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Trophic regulation constrains ecosystem carbon accumulation under global change

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Global change is rapidly reshaping the ecosystem carbon cycle, yet how trophic regulation—a fundamental driver of ecosystem biogeochemical cycling—mediates these responses remains poorly understood. Here we present a global synthesis of interactions between trophic regulation and major global change factors (GCFs: fertilization, warming, fire, increased precipitation, drought, and multiple GCFs), integrating 708 paired full-factorial experimental tests across 132 studies worldwide. We show that while GCFs alone increase ecosystem carbon stocks by 27% on average, their interactions with herbivores drive carbon losses of 23%, reversing the potential gains from individual GCF effects. Carbon losses are functionally localized in aboveground plant, litter, and microbial biomass carbon, with the most pronounced depletion occurring in the tropics, drylands, aquatic systems, and restoring ecosystems. Herbivore body size emerged as a directional trait shaping these outcomes, with small-bodied herbivores exerting disproportionately negative effects. Importantly, while excluding herbivores enhances carbon accumulation under global change, this sequestration benefit comes at the cost of reduced plant diversity, revealing an inherent trade-off between carbon-centric objectives and ecosystem integrity. Together, our findings demonstrate that carbon sequestration potential under global change cannot be evaluated independently of trophic regulation. Accounting for animal-mediated feedback is therefore essential for realistic Earth system model projections and for developing nature-based solutions that align climate mitigation with biodiversity conservation.

trophic interaction | global change | carbon cycling

Significance

Understanding how global change will affect ecosystem carbon storage is central to climate mitigation, yet most projections focus on climate and vegetation while largely underrepresenting trophic regulation. By synthesizing 708 full-factorial experiments worldwide, we show that herbivores can reverse the carbon gains otherwise expected from global change factors, reducing ecosystem carbon stocks by 23% on average. Crucially, while excluding herbivores enhances carbon storage under global change, this accumulation comes at the direct cost of reduced plant diversity. This fundamental tension between carbon-centric mitigation and ecosystem integrity demonstrates that realistic Earth system projections and nature-based solutions cannot manage carbon in isolation, but must explicitly account for animal-mediated trophic regulation.

Global change is reshaping ecosystem carbon dynamics (1, 2). While climate drivers explain much of the variability in carbon sequestration (3), a substantial proportion of sink dynamics remain unaccounted for within conventional abiotic frameworks. Animal consumers, as powerful biotic regulators, often coincide geographically with the unexplained gaps (4), yet their role in shaping carbon stocks under global change remains poorly quantified.

Evidence from case studies demonstrates the potency of these interactions. Bark beetle outbreaks intensify drought-driven tree mortality, accelerating forest carbon losses (5). Arctic reindeer grazing interacts with warming to reduce carbon storage beyond additive expectations (6, 7). Temperate grassland grazing frequently overrides climate effects on carbon storage and release (8). These examples highlight herbivores as regulators of ecosystem carbon balance, yet their impacts remain poorly represented in Earth system models, which conceptualize carbon dynamics largely as the product of abiotic drivers acting on vegetation (9). This disciplinary blind spot has been described as the "dark matter" of the carbon cycle.

Herbivores exert dual, context-dependent influences: they can amplify climate feedbacks by suppressing vegetation recovery (10, 11), or promote long-term carbon accumulation by facilitating recruitment of large, dense trees (12). Outcomes can vary with latitude: California forests show amplified carbon losses under drought–insect outbreaks (13), while Arctic herbivores may stabilize carbon by reshaping tundra vegetation structure (14, 15). These impacts not only directly affect carbon pools but can also indirectly influence ecosystem functions by altering plant community composition and diversity. Despite this evidence, no global quantitative synthesis has resolved how herbivores and global change factors (GCFs) interact to regulate carbon pools. In the literature to date, the effects of consumers on carbon stocks appear to be highly variable and context-dependent (7, 16, 17), making it hard to draw generalizations and to identify reliably where such interactions (e.g. through trophic rewilding) can reliably provide carbon sequestration or storage benefits.

Here we address this gap by compiling a global dataset of 708 full-factorial paired experimental tests from 132 studies worldwide (Fig. 1*A* and *SI Appendix*, Figs. S1 and S2), comprising 544 carbon-related effect sizes (525 involving herbivores and 19 involving predators) and 164 plant

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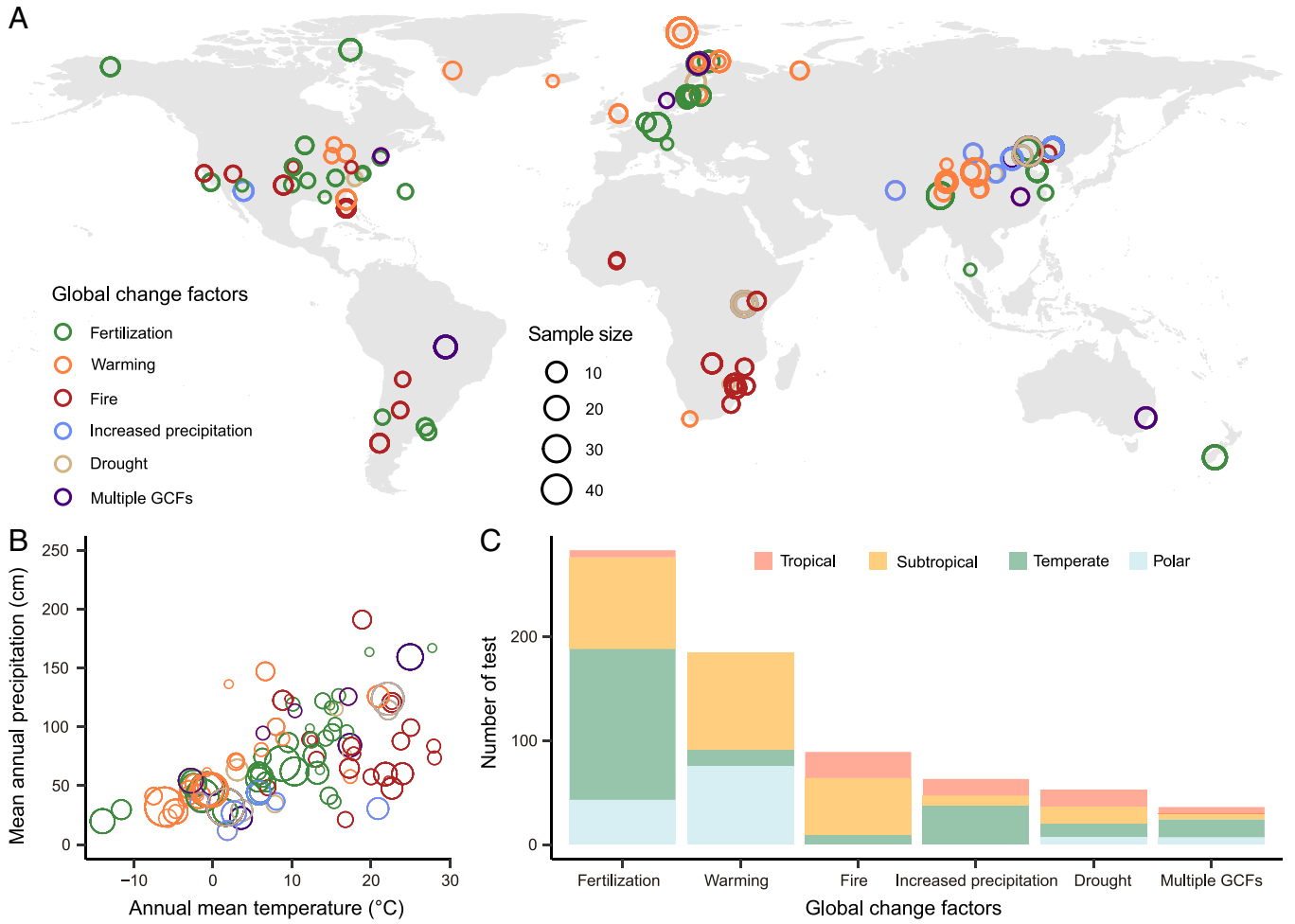


Fig. 1. Spatial and bioclimatic distribution of in situ experimental studies on the interactions between GCFs and consumers. (*A*) Geographic distribution of study locations included in this synthesis, representing experimental studies investigating GCFs–consumer interactions, with circle color indicating distinct GCF types and size proportional to number of tests. (*B*) Spatial projection of study sites onto bioclimatic gradients represented by mean annual temperature (MAT) and mean annual precipitation (MAP). (*C*) Distribution of experimental tests across different climatic zones, stratified by distinct types of GCFs.

diversity-related effect sizes. These tests integrate six major GCFs (fertilization, warming, fire, drought, increased precipitation, multiple GCFs) with consumer manipulations across broad temperature and precipitation gradients (Fig. 1 *B* and *C*). We assessed impacts on five carbon pools (aboveground biomass, belowground biomass, litter biomass, microbial biomass carbon, and soil organic carbon), as well as plant diversity (*SI Appendix*, Fig. S2), and asked: 1) what is the magnitude of carbon stock change driven by GCFs–herbivore interactions? 2) which pools are most vulnerable? and 3) under which environmental and biogeographic conditions are the strongest losses observed, and to what extent could these losses be mitigated through herbivore governance? By integrating GCFs and herbivore pressure into the analysis of ecosystem carbon cycling, our study highlights the pivotal role of herbivores as a key biotic interaction in shaping ecosystem carbon responses. These insights provide an essential foundation for improving predictions of biosphere-climate feedback and identifying ecological pathways to enhance natural climate solutions.

Amplified GCF–Herbivore Synergistic Effects On Carbon Stock Loss

Our results revealed that GCFs and herbivores drive divergent responses in ecosystem carbon dynamics. Although having heterogeneous impacts, GCFs caused a 27% (95% CI: 18 to 37%) increase in ecosystem carbon stocks (Fig. 2*A*), signaling a vast sequestration potential fueled by robust aboveground (+31%) and belowground (+19%) biomass accretion (Fig. 2 *B* and *C*) (18, 19). However, this vegetation-driven accumulation was counteracted by an average 9% loss in soil organic carbon (Fig. 2 *D*–*F*). Given that soil carbon stocks far exceed those in vegetation, this asynchronous coupling suggests that GCF-induced greening may mask a widespread but temporally uncertain depletion of soil carbon storage, given the short duration of most experiments (20, 21). In stark contrast, herbivores exerted potent top–down control, depleting vegetation stocks (e.g., −23% aboveground, −21% belowground biomass, and −38% litter biomass; Fig. 2 *B*–*D*) while producing only a minor increase in soil organic carbon stock (+2%), likely associated with herbivore-induced increases in soil bulk density (22).

Intriguingly, the combined effects of GCFs and herbivores (i.e., their overall impact when both factors concurrently influence ecosystem carbon) amplified carbon losses by an average of 23% (95% CI: −29 to −18%), a synergistic depletion that far exceeds the predicted additive sum of their individual impacts ($P < 0.0001$; Fig. 2*A*). This amplification was driven by declines across vegetation and microbial pools (Fig. 2 *B*–*E*), whereas soil organic carbon remained stable (+0.4%, Fig. 2*F*), potentially buffered by microbial necromass accumulation or delayed mineralization of mineral-associated organic matter (23). These divergent responses across specific carbon pools highlight the pressing need for future research to transition

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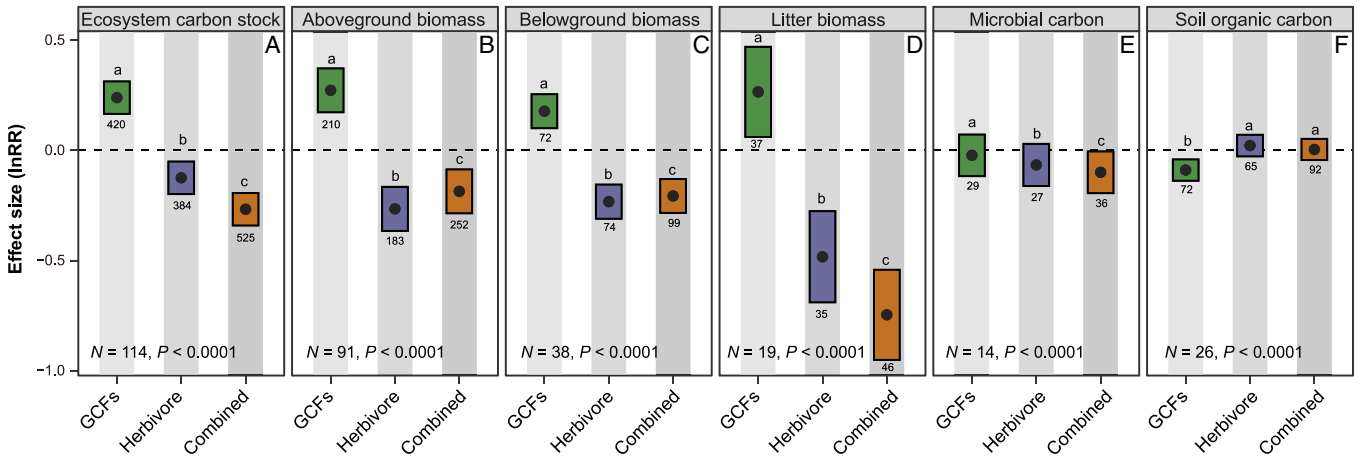


Fig. 2. Individual and combined effects of GCFs and herbivores on (*A*) ecosystem carbon stocks and (*B*–*F*) constituent pools. Mean effect sizes (represented by black circular points) and 95% CIs (depicted by the colored boxes) were estimated for (*A*) ecosystem carbon stock, (*B*) aboveground biomass, (*C*) belowground biomass, (*D*) litter biomass, (*E*) microbial biomass carbon, and (*F*) soil organic carbon. Effect sizes (calculation equation is detailed in "*Individual, Combined, and Interactive Effects of GCFs and Consumers*") are log response ratios (lnRR). The 95% CIs which do not overlap with zero (showing with horizontal dashed lines) indicate significant effects. Negative and positive mean effect values indicate corresponding directional impacts on ecosystem carbon stocks and constituent pools. The parameter *N* indicates the number of studies, and *P*-values were derived from the *Q*-statistics in the mixed-effects meta-analytic models. Sample sizes (number of tests) are specified below each box. Within each analysis, boxes that do not share the same letter demonstrate significant differences from one another. ($P < 0.05$, based on post hoc multiple comparisons with Holm correction).

toward holistic assessments of combined effects of GCFs and herbivores on net whole-ecosystem carbon stocks.

Such carbon loss amplification—likely underestimated due to a publication bias that underrepresents negative interactive effects (*SI Appendix*, Fig. S3 and Tables S1 and S2)—fundamentally challenges prevailing theoretical frameworks that assume additive interactions between GCFs and herbivores (*SI Appendix*, Fig. S4 *A*–*F*). Crucially, our findings expose a critical gap in current Earth system models, which largely neglect biotic factors and their nonlinear feedbacks (9, 24). Moreover, we demonstrated that these combined effects are governed by the functional identity of the GCFs: resource-type factors (e.g., fertilization) provide a buffer through compensatory plant growth, whereas disturbance-type factors (e.g., drought, fire) act synergistically with herbivores to accelerate carbon depletion (*SI Appendix*, Fig. S5). This divergence expands classical environmental stress models by demonstrating that plant–herbivore interactions are not governed by stressor intensity alone, but rather by the functional identity of GCFs (25). Incorporating these nonlinear biotic–abiotic feedbacks is therefore imperative for accurately predicting the future of the ecosystem carbon–climate feedback.

Regime, Body Size, and Ecosystem Context Shape Heterogeneous Carbon Pool Responses

Combined effects of GCFs and herbivores significantly depleted ecosystem carbon stocks, with the highest vulnerability observed in fast-cycling pools—specifically aboveground plant, litter, and microbial biomass (Fig. 3*A*). This loss was driven by negative interactive effects within vegetation and microbial pools (*SI Appendix*, Fig. S6), highlighting the susceptibility of unprotected, rapid-turnover carbon to compound stresses. The specific GCF regime (i.e., press vs. pulse) further modulated these outcomes (*SI Appendix*, Fig. S7). While press-type stressors (e.g., chronic drought) acted additively or synergistically with herbivores to severely deplete plant and litter biomass, pulse-type disturbances like fire exhibited an antagonistic interaction. This antagonistic shift suggests that acute pulses may trigger compensatory plant allocation or rapid microbial restructuring (26), potentially activating latent ecosystem homeostasis (27).

Herbivore size class, in contrast to dietary guild or provenance, emerged as a clear functional trait capturing the directional tendencies of ecosystem carbon responses to GCFs–herbivore interactions (Fig. 3*B* and *SI Appendix*, Figs. S8–S10). Specifically, carbon losses under combined GCF–herbivore effects were inversely related to body size: invertebrates and microherbivores induced significant carbon depletions (~18%), whereas large mesoherbivores (>100 kg) were associated with much smaller losses (~1.73%) (Fig. 3*B* and *SI Appendix*, Fig. S8). Given the relative scarcity of invertebrate studies, this distinct negative impact highlights the need for more targeted research on how smaller consumers influence carbon dynamics under global change. On the other hand, partitioning herbivores by evolutionary provenance or dietary guilds generally failed to yield consistent directional shifts across aggregated carbon pools, despite some pool-specific variations within certain subgroups (*SI Appendix*, Figs. S9 and S10). These findings extend the functional trait paradigm from plant communities to consumer-driven carbon dynamics, suggesting a conceptual shift from an animal's identity to its ecological role (28).

Herbivore biomass density further emerged as a key continuous predictor of carbon responses. Higher areal herbivore biomass combined with GCFs generally intensified carbon losses (*SI Appendix*, Fig. S11*A*), indicating that herbivore pressure, rather than provenance alone, is important for explaining variation in ecosystem carbon stocks. Although subgroup analyses showed no significant difference between wild herbivores and domestic livestock (*SI Appendix*, Fig. S12), domestic livestock often occur at higher densities; therefore, biomass density provides a more practical predictor of carbon responses than the wild-domestic distinction alone. Moreover, the biomass-density slope did not differ between wild and domestic populations (*SI Appendix*, Fig. S11*B*). Although our 100-kg threshold is conservative and likely masks the superior carbon-stabilizing potential of true megaherbivores (>1,000 kg) (29), restoring functional assemblages of large-bodied animals holds potential to synergize biodiversity conservation and climate mitigation via trophic rewilding (30). In contrast, GCFs–predator interactions had negligible effects (*SI Appendix*, Fig. S13), likely because the small size of sampled predators and durations (1 to 7 mo) were insufficient to capture the trophic cascades essential to systems where predators act as keystone species (31).

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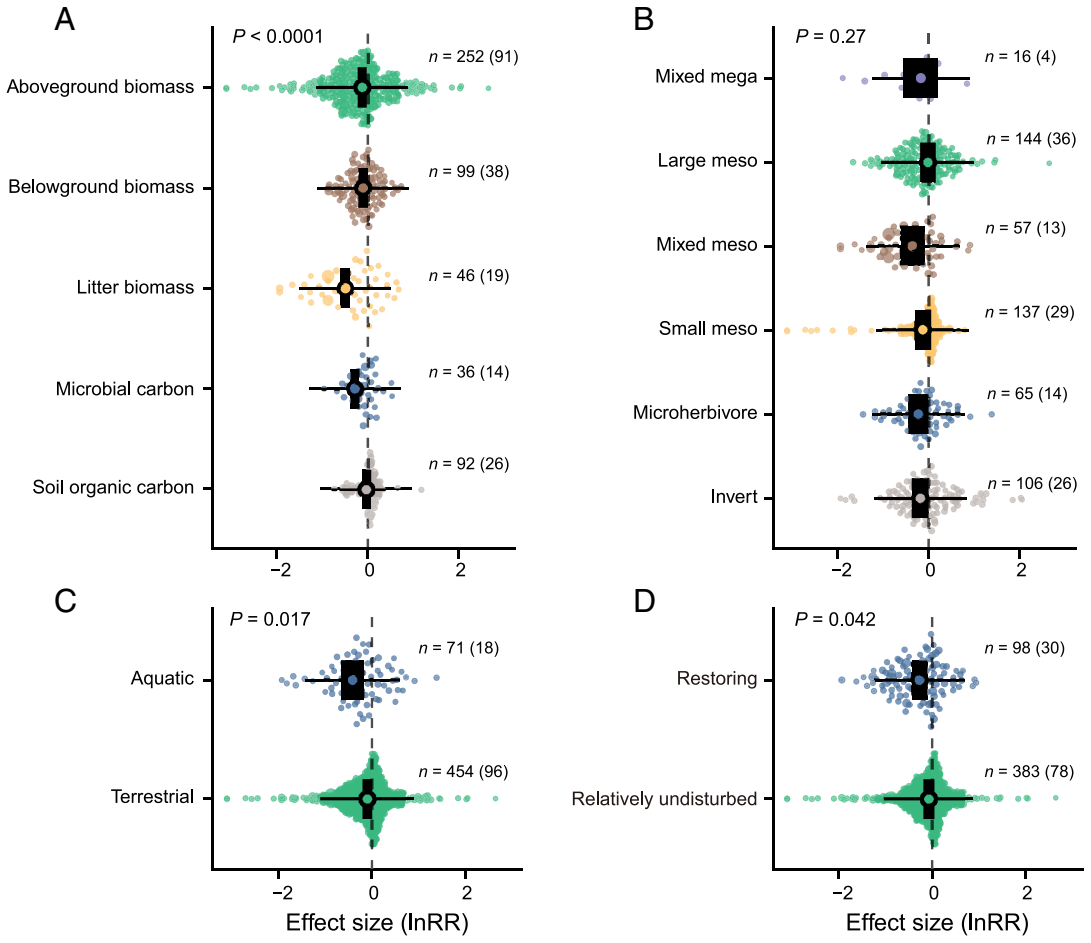


Fig. 3. Contextual dependency of combined effects of GCFs and herbivores on ecosystem carbon stocks. Heterogeneity in combined effects is mediated by (*A*) different carbon pools, (*B*) herbivore size class, (*C*) biome, and (*D*) site restoration status. Orchard plots show the overall effect sizes (represented by circles), 95% CIs (thicker lines), and 95% prediction intervals (thinner lines) derived from mixed-effects meta-analytic models. Effect sizes are expressed as log response ratios (lnRR), where positive values indicate an increase and negative values indicate a decrease in ecosystem carbon stocks or constituent pools. Effect sizes whose 95% CIs do not overlap zero are considered statistically significant. Point size denotes precision, which is proportional to the inverse of the variance. The *P*-values indicate the statistical significance of the omnibus test (Q_M) for differences within each subgroup. Parameter *n* indicates the number of effect sizes included in the meta-analysis, with the number in parentheses representing the number of independent studies from which these effect sizes were derived. The sample sizes in panel (*D*) are exclusively limited to data from field experiments. Abbreviations: Mixed mega: mixed megaherbivore, Large meso: large mesoherbivore, Mixed meso: mixed mesoherbivore, Small meso: small mesoherbivore, Invert: invertebrate.

Biomes (aquatic vs. terrestrial) and site restoration status (relatively undisturbed vs. restoring) also governed the impacts of GCFs–herbivore interactions (Fig. 3 *C* and *D* and *SI Appendix*, Figs. S14 and S15). Aquatic systems experienced more than threefold greater carbon loss (33.5%) than terrestrial systems (9.3%) (Fig. 3*C* and *SI Appendix*, Fig. S14*A*), driven by herbivore-mediated suppression of both above- and below-sediment biomass and the intense top–down control exerted by herbivorous invertebrates (i.e., scrapers) (*SI Appendix*, Figs. S2*D* and S9*B*) (32). Furthermore, herbivore-warming synergy disproportionately destabilized aquatic carbon pools (*SI Appendix*, Fig. S14*B*), suggesting that warming will further undermine aquatic vegetation via disrupted plant–herbivore interactions. While these negative combined effects are particularly pronounced in aquatic systems, separate subbiome analyses confirm that our primary trends remain robust across biomes (Fig. 2*A* and *SI Appendix*, Fig. S14 *C* and *D*). Simultaneously, site restoration status also significantly mediated this susceptibility (Fig. 3*D*), with restoring sites exhibiting markedly higher losses in litter and soil organic carbon than undisturbed ecosystems (*SI Appendix*, Fig. S15). Such heightened susceptibility, likely rooted in a dual legacy of persistent herbivore pressure and impaired microbial functions (11, 33), represents a critical biotic constraint on long-term carbon accrual.

Latitudinal, Temporal, and Climatic Drivers Moderating Carbon Stock Variations

While the interactive effects of GCF–herbivore interactions showed no latitudinal trend or variation across climatic zones (*SI Appendix*, Fig. S16), combined effects on ecosystem carbon stocks exhibited a significant latitudinal gradient ($P = 0.0008$, $R^2_{\text{marginal}} = 0.10$; Fig. 4*A*). Crucially, the substantial intralatitudinal variation observed at identical latitudes was modulated by digestive strategy ($P = 0.045$) rather than herbivore size class or dietary guild (*SI Appendix*, Table S3). This divergence was primarily driven by the opposing slopes of hindgut fermenters relative to other groups across the latitudinal gradient (Fig. 4*B*). Such a trait-contingent slope shift may underpin the polarized ecosystem responses observed across bioclimatic regions. At high latitudes, the positive gradient of ruminants—such as reindeer—contributes to the observed buffering trends, which may stem from herbivore-mediated compensatory regeneration and cryogenic carbon retention (*SI Appendix*, Table S4), suggesting trophic rewilding as a potential strategy for climate mitigation (30). Conversely, tropical ecosystems displayed high vulnerability to GCF–herbivore synergies, exhibiting disproportionate vegetation carbon losses (Fig. 4*C*). At these lower latitudes, GCF–herbivore interactions appear to counteract the baseline carbon gains typically driven by large hindgut

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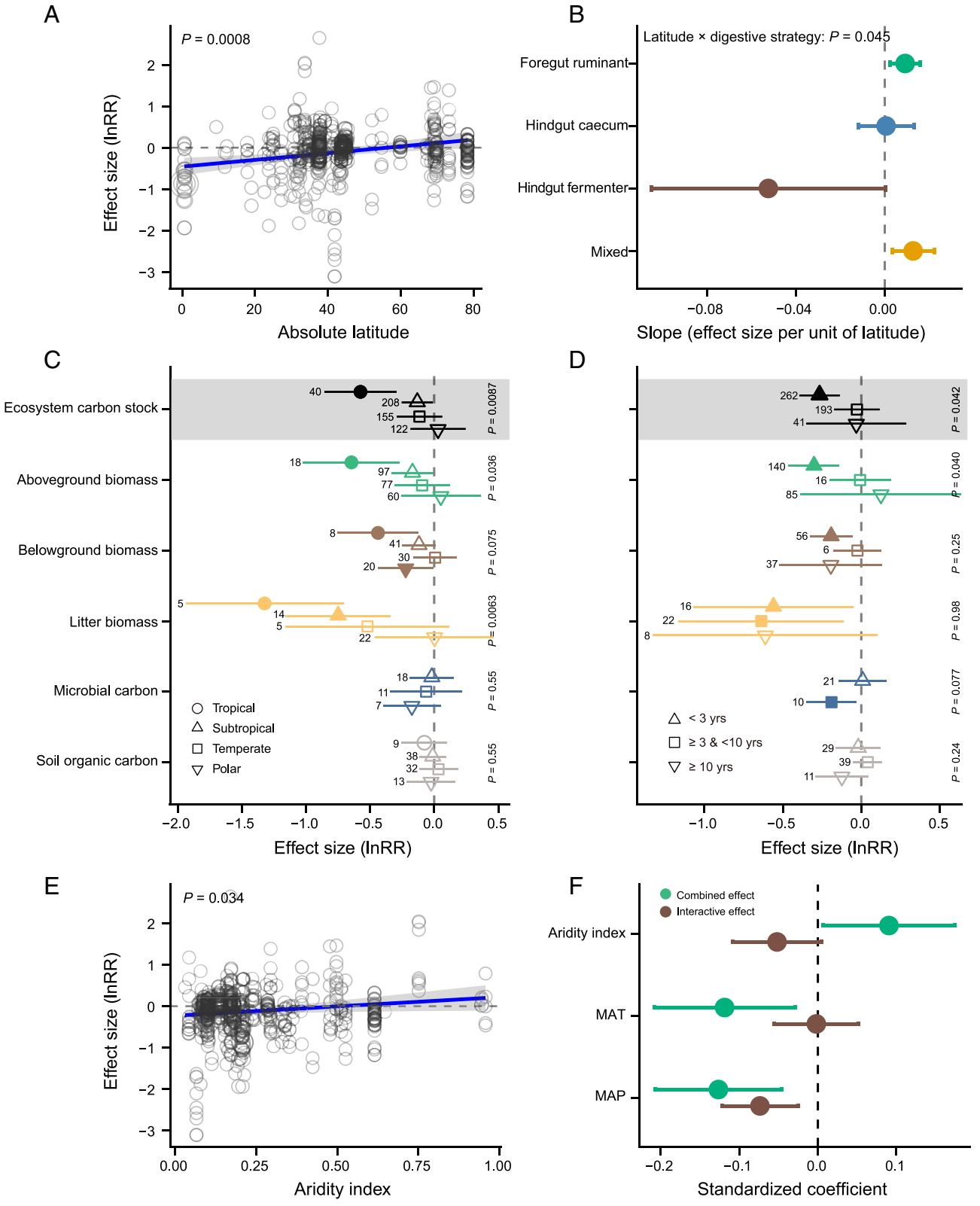


Fig. 4. Spatiotemporal patterns and climatic drivers of carbon stocks under the combined effects of GCFs and herbivores. (*A*) Combined effect sizes (lnRR) on ecosystem carbon stocks plotted as a function of absolute latitude, where bubble size is proportional to the weight (inverse of the variance) of each study, the blue solid line represents the linear regression, and the shaded area denotes the 95% CI. (*B*) Estimated slopes (with 95% CIs) of combined effect sizes as a function of absolute latitude across distinct herbivore digestive strategies, where the *P*-value indicates the significance of the absolute latitude × digestive strategy interaction. Combined effects on ecosystem carbon stocks and specific carbon pools moderated by (*C*) climatic zones and (*D*) experimental duration intervals, with numbers indicating sample sizes, error bars representing 95% CIs, and *Right*-margin *P*-values derived from the omnibus test (Q_M) indicating significant differences among groups; filled and open symbols denote significant ($P < 0.05$) and nonsignificant mean effect sizes, respectively. (*E*) Combined effect sizes on ecosystem carbon stocks plotted as a function of the aridity index, where lower values correspond to a drier climate, the blue solid line represents the linear regression, and the shaded area denotes the 95% CI. (*F*) Standardized coefficients (with 95% CIs) for the combined effect and interactive effect sizes as a function of key climatic variables, including the aridity index, MAT, and MAP. Dashed lines in all panels indicate an effect size of zero, and *P*-values in (*A*, *B*, *E*, and *F*) indicate the statistical significance of the respective regressions or interaction terms.

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fermenters like elephants, likely due to accelerated carbon release from intensified disturbances such as fire and drought (34, 35).

While combined and interactive effects of GCFs-herbivore showed no net change over time (*SI Appendix*, Fig. S17), they masked a profound temporal asynchrony among distinct carbon pools (Fig. 4*D*). Short-term studies (<3 y, n = 262) revealed that combined effects uniformly suppressed vegetation carbon. By mid-term (3 to 10 y, n = 193), the impact shifted: while vegetation recovered via rapid regeneration, the combined effects significantly depleted litter and microbial biomass by 47.2% and 17.3%, respectively (Fig. 4*D*). Over decadal timescales (≥10 y, n = 41), a sustained depletion emerged in litter biomass (–45.8%) and soil organic carbon (–11.7%), aligning with plant litter dominating soil carbon input (36). Meta-regression confirmed that experimental duration amplified the combined effect on aboveground biomass, but degraded that on microbial biomass carbon and marginally decreased that on soil organic carbon (*SI Appendix*, Table S5). This time-explicit reconfiguration implies that initial combined-effect shocks to vegetation cascade into decadal-scale carbon instability, necessitating a shift beyond static assessments in ecological risk frameworks (21, 37).

Meta-forest model identified the aridity index as the primary determinant of the combined effects of GCFs–herbivores on ecosystem carbon storage (*SI Appendix*, Fig. S18*A*). These combined effects were positively correlated with the aridity index (Fig. 4*E*), a trend consistently reflected in both aboveground and litter biomass (*SI Appendix*, Table S6). Consequently, the combined effects shifted from promoting net carbon accumulation in humid regions (aridity index > 0.75) to driving an 11.7% carbon depletion in arid zones (aridity index < 0.5) (*SI Appendix*, Fig. S18*C*). Within individual aridity levels, substantial variation in combined effects was dictated by herbivore body size rather than dietary guild or digestive strategy (*SI Appendix*, Table S3), identifying body size as a critical modulator of carbon dynamics under water-limited conditions. In contrast, the interactive effects between GCFs and herbivores remain stable across the gradient (*SI Appendix*, Fig. S18*D*), suggesting a potential buffering mechanism that may contribute to stabilizing carbon cycling against fluctuating global aridity (38).

Temperature and precipitation gradients further modulate how GCF–herbivore interactions govern carbon stocks. In warmer ecoregions, carbon pools declined through a decoupling effect, characterized by substantial vegetation depletion despite stable soil carbon retention (Fig. 4*F* and *SI Appendix*, Table S6). Such decoupling highlights the potential necessity of active vegetation management to mitigate climate-driven losses, particularly as warming expands herbivore ranges (39) and threatens to destabilize trophic cascades (40). Intriguingly, increasing precipitation also amplified carbon depletion, a trend primarily driven by vegetation carbon loss (Fig. 4*F* and *SI Appendix*, Table S6). Two synergistic mechanisms may reconcile this unexpected vulnerability with the typical carbon accumulation observed in humid regions: 1) higher precipitation intensifies the interactive pressures between GCFs and herbivores on biomass (Fig. 4*F* and *SI Appendix*, Table S6); and 2) enhanced moisture availability might improve plant nutritional quality, potentially exacerbating herbivore foraging pressure (41). By revealing these sensitivities, our results refine the paradigm that precipitation consistently facilitates carbon accrual, identifying biotic interactions as a potent regulator of ecosystem carbon dynamics.

Herbivore Management for Carbon Storage Under Global Change: A Complex Dilemma

Navigating the trade-off between carbon storage and biodiversity conservation presents a critical dilemma under global change. Our analysis reveals a stark contrast: while the combined effects of GCFs and herbivore exclusion significantly increased carbon stocks by 39%, driven primarily by the accumulation of aboveground, belowground, and microbial biomass (Fig. 5*A* and *SI Appendix*, Fig. S19*A*), this gain was accompanied by a 12% decline in plant diversity (Fig. 5*B*). The positive impacts on carbon stocks were more pronounced under fertilization, increased precipitation, and multiple GCFs (*SI Appendix*, Fig. S19*B*), whereas the detrimental impacts on plant diversity were more evident under fertilization and multiple GCFs (*SI Appendix*, Fig. S20*A*). Crucially, integrated studies monitoring both metrics provided direct evidence of this trade-off (*SI Appendix*, Fig. S21), suggesting that anthropogenic herbivore exclusion decouples carbon accrual from biodiversity loss under global change (42). Consequently, within the priority areas of the UN Decade on Ecosystem Restoration, herbivore management strategies under global change require a holistic management framework that transcends carbon-centric goals to balance competing functional priorities.

Accelerated carbon losses under global change are not uniform, but rather form a mosaic shaped by spatial context and consumer functional identity. Spatially, carbon depletion is disproportionately exacerbated in high-sensitivity zones, including tropical regions, drylands, aquatic systems, and restoring ecosystems (Figs. 3 *C* and *D* and 4 *C* and *E*). This regional divergence is stark: while high-latitude ecosystems exhibit a nonsignificant positive trend—which, when contextualized by the significant overall latitudinal gradient (Fig. 4*A*), hints at a potential for herbivores to buffer global change-driven carbon losses, possibly through altered snow-soil thermal regimes and localized trampling effects (43), tropical vegetation exhibits heightened vulnerability to herbivore pressure under global change (Fig. 4*C*). Critically, this vulnerability is modulated by consumer function. Unlike generalist biomass consumers, frugivore communities in intact rainforests facilitate vegetation carbon storage through seed dispersal and regeneration (44). This distinction suggests that targeted frugivore conservation offers a viable, biodiversity-driven approach to stabilize tropical carbon sinks, in sharp contrast to the risk-mitigation required for managing biomass consumers in sensitive areas. Ultimately, such pronounced spatial and functional variability underscores that "one-size-fits-all" interventions may be ineffective or even detrimental, necessitating adaptive management rigorously calibrated to local ecological contexts.

Crucially, our analysis highlights a potential misalignment in current mitigation: the exclusion of microherbivores yields significantly greater carbon gains than that of large herbivores (*SI Appendix*, Fig. S19). This finding reveals a discrepancy in management focus, as current interventions predominantly target large grazers while the substantial role of smaller herbivores in biomass dynamics remains less addressed. Because small herbivores provide indispensable ecological functions, including pollination and nutrient cycling (45, 46), their widespread suppression is ecologically unviable. Instead, herbivore management under global change should vary with restoration stage, herbivory intensity, and management objectives, reducing excessive herbivory where GCF–herbivore interactions pose high carbon-loss risks while maintaining herbivore functions where biodiversity and ecosystem integrity are primary objectives (11, 47). Implementing such an integrated paradigm may offer a viable pathway to safeguard biodiversity while simultaneously stabilizing carbon sinks in an era of accelerating global change.

Conclusion

Our study presents global-scale evidence that herbivores can interact with resource- and disturbance-type GCFs to exacerbate carbon losses. These interactions highlight a pivotal but often underrepresented role for herbivores in regulating carbon

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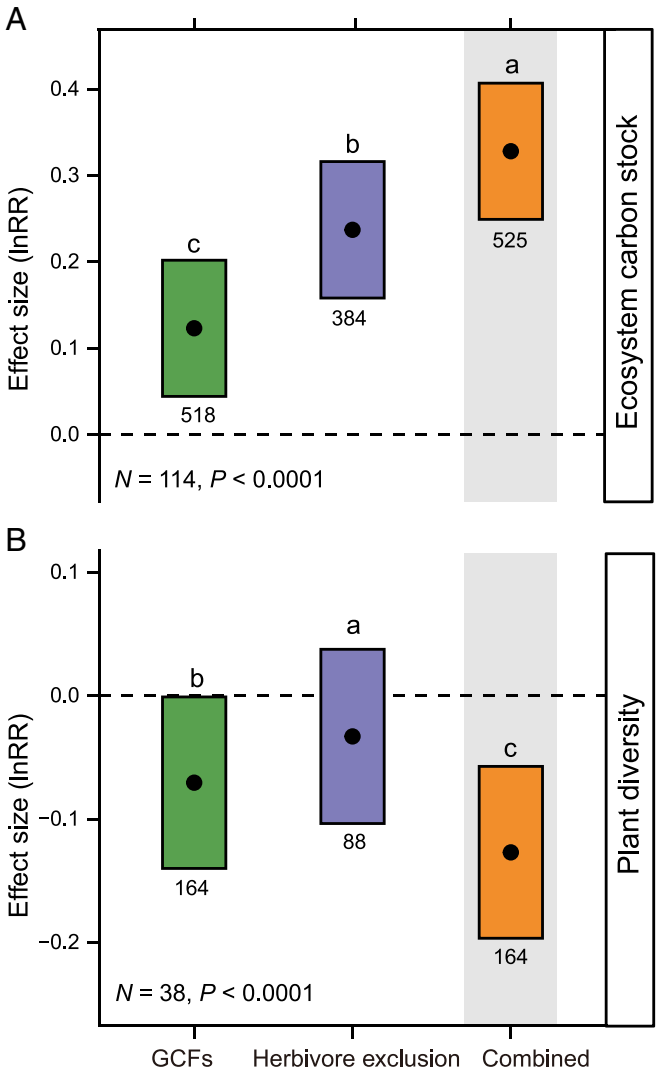


Fig. 5. Contrasting responses of (*A*) ecosystem carbon stocks and (*B*) plant diversity to the individual and combined effects of GCFs and herbivore exclusion. Mean effect sizes (black circles) and 95% CIs (colored boxes) represent the log response ratios (lnRR). A 95% CI that does not overlap with the horizontal dashed line (zero) indicates a significant effect, with positive and negative values denoting increased and decreased responses, respectively. *N* represents the total number of publications, and *P*-values are derived from the omnibus test (Q_M) indicating significant differences among groups. Sample sizes (number of tests) are displayed below each box. Different letters above the boxes indicate significant differences between treatments ($P < 0.05$, post hoc multiple comparisons with Holm correction).

cycling—a synergism currently simplified or less fully integrated in traditional Earth system frameworks (9). When biotic and climatic pressures collide, the resulting carbon stock vulnerability may emerge at lower thresholds or earlier stages than climate-only models predict. Recognizing these synergistic risks suggests that integrating herbivore functional roles into ecosystem processes could further refine our understanding of biosphere integrity boundaries (48). Moving beyond climate-only models toward a holistic biotic-abiotic synthesis represents a critical frontier for improving predictions of the future global carbon sink.

Our study highlights a potential trade-off in herbivore-based Nature-based Solutions (NbS): interventions optimized primarily for carbon sequestration may inadvertently compromise plant diversity, with potential cascading effects on animal and fungal diversity. Focusing strictly on narrow carbon objectives within current NbS frameworks may limit their efficacy under increasing ecological complexity (49). To address this challenge, herbivore management—including trophic rewilding—would benefit from a transition toward a valuation framework that is fundamentally defined by ecosystem-specific functional priorities, nuanced regional contexts, and the diverse roles of herbivore guilds. Adopting such a granular, multiobjective approach provides a pathway to balance these ecological targets. Ultimately, refining these biotic interventions within the broader NbS portfolio is essential for synergistically advancing the goals of both the Paris Agreement and the Kunming-Montreal Global Biodiversity Framework.

Materials and Methods

Database Assembly. We assembled a comprehensive database evaluating the combined effects of GCFs and trophic dynamics on ecosystem carbon stocks through a two-phase compilation process. First, foundational evidence was integrated from two published meta-analyses examining climate-grazing interactions on grassland carbon cycling (8, 50). To expand ecosystem and taxonomic coverage, we subsequently conducted systematic literature searches in both Web of Science and Scopus during March and July 2024 using the following search query: TITLE-ABS-KEY ("carbon storage" OR "carbon stock" OR "organic matter" OR productivity OR plant OR soil) AND TITLE-ABS-KEY ("global change" OR "climate change" OR "anthropogenic stressor" OR warm* OR temperatur* OR heat* OR drought OR fire OR burning OR precipitation OR rain* OR nutrient* OR fertiliz* OR eutroph*) AND TITLE (consumer* OR herbivor* OR graz* OR predator OR fauna* OR livestock OR "trophic cascade" OR pesticid* OR insecticide* OR nematicide*). Following PRISMA screening protocols (*SI Appendix*, Fig. S1), we assessed 4,327 studies and retained 132 peer-reviewed publications that met three specific inclusion criteria: 1) employed full-factorial designs investigating the interactive effects of GCFs with consumer manipulation; 2) measured responses of ecosystem carbon stocks across five critical pools (aboveground biomass, belowground biomass, litter biomass, microbial biomass carbon, and soil organic carbon); and 3) provided comprehensive statistical reporting (means/medians, sample sizes, and measures of variance) across a quadripartite experimental structure capturing four scenarios (control groups under ambient GCF, control groups under manipulated GCF, consumer-treated groups under ambient conditions, and consumer-treated groups under manipulated GCF).

Numerical data were extracted directly from text/tables or digitally from figures. To minimize statistical autocorrelation while maximizing data utilization, each unique GCF type/magnitude, consumer treatment, and distinct geographic location was treated as an independent observation, while a hierarchical coding system (shared "Study ID") was implemented for entries tracking multiple carbon pools or soil depths within the same experiment. For each entry, we compiled relevant ecological, methodological, and consumer trait covariates (detailed classification standards are provided in *SI Appendix*, Table S7). Background soil and climate parameters were standardized using global gridded datasets (HWSD v2.0 and WorldClim v2.1) (51, 52). To consistently evaluate drought severity across geographically diverse sites with contrasting absolute water budgets, we calculated a dimensionless aridity index (aridity index = MAP/PET) to capture relative ecosystem-level water stress via a universally comparable framework. Crucially, to eliminate confounding consumer-induced artifacts (e.g., trampling) on soil bulk density, standardized soil organic carbon stocks were computed using group-specific bulk densities predicted from organic carbon concentrations following Ren et al. (2024) (53) (see *SI Appendix, Supporting Information Text* for detailed *Method*).

Individual, Combined, and Interactive Effects of GCFs and Consumers. For each full-factorial study, we quantified the individual, combined, and interactive effects of GCFs and consumers using the natural logarithm of the response ratio (*lnRR*) as the primary metric (54). First, individual effects were calculated as

$$lnRR = \ln\left(\frac{X_a}{X_c}\right) \text{ or } lnRR = \ln\left(\frac{X_b}{X_c}\right), \quad [1]$$

$$Var = \frac{SD_a^2}{N_a \times X_a^2} + \frac{SD_c^2}{N_c \times X_c^2} \text{ or } Var = \frac{SD_b^2}{N_b \times X_b^2} + \frac{SD_c^2}{N_c \times X_c^2}. \quad [2]$$

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Then, the combined effects of both drivers were determined by

$$lnRR = \ln\left(\frac{X_{ab}}{X_c}\right), \quad [3]$$

$$Var = \frac{SD_{ab}^2}{N_{ab} \times X_{ab}^2} + \frac{SD_c^2}{N_c \times X_c^2}. \quad [4]$$

Finally, to model ecological interactions, we employed a multiplicative framework rather than a conservative additive approach, which was formulated as (55):

$$lnRR = \ln\left(\frac{X_{ab}}{X_a}\right) - \ln\left(\frac{X_b}{X_c}\right) = \ln\left(X_{ab} \times X_c\right) - \ln\left(X_a \times X_b\right), \quad [5]$$

$$Var = \frac{SD_c^2}{N_c \times X_c^2} + \frac{SD_a^2}{N_a \times X_a^2} + \frac{SD_b^2}{N_b \times X_b^2} + \frac{SD_{ab}^2}{N_{ab} \times X_{ab}^2}. \quad [6]$$

Here, X, SD, and N consistently represent the mean, SD, and sample size, respectively. Specifically, X_c, X_a, X_b, X_{ab} represent the sample means of the control group (ambient GCF, consumer absence), consumer-only group (ambient GCF, consumer presence), GCF-only group (manipulated GCF, consumer absence), and combined treatment group (manipulated GCF, consumer presence), respectively. This multiplicative framework provides a biologically realistic representation of trophic cascades and global change impacts (56), which typically propagate via proportional and interdependent shifts across trophic levels (57). Based on the 95% CIs of $lnRR_{interaction}$ and their directional alignment with individual effects, interactions were categorized into five regimes: additive (CIs overlapping zero), synergism+, synergism−, antagonism+, and antagonism− (*SI Appendix*, Fig. S22, see *SI Appendix, Supporting Information Text* for detailed *Method*) (58).

Multilevel Meta-Analytic Models. To account for dependencies and potential biases, effect sizes were analyzed using multilevel mixed-effects meta-analytic models via the *rma.mv* function in the *metafor* package (59). The random-effects structure nested "Study ID" (unique experiments) within "Publication ID" (unique publications) to explicitly control for variance–covariance structures and shared experimental environments. The total heterogeneity explained by categorical moderators was evaluated using the omnibus Q_M statistic. For continuous moderators, the R^2 statistic was calculated using the *r2_ml* function from the *orchaRd* package (60). All statistical analyses were performed in R version 4.5.2.

To justify the aggregation of diverse experimental designs and ensure our overarching synthesis was immune to idiosyncratic data structures, we executed a rigorous series of preliminary sensitivity frameworks prior to primary model execution. First, although simulated clipping cannot fully reproduce the selective feeding and biogeochemical effects of real herbivory, preliminary analyses revealed no significant moderating effect of consumer treatment (i.e., simulated clipping versus real-herbivore treatments; $P > 0.05$). Moreover, systematically excluding simulated-clipping studies left our core meta-analytic conclusions unchanged (*SI Appendix*, Fig. S23), indicating that their inclusion did not drive the overall trophic patterns. Second, omitting the limited subset of belowground herbivore studies yielded identical, stable primary outcomes (*SI Appendix*, Table S8). Third, to address potential directional biases from independently analyzing individual carbon pools, we performed a subanalysis restricted to experiments concurrently measuring above- and belowground components to derive a weighted, ecosystem-level net carbon stock, which consistently validated our main findings (*SI Appendix*, Table S8). Fourth, to decouple potential distortions from high-intensity, pulse experimental fertilization versus chronic, realistic nutrient deposition, we reevaluated our models by excluding all fertilization studies, confirming that overarching predictive trends remained highly robust (*SI Appendix*, Table S8). Based on these consistent cross-validations, data were pooled across these experimental regimes to maximize statistical power and macroecological generality.

Our statistical analysis proceeded hierarchically as follows. First, to establish an overarching baseline, we utilized a random-effects model to estimate the global mean effect sizes (with 95% CI) for both the combined and interactive effects of GCFs and consumers (including both herbivores and predators) on ecosystem carbon stocks. Because data limitations for predator effects precluded granular baseline segmentations, downstream analyses strictly focused on identifying the specific vulnerabilities within GCF–herbivore interactions. Consequently, we employed mixed-effects models to compare the mean effect sizes (with 95% CI) of GCF-only, herbivore-only, and combined GCF–herbivore treatments. This comparison was implemented across total ecosystem carbon stocks and recursively down into five individual constituent pools (aboveground, belowground, litter, microbial, and soil organic carbon), evaluated under both broad treatment groupings and specific GCF-type pairings. To stringently control the family-wise error rate across these multiple post hoc comparisons, *P*-values were adjusted using Holm's correction. Second, we isolated these pool-specific combined and interactive effects to determine if specific GCF types exerted disproportionate impacts when co-occurring with herbivores. Third, to identify the ecological drivers regulating these combined and interactive effects, we tested key environmental and biotic moderators (biome, site restoration status, climatic zone, consumer size class, dietary guild, and provenance) as fixed effects in separate models, and further compared biomass-density responses between wild herbivores and domestic livestock across distinct GCF regimes. Fourth, to capture temporal trajectories and continental-scale biogeographic gradients, separate multilevel meta-regressions and mixed-effects models were constructed for each carbon pool to evaluate the continuous or categorical influences of absolute latitude, herbivore biomass, bioclimatic gradients (MAT, MAP, and Aridity index) with in situ field data, and experimental duration intervals categorized into short-term (<3 y), medium-term (3 to 10 y), and long-term (≥10 y) regimes. Concurrently, to unravel the mechanisms driving variation in combined effects across identical latitudinal or aridity gradients, we employed meta-regression models incorporating the interaction between herbivore functional traits (including body size class, dietary guild, digestive strategies) and absolute latitude or aridity index with in situ field data, thereby quantifying and comparing the response slopes across distinct levels of herbivore traits.

Determining the Relative Importance of Moderators. To identify the key variables predicting the combined and interactive effects of GCFs and herbivores on ecosystem carbon stocks, we constructed a machine learning–based random forest model adapted for meta-analysis using the *metaforest* and *caret* packages (61). This approach integrated the retrospective variance and weights of each field experiment during model construction, providing robust protection against overfitting while effectively capturing nonlinear relationships and high-order interactive effects among predictors. The model incorporated 12 potential moderators stratified across four ecological dimensions: 1) climate factors (GCF type, MAT, MAP, and Aridity index); 2) soil properties (pH and total nitrogen); 3) herbivore traits (size class, dietary guild, and provenance); and 4) methodological/system features (experimental duration, carbon pool type, and biome). Following a structured variable screening and hyperparameter optimization protocol, we derived the relative importance metrics for each retained moderator.

Management Interventions. To systematically evaluate how herbivore exclusion modulates the impacts of GCFs on ecosystem carbon stocks and plant diversity, we quantified three standardized effect sizes (lnRR) for each experimental unit using the control plots (ambient GCF, herbivore presence) as the baseline framework (mathematical formulations detailed above). These metrics encapsulated: 1) GCF effects under herbivore presence; 2) herbivore exclusion effects under ambient GCF conditions; and 3) the combined effects of GCFs and herbivore exclusion (hereafter collectively designated as "the three effect categories"). Using these precalculated effect sizes as response variables, we respectively implemented multilevel mixed-effects models across total ecosystem carbon stocks and plant diversity metrics, treating the three effect categories as a fixed factor to resolve mean effect sizes and 95% CI. To compare whether the combined effects of herbivore exclusion and GCFs on carbon accumulation remain consistent across different carbon pools, GCF types, and herbivore size classes, we constructed separate, independent mixed-effects models with these factors set as fixed effects. The same moderators (except for carbon pool type) were also applied to plant diversity. Furthermore, we conducted mixed-effects model analyses on a subgroup dataset–comprising studies that simultaneously measured both ecosystem carbon stocks and plant diversity within the same paper–to perform cross-validation.

Publication Bias Evaluation. To evaluate potential publication bias within our database, we initially visualized the asymmetrical distribution of effect sizes using funnel plots, which revealed a characteristically asymmetrical pattern marked by a sparsity of small, negative effect sizes (*SI Appendix*, Fig. S3). Subsequent application of the trim-and-fill method confirmed this asymmetry

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(62), the imputed missing studies predominantly clustered within negative effect-size spectra, with the singular exception of interactive effects on litter biomass (*SI Appendix*, Tables S1 and S2). Because our empirical estimates of the combined and interactive GCF-consumer impacts on ecosystem carbon stocks were already predominantly negative, this systematic bias strongly indicates that our reported overall negative effect sizes are highly conservative. Finally, to examine temporal variations in publishing trends, we executed multilevel meta-regressions incorporating publication year as a fixed effect. These analyses demonstrated minimal temporal bias across the majority of our findings (*SI Appendix*, Tables S9 and S10). Significant temporal trajectories were restricted to: 1) a positive trend over time for the interactive effects of warming and multiple GCFs with consumers on ecosystem carbon stocks, potentially reflecting a growing methodological emphasis on stronger interactive regimes in recent literature; and 2) a negative temporal trend for fire–consumer interactions, capturing a historical shift toward reporting more pronounced or nuanced ecological responses over time.

Data, Materials, and Software Availability. All data used are available from the sources listed in the *SI Appendix*. The dataset and code can be accessed at Zenodo (https://doi.org/10.5281/zenodo.21350905) (63).

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