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Raubenheimer, S.L., Simpson, K.J., Ripley, B.S. et al. (2026) Interspecific competition negates CO2 benefits for most plant species. Nature Plants. ISSN: 2055-0278

https://doi.org/10.1038/s41477-026-02360-2

Interspecific competition negates CO_2 benefits for most plant species

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Elevated CO_2 (eCO_2) frequently stimulates plant growth and is widely assumed to enhance productivity in multispecies communities, yet species responses to eCO_2 vary widely with biotic and abiotic context. Whether eCO_2 relaxes competition or amplifies existing competitive hierarchies, shaping how growth benefits are distributed among species, remains poorly resolved. We synthesize data from 19 CO_2 enrichment experiments (glasshouse, chamber, and field studies), encompassing 97 plant species from grass-dominated ecosystems to quantify how competitive context alters species- and mixture-level responses. Although most species respond positively to eCO_2 without neighbours, over half show neutral or negative responses in mixtures. Despite this, dominant species often drive modest increases in total mixture biomass under eCO_2. Trait analyses indicate that acquisitive strategies, rather than intrinsic CO_2 sensitivity alone, predict success under competition. Together, our results indicate that under competition, eCO_2 redistributes growth benefits unevenly among species, favouring dominant species while many subdominants experience neutral or negative responses.

Rising atmospheric CO_2 is altering the productivity and composition of plant communities globally. Elevated CO_2 (eCO_2) often enhances plant photosynthesis and growth[1], but the magnitude of CO_2 fertilization varies widely among species and across biotic and abiotic contexts[2-6]. Within plant communities, individual responses emerge from interactions with neighbours, including potential positive facilitation as well as negative resource competition. For example, 24-year biomass responses of different herbaceous functional groups to eCO_2 were amplified in mixtures and further dependent on level of N availability[7]. However, whether interspecific competition consistently modifies CO_2-fertilization in species mixtures remains unresolved.

Here, we address this gap by synthesizing species-level responses to eCO_2 across contrasting ecological neighbourhoods (i.e. no neighbours, conspecific or interspecific neighbours) and examine whether functional traits shape these responses. Variation in plant responses to eCO_2 reflects traits that influence carbon use, growth, and competitive ability. For example, C_3 species often show stronger physiological responses to eCO_2 than C_4 species, whose photosynthesis is less carbon-limited[8], while growth form shapes how additional carbon is allocated to structure, water use, or species turnover[9]. However, consistent trait-based patterns remain elusive[1,10].

Evidence suggests that eCO_2 responses differ between isolated individuals and those subject to competition[1,4,11], and that the form of competition—whether within (monoculture) or among (mixture) species—can further shape species-level responses[12]. To synthesise these patterns, we adopt a conceptual framework that separates intrinsic growth responsiveness to eCO_2 from neighbour effects on plant performance, allowing species- and mixture-level outcomes to be considered jointly. In this framework (Fig. 1), species are positioned by their eCO_2 responsiveness and vulnerability to neighbours, with mixture-level responses emerging from their relative performance and dominance. Because CO_2 is well mixed in the atmosphere, plants are not expected to compete directly for CO_2; instead, eCO_2 relaxes carbon limitation to intensify competition for other limiting resources, particularly light, water, and nutrients[2,6,7,12]. eCO_2-driven biomass enhancement can therefore strengthen asymmetric competition for light, amplifying differences in growth and coexistence among species[13]. Because the axes in Fig. 1 are independent, realised eCO_2 effects reflect the joint effects of intrinsic responsiveness (i.e. responses when no limitations exist) and neighbour-mediated constraints, so growth stimulation in isolation may not translate to positive responses in mixtures (Fig. 1).

To examine these dynamics empirically, we extend prior syntheses of species-level CO_2 responses under competition[1] using a larger, more taxonomically diverse dataset (97 species across 19 studies) from grass-dominated CO_2 enrichment experiments, spanning functional groups (herbaceous vs. woody; C_3 vs. C_4) and neighbour contexts. We explicitly link species- and mixture-level CO_2 responses using a multilevel meta-analytic framework integrating plant trait data. Given limited comparable data from mature forests, grass-dominated ecosystems, which cover 37% of the world's vegetated land and support key ecosystem services[14], provide the strongest experimental basis for evaluating CO_2 × competition effects, where physiological responsiveness and competitive interactions jointly shape functional composition[11] and CO_2-driven growth responses.

We first quantify how competition from neighbours modifies species-level biomass responses to eCO_2 across competitive contexts (e.g. isolated vs. monoculture or multi-species mixture). Across studies, eCO_2 significantly enhanced plant biomass when species were grown in isolation (log eCO_2 response ratio (RR) intercept = 0.10, 95% CI: [–0.00, 0.20], $p < 0.06$), with 81% of species showing positive responses (Fig. 2a; Table S8a). As expected[1], this stimulation was markedly reduced when grown with neighbours, particularly in inter-specific mixtures (log eCO_2 RR Δ = –0.14, 95% CI: [–0.23, –0.06], $p < 0.001$), with no significant difference between monoculture and isolation. When competing for resources with other species, 56% of species exhibited negative biomass responses to eCO_2; i.e. roughly half as many (44%) responded positively as seen in isolation (81%). These effects were consistent across functional types (ICC = 0.00), suggesting that competition itself, rather than niche overlap within functional types, constrains eCO_2 responsiveness. Although we cannot directly test this, constraints on eCO_2 responses likely reflect limited availability of key resources such as nitrogen, phosphorus, and

water[6], which can suppress physiological benefits of eCO_2 and may be further shaped by mycorrhizal associations[15] and herbivore regimes[16].

We next examined whether species with lower vulnerability to neighbours retain stronger eCO_2 stimulation (log RCV response ratio (RR); Fig. 2B; Table S8B). On average, species showed significantly negative RCV values (log RCV RR intercept = –0.45, 95% CI: [–0.86, –0.03], $p < 0.05$), indicating that most species lost biomass under competition regardless of CO_2 treatment ($p = 0.60$) or competition type (monoculture or mixture; $p = 0.97$; Fig. 2b). These responses show that CO_2 enrichment does not inherently alleviate competitive suppression by boosting growth, contradicting earlier suggestions[17,18]. Notably, species that exhibited strong eCO_2 stimulation also tended to be less suppressed by competition, as shown by the strong positive correlation between eCO_2 RR and RCV RR (Fig. 2c; Table S8c; isolated vs. mixture: slope = 1.08, $R^2 = 0.75$; monoculture vs. mixture: slope = 0.81, $R^2 = 0.76$; both $p < 0.001$) and by a strong negative correlation between competitive suppression (log(mono/mix)) and eCO_2 responses in mixtures (Extended Data Fig. 1, Extended Data Table 1, slope = –0.65, $R^2 = 0.53$, $p < 0.001$). Although the 19 studies ranged from controlled chambers to field experiments, precision weighting and random study effects ($\tau^2 = 0.016$) accounted for contextual differences, revealing a consistent ecological signal. This pattern highlights a subset of species (e.g., the top 5 log eCO_2 RR under mixtures: *Vachellia karroo, Poa pratensis, Lupinis perenis, Panicum virgatum, Andropogon gerardi*) with dual advantages (high eCO_2 responsiveness and low competitive vulnerability) that may disproportionately benefit from eCO_2 in competitive environments, consistent with trait-based modeling[18] and species-level experimental outcomes[11]. Although species maintain their relative positions across CO_2 treatments, eCO_2 increases the performance gap between dominant and subordinate species, strengthening existing competitive hierarchies. This pattern does not require

rank reversals to generate strong mixture-level effects. Accordingly, positive mixture-level responses may arise as dominant species combine higher intrinsic responsiveness to eCO_2 with tolerance of competitive suppression, rather than because competition is relaxed or responses are uniform.

Shifting from species-level responses to mixture-level outcomes, despite negative average responses at the species level in mixtures (Fig. 2), plot-level biomass showed modest, non-significant, increases under eCO_2 in inter-specific mixtures (intercept = 0.04, 95% CI: [–0.01, 0.10], p = 0.13; Fig. 3a; Table S9a). Monocultures, by contrast, showed a significant positive response (Δ = 0.06, 95% CI: [0.02, 0.10], $p < 0.01$), mirroring the direction but not the magnitude of the stronger stimulation seen in isolated plants. However, the magnitude and direction of responses varied substantially, underscoring that the effect of eCO_2 is not uniform but contingent on competitive, environmental and trait contexts. Overall, eCO_2 effects on productivity were modest at the mixture scale (+8% in monocultures and +7% in mixtures, the latter not differing significantly from zero) and substantially lower than assumed in many ecosystem and Earth system models, which often assume uniform or plant function type specific productivity gains under eCO_2[19,20], indicating that competition dampens the CO_2 fertilization effect.

Modest mixture-level stimulation reflects dominant species maintaining performance under eCO_2 compensating for declines in subordinate species[11]. To test this interpretation, we examined species-level eCO_2 responses as a function of their relative dominance within mixtures (Fig. 3b; Table S9b). Species were grouped into quantile-based dominance categories (rare, subdominant, and dominant) based on adjusted biomass contribution, reflecting Grime's mass ratio theory that dominant species disproportionately influence ecosystem function[21]. Dominant species had the highest responses, subdominant species the second, and rare species the lowest: with both

dominant and subdominant species showing significantly stronger eCO_2 responses than rare species ($\Delta = 0.82$, $p < 0.001$) ($\Delta = 0.54$, $p < 0.05$). Mixture-level eCO_2 biomass responses are driven by dominant species, with eCO_2 selectively disadvantaging rarer species, likely through asymmetric resource capture of light, water and nutrients. Although mixture-level responses to eCO_2 were generally positive, variability among studies (Fig. 3) likely reflects interactions among dominance structure, functional composition, resource availability, and experimental duration; all factors that modulate CO_2 fertilisation and community reorganisation.

Building on the conceptual framework in Fig. 1, which highlights the dual roles of CO_2 responsiveness and competitive ability in shaping mixture outcomes, a key remaining question is which traits enable species to succeed in mixtures under eCO_2. To explore this, we grouped species into four "success" categories based on their combined eCO_2 responsiveness and competitive vulnerability: "Highly Successful", "CO_2 Responsive but Vulnerable", "Stable but Unresponsive", and "Less successful" (see Fig. 1), with most species falling into the two intermediate categories. These four groups differed significantly in multivariate trait space (Fig. 4a; Table S10a; Pillai's trace = 6.00, $p < 0.0001$), with "Highly Successful" species strongly separated along the first linear discriminant axis (LD1), largely due to acquisitive traits such as rapid growth rate, greater height, and lower specific stem density, with some showing reduced drought tolerance. We then tested which individual traits predicted success components (Fig. 4b; Table S10b). No individual trait significantly predicted eCO_2 responsiveness, whereas competitive vulnerability was consistently associated with traits linked to competitive performance under eCO_2, even after accounting for multiple testing (Table S10B). In isolated versus mixture settings, higher growth rate and lower drought tolerance were weakly associated with reduced vulnerability to competition (growth rate: $p < 0.02$, $p\_adj = 0.10$; drought tolerance: $p < 0.05$, $p\_adj = 0.10$). In monoculture versus mixture

comparisons, reduced vulnerability was most strongly associated with lower stem density ($p < 0.01$, $p_{adj} = 0.01$) and greater plant height ($p < 0.05$, $p_{adj} = 0.04$), with invasive status showing a similar association ($p < 0.05$, $p_{adj} = 0.04$). Leaf area and leaf carbon content showed weaker, non-significant trends in the same direction. These results suggest that acquisitive, and in some cases invasive, species are more likely to maintain high performance under eCO_2 and competition, indicating trait-based consistency among successful species rather than strict trait-based filtering. Such trait syndromes define the 'Highly Successful' group. Importantly, the association with invasive status likely reflects the relevance of traits linked to invasiveness under conditions of conspecific crowding, rather than a general effect of invasiveness on CO_2 responsiveness.

Our findings update, expand upon, and extend those of Poorter and Navas[1], who emphasized the role of acquisitive strategies in competition but found no consistent link between competitiveness and eCO_2 responsiveness. Here, we show that species with traits promoting rapid growth and resource capture often gain a dual advantage; reduced vulnerability to the presence of neighbours, which tends to have knock on positive effects on responses to eCO_2. This highlights how modern multilevel synthesis can uncover cross-scale patterns that were not detectable previously. By disproportionately increasing the abundance of dominant or invasive species, rising CO_2 may widen performance gaps within grass-dominated systems and promote biotic homogenization. Importantly, this amplification of dominance does not require changes in species rank order, but instead reflects strengthened competitive asymmetries that disproportionately suppress subdominant species under eCO_2. Since our synthesis focuses on grass-dominated systems, many functional groups and biomes remain underrepresented. Nevertheless, the consistent directional responses observed across diverse grass-dominated glasshouse, chamber, and field studies indicate that the patterns we report for the grassland biome are robust despite

contextual variation, a conclusion that is qualitatively supported by a small set of long-term, intact multispecies field experiments reporting changes in relative species or functional group abundance under eCO_2 (Table S11). More broadly, a lack of long-term, multispecies experiments explicitly designed to quantify competitive interactions under eCO_2 remains a major knowledge gap, limiting direct inference about how CO_2-driven changes in competition scale up to biodiversity change in natural ecosystems.

While slower-growing species may respond positively to eCO_2 under low-competition or over longer timescales, our results emphasize that competitive context and trait variation can jointly shape eCO_2 outcomes. Importantly, the responses synthesized here are necessarily constrained to experimental timescales, and competitive hierarchies may continue to reorganize over decades as species turnover, soil feedbacks, and disturbance regimes unfold, potentially modifying or even reversing short-term patterns. Incorporating these filters into models and predictions, where species-level or trait-based dynamics are of interest, will be critical for capturing the context-dependent nature of vegetation change under future climate scenarios. This shift in interpretation is consequential: mixture-level eCO_2 responses may be weak or neutral as eCO_2 amplifies dominance by a subset of species, with implications for biodiversity loss, invasion dynamics, and trait filtering under global change.

Methods

Data selection and extraction

A systematic literature search was conducted in Web of Science and Google Scholar (March 2023) using the search string**:** (‘elevated CO_2’ OR ‘high CO_2’ OR ‘rising CO_2’) AND (‘competition’ OR ‘mixture’) AND (‘grassland’ OR ‘savanna’ OR ‘woodland’ OR ‘shrubland’) AND (‘experiment’

196 OR ‘trial’ OR ‘FACE’ OR ‘free air CO_2 enrichment’ OR ‘OTC’ OR ‘open-top chamber’ OR
197 ‘glasshouse’ OR ‘growth chamber’ OR ‘conviron’)**.** This yielded 183 studies from Web of Science
198 and 146 from Google Scholar. Titles, abstracts, and full texts were manually screened to identify
199 studies reporting aboveground biomass for at least one competitive and one non-competitive
200 treatment under both ambient and eCO_2 conditions. Only studies on wild species were retained;
201 those focused on crops or involving fully mature woody plants were excluded. For studies that
202 included additional treatments (e.g. water, nutrient, or light manipulations), analyses were
203 restricted to treatment levels that allowed assessment of CO_2 and competition effects only. All
204 selected studies provided species-level aboveground biomass data (standardized to $g \cdot m^{-2}$ when
205 necessary). Ambient CO_2 (aCO_2) treatments ranged from 320–400 ppm, and eCO_2 treatments from
206 500–1000 ppm; studies using eCO_2 levels above 1000 ppm were excluded based on projected 2080
207 atmospheric scenarios. In total, 19 peer-reviewed studies were included, along with one additional
208 unpublished dataset known to the authors (full list in Table S1). The final dataset represents
209 experiments from five continents (see Fig. S1). Included studies comprised glasshouse and growth-
210 chamber experiments, open-top chamber studies, and FACE field experiments, and incorporated
211 both monocultures and experimentally imposed or naturally assembled species mixtures under
212 competitive and non-competitive conditions.

213 Species-level aboveground biomass data (as a measure of plant performance) were
214 extracted from text, tables, or figures using WebPlotDigitizer [22]. When biomass data were not
215 directly reported but inferred to exist based on the methods, corresponding authors were contacted
216 to request data. One dataset was obtained directly from the authors of this manuscript (see Table
217 S2). For each species within each study, mean and standard error of biomass were recorded for
218 each CO_2 and competition treatment. Species were assigned to one of three functional types based

on photosynthetic pathway and growth form: C_3 woody, C_3 herbaceous, or C_4 herbaceous. Competition context was classified into four categories: (1) Isolated (plants grown individually), (2) Monoculture (intraspecific competition), (3) Mixtures (interspecific competition). Pairwise experiments (those including two competing species) were classified within the "mixture" category to maintain consistency with broader multispecies comparisons. All biomass data were converted to standardized units of g m^{-2} to ensure comparability across studies. Mixture biomass was defined as the summed aboveground biomass of all species within a given plot or treatment, and comparisons were conducted separately for isolation versus inter-specific mixture and monoculture versus mixture designs to account for differences in experimental structure. Additional metadata were extracted to account for sources of heterogeneity in plant responses: experimental method, duration, CO_2 treatment difference, and soil volume. In total, biomass data from 97 species were compiled, including 25 young C_3 woody species, 49 C_3 herbaceous species, and 23 C_4 herbaceous species.

Effect size calculations

Species- and mixture-level responses to eCO_2 were calculated using log-transformed response ratios in R version 4.5.0[23]. For each species in each study and competition treatment, the eCO_2 response ratio (eCO_2 RR; Eq. 1) was calculated as the natural logarithm of the ratio of mean biomass under eCO_2 versus ambient CO_2 (aCO_2). To assess the effects of competitive context, relative competition vulnerability (RCV) was quantified as the log ratio of biomass in mixture versus either isolation or monoculture, depending on the study design (Eq. 2 and Eq. 3). These were computed separately under each CO_2 treatment to assess interaction effects. We interpret the log relative competitive vulnerability (RCV RR) as an operational measure of neighbour effect.

Less-negative (or more positive) RCV indicates higher competition tolerance (i.e., smaller proportional biomass loss in mixtures relative to isolation/monoculture), whereas more-negative RCV indicates higher competition vulnerability. As we excluded experimental categories that manipulated other resources (e.g., nutrient or water addition, imposed shade), the competition captured here reflects ambient resource limitation, most commonly light and soil nutrients. Mixture-level responses were assessed by summing aboveground biomass across all species within a plot and calculating the log-transformed response ratio between eCO_2 and aCO_2 treatments (Eq. 4). Variance for each log response ratio was estimated using the delta method (Eq. 5). Within mixture treatments, species dominance was quantified as the ratio of each species' biomass contribution to the total mixture biomass. Dominance ratio = biomass of focal species in mixture / total biomass of mixture. Species were binned into three quantile-based dominance groups (rare, subdominant, dominant) based on dominance ratio adjusted by species richness. Values are bounded in (0,1).

Eq. 1 $$eCO_2\ RR = \log(\frac{biomass_{eCO2}}{biomass_{aCO2}})$$

Eq. 2 $$RCV\ RR = \log(\frac{biomass_{mixture}}{biomass_{isolated}})$$

Eq. 3 $$RCV\ RR = \log(\frac{biomass_{mixture}}{biomass_{monoculture}})$$

Eq. 4 Mixture $$eCO_2\ RR = \log(\frac{community\ biomass_{eCO2}}{community\ biomass_{aCO2}})$$

Eq. 5 $$Var\ RR = \left(\frac{SE_{eCO2}}{Biomass_{eCO2}}\right) + \left(\frac{SE_{aCO2}}{Biomass_{aCO2}}\right) \text{ or } \left(\frac{SE_{mixture}}{Biomass_{mixture}}\right) + \left(\frac{SE_{iso\ or\ mono}}{Biomass_{iso\ or\ mono}}\right)$$

Effect sizes were synthesized using multilevel meta-analysis models (rma.mv in the *metafor* R package[24]), with random intercepts for study and functional type. Species- and mixture-

level eCO_2 responses were analyzed with competition treatment as a fixed effect (levels: Isolated, Monoculture, Mixture). RCV responses were analyzed using factorial models with CO_2 treatment and competition context (isolated vs. mixture; monoculture vs. mixture) as moderators. Estimates were weighted by the inverse of their sampling variance. Models were fit using restricted maximum likelihood (REML), and precision-weighted mean responses with 95% confidence intervals were extracted for each group. Individual effect sizes and fitted model estimates were visualized using forest-style plots. This hierarchical structure explicitly accounts for between-study and between-functional-type heterogeneity, ensuring that mean effects reflect consistent directional trends rather than artefacts of averaging across diverse experimental designs[25]. Variance components reported in Supplementary Table S8 show that most of the modest heterogeneity occurred among studies ($\tau^2 = 0.0156$), with negligible variance among functional-type groupings ($\tau^2 \approx 0.0000$). Thus, between-study differences were present but small, indicating that observed patterns are not driven by methodological inconsistency.

To assess potential publication bias and small-study effects, we followed the recommendations of Nakagawa et al.[25]. We visually inspected funnel plots of log response ratios (yi) against study precision (1/SE), with pseudo 95% confidence intervals centered on the model intercept (Figure S2). An Egger-style multilevel meta-regression tested for small-study effects by including the square root of the sampling variance ($\sqrt{vi}$) as a moderator. To evaluate robustness, we refitted the model after excluding low-precision studies (SE > 1); results were consistent with the original model (Table S2). We also conducted a leave-one-out influence analysis to assess the impact of individual studies. In all cases, changes in the intercept were minimal (maximum $\Delta = 0.075$), and the CO_2 effect remained consistently positive (Table S3, Figure S3), confirming that no single study disproportionately influenced the meta-analytic outcome. Finally, we performed a

trim-and-fill sensitivity analysis by excluding studies with extreme effect sizes (±2.5 SD from the mean). The resulting model (Table S4) showed slightly attenuated effect sizes but preserved the direction and significance of the mixture competition effect, supporting the robustness of the overall findings. We applied the same procedures to assess potential bias and robustness in the RCV meta-analysis. Funnel plots (Figure S4), Egger-style meta-regression, and exclusion of low-precision studies (Table S5) indicated no evidence of small-study effects. A leave-one-out analysis confirmed that no single study disproportionately influenced the RCV estimates (Figure S6, Table S6), and trimming outliers (±2.5 SD) had minimal effect on model outcomes (Table S7).

Trait data extraction and analysis

To determine which plant traits predict CO_2 responsiveness and competitive vulnerability, we compiled species-level trait data for all species in the meta-analysis. Continuous and categorical traits were extracted from the TRY[26] and AusTraits[27] databases, and supplemented with trait values from the original study manuscripts. The final dataset included the following traits: leaf area, leaf nitrogen content (Leaf N), leaf dry matter content (LDMC), specific stem density (SSD), specific leaf area (SLA), leaf carbon content (Leaf C), leaf C:N ratio (Leaf C:N), root:shoot ratio, maximum plant height, life strategy (annual, perennial, and deciduous), growth rate, lifespan, Grime strategy, resprouting ability, shade, fire, cold and drought tolerances (low, moderate, and high), and invasive status (manual assessment of reports of invasion occurrence using the CABI Invasive Species Compendium[28]). To assess potential multicollinearity among trait predictors, we calculated variance inflation factors (VIFs) for each model. All VIF values were below 3.3, indicating that collinearity was minimal and did not affect model inference.

Trait values were log-transformed (with offsets to avoid zeroes) and imputed using PCA-based imputation (`missMDA` package in R[29]) to complete missing values across the dataset. All

traits were standardized prior to analysis. Traits were then merged with species-level CO_2 response and competitive vulnerability metrics, and each species was classified into one of four success categories based on its position relative to median CO_2 response and RCV values: "Highly Successful," "eCO_2 Responsive but Vulnerable to Competition," "Stable but Unresponsive to eCO_2," and "Less successful". Discriminant Analysis of Principal Components (DAPC) was used to examine whether success categories occupy distinct multivariate trait spaces (Fig. 4A). Trait contributions to discriminant axes were used to identify key axes of variation, and significance of trait space separation was assessed via MANOVA and pairwise comparisons.

To quantify the contribution of each trait to CO_2 responsiveness and competitive vulnerability, linear mixed-effects models (LMMs; `missMDA` package in R[30]) were fitted with standardized trait predictors and random intercepts for study and functional type. Separate models were fitted for log-transformed eCO_2 RR, RCV RR from mixture versus isolation, and RCV RR from mixture versus monoculture. Standardized model coefficients and 95% confidence intervals were extracted and summarized in forest plots. All trait analyses were performed in R version 4.5.0[23].

Data availability

The data supporting the results of this study are available on DRYAD (https://doi.org/10.5061/dryad.8sf7m0d2q). This includes the raw biomass and trait data.

Code availability

The code supporting the results of this study are available on DRYAD (https://doi.org/10.5061/dryad.8sf7m0d2q). This includes the R scripts used for statistical analysis and trait imputation. The code is fully documented to ensure reproducibility of the analyses.

Acknowledgements

We would like to thank artist Elena Hartley/elabarts.com for the illustrations for Figure 1. This research was funded by The Institute for Global Change Biology (University of Michigan Biological Sciences Initiative Grant), the Natural Environment Research Council (NERC; NE/T000759/1), the National Science Foundation (NSF) Long-Term Ecological Research (LTER; DEB-1831944 and DEB-2425352), the Long-Term Research in Environmental Biology (LTREB; DEB-1753859), Biodiversity on a Changing Planet (DEB-2224854) and Biological Integration Institutes grant NSF-DBI-2021898.

Author contributions

SLR developed the idea, approach, and design for this study, with assistance from PBR. SLR conducted data analyses and wrote the initial draft of the manuscript. SLR, KJS, BSR, CPO, and PBR all contributed unpublished data. All authors contributed to revisions of the manuscript. We thank Dr. Thiago Gonçalves Souza for his advice on the manuscript.

Competing interests statement

There are no competing interests.

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Figure legends

Figure 1. Conceptual framework illustrating species- and mixture-level responses to elevated CO_2 (eCO_2) in competitive plant mixtures. (a) At the species level, success under eCO_2 depends on both a species' intrinsic responsiveness to CO_2 (i.e., responses in the absence of neighbors) and its ability to tolerate neighbours. Here, tolerance refers to a species' ability to maintain biomass with neighbours, while vulnerability is the proportional biomass loss when grown with neighbours. As studies/data altering other resources were excluded, "competition from neighbours" primarily reflects ambient growth limitation by light, nutrients and water. Species can be categorized into four quadrants: (1) *Less successful* (low eCO_2 responsiveness and low neighbour tolerance), (2) *CO_2 responsive but vulnerable* (high eCO_2 responsiveness but low neighbour tolerance), (3) *CO_2 unresponsive but tolerant* (low eCO_2 responsiveness but high neighbour tolerance), and (4) *Highly successful* (both high eCO_2 responsiveness and neighbour tolerance). The example species used in Fig 1A is a grass, but this could be any growth form. **(b)** At the mixture level, the overall biomass response to eCO_2 increases with the proportion of species classified as individually successful. However, this relationship is shaped by species' dominance and identity, meaning that mixture-level gains may occur even when many species respond negatively to eCO_2.

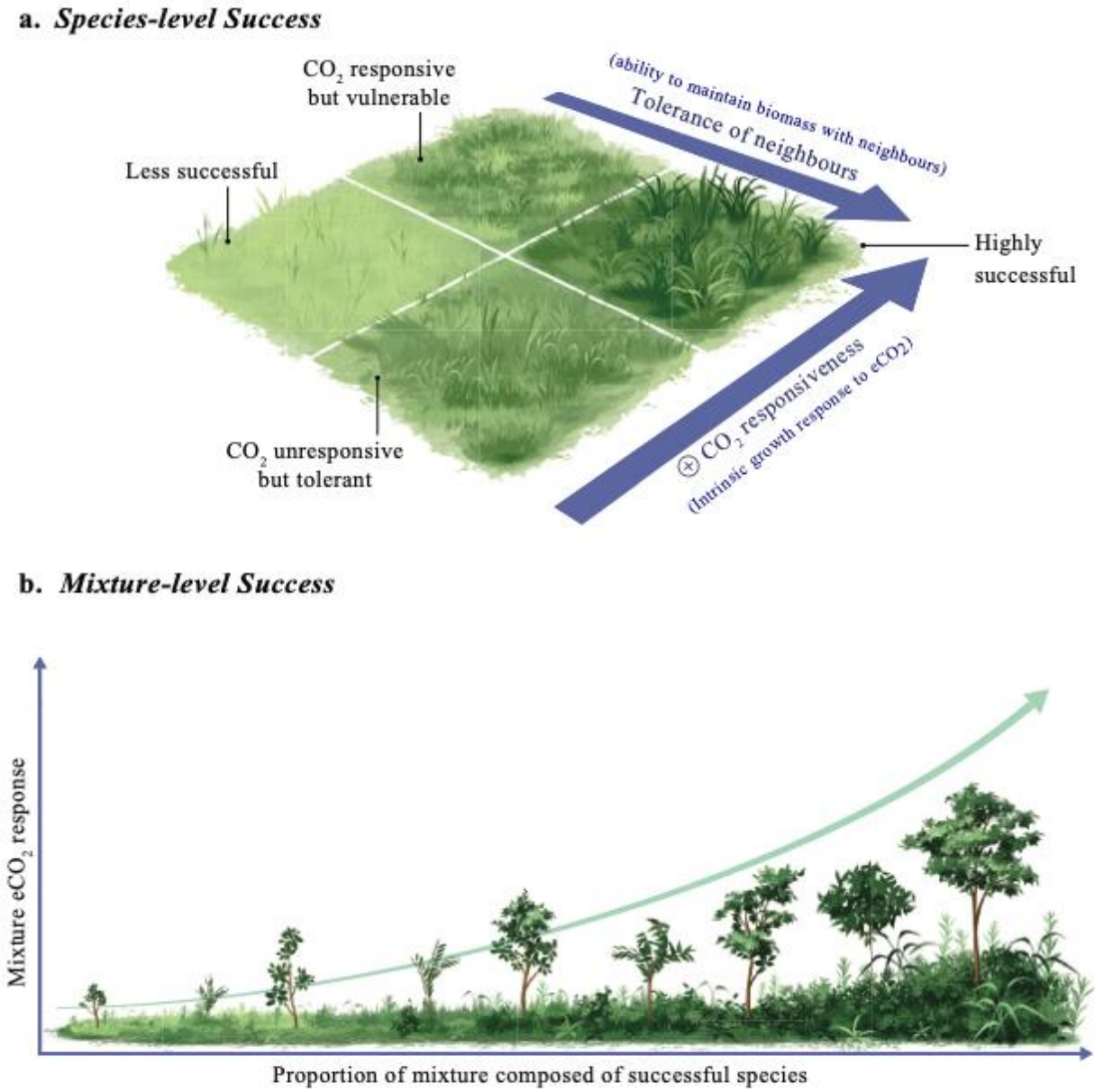
Figure 2. Effects of competition context on plant responses to elevated CO_2 (eCO_2) relative to ambient CO_2 (aCO_2) across functional types and experimental designs. (a) Mean log response ratios to eCO_2 (eCO_2 RR; biomass at eCO_2 / biomass at aCO_2) for plant biomass under three competition treatments: isolated (n = 41), monoculture (n = 47), and mixture (n = 96). Coloured points represent individual species-level responses, with point colour indicating functional type (young C_3 woody, C_3 herbaceous, C_4 herbaceous) and point size scaled by precision (1/SE). Black points and horizontal error bars show model-predicted group means and 95% confidence intervals from a multivariate meta-analysis. Model estimates: intercept = 0.10 (95% CI: −0.00 to 0.20, p = 0.06); mixture effect relative to isolation, $\Delta = -0.14$ (95% CI: −0.23 to −0.06, $p < 0.001$). **(b)** Mean log relative competitive vulnerability response ratios (RCV RR; biomass in mixture / biomass in isolated or monoculture), separated by CO_2 treatment: ambient (circles) and elevated (triangles). Coloured points show species-level responses with colours indicating functional type; black points and error bars indicate group means and 95% confidence intervals from a multivariate meta-analysis. High CO_2: diversity effect (n = 58), competition effect (n = 43); low CO_2: diversity effect (n = 57), competition effect (n =

42). Model estimates: intercept = −0.45 (95% CI: −0.86 to −0.03, $p < 0.05$); CO_2 treatment effect, $p = 0.60$; competition-type effect, $p = 0.97$. **(c)** Correlation between species' eCO_2 RR (y-axis) and RCV RR (x-axis) (n = 98). Solid and dashed lines represent fitted regression models for different competition comparisons (isolated vs. mixture: solid; monoculture vs. mixture: dashed). Shaded regions represent 95% confidence intervals around fitted linear regression lines. Point colours indicate functional type; regression equations and R^2 values are provided in the figure. Model slopes were 1.08 ($R^2 = 0.75$, $p < 0.001$) for isolated-versus-mixture comparisons and 0.81 ($R^2 = 0.76$, $p < 0.001$) for monoculture-versus-mixture comparisons.

Figure 3. Mixture level responses to elevated CO_2 (eCO_2) across competition context. (a) Meta-analysis of mixture-level eCO_2 response ratios (log-transformed) comparing monocultures (n = 51) and mixed-species (n = 35) competition treatments. Black points and error bars represent model-predicted means and 95% confidence intervals from a multilevel meta-analysis including random intercepts by study. Grey points show individual plot responses from each study, with size reflecting the inverse standard error (precision) of individual study estimates. The dashed line at x = 0 indicates no response to eCO_2. Model estimates: mixture intercept = 0.04 (95% CI: −0.01 to 0.10, $p = 0.13$); monoculture effect relative to mixtures, $\Delta = 0.06$ (95% CI: 0.02 to 0.10, $p < 0.01$). **(b)** Species-level responses to eCO_2 grouped by relative dominance within mixtures. Species were binned into three quantile-based dominance groups [rare (n = 31), subdominant (n = 30), dominant (n = 30)] based on dominance ratio adjusted by species richness. Points show individual species-level log response ratios, while large points and vertical error bars denote group means ± 95% confidence intervals. Sample sizes for each bin are indicated above. The dashed line at y = 0 indicates no response to eCO_2. Dominant and subdominant species exhibited stronger eCO_2 responses than rare species (dominant vs. rare: $\Delta = 0.82$, $p < 0.001$; subdominant vs. rare: $\Delta = 0.54$, $p < 0.05$).

Figure 4. Trait-based separation of plant success groups under elevated CO_2 and competition. (a) Discriminant Analysis of Principal Components (DAPC) shows separation among species classified into four success groups based on their CO_2 responsiveness and competitive vulnerability. Groups are plotted by the first two linear discriminants (LD1 and LD2), with ellipses representing 68% confidence intervals. Arrows indicate trait loadings, scaled by

correlation strength with the DAPC axes. Success groups differed significantly in multivariate trait space (Pillai's trace = 6.00, $p < 0.0001$). **(b)** Standardized coefficients (±95% CI) from linear mixed-effects models showing how individual traits predict species' CO_2 response (left) and competitive vulnerability (right). Significant predictors ($P < 0.05$) are shown in red. Trait effects are shown for eCO_2 response ratios (n = 99), relative competitive vulnerability response ratios for isolated versus mixture comparisons (n = 88), and relative competitive vulnerability response ratios for monoculture versus mixture comparisons (n = 110). Error bars indicate 95% confidence intervals around standardized coefficient estimates. No individual trait significantly predicted eCO_2 responsiveness. In isolated-versus-mixture comparisons, higher growth rate ($p < 0.02$, p-adj = 0.10) and lower drought tolerance ($p < 0.05$, p-adj = 0.10) were associated with reduced competitive vulnerability. In monoculture-versus-mixture comparisons, reduced vulnerability was associated with lower stem density ($p < 0.01$, p-adj = 0.01), greater plant height ($p < 0.05$, p-adj = 0.04), and invasive status ($p < 0.05$, p-adj = 0.04). **Trait abbreviations:** Cold tol. – cold tolerance (ordinal: 1 = low to 10 = high); Drought tol. – drought tolerance (ordinal: 1 = low to 10 = high); Fire tol. – fire tolerance (ordinal: 1 = low to 10 = high); Grime strat. – Grime's strategy classification (e.g., C, S, R types); Growth form – life strategy (annual, perennial, deciduous); Growth rate – growth speed (fast- or slow-growing); Height – maximum vegetative height (cm); Invasive – invasive status (classified as invasive: yes/no); LA – leaf area (mm^2); Leaf C – leaf carbon content (%); Leaf C:N – leaf carbon-to-nitrogen ratio (unitless); Leaf N – leaf nitrogen content (%); LDMC – leaf dry matter content (g/g); Lifespan – estimated lifespan (years); LMA – leaf mass per area (g/m^2); Resprouting – resprouting ability (yes/no); Root:Shoot – root-to-shoot biomass ratio (unitless); Shade tol. – shade tolerance (ordinal: 1 = low to 10 = high); SLA – specific leaf area (mm^2/mg); SSD – stem specific density (g/cm^3).



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495 Figure 1.

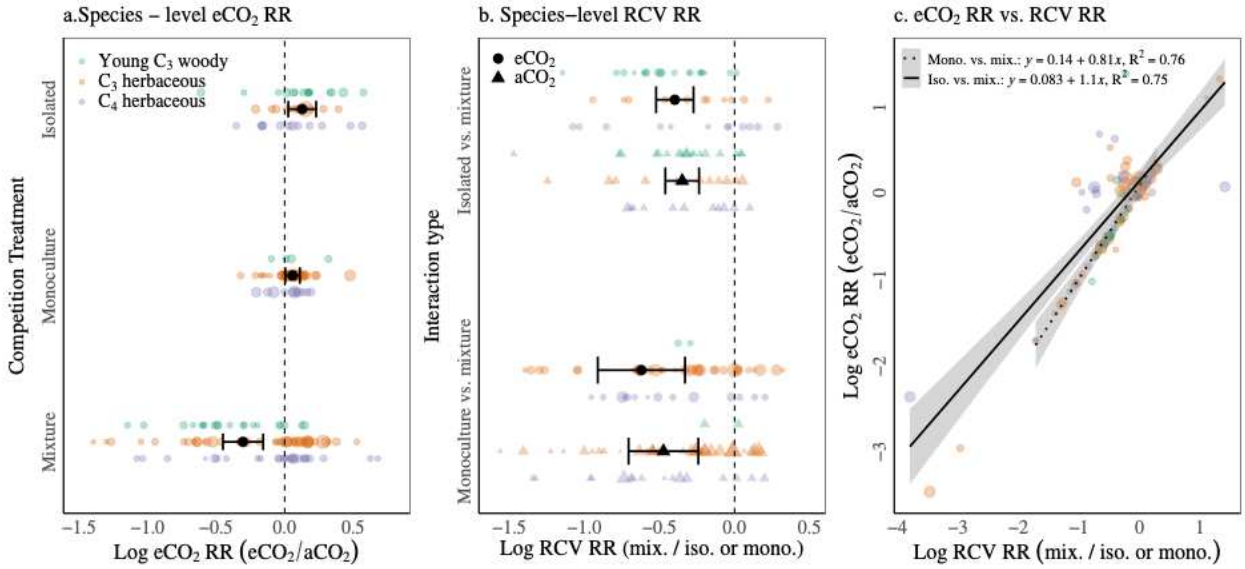
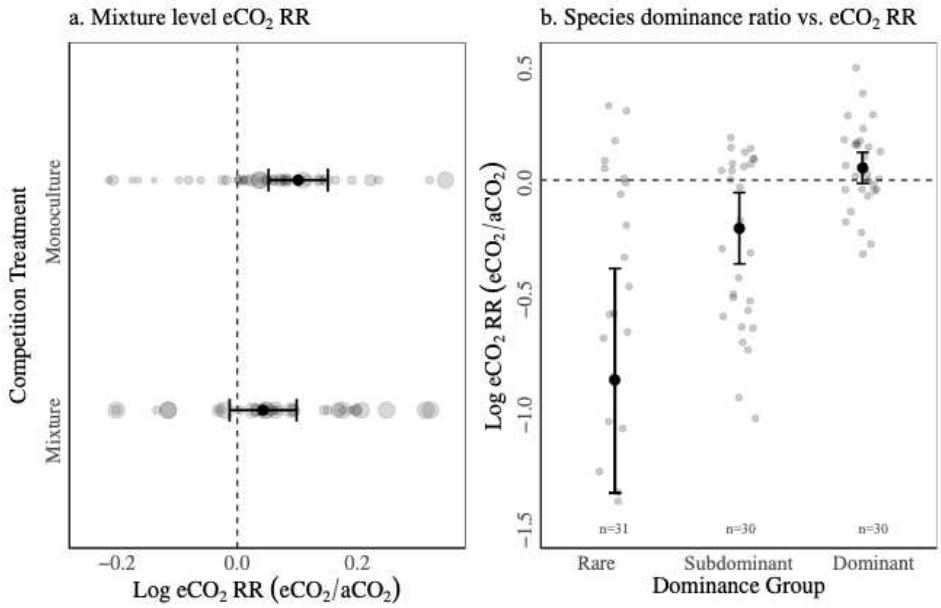

a.Species – level eCO2 RR
Young C3 woody
C3 herbaceous
C4 herbaceous
Competition Treatment
Isolated
Monoculture
Mixture
−1.5 −1.0 −0.5 0.0 0.5
Log eCO2 RR (eCO2/aCO2)
b. Species–level RCV RR
eCO2
aCO2
Interaction type
Isolated vs. mixture
Monoculture vs. mixture
−1.5 −1.0 −0.5 0.0 0.5
Log RCV RR (mix. / iso. or mono.)
c. eCO2 RR vs. RCV RR
Mono. vs. mix.: y = 0.14 + 0.81x, R2 = 0.76
Iso. vs. mix.: y = 0.083 + 1.1x, R2 = 0.75
Log eCO2 RR (eCO2/aCO2)
−4 −3 −2 −1 0 1
Log RCV RR (mix. / iso. or mono.)

Figure 2.

500



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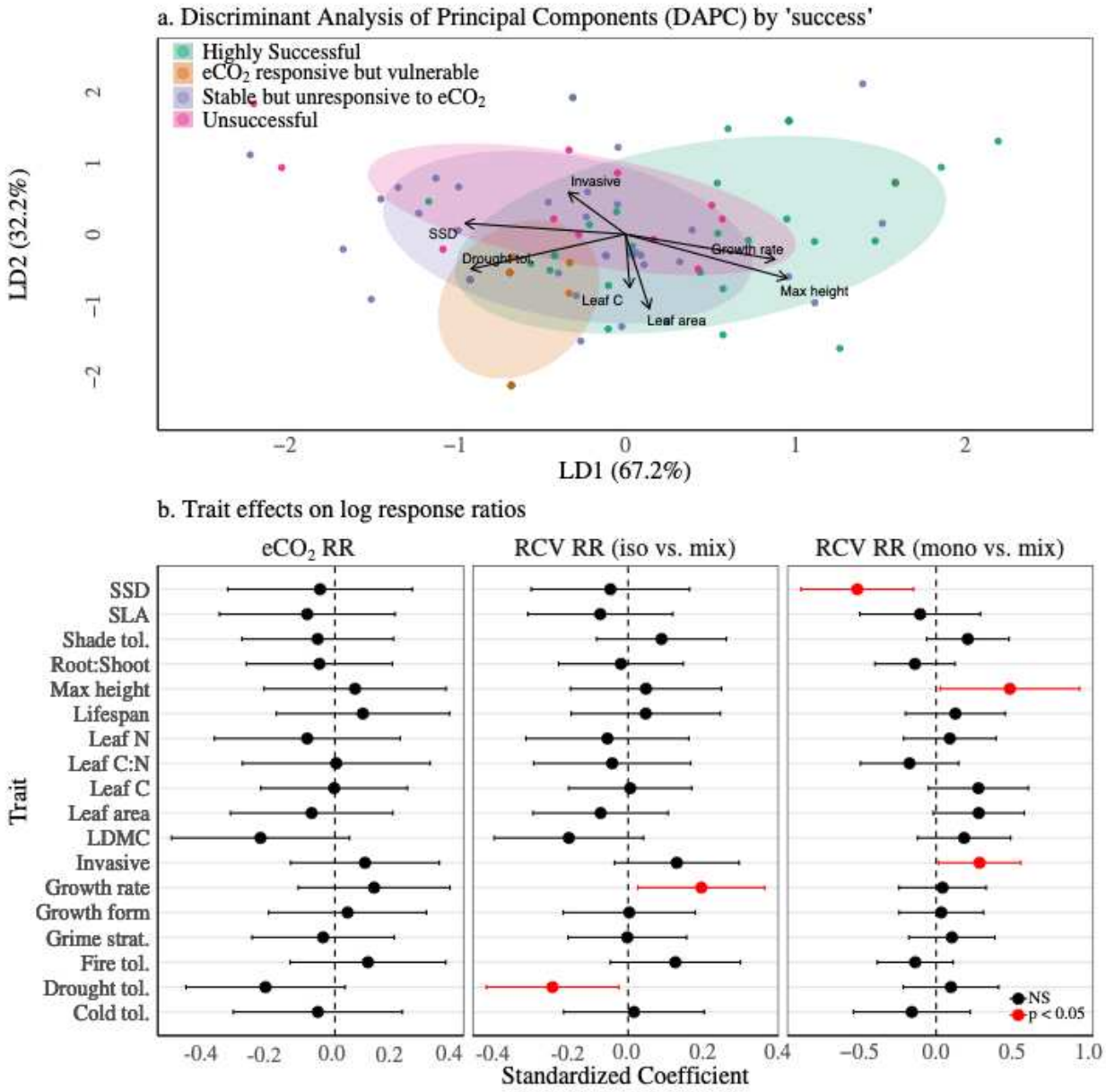
502 Figure 3.



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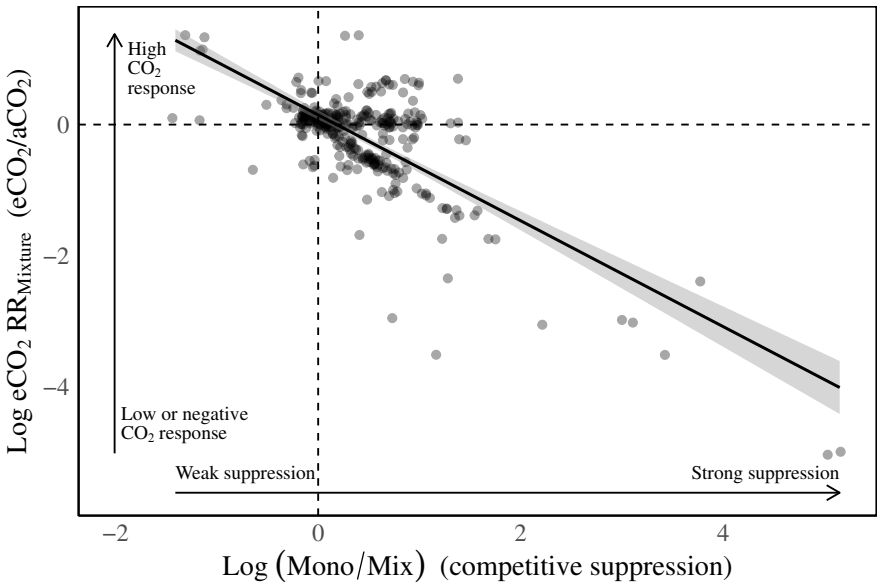
504 Figure 4.

Extended Data

ED 1. eCO_2 response in mixtures vs competitive suppression



Extended Data Figure 1. CO_2 responsiveness in mixtures as a function of competitive suppression. Species that experience stronger biomass suppression in mixtures relative to monocultures (higher log mono/mix values) show weaker or negative biomass responses to elevated CO_2 (log eCO_2 RR). Competitive suppression was negatively associated with eCO_2 responses in mixtures (slope = −0.65, $R^2 = 0.53$, $p < 0.001$). Species that are less suppressed by neighbours retain more positive eCO_2 responses. This pattern indicates that competitive context strongly constrains the expression of intrinsic CO_2 responsiveness.

Extended Data Table 1. Linear model results testing the correlation between species' CO_2 responsiveness in mixtures and competitive suppression. The model relates species' log-transformed biomass response ratios to elevated CO_2 in mixtures (eCO_2 RR_mix) to their competitive suppression (log(mono/mix)). The table reports the intercept and slope for eCO_2 RR_mix, along with associated standard errors, 95% confidence intervals, and p-values. Model fit is summarized using R-squared (R^2).

ED Table 1. CO_2 responsiveness in mixtures vs. competitive suppression

	Term	Estimate	SE	X95..CI	p.value
Mixture correlation model	(Intercept)	0.304	0.028	[0.249, 0.359]	< 0.001
Mixture correlation model	X	-0.652	0.035	[-0.720, -0.583]	< 0.001
Model Fit	R-squared	0.526			

Supplementary materials

S1. Studies included in meta−analysis

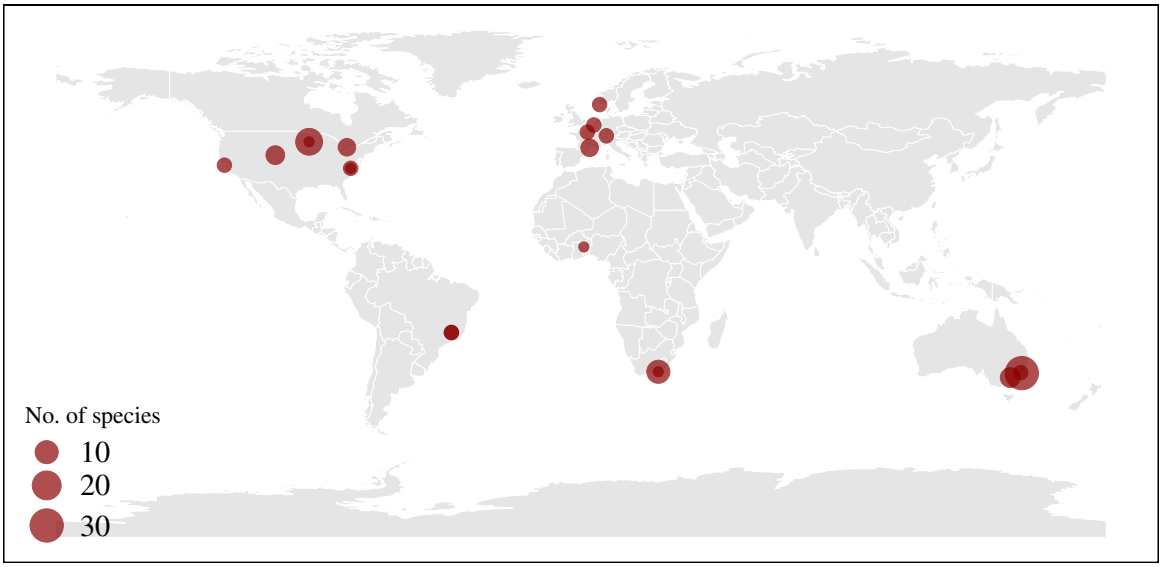


Fig. S1. Geographic distribution of studies included in the meta-analysis. Points indicate study locations, with symbol size scaled by the number of species assessed in each study. The dataset includes 19 studies spanning temperate, tropical, and Mediterranean regions across six continents. Coordinates and species richness were extracted from original publications or supplementary materials.

Table S1. Summary of studies used in the meta-analysis

Table S1.

Data source	Location	Experimental conditions	CO_2 treatment levels	Duration of experiment (days)	Species	Functional type
Bloor *et al.*, 2009[1]	Orsay, France	Glasshouse growth chambers (CO_2-enriched); experimentally sown, potted tree seedlings grown alone or with grass competitors	380, 645	105	*Dactylis glomerata*	C_3 Herbaceous
				75	*Fraxinus excelsior*	C_3 Woody
Collins *et al.*, 2018[2]	Sydney, Australia	Field (FACE); naturally assembled temperate eucalypt woodland with transplanted woody seedlings grown with or without herbaceous neighbours	400, 550	1825	*Eucalyptus tereticornis*	C_3 Woody
					Hakea sericea	C_3 Woody
Dijkstra *et al.*, 2010[3]	Central Plains Experimental Range, Colorado	Glasshouse (CO_2-enriched); experimentally sown, potted monocultures and five-species mixtures	400, 780	85	*Artemisia frigida*	C_3 Herbaceous
					Bouteloua gracilis	C_4 Herbaceous
					Hesperostipa comata	C_3 Herbaceous
					Linaria dalmatica	C_3 Herbaceous
					Pascopyrum smithii	C_3 Herbaceous

Hager *et al.*, 2020[4]	Guelph, Canada	Glasshouse CO_2-controlled chambers; experimentally sown, potted grass monocultures and native–invasive species mixtures	390, 700	98	*Andropogon gerardii*	C_4 Herbaceous
					Elymus virginicus	C_3 Herbaceous
					Koeleria macrantha	C_3 Herbaceous
					Panicum virgatum cv. Cave-in-Rock	C_4 Herbaceous
Goncalves de Oliviera et al. 2021[5]	Federal University of Viçosa, Campus Florestal, Brazil	Open-top chambers; experimentally sown; isolated or 2 species mixture	350, 100	270	*Melinis minutiflora*	C_4 Herbaceous
					Stylosanthes capitata	C_3 Herbaceous
Jongen & Jones, 1997[6]	Dublin, Ireland	Open-top chambers; experimentally sown, potted grass monocultures (density manipulation) and four-species mixtures	354, 700	80	*Cynosurus cristatus*	C_3 Herbaceous
					Holcus lanatus	C_3 Herbaceous
					Lolium perenne	C_3 Herbaceous
Lau *et al.*, 2010[7]	Cedar Creek, Minnesota, USA	Field (FACE); potted plants grown with experimentally imposed competition (none, intraspecific, C_3 or C_4 grass competitors)	368, 560	35	*Arabidopsis thaliana*	C_3 Herbaceous
Manea & Leishman, 2011[8]	Sydney, Australia	Glasshouse (CO_2-enriched); experimentally sown, potted native–invasive species pairs grown singly or with heterospecific neighbours. Additional data that is not in Manea and Leishman (2011) was provided by the authors on request.	380, 675	84	*Acacia implexa*	C_3 Woody
					Acacia parramattensis	C_3 Woody
					Acetosa sagittata	C_3 Herbaceous
					Araujia sericifera	C_3 Herbaceous
					Atriplex semibaccata	C_3 Herbaceous
					Bidens pilosa	C_3 Herbaceous
					Bothriochloa macra	C_4 Herbaceous
					Chloris gayana	C_4 Herbaceous
					Chloris truncata	C_4 Herbaceous
					Convolulus erubescens	C_3 Herbaceous
					Conyza bonariensis	C_3 Herbaceous
					Dichanthium sericeum	C_4 Herbaceous
					Digitaria sanguinalis	C_4 Herbaceous
					Einadia hastata	C_3 Herbaceous
					Eragostis brownii	C_4 Herbaceous
					Eragrostis curvula	C_4 Herbaceous
					Glycine microphylla	C_3 Herbaceous
					Ligustrum sinense	C_3 Woody
					Olea europaea subsp cuspidata	C_3 Woody
					Paspalum dilatatum	C_4 Herbaceous
					Phytolacca octandra	C_3 Herbaceous
					Plectranthus parviflorus	C_3 Herbaceous
					Sida rhombifolia	C_3 Herbaceous
					Sigesbeckia orientalis	C_3 Herbaceous
					Sorghum halepense	C_4 Herbaceous

					Sporobolus creber	C_4 Herbaceous
					Sporobolus indicus	C_4 Herbaceous
					Themeda australis	C_4 Herbaceous
Melo *et al.*, 2018[9]	Viçosa, Brazil	Field (open-top chambers); experimentally established tree seedlings grown in soil with density-manipulated herbaceous neighbours	380, 700	320	*Hymenaea stigonocarpa*	C_3 Woody
					Melinis minutiflora	C_4 Herbaceous
Miranda-Apodaca *et al.*, 2015[10]	Leioa, Spain	Growth chamber (CO_2-controlled); experimentally sown, potted monocultures and interspecific mixtures	370, 740	38	*Agrostis capillaris*	C_3 Herbaceous
					Festuca rubra	C_3 Herbaceous
					Trifolium pratense	C_3 Herbaceous
					Trifolium repens	C_3 Herbaceous
Moore & Field, 2006[11]	Stanford, California, USA	Field (open-top chambers); experimentally sown grassland microcosms grown as monocultures or two-species mixtures	400, 700	365	*Avena barbata*	C_3 Herbaceous
					Hemizonia congesta	C_3 Herbaceous
Raubenheimer & Ripley, 2022[12]	Grahamstown/Makhanda, South Africa	Field (open-top chambers); potted tree seedlings grown with density-manipulated grass competition	400, 800	180	*Vachellia karroo*	C_3 Woody
RUECF NERC Experiment (unpublished data)	Grahamstown/Makhanda, South Africa	Field (open-top chambers); potted tree seedlings grown with density-manipulated grass competition	400, 550	360	*Senegalia burkeii*	C_3 Woody
					Senegalia caffra	C_3 Woody
					Senegalia nigrescens	C_3 Woody
					Vachellia erioloba	C_3 Woody
					Vachellia exuvialis	C_3 Woody
					Vachellia gracilis	C_3 Woody
					Vachellia karroo	C_3 Woody
					Vachellia nilotica	C_3 Woody
					Vachellia robusta	C_3 Woody
					Vachellia sieberiana	C_3 Woody
					Vachellia swazica	C_3 Woody
					Vachellia tortilis	C_3 Woody
Reich et al., 2024[13]	Cedar Creek, Minnesota, USA	Field (FACE); plot-level experimentally sown monocultures and 16-species mixtures	415, 550	8395	*Achillea millefolium*	C_3 Herbaceous
					Agropyron repens	C_3 Herbaceous
					Amorpha canescens	C_3 Woody
					Andropogon gerardii	C_4 Herbaceous
					Anemone cylindrica	C_3 Herbaceous
					Asclepias tuberosa	C_3 Herbaceous
					Bouteloua gracilis	C_4 Herbaceous
					Bromus inermis	C_3 Herbaceous
					Koeleria cristata	C_3 Herbaceous
					Lespedeza capitata	C_3 Woody
					Lupinus perennis	C_3 Woody
					Petalostemum villosum	C_3 Woody
					Poa pratensis	C_3 Herbaceous
					Schizachyrium scoparium	C_4 Herbaceous
					Solidago rigida	C_3 Herbaceous

					Sorghastrum nutans	C_4 Herbaceous
Tom-Dery *et al.*, 2019[14]	Tolon, Ghana (experiment carried out in Germnay)	Glasshouse growth chambers (CO_2-controlled); potted tree seedlings grown alone or with grass competitors	400, 950	112	*Vitellaria paradoxa*	C_3 Woody
Van De Velde *et al.*, 2019[15]	Wilrijk, Belgium	CO_2- and climate-controlled chambers; experimentally sown, potted monocultures and interspecific mixtures	400, 620	90	*Lolium perenne*	C_3 Herbaceous
					Plantago lanceolata	C_3 Herbaceous
Van Kleunen *et al.*, 2006[16]	Basel, Switzerland	Field (FACE); experimentally assembled monocultures and two-species mixtures across planting-density gradients	400, 600	365	*Bromus erectus*	C_3 Herbaceous
					Carex flacca	C_3 Herbaceous
Wray & Strain, 1987[17]	Durham, North Carolina, USA	Glasshouse (CO_2-controlled); experimentally sown, potted monocultures and two-species replacement-series mixtures	350, 500	63	*Andropogon virginicus*	C_4 Herbaceous
					Aster pilosis	C_3 Herbaceous
Yu *et al.*, 2019[18]	Durham, North Carolina, USA	CO_2-controlled growth chambers; experimentally sown, potted monocultures and two-species mixtures	400, 800	120	*Bouteloua eriopoda*	C_4 Herbaceous

Table S2. Description of unpublished data used in the meta-analysis

Unpublished study	Description
RUECF NERC Experiment	The unpublished data are from the Rhodes University Elevated CO_2 Facility NERC (National Ecological Research Council.) experiment which is a collaboration between Rhodes University, South Africa, Sheffield and Edinburgh Universities, UK. This study was conducted at the Rhodes University Elevated CO_2 Facility in Open-Top Chambers (OTCs) as described by Raubenheimer and Ripley[12]. In this experiment[19], 12 C_3 woody species were grown either individually or in competition with the C_4 grass species *Themeda triandra* at two CO_2 treatment levels (400 or 550 ppm) for a total of 360 days in 37.L pots.

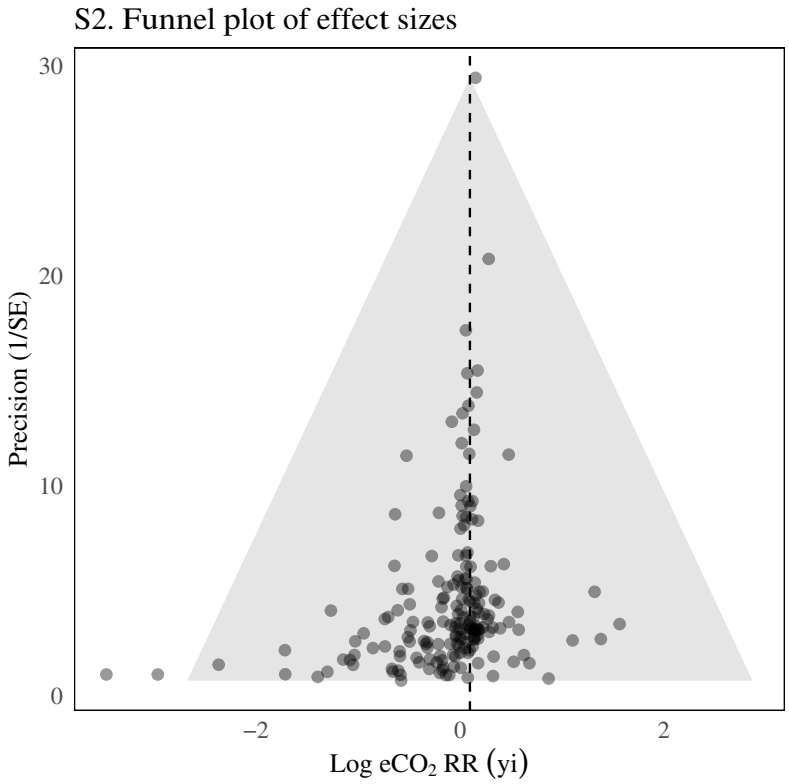


Figure S2. Funnel plot showing the distribution of log elevated CO_2 response ratios (yi) against study precision (1/SE) for all species-level estimates included in the meta-analysis. The dashed vertical line indicates the overall estimated effect size under ambient competition conditions, and the shaded triangle represents the expected 95% pseudo confidence region in the absence of publication bias. Asymmetry in the plot suggests the presence of small-study effects, motivating the sensitivity analysis presented in Table S2. n = 97.

Table S2. Comparison of meta-analysis results including all studies (Original Model) and excluding low-precision studies (Sensitivity Model; SE > 1). Estimates represent the log response ratio to elevated CO_2 across competition treatments. The similarity of estimates between models indicates that the main findings are robust to the influence of low-precision studies.

Table S2. Comparison of meta-analysis results with and without low-precision studies (SE > 1)

Term	Estimate	SE	95% CI	p-value	Estimate	SE	95% CI	p-value	Δ Estimate
intrcpt	0.10	0.05	[-0.004, 0.196]	0.059	0.10	0.05	[-0.001, 0.198]	0.051	0.003
Monoculture vs Isolated	-0.03	0.05	[-0.127, 0.067]	0.543	-0.03	0.05	[-0.130, 0.063]	0.494	-0.004
Mixture vs Isolated	-0.14	0.04	[-0.227, -0.057]	0.001	-0.14	0.04	[-0.225, -0.055]	0.001	0.002

S3. Influence of individual studies on eCO_2 RR estimate

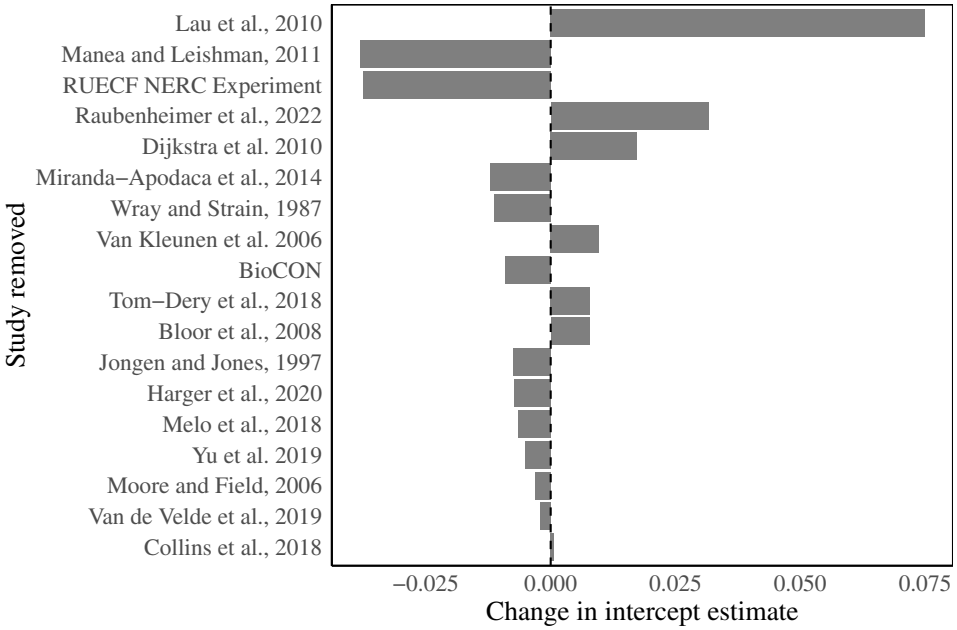


Figure S3. Influence diagnostics based on leave-one-out meta-analysis. Each bar represents the change in the overall intercept (CO_2 response estimate under isolated conditions) when a single study is removed from the model. The dashed line indicates the full-model estimate. While a few studies notably shift the intercept (e.g., Lau et al., 2010; Raubenheimer et al., 2022), the overall effect direction remains consistent, suggesting that findings are not driven by any single influential study.

Table S3. Results of leave-one-out influence analysis for the meta-analysis of plant biomass response to elevated CO_2 under isolated conditions. Each row shows the estimated intercept (CO_2 effect) when a single study is excluded from the model. The difference from the full-model estimate (Δ Intercept) and the absolute value of that difference (|Δ| Intercept) indicate the relative influence of each study. Larger values suggest greater influence on the overall result, though no single study qualitatively altered the direction or significance of the effect.

Table S3. Leave-one-out influence analysis: effect of excluding each study on the estimated CO_2 response under isolated competition.

Study (Paper)	Intercept (LOO)	Δ Intercept	|Δ| Intercept
Lau et al., 2010	0.171	0.075	0.075
Manea and Leishman, 2011	0.058	-0.038	0.038
RUECF NERC Experiment	0.059	-0.037	0.037
Raubenheimer et al., 2022	0.128	0.032	0.032
Dijkstra et al. 2010	0.113	0.017	0.017
Miranda-Apodaca et al., 2014	0.084	-0.012	0.012
Wray and Strain, 1987	0.085	-0.011	0.011
Van Kleunen et al. 2006	0.106	0.010	0.010
BioCON	0.087	-0.009	0.009
Tom-Dery et al., 2018	0.104	0.008	0.008
Bloor et al., 2008	0.104	0.008	0.008
Jongen and Jones, 1997	0.089	-0.007	0.007

Table S3. Leave-one-out influence analysis: effect of excluding each study on the estimated CO_2 response under isolated competition.

Study (Paper)	Intercept (LOO)	Δ Intercept	|Δ| Intercept
Harger et al., 2020	0.089	-0.007	0.007
Melo et al., 2018	0.089	-0.007	0.007
Yu et al. 2019	0.091	-0.005	0.005
Moore and Field, 2006	0.093	-0.003	0.003
Van de Velde et al., 2019	0.094	-0.002	0.002
Collins et al., 2018	0.097	0.001	0.001

Table S4. Comparison of meta-analysis results before and after excluding small-study outliers (trim-and-fill adjustment). Estimates represent the log response ratio to elevated CO_2 under different competition treatments. While the trimmed model yielded slightly smaller absolute effect sizes, the direction and significance of the mixture competition effect remained consistent, indicating that the main results are robust to the influence of outlier studies.

Table S4. Comparison of meta-analysis results before and after trim-and-fill adjustment

Term	Estimate (Orig)	SE (Orig)	95% CI (Orig)	p-value (Orig)	Estimate (Trimmed)	SE (Trimmed)	95% CI (Trimmed)	p-value (Trimmed)	Estimate Diff
Intercept	0.10	0.05	[-0.00, 0.20]	0.059	0.08	0.05	[-0.01, 0.18]	0.093	-0.01
Monoculture vs Isolated	-0.03	0.05	[-0.13, 0.07]	0.543	-0.02	0.05	[-0.12, 0.07]	0.624	0.01
Mixture vs Isolated	-0.14	0.04	[-0.23, -0.06]	0.001	-0.13	0.04	[-0.21, -0.04]	0.003	0.01

S4. Funnel plot of RCV effect sizes

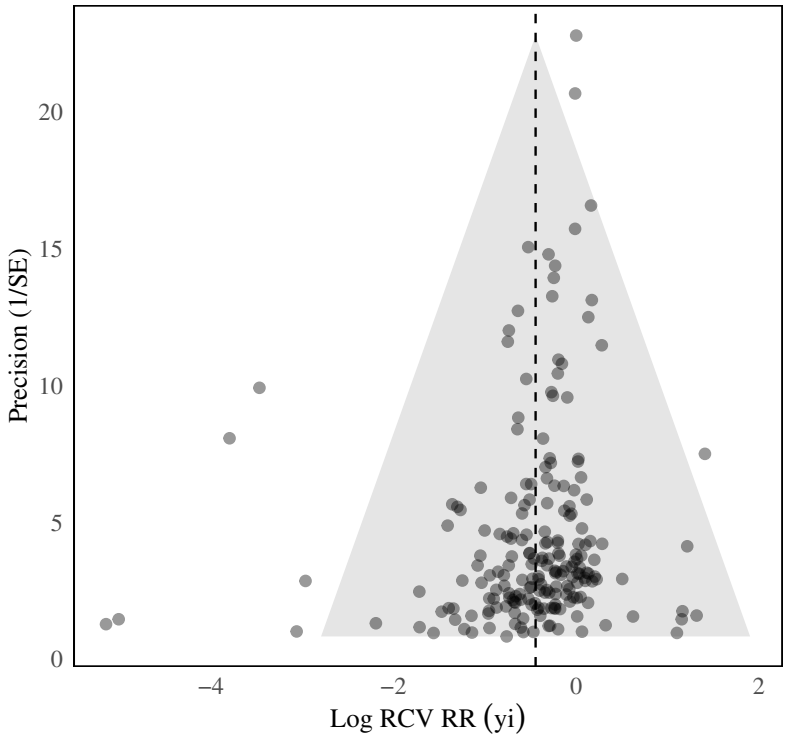


Figure S4. Funnel plot showing log response ratios of relative competitive vulnerability (RCV RR; *yi*) plotted against study precision (1/SE). The shaded triangle represents pseudo 95% confidence limits centered on the model intercept (dashed line). Points represent individual effect sizes; their vertical spread reflects variation in study precision. The symmetrical shape suggests limited evidence for publication bias in the RCV data. n = 97.

Table S5. Comparison of meta-analysis estimates for relative competitive vulnerability (RCV) with and without low-precision studies (SE > 1). Values represent model estimates, standard errors, 95% confidence intervals, and p-values for each fixed effect term. The final column shows the difference in estimates between the original and sensitivity analyses. Minimal changes suggest robust results.

Table S5. Comparison of RCV meta-analysis with and without low-precision studies (SE > 1)

Term	Estimate	SE	95% CI	p-value	Estimate	SE	95% CI	p-value	Δ Estimate
intrcpt	-0.44	0.21	[-0.860, -0.030]	0.036	-0.45	0.21	[-0.864, -0.026]	0.037	-0.01
Low CO_2 vs High CO_2	0.03	0.06	[-0.093, 0.160]	0.602	0.03	0.06	[-0.093, 0.161]	0.601	0.00
Diversity vs Competition	-0.01	0.26	[-0.510, 0.492]	0.972	-0.01	0.26	[-0.515, 0.497]	0.971	0.00
Interaction: Low CO_2 × Diversity	0.03	0.07	[-0.107, 0.169]	0.657	0.03	0.07	[-0.109, 0.168]	0.676	0.00

S6. Influence of individual studies on RCV estimate

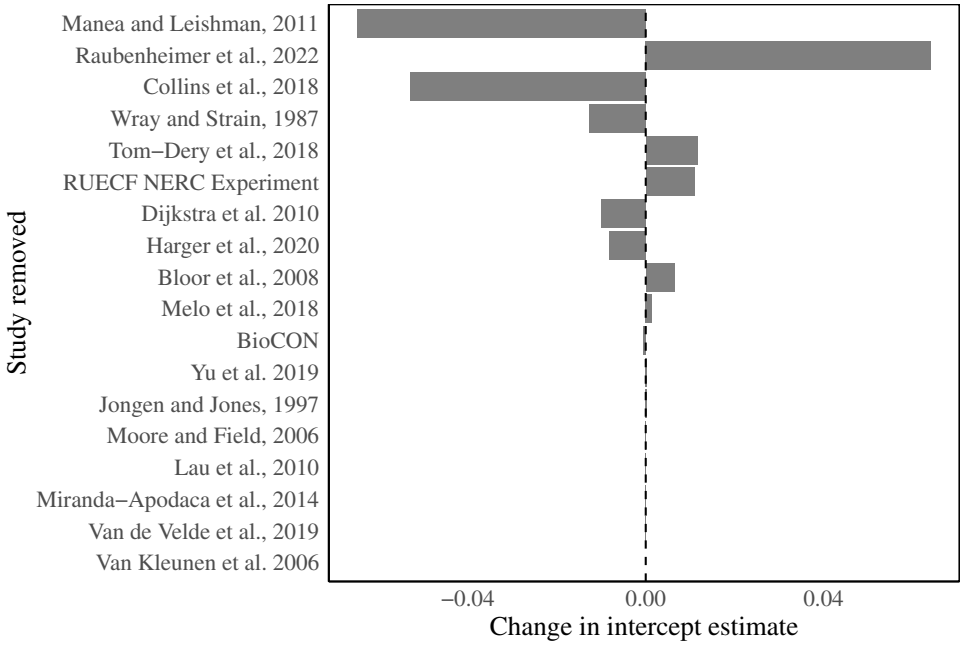


Figure S6. Leave-one-out influence analysis of individual studies on the RCV meta-analysis intercept estimate. Each bar shows the change in the estimated intercept when the corresponding study is removed from the model. The dashed line represents the full-model intercept. The modest magnitude of all changes ($|\Delta| < 0.05$) indicates that no single study unduly influenced the overall estimate of relative competitive vulnerability.

Table S6. Leave-one-out influence analysis for RCV meta-analysis: effect of excluding each study on the estimated log response ratio under high CO_2 and competitive conditions. The table shows the model intercept when each study is excluded (Intercept (LOO)), the change from the full model estimate (Δ Intercept), and the absolute magnitude of this change (|Δ| Intercept).

Table S6. Leave-one-out influence analysis: effect of excluding each study on the estimated RCV under high CO_2 × competition.

Study (Paper)	Intercept (LOO)	Δ Intercept	|Δ| Intercept
Manea and Leishman, 2011	-0.51	-0.06	0.06
Raubenheimer et al., 2022	-0.38	0.06	0.06
Collins et al., 2018	-0.50	-0.05	0.05
Wray and Strain, 1987	-0.46	-0.01	0.01
Tom-Dery et al., 2018	-0.43	0.01	0.01
RUECF NERC Experiment	-0.43	0.01	0.01
Dijkstra et al. 2010	-0.45	-0.01	0.01
Harger et al., 2020	-0.45	-0.01	0.01
Bloor et al., 2008	-0.44	0.01	0.01
Melo et al., 2018	-0.44	0.00	0.00
BioCON	-0.45	0.00	0.00
Yu et al. 2019	-0.44	0.00	0.00
Jongen and Jones, 1997	-0.44	0.00	0.00
Moore and Field, 2006	-0.44	0.00	0.00

Table S6. Leave-one-out influence analysis: effect of excluding each study on the estimated RCV under high CO_2 × competition.

Study (Paper)	Intercept (LOO)	Δ Intercept	|Δ| Intercept
Lau et al., 2010	-0.44	0.00	0.00
Miranda-Apodaca et al., 2014	-0.44	0.00	0.00
Van de Velde et al., 2019	-0.44	0.00	0.00
Van Kleunen et al. 2006	-0.44	0.00	0.00

Table S7. Comparison of RCV meta-analysis results before and after outlier trimming. Meta-analysis fixed effects estimates for log(RCV) vulnerability ratios under high CO_2 × competition conditions, comparing the original model (all studies) to a trimmed model excluding extreme outliers (yi values beyond ±2.5 SD from the mean). Estimates, standard errors (SE), confidence intervals (95% CI), and p-values are reported for each model, along with the difference in effect estimates (Δ Estimate). Trimming had minimal influence on effect estimates, indicating model robustness.

Table S7. Comparison of RCV meta-analysis results before and after outlier trimming (±2.5 SD)

Term	Estimate (Orig)	SE (Orig)	95% CI (Orig)	p-value (Orig)	Estimate (Trimmed)	SE (Trimmed)	95% CI (Trimmed)	p-value (Trimmed)	Estimate Diff
intrcpt	-0.44	0.21	[-0.86, -0.03]	0.036	-0.45	0.19	[-0.81, -0.08]	0.017	-0.00
Low CO_2 vs High CO_2	0.03	0.06	[-0.09, 0.16]	0.602	0.03	0.06	[-0.10, 0.16]	0.636	-0.00
Diversity vs Competition	-0.01	0.26	[-0.51, 0.49]	0.972	0.23	0.22	[-0.21, 0.67]	0.298	0.24
Interaction: Low CO_2 × Diversity	0.03	0.07	[-0.11, 0.17]	0.657	-0.05	0.07	[-0.19, 0.09]	0.501	-0.08

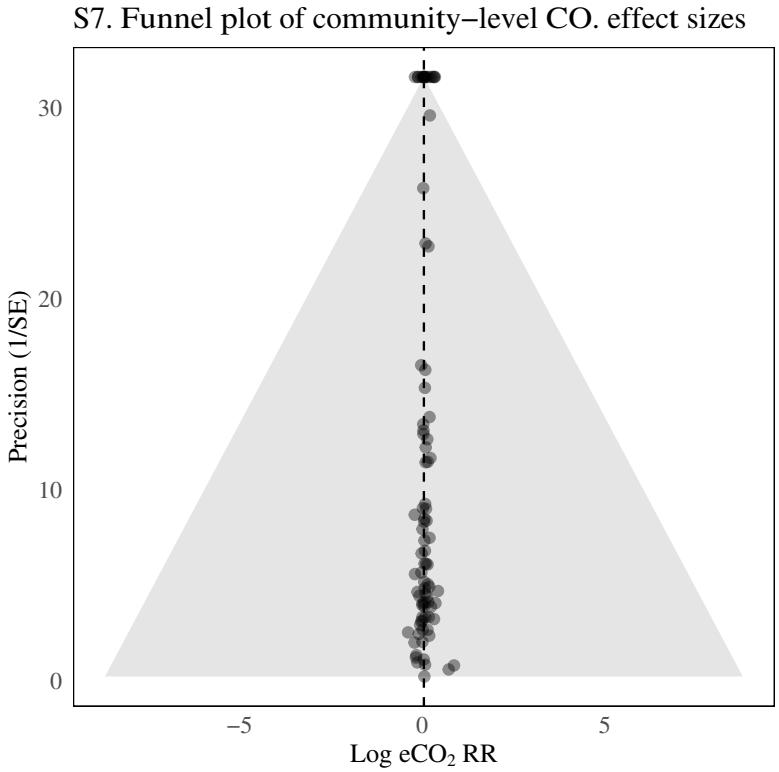


Figure S7. Funnel plot of mixture-level CO_2 effect sizes (log response ratios, *yi*) plotted against study precision (1/SE). The shaded triangle represents pseudo 95% confidence limits centered on the model intercept (dashed line). Each point corresponds to an individual site-level estimate. The overall symmetry of the plot and lack of extreme outliers suggest minimal evidence of small-study effects or publication bias in the mixture-level dataset.

Table S8a. Meta-analysis results for species-level log-transformed biomass response ratios to elevated CO_2 across competition treatments (log eCO_2 RR). Fixed effects represent estimated differences in eCO_2 response between monoculture or mixture treatments relative to isolated plants. The model was fit using a multivariate random-effects meta-analysis (`rma.mv`) with restricted maximum likelihood (REML), including random intercepts for study (`Study`) and functional type (`FT`). Variance components, model fit metrics (AIC and log-likelihood), and intra-class correlation coefficients (ICC) are reported to quantify between-study and between-functional-type heterogeneity.

Table S8a: Species-level meta-analysis results – log(eCO_2 response ratio)

	Term	Estimate	SE	X95..CI	p.value
Fixed Effects	intrcpt	0.096	0.051	[-0.004, 0.196]	0.059
Fixed Effects	Monoculture vs Isolated	-0.030	0.049	[-0.127, 0.067]	0.543
Fixed Effects	Mixture vs Isolated	-0.142	0.043	[-0.227, -0.057]	0.001
Model Fit	AIC	321.52			
Model Fit	Log Likelihood	-155.76			
Random Effects	Study	0.015622	0.124987		
Random Effects	Functional type	0.000000	0.000005		
Variance Partitioning (ICC)	Study	1.000			
Variance Partitioning (ICC)	Functional type	0.000			

Table S8b. Meta-analysis results for species-level log-transformed relative competitive vulnerability ratios (RCV RR) across CO_2 treatments and competition contexts. Fixed effects represent differences in RCV RR between ambient and elevated CO_2 conditions (Low CO_2 vs High CO_2), between diversity-based and competition-based contrasts (Diversity vs Competition), and their interaction. The model was fit using a multivariate random-effects meta-analysis (`rma.mv`) with restricted maximum likelihood (REML), including random intercepts for study (`Study`) and functional type (`FT`). Variance components, model fit metrics (AIC and log-likelihood), and intra-class correlation coefficients (ICC) are reported to quantify between-study and methodological heterogeneity.

Table S8b: Meta-analysis Results – log(RCV vulnerability ratio)

	Term	Estimate	SE	X95..CI	p.value
Fixed Effects	intrcpt	-0.445	0.212	[-0.860, -0.030]	0.036
Fixed Effects	Low CO_2 vs High CO_2	0.034	0.065	[-0.093, 0.160]	0.602
Fixed Effects	Diversity vs Competition	-0.009	0.256	[-0.510, 0.492]	0.972
Fixed Effects	Interaction: Low CO_2 × Diversity	0.031	0.070	[-0.107, 0.169]	0.657
Model Fit	AIC	1704.42			
Model Fit	Log Likelihood	-846.21			
Random Effects	Paper	0.015622	0.124987		
Random Effects	Functional type	0.000000	0.000005		
Variance Partitioning (ICC)	Paper	1.000			
Variance Partitioning (ICC)	Functional type	0.000			

Table S8c. Linear model results testing the correlation between species' log-transformed biomass response ratios to elevated CO_2 (eCO_2 RR) and their relative competitive vulnerability (RCV RR). Separate models are presented for diversity-based (isolated vs. mixture) and competition-based (monoculture vs. mixture) contrasts. Each model includes an intercept and slope for RCV RR, along with associated standard errors, 95% confidence intervals, and p-values. Model fit is summarized using R-squared (R^2) for each contrast.

Table S8c: Correlation between eCO_2 response and competitive vulnerability

	Term	Estimate	SE	X95..CI	p.value
Isolated vs. mixture	(Intercept)	0.083	0.056	[-0.030, 0.196]	0.147
	yi_RCV	1.077	0.098	[0.880, 1.274]	< 0.001
Monoculuture vs. mixture	(Intercept)	0.138	0.065	[0.007, 0.269]	0.039
	yi_RCV	0.812	0.063	[0.685, 0.939]	< 0.001
Model Fit	R-squared (Mono v. mix)	0.757			
Model Fit	R-squared (Iso v. mix)	0.748			

Table S9a. Meta-analysis results for mixture-level log-transformed biomass response ratios to elevated CO_2 (log eCO_2 RR). Fixed effects represent differences in eCO_2 response between monoculture and mixture treatments, with the intercept corresponding to mixed-species communities. The model was fit using a multivariate random-effects meta-analysis (`rma.mv`) with restricted maximum likelihood (REML), including a random intercept for study (`Study`). Variance components, model fit metrics (AIC and log-likelihood), and intra-class correlation coefficients (ICC) are reported to quantify between-study heterogeneity.

Table S9a: Meta-analysis Results - mixture log(eCO_2 response ratio)					
	Term	**Estimate**	**SE**	**X95..CI**	**p.value**
Fixed Effects	Intercept (Mixture)	0.043	0.028	[-0.013, 0.099]	0.131
Fixed Effects	Monoculture vs Mixture	0.058	0.021	[0.018, 0.099]	0.005
Model Fit	AIC	165.30			
Model Fit	Log Likelihood	-79.65			
Random Effects	Study	0.007284	0.085346		
Variance Partitioning (ICC)	Study	1.000			

Table S9b. Mixed-effects model summary of species-level biomass responses to elevated CO_2 (eCO_2 RR) as a function of relative dominance within communities. Fixed effects represent differences in eCO_2 response across dominance categories, with the intercept corresponding to the "Rare" group. The model was fit using a linear mixed-effects model (`lmer`) with random intercepts for study (`Study`) and functional type (`FT`). The table reports fixed effects, random standard deviations, model metrics (R^2, AIC, sample sizes), and pairwise comparisons between dominance categories based on estimated marginal means.

Table S9b: Mixed-effects model summary: fixed effects, random SDs, model metrics, and pairwise comparisons.					
Term	Estimate	Std. Error	df	t value	Pr(>|t|)
(Intercept)	-0.79	0.19	32.00	-4.26	0.000
Dominance: Subordinate	0.54	0.23	87.36	2.39	0.019
Dominance: Dominant	0.82	0.23	80.91	3.53	0.001
Random SD: Study	0.28				
Random SD: FT	0.00				
Random SD: Residual	0.81				
Marginal R^2	0.15				
Conditional R^2					
AIC	242.90				
n (total obs)	92.00				
n (Study groups)	16.00				
n (FT groups)	3.00				
Contrast: Rare vs. Subordinate	-0.54	0.24		-2.24	0.070
Contrast: Rare vs. Dominant	-0.82	0.25		-3.32	0.004
Contrast: Subordinate vs. Dominant	-0.28	0.22		-1.25	0.429

Table S10a.1. MANOVA results testing for trait space separation across species success groups using four multivariate test statistics (Pillai's Trace, Wilks' Lambda, Hotelling–Lawley Trace, and Roy's Largest Root). The analysis was performed on the first two discriminant axes from a discriminant analysis of principal components (DAPC). Residual sums of squares (SS), residual degrees of freedom, and standard errors (SE) are reported for LD1 and LD2.

Table S10a.2. Pairwise comparisons among species success groups along the first two DAPC axes (LD1 and LD2). P-values are reported both as raw values and after Benjamini–Hochberg (BH) correction for multiple testing. Comparisons were conducted using Tukey's HSD test following ANOVA on each discriminant axis.

Table S10a.1: MANOVA results for trait space separation across success groups				
Test	F	Num.df	Den.df	p-value
Pillai	5.63	6	190	0.0000

Table S10a.1: MANOVA results for trait space separation across success groups

Test	F	Num.df	Den.df	p-value
Wilks	5.63	6	188	0.0000
Hotelling-Lawley	5.62	6	186	0.0000
Roy	7.77	3	95	0.0001
Residual SS (LD1)	95.00			
Residual SS (LD2)	95.00			
Residual df	95.00			
Residual SE (LD1)	1.00			
Residual SE (LD2)	1.00			

Table S10a.2: Pairwise comparisons of success groups across DAPC axes (BH-adjusted)

Comparison	Raw.p	Adj..p..BH.	Axis
Highly Successful-CO_2 Responsive but Vulnerable	0.0143665582	0.034933689	LD1
Stable but Unresponsive-CO_2 Responsive but Vulnerable	0.9943892211	0.999941837	LD1
Less Successful-CO_2 Responsive but Vulnerable	0.9999418373	0.999941837	LD1
Stable but Unresponsive-Highly Successful	0.0003122387	0.001873432	LD1
Less Successful-Highly Successful	0.0174668445	0.034933689	LD1
Less Successful-Stable but Unresponsive	0.9977874607	0.999941837	LD1
Highly Successful-CO_2 Responsive but Vulnerable	0.0661265945	0.132253189	LD2
Stable but Unresponsive-CO_2 Responsive but Vulnerable	0.0058786531	0.019811111	LD2
Less Successful-CO_2 Responsive but Vulnerable	0.0145175015	0.064185091	LD2
Stable but Unresponsive-Highly Successful	0.9108633281	0.910863328	LD2
Less Successful-Highly Successful	0.5431766976	0.814765046	LD2
Less Successful-Stable but Unresponsive	0.8100422308	0.910863328	LD2

Table S10b. Standardized coefficients from linear mixed-effects models (`lmer`) predicting log-transformed species responses to elevated CO_2 (eCO_2 RR) and competitive vulnerability (RCV RR) from plant functional traits. Separate models were fit for each response: eCO_2 RR, RCV RR (isolated vs. mixture), and RCV RR (monoculture vs. mixture). Models included random intercepts for study (`Study`) and functional type (`FT`). Coefficients, standard errors (SE), 95% confidence intervals (CI), and p-values are reported for each trait predictor. Traits were log-transformed prior to analysis using safe offsets, and model parameters were standardized by refitting with scaled predictors.

Table S10b: Standardized coefficients (LMM) predicting CO_2 and competition responses from plant traits. Raw p-values and Benjamini–Hochberg FDR-adjusted p-values are shown; adjustment applied within biologically defined trait groups.

Response	Trait	Coefficient	SE	CI low	CI high	p	p adj
RCV RR (iso vs. mix)	Growth rate	0.20	0.09	0.03	0.36	0.02	0.10
	Drought tol.	-0.20	0.09	-0.38	-0.03	0.03	0.10
	LDMC	-0.16	0.10	-0.36	0.04	0.12	0.72
	Invasive	0.13	0.08	-0.04	0.30	0.13	0.13
	Fire tol.	0.13	0.09	-0.05	0.30	0.15	0.31
	Shade tol.	0.09	0.09	-0.08	0.26	0.31	0.41
	Leaf area	-0.07	0.09	-0.25	0.11	0.42	0.83
	SLA	-0.07	0.10	-0.27	0.12	0.45	0.83
	Leaf N	-0.06	0.11	-0.27	0.16	0.62	0.83
	Max height	0.05	0.10	-0.15	0.25	0.64	0.66

Table S10b: Standardized coefficients (LMM) predicting CO_2 and competition responses from plant traits. Raw p-values and Benjamini–Hochberg FDR-adjusted p-values are shown; adjustment applied within biologically defined trait groups.

Response	Trait	Coefficient	SE	CI_low	CI_high	p	p_adj
	Lifespan	0.05	0.10	-0.15	0.25	0.64	0.98
	SSD	-0.05	0.11	-0.26	0.16	0.66	0.66
	Leaf C:N	-0.04	0.11	-0.25	0.17	0.69	0.83
	Root:Shoot	-0.02	0.08	-0.19	0.15	0.82	0.82
	Cold tol.	0.02	0.09	-0.17	0.20	0.87	0.87
	Leaf C	0.01	0.08	-0.16	0.17	0.95	0.95
	Growth form	0.00	0.09	-0.17	0.18	0.97	0.98
	Grime strat.	0.00	0.08	-0.16	0.16	0.98	0.98
RCV RR (mono vs. mix)	SSD	-0.52	0.18	-0.88	-0.15	0.01	0.01
	Max height	0.48	0.23	0.03	0.94	0.04	0.04
	Invasive	0.28	0.13	0.02	0.55	0.04	0.04
	Leaf area	0.28	0.15	-0.02	0.58	0.07	0.29
	Leaf C	0.28	0.16	-0.05	0.60	0.10	0.29
	Shade tol.	0.21	0.14	-0.06	0.48	0.13	0.52
	LDMC	0.18	0.15	-0.12	0.49	0.23	0.43
	Leaf C:N	-0.17	0.16	-0.50	0.15	0.28	0.43
	Fire tol.	-0.14	0.12	-0.39	0.11	0.28	0.54
	Root:Shoot	-0.14	0.13	-0.40	0.12	0.29	0.29
	Cold tol.	-0.16	0.19	-0.54	0.22	0.41	0.54
	Lifespan	0.13	0.16	-0.20	0.45	0.44	0.81
	Grime strat.	0.10	0.14	-0.18	0.38	0.46	0.81
	Drought tol.	0.10	0.16	-0.21	0.41	0.54	0.54
	Leaf N	0.09	0.15	-0.21	0.39	0.56	0.60
	SLA	-0.10	0.20	-0.50	0.29	0.60	0.60
	Growth rate	0.04	0.14	-0.24	0.33	0.77	0.81
	Growth form	0.03	0.14	-0.24	0.31	0.81	0.81
eCO_2 RR	Drought tol.	-0.22	0.13	-0.47	0.03	0.09	0.35
	LDMC	-0.24	0.14	-0.52	0.05	0.10	0.60
	Growth rate	0.12	0.12	-0.12	0.36	0.31	0.75
	Fire tol.	0.10	0.12	-0.14	0.35	0.40	0.69
	Invasive	0.10	0.12	-0.14	0.33	0.42	0.42
	Lifespan	0.09	0.14	-0.19	0.36	0.52	0.75
	SLA	-0.09	0.14	-0.37	0.19	0.53	0.85
	Leaf N	-0.09	0.15	-0.38	0.21	0.55	0.85
	Leaf area	-0.07	0.13	-0.33	0.18	0.57	0.85
	Shade tol.	-0.05	0.12	-0.29	0.19	0.65	0.69
	Max height	0.06	0.14	-0.22	0.35	0.66	0.75
	Root:Shoot	-0.05	0.12	-0.28	0.18	0.67	0.67
	Cold tol.	-0.05	0.13	-0.32	0.21	0.69	0.69
	Grime strat.	-0.04	0.11	-0.26	0.19	0.74	0.75
	SSD	-0.05	0.15	-0.34	0.24	0.75	0.75
	Growth form	0.04	0.13	-0.21	0.29	0.75	0.75
	Leaf C	0.00	0.12	-0.23	0.23	0.98	0.98
	Leaf C:N	0.00	0.15	-0.29	0.30	0.98	0.98

Table S11. Summary of field experiments exposing intact, multi-species plant communities to elevated CO_2 (eCO_2), showing ecosystem type, experimental approach, and whether eCO_2 was associated with changes in total community biomass and/or relative species abundance. This table is included to support the idea that community-level responses to eCO_2 rarely reflect uniform stimulation across all species; instead, increases in community biomass, where observed, typically

arise from heterogeneous species responses in which some taxa respond positively while others show weak, neutral, or negative responses. By documenting whether relative abundance or dominance shifts were reported across systems, the table provides qualitative evidence that competitive interactions under eCO_2 can structure community outcomes.

Study (site)	**Ecosystem / vegetation type**	**Experimental design (FACE / OTC / in situ)**	**Reported change in total community biomass under eCO_2**	**Change in relative species abundance under eCO_2?**
Morgan et al. 2011[20] (CPER, CO, USA)	Semi-arid shortgrass steppe grassland	OTC	Variable; precipitation-dependent	Yes — C_3 grasses favoured under eCO_2; warming favoured C_4 grasses
Nowak et al. 2004[21] (multiple sites)	Forests, grasslands, deserts	FACE (review of multiple experiments)	Generally positive but variable across systems	Indirect — review synthesizes species-specific and dominance-driven responses in intact communities but does not quantify abundance shifts
Seiler et al. 2009[22] (Merritt Island, FL, USA)	Fire-regenerated scrub-oak ecosystem	OTC	Increase	Yes — community-level response driven primarily by dominant species
Hovenden et al. 2006[23] (TasFACE, Tasmania, Australia)	Mixed native grassland (C_3/C_4)	FACE	Increase	No — productivity increased under eCO_2 without sustained changes in community composition
Owensby et al. 1999[24] (Konza Prairie, KS, USA)	Tallgrass prairie (C_4-dominated)	OTC	Increase in dry years; little effect in wet years	Yes — functional group shifts (decline of C_3 grasses; increase of C_3 forbs and sedges)
Niklaus & Körner 2004[25] (Nenzlingen, Switzerland)	Temperate calcareous grassland	In situ CO_2 enrichment	Increase	Yes (subtle) — increased evenness via positive responses of subdominant sedges and bryophytes
Mueller et al. 2016[26] (PHACE, WY, USA)	Semi-arid northern mixed-grass prairie	FACE	eCO_2 alone: variable; eCO_2 + warming: consistent increase	Yes (strong) — long-term reversal of dominance from C_4 grasses to C_3 graminoids

Dijkstra et al., 2002[27] (Merritt Island, FL, USA)	Fire-regenerated scrub-oak ecosystem	OTC	Increase	Yes — biomass gains were species-specific and dominated by Quercus myrtifolia; subdominant species showed weak or no response

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