



RESTORATION ECOLOGY

Herbivory limits success of vegetation restoration globally

Changlin Xu¹, Brian R. Silliman², Jianshe Chen¹, Xincheng Li¹, Mads S. Thomsen^{3,4}, Qun Zhang¹, Juhung Lee^{5,6}, Jonathan S. Lefcheck^{7,8}, Pedro Daleo⁹, Brent B. Hughes¹⁰, Holly P. Jones¹¹, Rong Wang¹², Shaopeng Wang¹³, Carter S. Smith², Xinqiang Xi¹⁴, Andrew H. Altieri¹⁵, Johan van de Koppel^{16,17}, Todd M. Palmer¹⁸, Lingli Liu¹⁹, Jihua Wu²⁰, Bo Li²¹, Qiang He^{1*}

Restoring vegetation in degraded ecosystems is an increasingly common practice for promoting biodiversity and ecological function, but successful implementation is hampered by an incomplete understanding of the processes that limit restoration success. By synthesizing terrestrial and aquatic studies globally (2594 experimental tests from 610 articles), we reveal substantial herbivore control of vegetation under restoration. Herbivores at restoration sites reduced vegetation abundance more strongly (by 89%, on average) than those at relatively undegraded sites and suppressed, rather than fostered, plant diversity. These effects were particularly pronounced in regions with higher temperatures and lower precipitation. Excluding targeted herbivores temporarily or introducing their predators improved restoration by magnitudes similar to or greater than those achieved by managing plant competition or facilitation. Thus, managing herbivory is a promising strategy for enhancing vegetation restoration efforts.

Vegetation is a primary foundation of Earth's ecosystems, spanning from rainforests and grasslands on land to seagrass beds and kelp forests in coastal oceans. Vegetation in many ecosystems, however, has been extensively degraded, resulting in the loss of biodiversity and critical services to humanity (1, 2). The restoration of degraded vegetation has been increasingly adopted to recover ecosystem functions and services (e.g., carbon sequestration and flood mitigation), which contributes to efforts to achieve many of the United Nations (UN) Sustainable Development Goals (3, 4). To fulfill commitments in the UN Decade on Ecosystem Restoration, governments, nongovernmental organizations, and local communities are seeking effective strategies to restore vegetation.

Restoration of vegetated ecosystems has traditionally adopted a bottom-up framework (i.e., the “Field of Dreams” hypothesis), which posits that plants (and subsequently higher trophic levels) will recover through natural plant propagation if the cause of degradation (e.g., tree logging, farming, or plant invasion) is removed, sometimes with additional activities

to ameliorate changes to the physical environment (e.g., hydrological modification or soil amendment) (5). We refer to this restoration approach as natural regeneration (also known as passive restoration) (5). A more active approach is planting seeds, seedlings, or other plant propagules to expedite vegetation recovery. We refer to this approach as planted restoration (also known in some literature as active restoration) (6, 7).

Plant abundance and diversity in ecosystems that are restored by these bottom-up approaches often do not fully recover, even after decades (but there are exceptions, especially at tropical sites) (7, 8). This limited recovery may be caused by unrecognized top-down control of vegetation by herbivores or indirectly by the loss of predators that control herbivore populations (9, 10), which limits vegetation establishment or growth at restoration sites. Top-down control has been documented extensively as a key force that structures vegetation in relatively undegraded ecosystems where trophic interactions among plants, herbivores, and predators have stabilized (11, 12). Despite studies on specific ecosystems or consumers (13, 14),

there has not yet been a global assessment of top-down effects on restoration. This gap hinders progress in upscaling restoration and leaves the recent initiative of trophic rewilding, in which reintroducing predators is recommended to promote biodiverse and self-regulating ecosystems (15), unsubstantiated by broad empirical evidence.

We present an assessment of top-down control of vegetation under restoration globally by assembling a dataset of consumer effects on vegetation, with 1898 field experimental tests conducted in 64 countries and published in 451 articles [the Global Consumer Effects dataset (16); see figs. S1 and S2, table S1, and materials and methods (17)]. This dataset includes tests of consumer effects on vegetation by herbivore exclusion or addition (1883 tests) or predator reintroduction (15 tests) at relatively undegraded (550 tests), natural regeneration (1049 tests), and planted restoration (299 tests) sites. We considered relatively undegraded sites (hereafter, undegraded sites) to be those not impaired by recent anthropogenic disturbance, although we recognize that few sites on Earth remain completely undisturbed. These tests encompassed terrestrial and aquatic (freshwater and marine) biomes across all six vegetated continents (Fig. 1A) and spanned tropical, subtropical, and temperate regions (274, 773, and 851 tests, respectively, with tropical aquatic studies considerably less represented; Fig. 1C) and broad gradients of temperature and precipitation (Fig. 1B). Each test included measures of vegetation abundance (density, percent cover, biomass, or survival; 1434 tests) or diversity (species richness, Shannon diversity, Simpson's evenness, or Pielou's evenness; 464 tests), both in control (X_C) and in herbivore exclusion or predator reintroduction (X_T) treatments [the relatively small number of herbivore addition studies were omitted in our main analyses (17); fig. S3]. These vegetation measures represent proxies for desirable restoration outcomes because they correlate with valued ecosystem functions such as carbon sequestration and ecosystem stability (18, 19). For each test, we calculated the effect size of herbivores on vegetation abundance and diversity using the log response ratio, $\ln(X_C/X_T)$, with negative and

¹MOE Key Laboratory for Biodiversity Science and Ecological Engineering, National Observations and Research Station for Wetland Ecosystems of the Yangtze Estuary, School of Life Sciences, Fudan University, Shanghai, China. ²Nicholas School of the Environment, Duke University, Beaufort, NC, USA. ³Marine Ecology Research Group and Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury, Christchurch, New Zealand. ⁴Department of Bioscience, Aarhus University, Roskilde, Denmark. ⁵Marine Science Center, Northeastern University, Nahant, MA, USA. ⁶Department of Oceanography and Marine Research Institute, Pusan National University, Busan, Republic of Korea. ⁷Tennenbaum Marine Observatories Network and MarineGEO Program, Smithsonian Environmental Research Center, Edgewater, MD, USA. ⁸University of Maryland Center for Environmental Science, Cambridge, MD, USA. ⁹Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMdP, CONICET, Mar del Plata, Argentina. ¹⁰Department of Biology, Sonoma State University, Rohnert Park, CA, USA. ¹¹Department of Biological Sciences and Institute for the Study of the Environment, Sustainability, and Energy, Northern Illinois University, DeKalb, IL, USA. ¹²School of Ecological and Environmental Sciences, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, East China Normal University, Shanghai, China. ¹³Institute of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing, China. ¹⁴Department of Ecology, School of Life Science, Nanjing University, Nanjing, Jiangsu, China. ¹⁵Department of Environmental Engineering Sciences, University of Florida, Gainesville, FL, USA. ¹⁶Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research, Yerseke, Netherlands. ¹⁷Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, Netherlands. ¹⁸Department of Biology, University of Florida, Gainesville, FL, USA. ¹⁹State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China. ²⁰State Key Laboratory of Herbage Improvement and Grassland Agro-Ecosystems, and College of Ecology, Lanzhou University, Lanzhou, Gansu, China. ²¹Yunnan Key Laboratory of Plant Reproductive Adaptation and Evolutionary Ecology and Centre for Invasion Biology, Institute of Biodiversity, School of Ecology and Environmental Science, Yunnan University, Kunming, Yunnan, China.

*Corresponding author. Email: he_qiang@hotmail.com

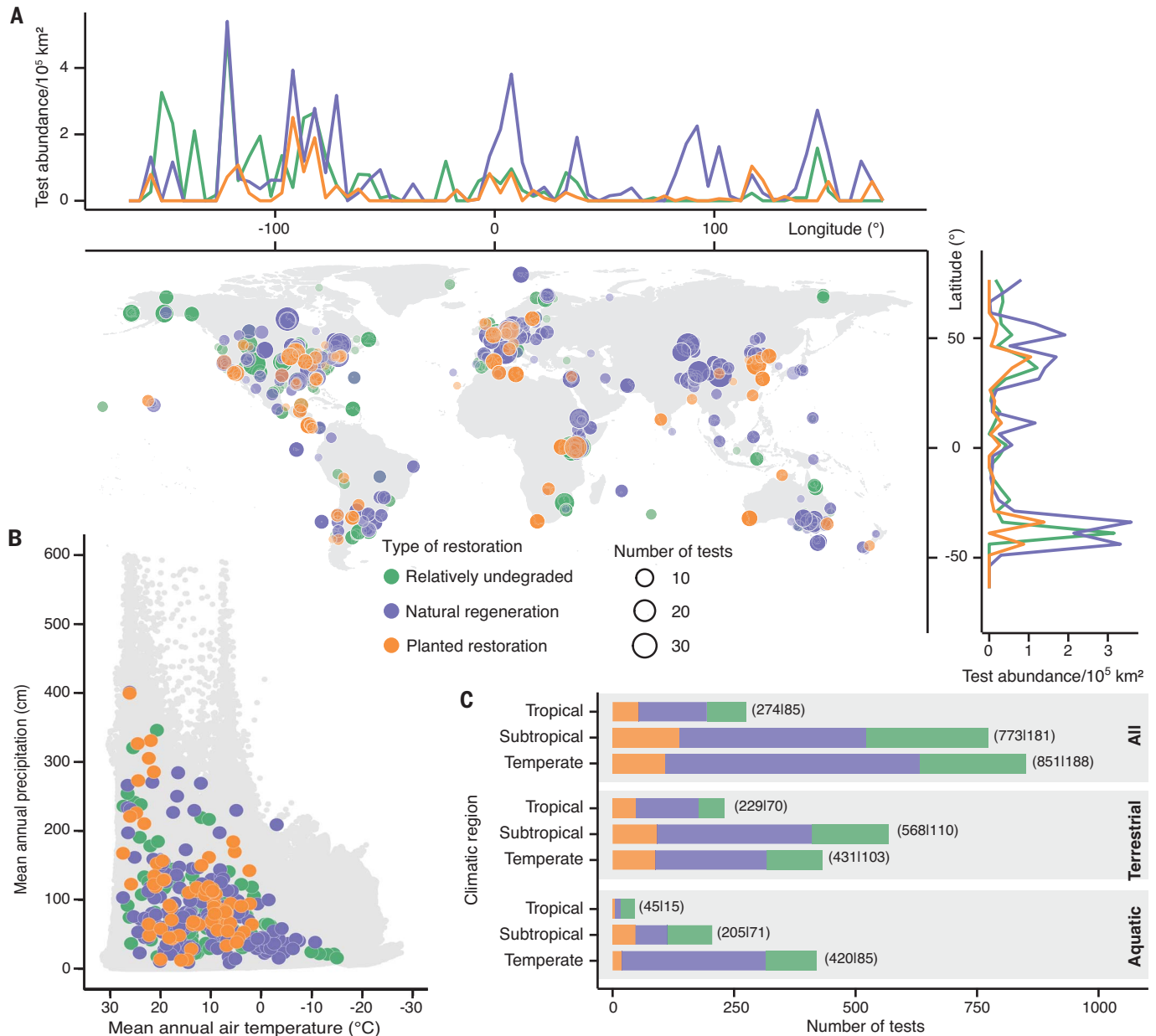


Fig. 1. Global patterns in the study of consumer effects on vegetation.

(A) Global distribution of tests at natural regeneration, planted restoration, and relatively undegraded sites. The insets show the distributions of the abundance of tests per 10^5 km² of land area (excluding Antarctica) along latitudinal and longitudinal gradients (one point of test abundance, 41, between longitude -165° and -170° was omitted from the figure for visual clarity). Tests on aquatic vegetation that occur primarily along shorelines were also included to compute test abundance per unit land area. The equidistant cylindrical projection, instead of an equal-area

projection, is used for the background map to align it with the insets that show test abundance. (B) Distribution of tests in the global climate space defined by MAT and MAP (gray points represent 1,000,000 randomly sampled points of global land areas, and colored points represent tests included in our dataset; 88 of the 574 coastal marine tests that did not have standardized climate data were omitted from the figure). (C) Number of tests in different biomes (terrestrial and aquatic) and climatic regions (tropical, subtropical, and temperate). Sample sizes are shown as number of tests|number of articles to the right of each bar.

positive values indicating negative and positive effects of herbivores, respectively. For each test, we also collected several covariates to identify moderators of variation in effect sizes (17): biotic (e.g., plant life forms such as macroalgal, herbaceous, or woody; herbivore size classes such as invertebrate, small vertebrate, and large vertebrate; the provenance of plants and herbivores), climatic [mean annual air temperature

(MAT) and mean annual precipitation (MAP)], and methodological (e.g., study duration and plot size, that is, the area where herbivores were removed).

Additionally, to assess the effect size of managing herbivory (through herbivore exclusion or predator reintroduction) versus managing other widely considered biotic drivers of vegetation restoration, we assembled a global

dataset of 696 tests on the effects of managing plant competition and facilitation from 167 articles [the Global Plant Interactions and Restoration dataset (16); fig. S1 and table S1] (17). Each of these tests measured vegetation abundance in control (X_C) and in competitor removal or facilitator inclusion (X_T) treatments at a natural regeneration or planted restoration site. Effect sizes of competitor removal or

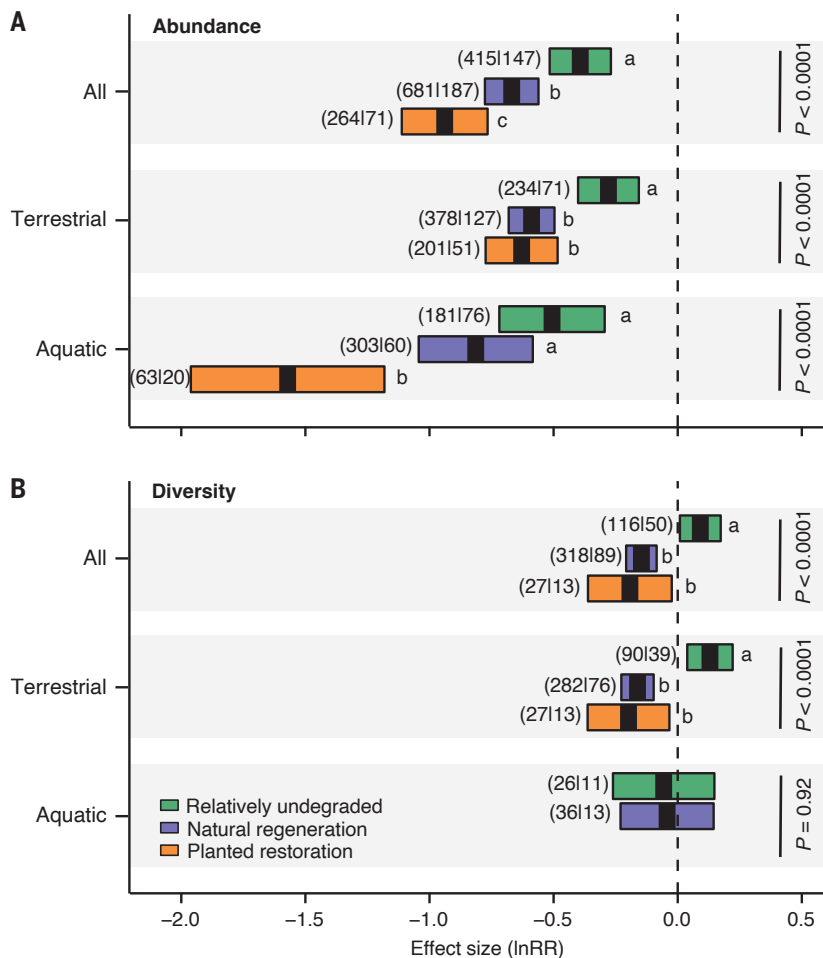


Fig. 2. Herbivores exert stronger effects on vegetation at restoration sites than at undegraded sites globally. (A and B) Herbivore effect sizes on plant abundance (A) and diversity (B) at natural regeneration, planted restoration, and relatively undegraded sites. Analyses were conducted for studies in terrestrial, aquatic, and all (combined) biomes. Effect sizes are log response ratios (lnRR), with negative and positive values indicating negative and positive effects of herbivores, respectively. Center bolded lines represent mean effect sizes, and error bars represent 95% CI. Sample sizes are shown as number of tests|number of articles to the left of each bar. Statistical significances are shown with *P* values. Within each analysis (shaded area), bars that share a letter (i.e., a, b, or c) do not differ significantly from one another ($P > 0.05$, based on post hoc multiple comparisons with Holm correction). Relatively undegraded, natural regeneration, and planted restoration sites are indicated with green, purple, and orange boxes, respectively.

facilitator inclusion were calculated as $\ln(\bar{X}_T/\bar{X}_C)$, with positive values indicating positive effects of management. We then compared these effect sizes with those of herbivore exclusion or predator reintroduction calculated for tests in the Global Consumer Effects dataset. Our analyses are robust to inclusion of tests with zero values (table S2) and potential publication bias (fig. S4 and tables S3 to S6).

Global, amplified effects of herbivores on vegetation under restoration

We first assessed the mean effect sizes [with 95% confidence interval (CI)] of herbivores at restoration (natural regeneration and planted restoration) sites in comparison to undegraded sites. We found strong negative effects of her-

bivores on the abundance of vegetation under restoration across terrestrial and aquatic biomes globally. Although herbivores naturally reduced vegetation abundance at undegraded sites (-32% on average), reductions were significantly stronger at restoration sites (-52% ; Fig. 2A). This finding was corroborated by supplementary analyses that (i) focused on studies that tested herbivore effects at both undegraded and natural regeneration sites (fig. S5), (ii) used more-specific vegetation performance measures (fig. S6), (iii) accounted for differences in sample size through bootstrap resampling (table S7) (17), and (iv) accounted for potential effects of covariates through multivariate modeling (table S8) (17). Subsequently, vegetation recovery was often slower and less

complete if herbivores were unchecked at restoration sites (fig. S7). Indeed, herbivore density was generally higher at restoration sites than at undegraded sites, and greater densities of herbivores often more strongly suppressed vegetation abundance (fig. S8). Herbivores (generalists in particular) can retreat during disturbance and rapidly reestablish (20), which likely contributes to amplified herbivore effects at restoration sites. Although herbivores might suppress vegetation abundance more strongly at high productivity sites (fig. S9), plant productivity was often lower at restoration sites than at undegraded sites (fig. S9) and thus could not explain the amplified herbivore effects at restoration sites.

We also examined whether the amplified effects of herbivores on vegetation abundance at restoration sites were consistent among different biomes, climatic regions, and types of restoration. We found amplified herbivore effects in both terrestrial and aquatic biomes (Fig. 2A) for both natural regeneration and planted restoration, which used different types of propagules like seeds, seedlings, or adults (Fig. 2A and table S9), and in tropical and subtropical regions (fig. S10). In temperate regions, however, herbivore effects were strongly negative at both undegraded and restoration sites (fig. S10). Our results also revealed some fundamental differences in herbivore effects between terrestrial and aquatic biomes. Herbivore effects on vegetation abundance were similar between natural regeneration and planted restoration sites in terrestrial biomes (grasslands and forests), whereas in aquatic biomes (freshwater wetlands and marine vascular plant systems; table S10), herbivore effects were much stronger at planted restoration sites than at natural regeneration sites (Fig. 2A and fig. S11). This pattern, however, held only when natural regeneration sites had target plants already present at the beginning of the study (fig. S12). This is likely in part because aquatic herbivores are more generalized in habitat use relative to their terrestrial counterparts (21) and may tend to concentrate on immature, regenerating plants rather than mature, defended plants.

Herbivores have generally been shown to increase plant diversity in naturally productive ecosystems by reducing the dominance of competitively superior plant species (22). Our global synthesis corroborates this paradigm at undegraded sites but also reveals that herbivores generally reduced plant diversity at restoration sites (Fig. 2B and fig. S13) (17). This reversal was found mainly in terrestrial biomes (from 14% at undegraded sites to -15% at restoration sites; Fig. 2B), which included grasslands and forests (fig. S11) across different climatic regions (fig. S10). Supplementary analyses showed that plant productivity was lower at restoration sites than at undegraded sites (fig. S9) and that herbivores more strongly

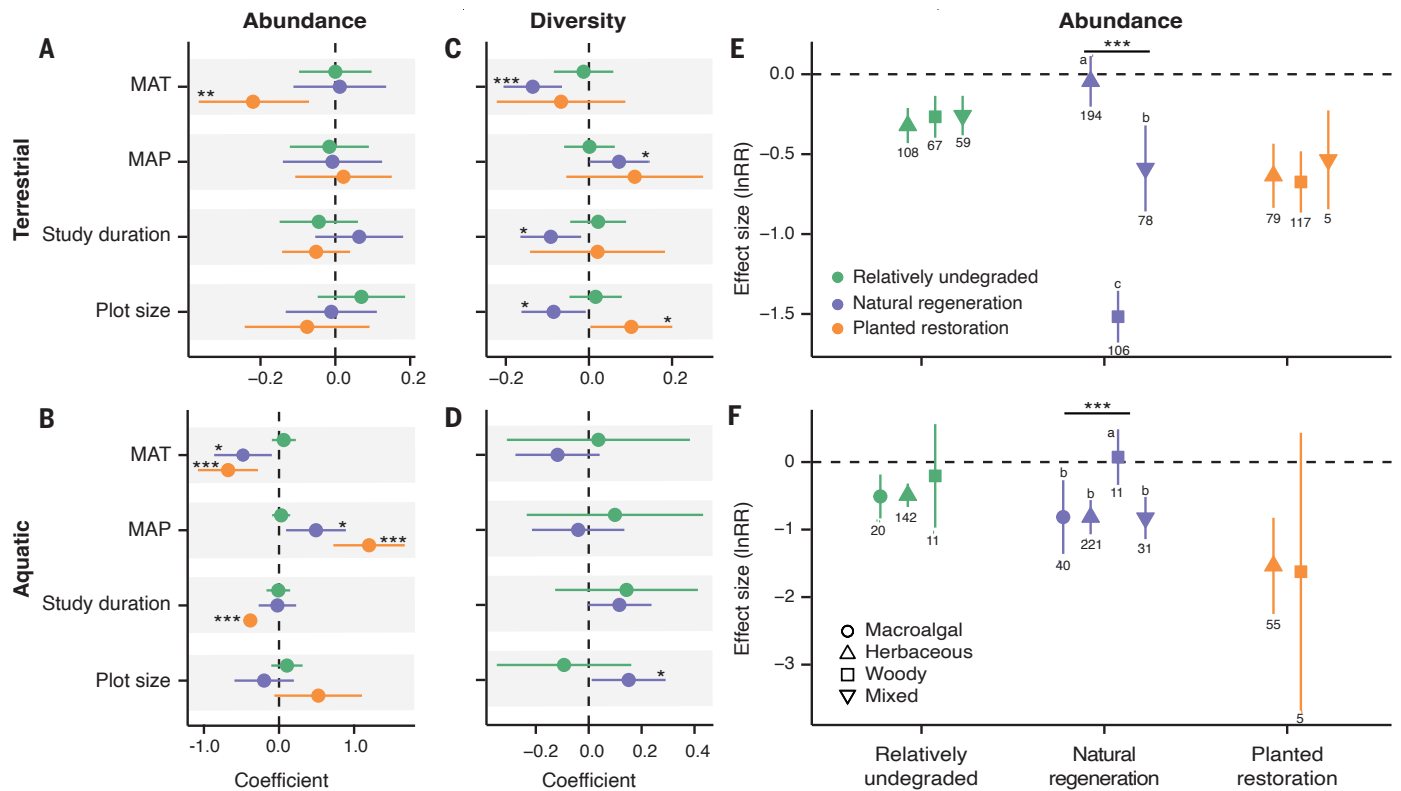


Fig. 3. Herbivore effects are contingent on climatic and biotic factors.

(A and B) Coefficients of continuous covariates for the effect size of herbivores on vegetation abundance, estimated using a global model that included all covariates considered (17). (C and D) Coefficients of continuous covariates estimated using mixed-effects models on plant diversity (no studies were available for planted restoration in aquatic biomes). In (A) to (D), all coefficients were estimated using covariates that were standardized to have a mean of zero and a standard deviation of one; negative and positive coefficients indicate that the negative effects of herbivores strengthen and weaken with increases in a covariate, respectively (see fig. S15 for changes in the effect sizes of herbivores with covariates in original, untransformed units). (E and F) Mean effect sizes of herbivores on the abundance of different plant life forms (the number of tests

is shown below each bar; see figs. S16 to S18 for additional categorical covariates). Effect sizes are log response ratios (lnRR), and negative values correspond to negative effects of herbivores on vegetation abundance. Panels (A), (C), and (E) show data for terrestrial biomes, and panels (B), (D), and (F) show data for aquatic biomes. In all panels, data are shown as means \pm 95% CI. Statistical significances are indicated: *** P < 0.001, ** P < 0.01, and * P < 0.05. In (E) and (F), bars that share a letter (i.e., a or b) do not differ significantly from one another (P > 0.05, based on post hoc multiple comparisons with Holm correction). Groups with <5 tests (which require further research) were omitted from the figures and discussions throughout this paper. In all panels, natural regeneration, planted restoration, and relatively undegraded sites are indicated by purple, orange, and green symbols, respectively.

suppressed plant diversity where plant productivity was lower (fig. S14), possibly owing to lower productivity sites having smaller plant populations that are more easily eliminated. This explanation for the reversal is supported by multiple studies that show that herbivores increase plant diversity at high-productivity sites but decrease it at low-productivity sites (22, 23). Additionally, degraded ecosystems were often characterized by a higher density of generalist herbivores that are more likely to suppress plant diversity by removing early successional plant species (fig. S8) (24), which invest more in tolerance to environmental stressors than in defenses against herbivory (25). However, no such reversal was detected in aquatic biomes (Fig. 2B), where plant diversity is generally low and restoration efforts often targeted a single foundation species (26). We found no significant effect of herbivores on the recovery rate and completeness of plant

diversity, although studies remained relatively few (fig. S7) or often lasted only a few years (table S11).

Climatic conditions are among the key moderators of herbivore effects at restoration sites

Exploring variation in the effect sizes of herbivores (17), we found that moderators of herbivore effects often differed between restoration and undegraded sites. First, we found climatic conditions, including MAT and MAP, to be among the key moderators at restoration sites but not at undegraded sites (Fig. 3, A to D; fig. S15; and tables S12 and S13). In both terrestrial and aquatic biomes, herbivores often more strongly suppressed vegetation abundance at sites with higher MAT (but this pattern was absent at terrestrial natural regeneration sites; Fig. 3). This finding corroborates the view that high temperatures generally increase herbivory

(27), although this effect of temperature may be amplified or offset by its effect on plant growth, which varies depending on habitat moisture (28). In terrestrial biomes, herbivore effects on vegetation abundance did not vary significantly with MAP, whereas in aquatic biomes, effects were more negative with lower MAP (Fig. 3), perhaps because aquatic vegetation is more stressed from periodic drying and higher densities of herbivores during dry periods (29). Climate also explained variation in herbivore effects on plant diversity at natural regeneration sites, with herbivores exerting stronger negative effects in regions with high MAT and low MAP, a pattern that is significant in terrestrial biomes but not in low-diversity aquatic biomes (Fig. 3). In contrast to restoration sites, these climatic signals were nonsignificant at undegraded sites (Fig. 3, A to D). This difference suggests that systems under restoration may be more vulnerable to herbivory in warmer, drier climates.

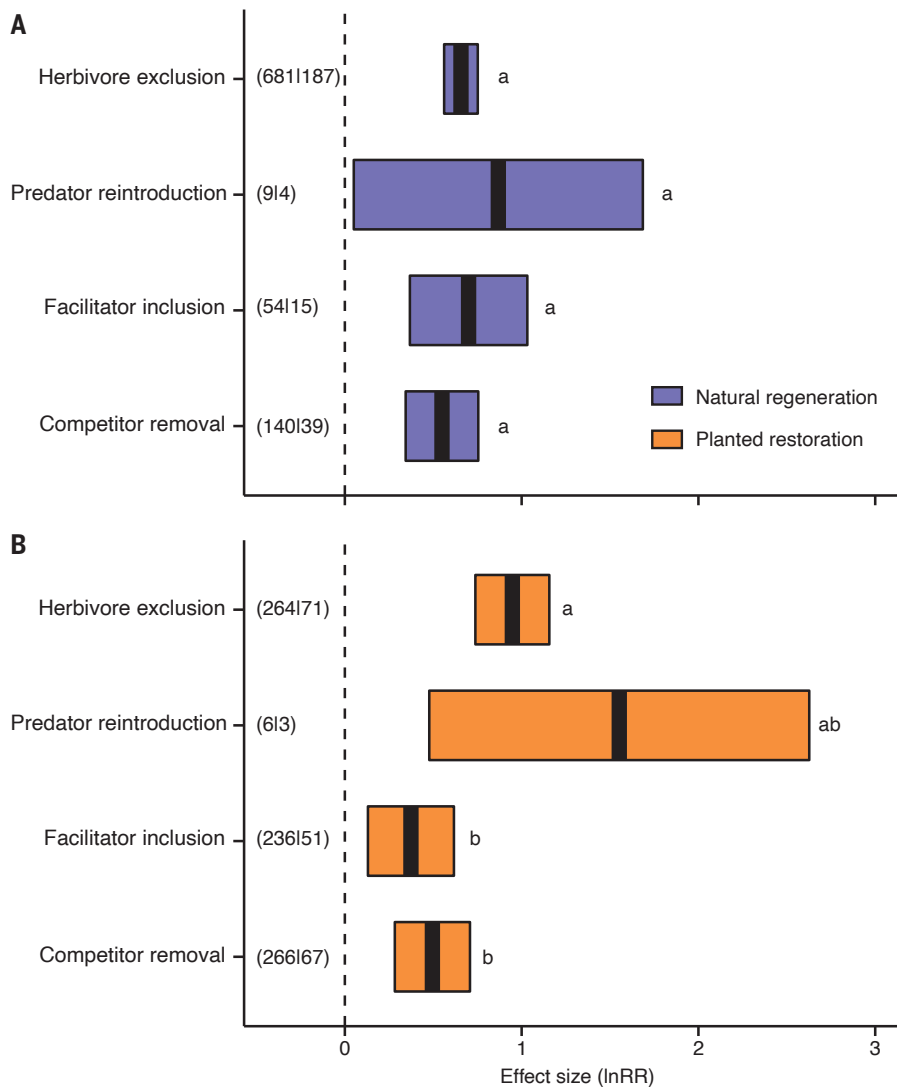


Fig. 4. Effects of managing herbivory in comparison to managing plant-plant interactions. Management of herbivory occurred by herbivore exclusion or predator reintroduction, whereas management of plant-plant interactions occurred by facilitator inclusion or competitor removal. **(A and B)** Effect sizes of management for natural regeneration (A) and planted restoration (B). Effect sizes are log response ratios (lnRR), and positive values indicate that management enhanced vegetation abundance. Center bolded lines represent mean effect sizes, and error bars represent 95% CI. Sample sizes are shown as number of tests|number of articles to the left of each bar. Bars that share a letter (i.e., a and/or b) do not differ significantly from one another ($P > 0.05$, based on post hoc multiple comparisons with Holm correction).

The effect sizes of herbivores at restoration sites also varied across plant functional groups. Herbivores more strongly reduced the abundance of woody versus herbaceous and mixed vegetation under natural regeneration in terrestrial biomes (Fig. 3E), where early successional shrubs and trees often have relatively few defenses against herbivory (25). This finding corroborates studies that have shown that herbivore exclusion accelerates woody encroachment in grasslands (30) and might decrease plant functional diversity in tropical forests (31). In aquatic biomes, however, herbivore effects were stronger for herbaceous and macroalgal vegetation than for woody vegetation under

natural regeneration (Fig. 3F), likely because woody plants in aquatic biomes are less palatable or better defended against herbivory (32). Nonetheless, these patterns disappeared with planted restoration, where herbivore effects were generally strong regardless of biome and plant life form (Fig. 3, E and F). This finding suggests that the susceptibility of propagules used in planted restoration may not mirror that of naturally regenerating plants (33). Furthermore, herbivores often reduced the abundance of naturally regenerating native plants more than exotic plants (fig. S16), a pattern consistent with the enemy release hypothesis (34).

Not surprisingly, variations in the effect size of herbivores on vegetation abundance and diversity were additionally explained by herbivore functional groups, the cause of degradation, and the study methodology, including plot size and study duration (Fig. 3 and figs. S15, S17, and S18). For example, herbivore effects might strengthen with study duration (Fig. 3, A to D). This supports the idea that herbivores have accumulating effects across plant generations or successional stages (25), although the regeneration of woody plants can take much longer than the time period covered in most studies (table S11). Herbivore effects on plant diversity might strengthen or weaken with plot size, whereas effects on plant abundance at restoration sites were generally observed regardless of plot size (Fig. 3, A to D). Although aquatic restoration studies often used small plots (table S11), many terrestrial natural regeneration studies with >1 -ha plots consistently reported strong herbivore effects on vegetation abundance (mean effect size: -0.73 ; 95% CI: -1.00 to -0.46) and diversity (mean effect size: -0.31 ; 95% CI: -0.54 to -0.09). These findings, along with well-documented large-scale impacts of changes in herbivore populations on vegetation (9, 35), suggest that the effects of herbivores may scale up to real-world restoration settings.

Managing herbivory to enhance restoration success

The effects of herbivores at restoration sites can be managed through plant-based interventions, such as prioritizing revegetation at sites less affected by herbivores or using planting strategies that are robust to herbivory (e.g., planting at high densities or with grazing-resistant species). Our synthesis found that excluding herbivores with physical enclosures, insecticides, or deterrents, which is a consumer-based intervention more suited for small-scale restoration, increased vegetation abundance by 93 and 158% at natural regeneration and planted restoration sites, respectively, relative to plots open to herbivores (Fig. 4). Introducing predators, another consumer-based intervention, increased vegetation abundance by 138 and 372% at natural regeneration and planted restoration sites, respectively (variations in these effects were likely inflated by small sample size; Fig. 4), which supports calls for trophic rewilding (15). Both types of consumer-based intervention generally improved restoration by magnitudes that were comparable to or greater than those achieved by managing plant competition or facilitation (Fig. 4) across terrestrial and aquatic biomes (table S14) in tropical, subtropical, and temperate regions (fig. S19), including when accounting for sample-size differences through bootstrap resampling (table S15) (17).

Our findings offer insights toward achieving myriad restoration commitments. Massive

revegetation efforts are being implemented globally, including the Bonn Challenge (36), Africa's Great Green Wall (37), and the Blue Carbon Initiative (38). By demonstrating global, substantial impacts of herbivores on the abundance and diversity of vegetation under restoration, our study suggests that revegetation efforts, if implemented merely by removing the cause of degradation, recreating abiotic conditions, or planting propagules, are unlikely to achieve maximal outcomes. Rather, substantial improvements can be achieved by comanaging herbivory (by either plant- or consumer-based approaches). By revealing climates and other moderators of variations in herbivore effects at restoration sites, our study can help restoration practitioners pinpoint where and when managing herbivory may be particularly crucial, including in the tropics (Fig. 1C), where global priority areas for vegetation restoration are concentrated (39), and in hot, dry regions as well as in the years ahead with respect to future climates. Indeed, as climate change and human activities, which are often beyond the immediate control of local managers, continue to disrupt food webs and affect vegetation through top-down processes (10, 40, 41), managing herbivory may become increasingly relevant and tractable for enhancing recovery and resilience (42).

Interpretation of our results within the following context can provide guidelines for restoration practice. First, the causes of amplified herbivore effects are often site-specific, including (i) predator loss (9), (ii) increases in herbivore density or consumption (43), and/or (iii) decreases in plant resource and resistance (40), each of which requires distinct interventions. For certain herbivore species that are endangered or threatened or that may facilitate plant establishment through ecosystem engineering, by preferentially consuming competitive weeds or by promoting seed dispersal at low population densities (44, 45), plant-based interventions may be more appropriate than consumer-based interventions, so that vegetation restoration serves as a foundation for restoring the whole ecosystem, including endangered or threatened fauna. Second, restoration practices should be bounded within the broader socioeconomic context. Reintroducing wild predators, for example, may be undesirable because of human-wildlife conflicts in farmed landscapes or urban environments. In such cases, managing herbivory through plant-based interventions or by introducing

predator cues (mimics, sounds, or chemical signatures) may be possible solutions, especially where predator effects are predominantly driven by fear (46). Third, although we focused on herbivores (17), best practices should combine approaches and account for other biotic (e.g., parasites, omnivores, and microbes) and abiotic (e.g., nutrient and hydrology) factors (11, 47), including potential synergistic or additive interactions of herbivores with abiotic stressors at restoration sites (47). Developing more-integrative restoration approaches is critical for fulfilling vegetation's enormous capacity for mitigating climate change, supporting biodiversity, and promoting sustainable development.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.add2814
Materials and Methods

Figs. S1 to S19

Tables S1 to S15

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Herbivory limits success of vegetation restoration globally

Changlin Xu, Brian R. Silliman, Jianshe Chen, Xincheng Li, Mads S. Thomsen, Qun Zhang, Juhung Lee, Jonathan S. Lefcheck, Pedro Daleo, Brent B. Hughes, Holly P. Jones, Rong Wang, Shaopeng Wang, Carter S. Smith, Xinqiang Xi, Andrew H. Altieri, Johan van de Koppel, Todd M. Palmer, Lingli Liu, Jihua Wu, Bo Li, and Qiang He

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Editor's summary

Restoring vegetation to degraded areas, either through planting or by encouraging natural generation, is a prominent strategy for conservation and nature-based climate solutions. However, restoration efforts are not always successful and can take a long time to reach pristine conditions. Xu *et al.* performed a global meta-analysis to ascertain how herbivory affects restoration success in both terrestrial and aquatic systems (see the Perspective by Villar). They found that herbivory has negative effects on plant abundance and diversity at restoration sites, even more than in undisturbed ecosystems, and this effect was strongest at sites with actively planted vegetation. Their findings suggest that excluding herbivores or reintroducing predators may aid restoration efforts in many locations. —Bianca Lopez

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