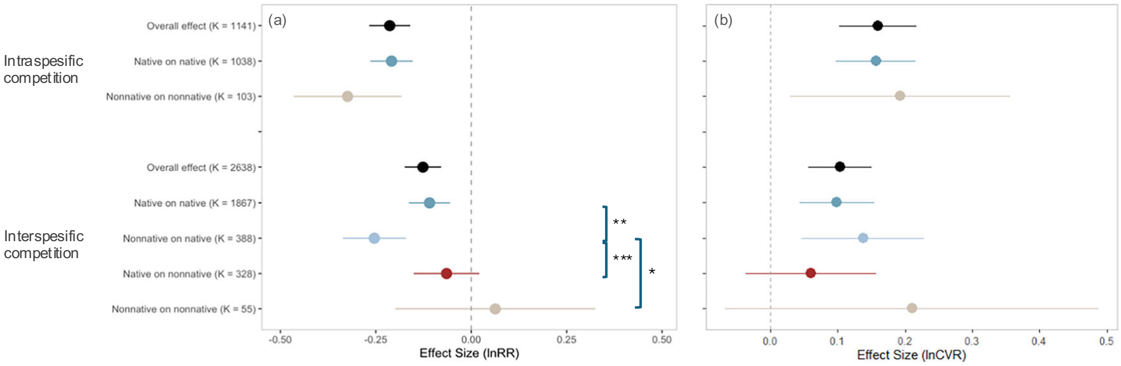

Fig. 5 | Forest plots of effect sizes for traits in response to intra- vs. interspecific competition under four species provenance scenarios. a Trait means, expressed as log-response ratios (lnRR) between competition and control groups. **b** Trait variation, expressed as log-coefficients of variation ratio (lnCVR). Effect sizes are shown as mean values ± 95% confidence intervals (CIs). K denotes the number of effect-size estimates derived from $N = 346$ studies (see Supplementary Data 1) and two-sided Tukey post hoc comparisons. Statistical details are provided in Supplementary Data 2. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

significant shifts in both trait means and variation were observed only under intraspecific competition, with no significant changes under interspecific interactions.

Discussion

Our study provides a quantitative synthesis of how competition shapes trait distributions within species, depending on species provenance. By integrating meta-analysis with bibliometric analysis (Supplementary Fig. S2), we focused on three key ecological modifiers (organism type, trait type, and competition type) frequently referenced in the literature and evaluated their influence across four provenance scenarios. Our analysis revealed several key findings. First, competition generally led to directional-disruptive trait shifts, characterized by reduced trait means and increased variation. Second, species provenance shaped this response. Native species exhibited trait shifts under competition, while nonnative species showed little change when competing with natives, suggesting competitive asymmetry. Third, ecological context modulated these patterns. Trait responses varied with organism, trait, and competition types, each interacting with species provenance to influence outcomes. Notably, the global dataset was dominated by studies on plants and morphological traits, likely reflecting practical constraints on study systems and trait measurements. Despite the overall pattern, notable exceptions were observed, particularly among animals and chemical/physiological traits. We discuss these patterns and their implications in the sections that follow.

Directional-disruptive trait responses to competition are shaped by species provenance

Across a wide range of taxa and ecological settings, our synthesis revealed a consistent pattern. Competition tended to shift trait distributions in a directional-disruptive manner, lowering trait means while increasing trait variation. This response aligned with theoretical expectations and empirical findings, linking resource limitation to trait change. Resource limitation under competition could constrain individual performance, often suppressing traits (e.g., total biomass[30,31] or leaf dry matter content[31,32]). Meanwhile, resource limitation could amplify trait divergence as individuals may need to explore alternative niche strategies under competition. For example, legumes in species-rich plant communities within the Jena Experiment exhibited greater variation in light-acquisition traits (e.g., in terms of lateral branch number and leaf number) compared to competition-absent monocultures[32,33], likely reflecting niche partitioning under intense competition. Similarly, *Spea multiplicata* tadpoles developed two distinct dietary morphotypes, omnivorous and carnivorous, with increased morphological diversity (e.g., notable changes in eye, nasal tip positioning, and oral protrusion) as carnivorous frequency rose[33,34]. Consistent with these case studies, our synthesis revealed that competition promoted trait variation, often coupled with reduced means. Note that in rarer cases, however, increased variation could be accompanied by elevated trait means (a different directional-disruptive pattern), potentially driven by self-thinning dynamics, as competitively inferior individuals (e.g., those with smaller body size[34,35] or shorter roots[35,36]) were excluded. Despite such variation across systems, the directional-disruptive response emerged as a dominant signature of competition.

We further found that the provenance of interacting species modulated trait responses to competition. Trait shifts differed depending on whether species were native or nonnative, a factor deeply relevant to understanding biological invasions. Native species exhibited directional-disruptive trait responses when competing with nonnatives. In contrast, nonnative species often exhibited no significant change when competing with natives (Fig. 2), suggesting a competitive asymmetry[36–38]. These findings support prior meta-analysis[39,40] on pairwise competition between native and nonnative plants, which showed that nonnatives tend to be stronger competitors and exert greater negative effects on native plant biomass and size, and align with the Evolution of Increased Competitive Ability hypothesis[19]. Our broader synthesis, spanning taxa and trait types, indicated that these patterns might be broadly generalizable. Nonnatives are frequently characterized by physiological advantages[36,38], release from natural enemies[4,40,41], and rapid evolutionary shifts[19], all contributing to their strong competitive performance[42,43]. Our results revealed a clear asymmetry in trait responses between native and nonnative species, emphasizing the need to consider species provenance in understanding the ecological consequences of competition. These findings underscore the complexity of species interactions, showing that competition shapes trait distributions in ways that reflect the deep evolutionary and biogeographic histories of interacting species.

Organism type modulates provenance-dependent trait responses to competition

While overall patterns of directional-disruptive trait shifts were broadly consistent across taxa, nuances emerged between plants and animals when species provenance was taken into account. In plants, when nonnative species acted as competitors, whether the focal species were nonnatives or natives, competition consistently led to directional-disruptive trait shifts. By contrast, animals showed little change under similar scenarios. A notable exception occurred in the native on nonnative scenario, where nonnative animals facing competition from native species exhibited pronounced increases in trait variation, a pattern not observed in plants. While sample sizes for animals in some provenance scenarios were limited, resulting in wider confidence intervals, these outcomes aligned with ecological expectations grounded in fundamental differences in mobility, behavioral plasticity, and life history. The mobility of animals might buffer them against localized competitive exclusion. In scenarios where nonnative animals were the competitors, dispersal likely reduced competitive interactions. Dispersal, through source-sink dynamics, might enable persistence of individuals with lower-fitness traits in populations of small mammals, leopards, and birds[43–45], thereby mitigating trait-level consequences of competition[46,47]. Microbial taxa were not included in our synthesis due to limited trait data and the ambiguity of “nonnative” or “invasive” designations, which often reflect host associations rather than true biological invasion. By contrast, plant traits were far more frequently reported, a disparity likely stemming from the stationary nature of plants and the relative ease of trait measurement. This taxonomic imbalance might introduce bias in global pattern detection, underscoring the need for broader trait-based studies across underrepresented taxa.

Trait responses to competition vary by functional category

Trait responses to competition varied markedly across trait types. Morphological and life-history traits consistently exhibited directional-disruptive responses, whereas chemical/physiological traits were less affected. These patterns are intuitive, as organisms tend to develop smaller body sizes (e.g., morphological traits) and slower growth rates (e.g., life-history traits) under competition, while chemical traits may be governed by different or opposing competitive pressures or trade-offs. For example, in a competition experiment between Aleppo pine (*Pinus halepensis*) and downy oak (*Quercus pubescens*), both species exhibited decreases in morphological traits, such as height, diameter, aerial and root biomass, and root/shoot ratio, whereas chemical traits were inconsistent. Phenolic content remained unchanged, and only downy oak increased phenolic allocation, with no noticeable changes in the variation of chemical traits[47,48]. These findings suggested that chemical traits may not shift predictably under competition, likely due to complex trade-offs with structural or growth-related traits. While the above study involved only native species, stronger effects might emerge if invasive species were involved, especially through allelopathy[47], as predicted by the Novel Weapons hypothesis[27], which posits invasive species could gain a competitive advantage through unfamiliar biochemical traits to which native species were not adapted.

Traits of the same organisms have often been studied separately. For example, morphological and physiological trait changes in *Anolis* lizards have been reported in separate studies. However, empirical studies increasingly reveal tight phenotypic integration across traits. A competition experiment by Perez-Ramos and colleagues[48,49] showed that annual plant species under nutrient limitation experienced simultaneous changes in traits, such as lowered specific leaf area, increased water-use efficiency, and elevated leaf carbon content, synergistically enhancing competitive ability. These observations aligned with classic ecology theories, such as r/K selection[49,50] and CSR triangle models[50,51], which also suggested trade-offs across trait axes. By synthesizing a global dataset, our study revealed that competition was more likely to drive changes in morphological and life-history traits relative to chemical/physiological traits, offering an insight into how competition shapes different dimensions of trait space of populations. Although the complex architecture of trait networks is beyond the scope of our synthesis, the potential for coordinated or compensatory trait shifts underscores the importance of future research into phenotypic integration and trait covariance.

Intraspecific competition drives stronger trait shifts than interspecific competition

Both intra- and interspecific competition induced directional-disruptive shifts in trait distribution, but their magnitudes differed markedly. Intraspecific competition consistently caused stronger trait shifts, likely due to greater niche overlap among conspecifics competing for similar or even identical resources[51,52]. These dynamics were further modulated by species provenance. Among nonnative species, intraspecific competition drove directional-disruptive shifts, whereas interspecific competition showed negligible effects. When competition is niche-based, nonnative species may have distinct adaptation histories, resulting in a much lower chance of two distinct nonnative species exploiting the same resources, thus reducing the intensity of competition. Alternatively, nonnative species may facilitate one another. According to the Invasional Meltdown hypothesis[27,52], early-arriving nonnative species can modify environments in ways that benefit later-arriving nonnative species. This facilitation might mitigate competitive interactions, resulting in weak net effects. The likelihood of establishment for nonnative species, however, also depends on interactions with natives of varying phylogenetic relatedness. Darwin's Naturalization hypothesis[53] posits that close phylogenetic relatedness increases niche overlap and biotic resistance from natives. Together, our findings highlight the central role of intra- and interspecific competition between natives and nonnatives and provide a predictive framework for assessing how biological invasions may reshape the trait space of native communities.

Implications and conclusions

Biological invasions pose a pressing threat to global biodiversity, yet the trait-level consequences of competitive interactions between natives and nonnatives remain largely unresolved. Our synthesis uncovers two consistent patterns: prevalent directional-disruptive shifts in trait distributions across most scenarios, and a lack of significant trait change when nonnative species compete with natives. These patterns underscore how ecological context modulates trait responses. Despite these insights, key knowledge gaps remain. Trait-based studies have been disproportionately focused on plants, limiting generalization across evolutionary lineages. Data on competition among nonnative species are sparse, leaving their interaction dynamics underexplored. While our synthesis provides a quantitative baseline for competition-driven trait shifts, useful as null hypotheses for future work, it also underscores the need for targeted experiments and comparative analyses across taxa and ecological contexts. A critical next step is to determine whether trait changes driven by competition during invasions feedback to influence invasion success itself. Although our data cannot yet resolve this question, it represents a promising and practically important direction for future work. Ultimately, disentangling how competition shapes trait dynamics under invasion will be key to predicting ecological trajectories and informing biodiversity conservation in an increasingly invaded world.

Methods

Literature search and bibliometrics analysis

Our literature search was conducted in accordance with the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)[54]. The PRISMA diagram (Supplementary Fig. S1) and PRISMA checklist are available in the Supplementary Code 1 and at https://osf.io/78vgt/. Our initial aim was to examine how competition influences trait shifts. To do this, we conducted a preliminary literature search on ISI Web of Science using the search term (competition AND trait). After establishing a database of relevant articles, we systematically screened them to extract all available data. We then applied bibliometric analysis to identify key modifiers shaping trait shifts, which helped refine the focus of our study on species provenance. To ensure comprehensive coverage of related papers, we conducted additional targeted searches: (invasion AND competition AND trait), and then, (competition AND trait) OR (competition AND life-history trait) OR (competition AND chemical trait) OR (competition AND morphological trait) OR (intraspecific competition AND trait) OR (interspecific competition AND trait) OR (competition AND plant AND trait) OR (competition AND animal AND trait) OR (competition AND microbe AND trait). No new papers were discovered. Although microbial studies were initially identified during literature screening, sample sizes ($N = 21$, $K = 105$; Supplementary Data 1) were too limited for inclusion in the meta-analysis. We limited our selection to papers that are in English and have been formally accepted for publication. As of December 2023, after removing duplicates, we initial search yielded 15,834 records.

We applied three criteria to screen eligible studies. First, studies exposed focal organisms to both "control" and "competition" conditions with replication, allowing for trait comparisons between the two settings. These conditions were typically established through experimental manipulations (e.g., presence/absence or addition/removal of competing species) or through observational gradients in competitor presence/absence or abundance, with low-abundance scenarios serving as controls under otherwise comparable environmental settings. Second, studies were required to report trait mean, sample size, and measures of variance (standard error, standard deviation, or confidence interval) to enable effect size estimation. Third, focal organisms needed to show clear individual growth within a population for trait manifestation. Data were excluded when the establishment failed, or individuals experienced poor growth under stressful conditions. To ensure data independence, we retained only the final measurement for traits recorded multiple times within a study, following the approach of Vila and Weiner[39,40].

We extracted data from texts, tables, and raw data sheets provided by the studies. Data presented in graphs were extracted using PlotDigitizer (https://plotdigitizer.com/app). To summarize the 346 studies included in the meta-analysis, we used the "bibliometrix" R package[55] and conducted two most-frequent-words (unigrams and bigrams) analyses based on study abstracts (Fig. S2). Unigrams identified the most representative keywords, while bigrams provided contextual information. After excluding general terms (e.g., "effects," "competitive," "results," and "conditions"), the most frequent terms included organism type, trait type, and competition type. Among these studies, plants are more frequently studied than animals. In this study, we classified trait types into three functional categories: morphological traits, life-history traits, and chemical/physiological traits (Supplementary Data 1). We considered traits that quantify physical characteristics as morphological traits[56,57], and non-morphological characteristics, including chemical defense, chemical composition and production, and physiological activities, as chemical/physiological traits (see Supplementary Data 1 for trait examples). We considered traits directly related to reproduction as life-history traits[58,59]. Competition types were categorized as intraspecific or interspecific.

We classified the provenance of competing species as native or nonnative. Native species are naturally occurring in a specific geographic area. Note that the term "native" is often not specifically mentioned in the literature. Nonnative species, in contrast, establish populations in novel environments. Terms such as "invasion," "invasive," "exotic," "alien," "non-native," "nonnative," "naturalized," "introduced," "non-indigenous," and "foreign" were used as indicators for nonnative species. In cases of ambiguity, we consulted additional publications and electronic floras to verify species origins. Notably, many invasion-related studies mentioned "competition" in their abstracts without specifically addressing invasion, which reinforced our decision to prioritize competition in the initial literature search.

In total, we retained 346 studies (N) and 3779 observations (K) for the meta-analysis. The majority of the studies employed experimental methods ($N = 333$, $K = 3700$; Fig. 1), with a smaller subset using observational approaches ($N = 13$, $K = 79$). Data were sourced through three methods: directly from the article or tables ($N = 78$, $K = 717$), extracted from graphs using the PlotDigitizer Online App (https://plotdigitizer.com/app) ($N = 229$, $K = 1896$), and from raw data provided in the papers ($N = 39$, $K = 1166$).

Effect size calculation and statistical analyses

We calculated effect sizes and performed the subsequent analyses using the "metafor" package in R (v.3.4.4)[60]. For trait means, we used the log-response ratio (lnRR) between the competition group and control group. For trait variation, we used the log-coefficient of variation ratio (lnCVR)[28,29], which controls for the potential correlation between means and variances[61]. A positive value of lnRR or lnCVR indicated competition increased trait mean or variation, whereas a negative value indicated competition reduced trait mean or variation.

To examine the significance of trait shifts, we employed multilevel mixed effect models ("rma.mv" function). For random effects, we incorporated an observation-level identifier for each effect size nested within study identification (Study), along with publication year, ecosystem type (aquatic, terrestrial ecosystems, and artificial ecosystems with model organisms), and study type (observational vs. experimental; indoor vs. outdoor) as random effects in all models. To examine the overall effect of provenance scenarios, we included it as a fixed effect (moderator) with four levels: (1) focal native species competing with native species (native on native), (2) focal native species competing with nonnative species (nonnative on native), (3) focal nonnative species competing with native species (native on nonnative), and (4) focal nonnative species competing with nonnative species (nonnative on nonnative). To further examine how these responses would be affected by other factors, we combined the levels of provenance scenario with the levels of organismal type, trait type, and competition type as moderators to examine the effect of each combined level[62]. Post hoc tests across factors were conducted using the "glht" function in the "multcomp" package[63].

Publication bias and sensitivity analysis

To evaluate potential publication bias, we first created and visually inspected funnel plots and then applied an extended Egger's regression method adapted for multilevel meta-regression in both trait means and variation. In this analysis, we included the publication year and study setting (indoor experimental, outdoor experimental, and outdoor observational) as moderators to account for publication bias[64] and found no significant effect (Supplementary Figs. S7 and S8). We then conducted a series of sensitivity analyses to confirm the robustness of our results against various factors, including influential outliers, extreme variances, and ecosystem type (aquatic, model organisms, and terrestrial). Influential outliers were identified by comparing hat values to the average value, following the approach of Habeck and Schultz[65]. Given the broad range of sampling variances in complex datasets, we specifically examined the impact of extreme variances by capping vi values outside the normal ranges (the 2.5th and 97.5th percentiles) at those quantile thresholds. The results remained consistent across these tests, confirming the robustness of the results (Supplementary Code 1).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data generated in this study are deposited in the Open Science Framework (OSF) repository at https://doi.org/10.17605/OSF.IO/78VGT. All data and code required to reproduce the results and figures (Supplementary Code 1, Supplementary Data 1 and Supplementary Data 2) are provided with this paper.

Code availability

All codes used in this study are provided in Supplementary Code 1 and are deposited in the Open Science Framework (OSF) repository at https://doi.org/10.17605/OSF.IO/78VGT.

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Acknowledgements

This work was supported by the US National Science Foundation (MCB-2300058 to N.W. and 2300057 to J.T.); the Gordon and Betty Moore Foundation Symbiosis in Aquatic Systems Initiative (10635 to J.T.); and the Louisiana Board of Regents Support Fund (LEQSF(2023–26)-RD-A-14 to J.T. and N.W.); the Chinese Academy of Sciences (E529990101 and E455990101 to N.W.). We thank Morgan Kelly, Bret Elderd, Lizhe Xu, and anonymous reviewers for their discussion and comments.

Author contributions

J.T. and N.W. conceived the idea and designed the study; Y.C., X.F., and J.T. conducted the literature search and data collection; Y.C. performed the secondary screening and data analysis; L.L. and N.W. provided methodological suggestions; Y.C., N.W., and J.T. drafted the manuscript, and all authors reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-025-65639-6.

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Peer review information *Nature Communications* thanks Jian Song and the other anonymous reviewer(s) for their contribution to the peer review of this work. A peer review file is available.