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Review

Enhanced but highly variable biodiversity outcomes from coastal restoration: A global synthesis

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SUMMARY

Coastal ecosystems are being restored to combat environmental degradation and biodiversity loss. Colonization of restored sites by non-habitat-forming animals improves outcomes for ecosystems and society, yet there has been no review of how animals respond to coastal restoration. Here, we extracted 5,133 response ratios from 160 studies to show how coastal ecosystem restoration benefits animals as individuals, populations, and communities. Abundances and diversity at restored sites were greater than at degraded (61% and 35%, respectively) and unstructured (42% and 37%) control sites and similar to those at natural reference sites (both within 2%). Individuals in restored sites were similar in condition to those within control and reference sites. However, responses among projects were highly variable and rarely related to restored site maturity or characteristics, presenting a challenge for predicting outcomes and highlighting the need to improve restoration techniques, monitoring, and reporting. Nevertheless, studies so far suggest coastal restoration benefits biodiversity.

INTRODUCTION

The pace and severity of environmental degradation necessitates billions of dollars of investment to restore lost ecosystems and save imperiled biodiversity.[1–4] At the interface of land and sea, coastal areas attract dense human populations and are highly affected.[5,6] Bolstered by international calls to action, including the United Nations (UN) Decade of Ecosystem Restoration[7] and the Kunming-Montreal Global Biodiversity Framework,[8] global efforts to restore saltmarshes, mangroves, seagrasses, macroalgae, and coral and shellfish reefs are accelerating.[7,9] While restoration planning, actions, and monitoring have focused historically on changes in abiotic and vegetation indicators and ecosystem services benefits,[10] attaining the optimum outcomes also requires an understanding of how restoration affects non-habitat-forming animals (hereafter, animals). Outcomes for animals are often a central goal of restoration plans and animal recovery may be part of policy commitments. For example, delivering sufficient recovery for threatened species can be legal requirement in environmental offset programs[11,12]; maximizing biodiversity is a core principle in conservation initiatives (e.g., the “Mangrove breakthrough”[13]), and habitat restoration can be a priority action for protected species conservation.[14] Animals also support vital functions that facilitate habitat recovery and support ecosystem services,[15–17] and they provide commercial and cultural incentives that bolster public and political support for restoration.[18–20]

How animals respond to coastal restoration efforts, however, is largely unknown. Combined with the high level of uncertainty in restoration outcomes more broadly, this presents a possible challenge for managers seeking biodiversity outcomes from coastal restoration and for policy makers setting targets.[21] Uninformed restoration targets and policies have implications for the effectiveness of restoration actions and for how the public and policy makers view restoration.[22] Synthesizing knowledge about how animals respond to coastal restoration and the variability around these estimates can form the basis for better predicting outcomes. This will help to develop restoration practices that more reliably meet targets, inform strategies to anticipate and plan for risks and uncertainty, and lead to more scientifically credible restoration targets and policy.[23]

Currently, it is often assumed that restoring habitat will guarantee animal recolonization; this is known as the Field of Dreams hypothesis (i.e., “if you build it, [they] will come”).[24] The unassisted return of animals to restored sites, however, may not occur.[25] Evidence from meta-analyses at high levels of biological organization and broad ecosystem groups on animal recovery rates and trajectories within restored sites (including freshwater wetlands and terrestrial systems) suggests that recovery has been lacking,[26] slow,[27] or slowing down over time as natural levels are approached but not reached.[28–30] Habitat suitability and animal occupation of restored sites might change through time as different resources are returning. For instance, bird guilds can vary in terms of when they recolonize replanted sites as a function of when their required habitat resources develop.[31] Quantifying animal responses to coastal restoration can reveal variation in how different taxa respond to restoration, which helps identify opportunities for improving restoration actions.[28,32] Syntheses of available animal data across multiple coastal systems and taxonomic groups is useful for informing restoration projects and predicting outcomes, and meta-analyses can provide rigorous theoretical tests about restoration trajectories and evaluations of strategies to maximize outcomes.[28]

There are two aspects of animal responses to restoration that need to be quantified. The first is population- and community-level responses, which are relatively well studied. A second need is to quantify whether the animals colonizing restored sites contribute to population persistence. It is important that restoration sites provide a suitable environment for animals to survive, grow, and reproduce, rather than being sinks that rely on constant immigration of new animals.[33] The likely contribution to population persistence can be estimated by measuring survival, reproductive rates, and individual condition. A mismatch between population and fitness outcomes is concerning because it could indicate that restored sites attract animals but are suboptimal for population persistence because other drivers of degradation, such as pollution, remain (e.g., where the restored habitat functions as an ecological trap[34]). For instance, some freshwater marsh restoration sites have similar population abundances to reference sites, but animal survival and reproduction is lower in the restored sites.[35,36] A synthesis of community-, population-, and individual-level measures is therefore necessary to comprehensively evaluate coastal restoration initiatives.

A quantitative synthesis of research into animal responses to restoration in coastal ecosystems can also guide future practice and identify research trends and gaps.[37,38] Although some ecosystem- and taxon-specific analyses are starting to be published,[29,39,40] there has been limited attention on comparisons across broad taxonomic groups and habitat types, particularly on comparing metrics of animal fitness with abundance and community indicators.

We used a quantitative synthesis of research into animal responses to coastal restoration for the objective of identifying (1) trends in the study of animals in restoration across habitats, response metrics, animal taxa, and the globe; (2) whether and how much restoration benefits animals; (3) how benefits vary by response metric, taxa, habitat, and restoration method; and (4) the trajectory of animal responses. Using a systematic literature search and meta-analysis, we analyzed how animals responded to the restoration of saltmarshes, mangroves, seagrasses, macroalgae, and coral and shellfish reefs. We found that abundances and diversity at restored sites were greater than at degraded and unstructured (e.g., bare substrate) control sites and similar to those at natural reference sites. Individuals in restored sites were similar in condition to those within control and reference sites. Across habitat types and taxa, animal responses to restoration were highly variable and were rarely related to restored site maturity or characteristics. Such high variability presents a challenge for predicting restoration outcomes, potentially leading to a mismatch between realized outcomes and policy targets. However, our synthesis suggests that coastal restoration is likely to benefit animal biodiversity and can inform restoration planning, practice, target setting, and social and policy expectations.

RESULTS

Summary of studies measuring animal responses

Our final dataset contained 5,133 response ratios from 160 papers (see Table S1 for a summary of the studies included in the formal meta-analysis). Studies documenting animal responses to coastal restoration were overwhelmingly conducted in the United States (87 papers), followed by China (13), Indonesia (seven), Philippines (six), and Australia (five; Figure 1A). The number of studies reporting animal responses has increased approximately in proportion with the increase in studies on coastal restoration more generally (Figure 1D). In terms of the distribution of studies across ecosystem types, the trend is toward evenness (except for the understudied macroalgae) following an early (pre-2008) dominance of saltmarsh studies, and a more recent increase in oyster reefs (Figure 1D). However, the number of response ratios extracted varied considerably among ecosystem types, with saltmarsh and oyster reefs having the most response ratios (Figure 2). The median time from restoration to when animals were monitored was 4 years (6.4 ± 8.6 years; mean ± SD), and 34% of studies (54 out of 160) monitored sites across multiple years.

The three most common monitoring methods for population and community metrics were collections (e.g., netting, 85% and 80%, respectively), visual surveys (13% and 18%), and camera surveys (1% and 2%; Table S2). Given the strong bias toward collections, we did not attempt to evaluate differences among methods. Individual and fitness metrics were evaluated on collected animals (93% and 53%, respectively), with enclosures (17%), tethering (14%), and visual methods (10%) also used to measure fitness (Table S2).

Saltmarshes were the most studied of the six ecosystems, followed by oyster reefs, mangroves, seagrass, coral reefs, and macroalgae reefs (Figure 2). Crustaceans and fish (including where the collective term "nekton" was used) were the most studied taxa, followed by gastropods, worms, bivalves, and birds, with a statistically significant difference in the distribution of taxonomic groups across ecosystem types (Figure 2; $\chi^2_{40} = 65.9$, $p = 0.006$). More than half of the studies compared animals in restored sites to a natural reference site (68%), while 33% used a degraded control site and 24% used an unstructured control site (note here and below that percentages can sum to greater than 100 as many studies include multiple levels of each factor). Animal responses related to populations (e.g., abundance) were quantified in 93% of studies, while those related to community (e.g., richness; 56%), individuals (e.g., size; 15%), and fitness (e.g., survival; 8%) were quantified less frequently.

For individual and fitness metrics, saltmarshes were the most studied of the six ecosystems, fish were the most studied taxon, and size was the most measured metric (Figure 2).

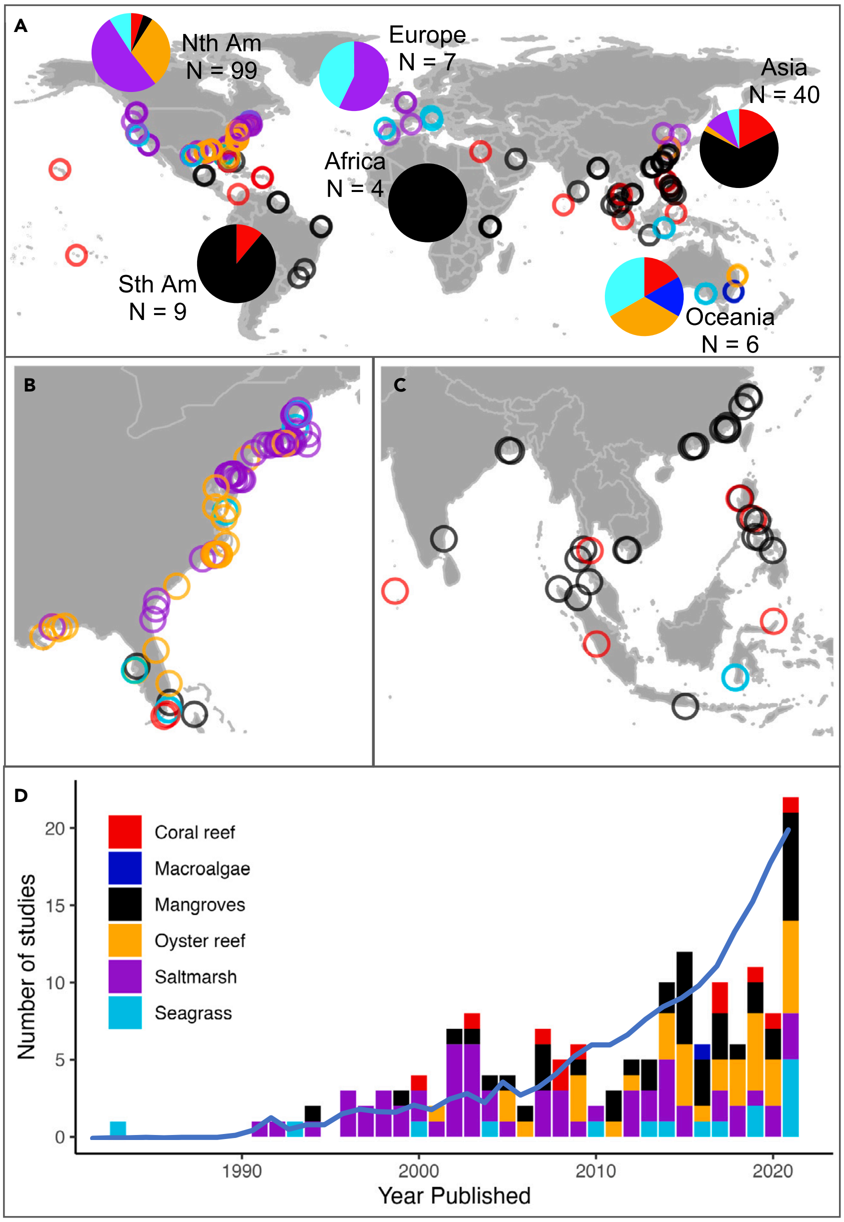

Figure 1. Research effort for studies quantifying animal metrics in both restored and control/reference sites

Location of sites (A) globally, in (B) east coast United States, and in (C) Asia (points are jittered to aid visualization), and (D) the number of studies published per ecosystem type, with the general trend in all publications on coastal restoration over the same period (blue line; N = 20,776); Web of Science search: coast* OR reef OR coral OR oyster OR shellfish OR kelp OR alga* OR seaweed OR saltmarsh OR “salt marsh” OR “tidal marsh” OR eelgrass OR seagrass* OR “sea grass” OR mangrove* or mangal*) AND (restoration OR rehabilitation). N values are the papers included in the formal meta-analysis (N_{TOTAL} = 165 papers, since five studied two habitat types and so are shown twice in A).

Comparisons to degraded and unstructured controls

Metrics of animal communities, populations, and individuals are higher in restored sites compared to degraded and unstructured controls. Animal communities were 35% more diverse at restored sites than degraded (95% confidence interval [CI], 16%–56%) and 37% more diverse than unstructured (21%–57%) controls (Figure 3). Animal communities were significantly (i.e., non-overlap of 95% CIs with zero) more diverse in restored sites for coral reefs relative to degraded sites (mean: 165%); oyster reefs relative to unstructured sites (77%), and fish relative to degraded (61%) and unstructured (132%) sites (Figure 4; see Table S5 for all percentage changes). Different community metrics—richness, diversity, and evenness—showed similar patterns (Figure S1).

Animal populations were 61% more abundant at restored sites compared to degraded (95% CI, 34%–93%) and 42% more abundant than unstructured (12%–81%) controls (Figure 3). Animal populations were significantly more abundant in restored sites for coral reefs relative to degraded sites (mean: 220%); oyster reefs (46%) and saltmarshes (232%) relative to unstructured sites; crustaceans (116%) and fish (77%) relative to degraded sites; and birds (508%), bivalves (216%), crustaceans (58%), gastropods (73%), and worms (86%) relative to unstructured sites (Figure 4; see Table S5 for all percentage changes). Population responses for individual taxa by habitat type combinations showed similar trends, although with very high variance for most combinations (Figure S2).

Individual metrics (e.g., size, mass) were similar in restored sites compared to degraded (9%; −12% to 35%) and unstructured (9%; −26% to 60%) sites, while animal fitness (e.g., survival, condition) in restored sites was higher relative to degraded sites (127%; 27%–305%) and similar to unstructured sites (−22%; −64% to 67%; Figure 3). Significant positive effects, where individual animal metrics were greater in restored sites, existed for: coral reefs relative to degraded sites (102%); oyster reefs relative to unstructured sites (7%); and fish relative to unstructured sites (7%; Figure 5). Significant positive effects for fitness, where animal fitness was greater in restored sites, existed for fish relative to degraded sites (133%; Figure 5). There were no significant negative effects (see Table S6 for all percentage changes).

Comparisons to natural reference sites

Animal populations were comparable between restored and natural reference sites (2%; −11% to –18%; Figure 3), showing that restored sites reach parity with respect to abundance and biomass metrics. A significant positive response was found for gastropods (52%), while the only negative response was for crustaceans (−20%; Figure 4). Population responses for individual taxa by habitat type combinations showed similar trends,

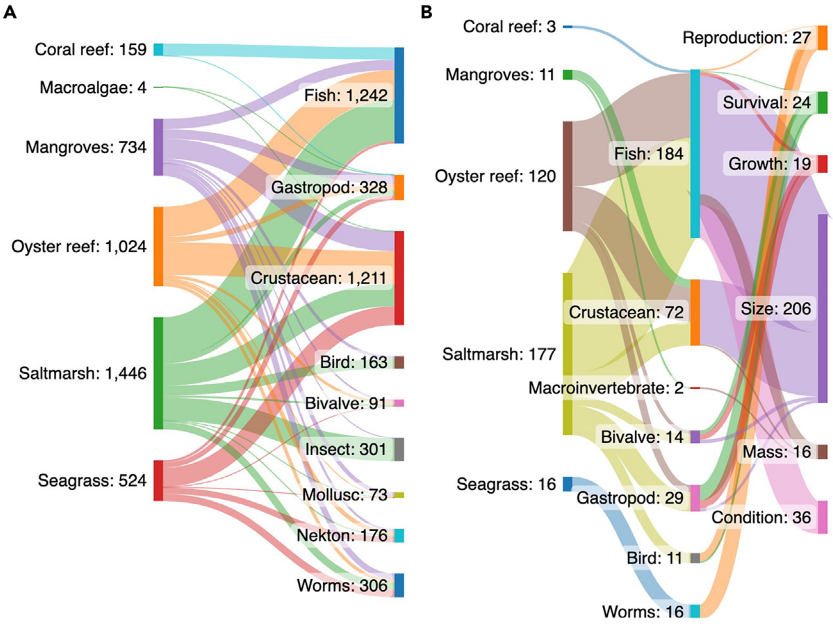

Figure 2. The division of study effort across ecosystem types and taxa

Sankey diagram showing the number of response ratios by ecosystem type and taxonomic group for (A) the entire dataset and (B) the individual and fitness metrics.

with very high variance for most combinations (Figure S2). Similarly, animal communities were comparable between restored and natural reference sites (−1.5%; −11% to 9%; Figure 3). Significant positive responses existed for birds (34%) and nekton (23%), while negative responses were found for macroalgae (−71%) and gastropods (−23%; Figure 4). Individual (11%; −8% to 35%) and fitness (47%; −10% to 141%) metrics were also similar in restored and reference sites (Figure 5). Individual animal metrics were significantly greater in restored sites for mangroves (94%) and significantly lower for crustaceans (−15%; Figure 5). Significant positive responses for animal fitness existed for seagrass (920%) and worms (920%; Figure 5).

A lack of trajectories as restored sites mature

We tested for an effect of time since restoration (TSR) on animal responses. We tested a three-way interaction of restored habitat type, control/reference site type, and taxonomic group, finding significantly different trends through time for population metrics ($F_{22} = 1.45$, $p = 0.048$; Table S3, but note that many combinations of these factors did not exist in the database). Of the combinations that existed, 77% of the trajectories did not significantly change as restored sites mature. This was true whether we used only data from sites with more than one temporal data point (Figure 6), all data with a TSR value (Figure S3), or when the dataset was condensed by summing the raw abundances for each species into a single value per taxa per site (Figure S4). Population abundances within mangroves and saltmarsh showed negative trends in restored relative to reference sites, whereby restored sites had greater abundances initially, which converged toward, or even below, reference sites over time (Figure 6, blue curves). None of the three factors or their interactions were significant for community-level response trajectories, and we found no evidence of community-metric trajectories significantly increasing or decreasing as restored sites matured (Figures S5 and S6). There were insufficient data on individual and fitness metrics.

The effect of restoration methods and characteristics

Overall, restoration methods that change habitat faster, and larger sizes of restored habitats, did not have greater positive effects on animal metrics. Although two methods that change habitat quickly—exotic species removal in saltmarshes (exclusively *Phragmites australis*) and planting of seagrasses—showed some evidence of stronger positive effects on population-level metrics than other, often slower, restoration methods (Figure 7); these were not consistent across comparator sites (i.e., across reference, degraded, and unstructured sites). Overall, different restoration methods generally led to similar mean responses (with high variability; Figure 7). The long-term effects of these practices is not so clear; for instance, removal of exotic species may provide quick returns in species abundance, but these effects may not be lasting without continuous removal. No clear differences existed for community metrics by restoration method (Figure S8), and there were insufficient data on individual and fitness metrics.

We evaluated the influence of restored habitat size on population-level responses for the two ecosystem types with sufficient data and those for which we could be confident in the sizing (e.g., habitat size for patchy ecosystems such as seagrass, oyster, and coral reefs was often difficult to discern). We found no evidence that responses differed based on restored area, despite size differences of several orders of magnitude (Figures S9 and S10), and there were insufficient data on community, individual, and fitness metrics.

DISCUSSION

How animals respond to coastal restoration efforts is crucial to inform on restoration planning, target setting, and providing realistic expectations; however, this information is largely unknown. We found that animal population sizes and community diversity within restored coastal habitats were on average between 35% and 61% higher than in degraded and unstructured control sites. These metrics also reached parity with natural reference sites, contrary to our hypothesis that they would not. Restored sites also harbored individuals that were in similar or better condition than those in control and reference sites. However, across ecosystem types, taxonomic groups, response metrics, and restored site characteristics, there was very high variability in how animals responded to restoration.

Still, some strong trends for population metrics highlight the benefits restoration can bring to meeting the conservation and food production objectives that often underlie restoration. For example, overall coral reef restoration was effective for restoring

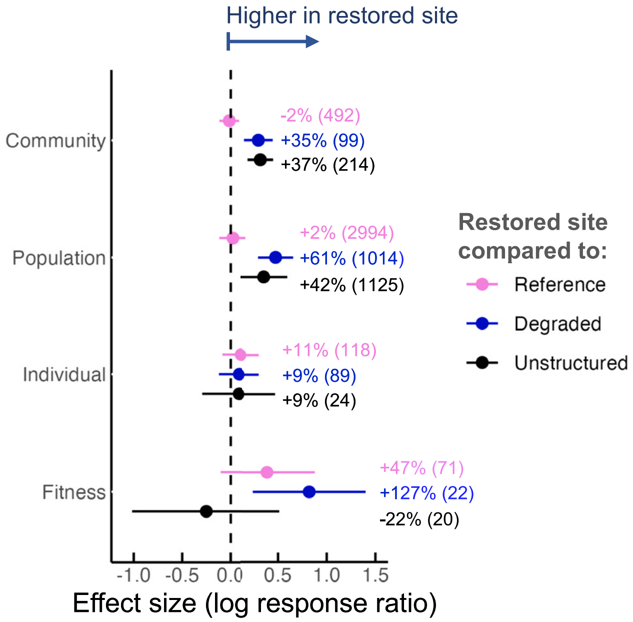

Figure 3. Forest plots of response ratios (and 95% CI) of community, population, individual, and fitness metrics, pooling across ecosystem type and taxonomic group

Values represent mean percentage difference between restored and reference/control, and sample size is shown in parentheses. Positive effect sizes mean the value for that metric was higher in restored sites, whereas negative values mean the value was lower in restored sites.

animal populations relative to degraded sites (e.g., Ferse, Ku'ulei et al., and Lecchini[41–43]). Since a core goal of coral reef restoration is often to enhance fish biomass for fisheries and the aesthetics of reefs for tourists, positive recovery of animals suggests that reef restoration can contribute to these goals, even if at small scale. Across ecosystem types, fish and crustaceans had consistent positive outcomes relative to degraded sites (e.g., De Santiago et al. and Kimball et al.[44,45]). Increased abundance of these taxa is often desired to meet recreational fishing or food security goals, so our results also provide support for restoration schemes that seek to enhance these opportunities. Less conspicuous taxonomic groups that provide important functions for restored ecosystem persistence and resilience[16] also benefited from restoration, such as the bivalves, gastropods, and worms, which often responded positively across ecosystem types.[46–48] Additionally, several threatened fish species (e.g., *Anguilla rostrata*, *Cynoscion regalis*, and *Pomatomus saltatrix*) responded positively to restoration,[49,50] suggesting restoration can contribute to threatened species conservation and management.

Individual and fitness responses suggest that restored sites, in general, are providing suitable habitat and the resources necessary for potential persistence. Although data—particularly with respect to long-term datasets—were scarce, animals were in similar condition within restored sites relative to reference sites. The much higher fitness (920%) of worms within restored seagrass relative to reference sites comes from Bell et al.,[51] who found substantially different reproductive metrics in the polychaete *Kinbergonuphis simoni*. Similar benefits of tidal restoration of a saltmarsh for the fitness of mummichog *Fundulus heteroclitus* were observed following tidal restoration.[52] Collectively, our results demonstrate that coastal restoration is providing benefits for animals and biodiversity.

Although our findings lend support to the Field of Dreams hypothesis that animals will come,[24,53] we observed very high variability across most responses, suggesting that positive animal responses are far from guaranteed. For instance, while coral reef fishes as a whole responded positively to restoration, in some key instances, larger-bodied reef fish showed negative or neutral trends across multiple sites.[54] Further, although birds typically responded positively to restoration, some work shows that restored saltmarsh sites do not provide suitable nesting habitat for threatened species such as the saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*).[55] The high variability in some restoration projects makes it difficult to discern clear trends or differences due to restored site characteristics (e.g., site age and size) or restoration methods. Capacity to delineate ecosystem types by how strongly or quickly they attract animals, or to delineate taxonomic groups with respect to how strongly or quickly they respond to restoration, was similarly challenging. Since attracting animals to, and supporting animals within, restored sites can improve ecosystem function; resilience and persistence; ecosystem service provision; and the capacity to meet environmental, social, and policy requirements, understanding the drivers of variability is critical. We therefore focus the rest of the discussion on unpacking several non-mutually exclusive drivers of high variability and the broader implications of our findings.

DRIVERS OF HIGH VARIABILITY IN ANIMAL RESPONSES TO COASTAL RESTORATION

Our results support previous suggestions that ecological responses to restoration actions at a site level can be hard to predict.[21,23,56] Although our analysis of 5,000+ datapoints revealed some overarching trends, responses across individual studies, taxa, and systems were highly variable, suggesting biodiversity benefits are not guaranteed. The variability we have captured might truly reflect variability in outcomes for animals at restored sites, which can be important for reducing biotic homogenization via promoting higher-level diversity.[23] Nevertheless, a lack of understanding of the drivers of variability can impede effective and efficient restoration, whereas the capacity to explain variability and predict outcomes can improve the cost-effectiveness of restoration and allow better planning around expected consequences.[21] In addition to general ecological stochasticity,[57] high variability in most responses observed is likely due to several interrelated drivers, including (1) community dynamics and ecological succession, (2) unmeasured and unaccounted covariables, (3) monitoring program design and reporting, and (4) review-specific features and limitations.

Community dynamics and ecological succession

Monitored population and community metrics across many taxa and ecosystem types did not increase as restored sites matured. The lack of trends may be partly related to our analysis focusing on restoration interventions directly aimed toward habitat-forming species (e.g., planting and reef creation), which consequently did not account for whether stressors and threatening processes

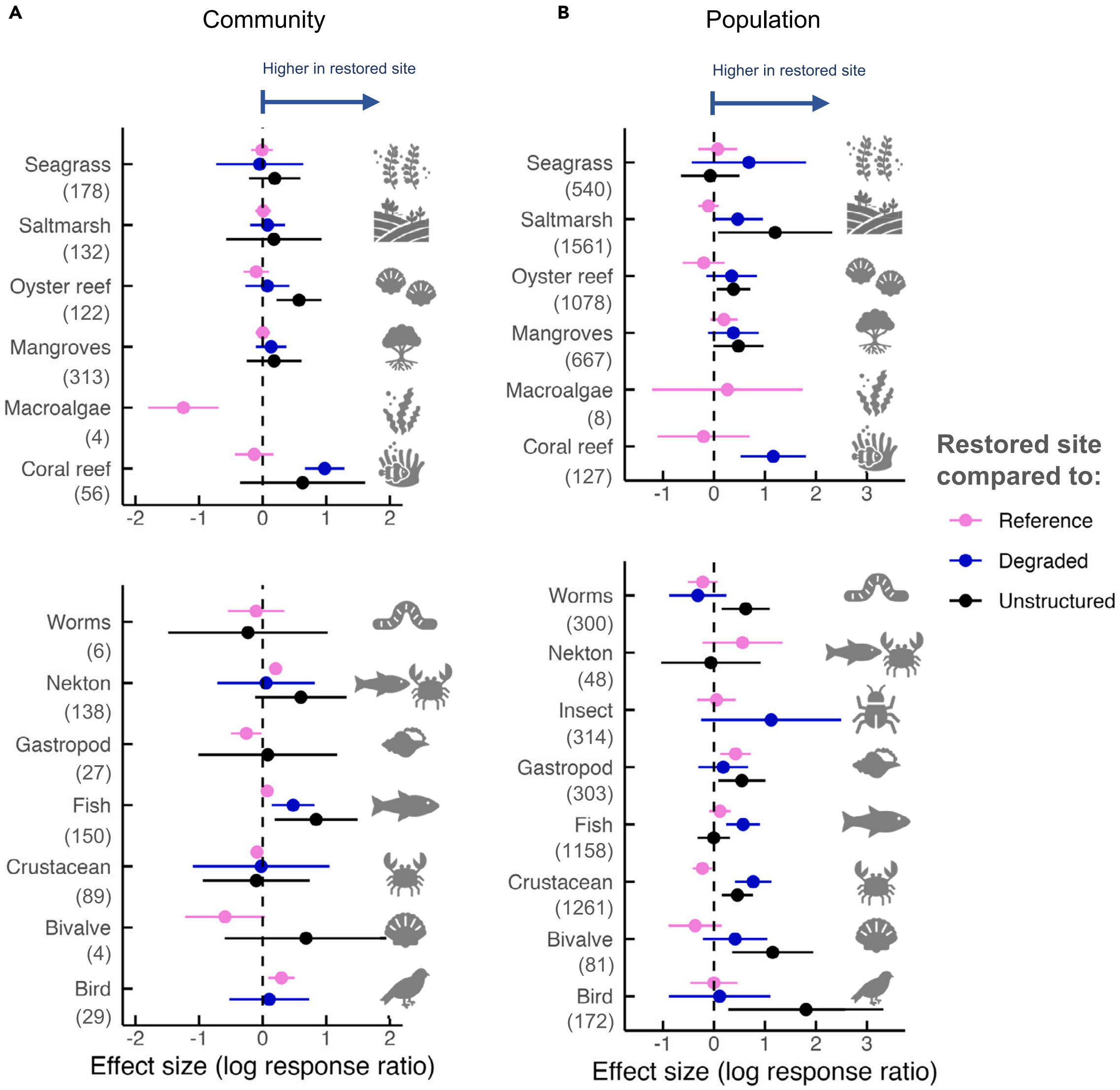

Figure 4. Forest plots of response ratios (and 95% CIs) of community and population metrics

(A) Community metrics.

(B) Population metrics. Presented are analyses for restored habitat types and taxonomic groups. All mixed models contained study ID and site ID as random factors. Values are the number of response ratios (summed across reference, degraded, and unstructured comparator sites). Positive effect sizes mean the value for that metric was higher in restored sites, whereas negative values mean the value was lower in restored sites.

(e.g., fishing) were removed prior to restoration. Thus, in some cases the recovery of animals may be slow if threatening processes are not first ameliorated.

Animals within mangroves and saltmarsh did show some significant negative trends through time for the abundance of certain taxa, counter to our hypothesis. Some negative trajectories saw higher initial values in restored sites later reach parity with natural reference sites (e.g., crustaceans and worms in mangroves), suggesting an initial high abundance of early colonizers giving way to less abundant late colonizers. Some taxa might therefore overshoot carrying capacities at restoration sites during the early colonization period, analogous to what typically happens in ecosystems during the expansion phase (r phase) of community succession.[58] As such, early (i.e., low TSR) evaluations of animal abundance may be overinflated in some cases.

Changes in composition as the system matures and communities re-assemble may be masked by a reliance on basic metrics such as species richness (the most common community-level metric in our dataset) or aggregate abundance of species within a taxon. More effective metrics, such as those related to functional diversity, species interactions, and the contribution of individuals to populations, may reveal important differences between restored habitats and reference and control sites.[59–61] Further, changes in assemblages are hard to interpret in a meta-analysis, because knowledge of local context is required to understand whether assemblage structure is shifting toward, or away from, an ecological baseline. Resolving assemblage changes would benefit from long-term and high-temporal-resolution monitoring and be most suitably interpreted on a site-by-site basis. The dearth of studies that monitor animal responses

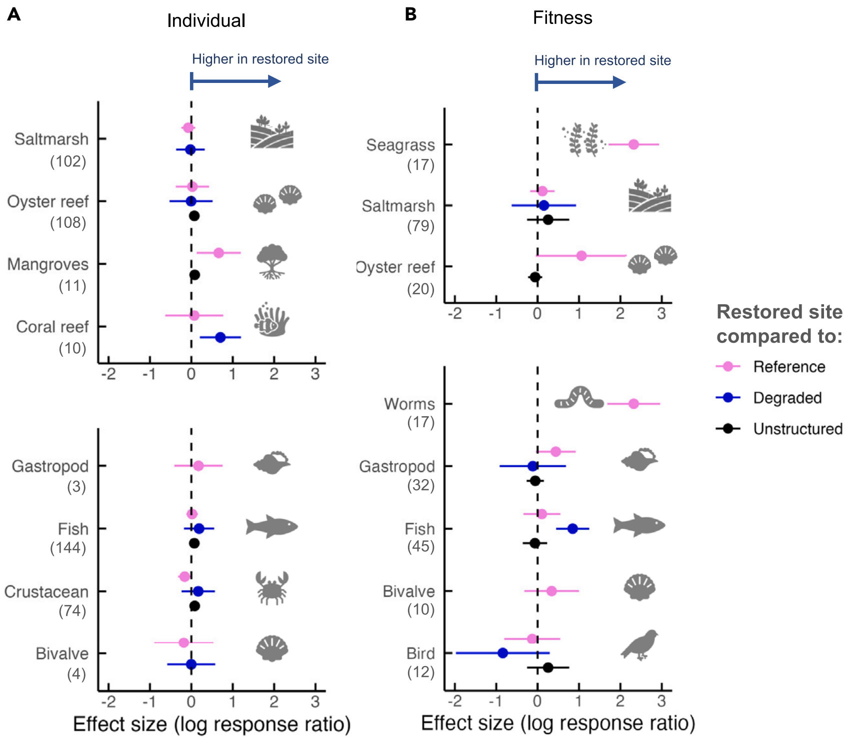

Figure 5. Forest plots of response ratios (and 95% CIs) of individual and fitness metrics

(A) Individual metrics.

(B) Fitness metrics. Presented are analyses for restored habitat types and taxonomic groups. All mixed models contained study ID and site ID as random factors. Values are the number of response ratios (summed across reference, degraded, and unstructured comparator sites). Positive effect sizes mean the value for that metric was higher in restored sites, whereas negative values mean the value was lower in restored sites.

through time, particularly with long-term datasets, limits capacity to more accurately identify the shapes and drivers of response trajectories; this is a consistent finding in similar reviews.[36] Developing this knowledge can enhance capacity to predict restoration outcomes and understand the drivers of variability in comparative studies, providing guidance toward expectations of animal colonization, inhabitation, and habitat use of restored sites as they mature.

Unmeasured and unaccounted covariables

Numerous factors can influence animal responses to coastal restoration, many of which were not measured or presented within studies. For instance, land-use legacies and the intensity of locally important stressors could affect animal utilization of, and how well animals fare in, restored habitats.[62] Further, spatial connectivity with alternative ecosystem types and source populations influences colonization rates and residency of animals in restored habitats, particularly in the short term.[63–65] Such cross-boundary connectivity can enhance ecological functions within restored sites,[66] and so habitat positioning within the seascape and the condition of connected habitats should be considered when undertaking evaluations of restoration outcomes and designing projects.[65] These and other unmeasured and unaccounted-for covariables are often not quantified in individual studies and could not be captured retrospectively in our meta-analysis. More work is needed to quantify the effect of covariables[9] and contrast outcomes based on various restoration methods and characteristics.[21]

Monitoring program design and reporting

Variability in monitoring design and the choice of indicator metrics might contribute to the variability in animal responses reported in our meta-analysis. The effectiveness of monitoring programs can vary in response to a range of factors, such as how well their objectives and design are grounded in ecological theory, their level of resourcing, and the objectivity of reporting of outcomes.[67,68] Many coastal restoration projects do not have clear objectives or an adequate design and include monitoring metrics poorly aligned with project objectives.[69] For instance, monitoring the survival of planted seedlings is a standard metric to determine the success of a mangrove restoration project, even though the primary goal may be improving fisheries production. We could not obtain data on the match between monitored variables and restoration objectives (in many cases it was not documented), so it was not accounted for in our analyses. Monitoring and reporting on outcomes from restoration activities are ultimately crucial for enabling adaptive management and evaluation of restoration techniques and actions.[70] Without effective monitoring and reporting, evaluating the success or failure of particular restoration projects, or identifying the reasons for the observed outcomes, is difficult. The Society for Ecological Restoration provides guidance on defining clear targets and planning a monitoring plan based on the project's objectives.[3]

Review-specific features and limitations

Our analysis has the typical limitations and biases of ecological meta-analyses and systematic reviews. Despite having >5,000 response ratios from 160 publications, when divided (unevenly) across ecosystem types, taxonomic groups, response types, comparator type (i.e., reference, degraded, and unstructured controls), and restored site maturity, sample sizes are lowered and effects were sometimes influenced by a handful of studies. Further, there are potential effects of geographic/language,[71] ecosystem type,[72] and taxonomic biases[73] that pervade the scientific literature and meta-analyses. We acknowledge the limitations these biases create for our results and concur with pushes toward more equitable and diverse science and improved global syntheses. We also focus on peer-reviewed published literature under the assumption that a peer-review process is preferred before data should be used to develop hypotheses or incorporated into broader studies. However, gray literature contains a wealth of useful information, and peer-reviewed studies may be biased toward successful restoration attempts (although extracting data from the

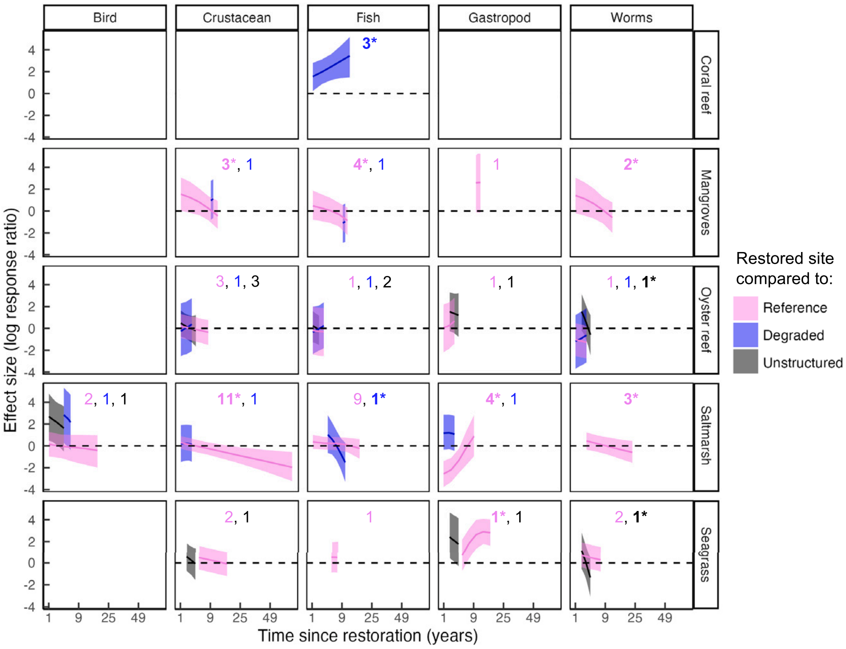

Figure 6. Response trajectories (and 95% CIs) in population-level metrics as restored sites mature for the most monitored taxa

Data are from studies that presented more than 1 year's worth of monitoring data for at least one site. Values are the number of studies from which data came, and asterisks signify statistically significant trajectories. TSR is square-root transformed, and GAMs are fitted with overall splines by control type and splines for control type by taxa and control type by habitat type. All mixed models contained study ID as a random factor. See Note S2 for full GAM models. For plots with all taxa, see Figure S7; for plots of all data with a TSR, see Figure S3; for plots of the dataset after it was condensed by summing the raw abundances for each species into a single value per taxonomic group per site, see Figure S4.

supplementary material—as done here—can reduce this bias[74,75]). Therefore, while our review is non-exhaustive, biased toward well-studied locations, ecosystems, and taxa, it provides a data-rich, quantitative synthesis valuable for understanding animal responses to coastal restoration efforts.

Moving forward

We found animal populations benefited from restoration, on average, but responses were highly variable. High variability presents a potential challenge for managers and policy makers seeking animal outcomes from restoration, because specific responses are not guaranteed on a project-by-project basis. Future work can use these quantitative estimates of animal responses to restoration actions and the uncertainty around those responses to better predict outcomes and, thus, to make future efforts more targeted with respect to how, what, and why we restore. In addition, this insight can inform offset schemes, restoration targets, and other policy commitments that may need to account for uncertainty in animal responses. Future work could also aim to identify how to deal with uncertainty, such as by quantifying appropriate multipliers for biodiversity offsets.[76,77] Despite clear benefits for animals from coastal restoration, in some cases, highly variable and thus uncertain outcomes may require planning for higher ratios of projects to expected outcomes to account for potential failures and help ensure positive outcomes ensue. Alternatively, portfolio approaches that spread risk may be required where biodiversity benefits could be low or highly uncertain.[78]

We finish by suggesting three strategies to help ensure that animal responses to restoration are better evaluated, and knowledge better utilized, in coastal restoration efforts. We need long-term monitoring of metrics that adequately measure what the goal is; metrics need to be simple enough to be used but meaningful enough to be informative. With this in mind, we acknowledge the additional resources required to meet the following ambitious strategies.

(1) Couple measures of abundance or diversity with information about animal fitness.[34,36] Although we found no evidence for lower fitness within restored sites relative to reference sites, fitness data were scarce. Therefore, the lack of evidence for lower fitness in restored sites could be due to a paucity of fitness data, be an accurate reflection of how restored sites are supporting animals, or be biased because fitness metrics were primarily measured on hardy or common species that may be less susceptible to poor habitat quality. Regardless, improved knowledge of fitness responses could improve our understanding of changes or differences in population- and community-level metrics and help us understand why some projects achieve desirable outcomes for animals whereas others do not.

(2) Ensure that the interactions, roles, and functions of animals are considered more frequently, including prior to restoration. Setting ambitious recovery targets necessitates that these interactions are accounted for, and one way to address this could be to adapt the methods proposed by Akçakaya et al.[60] to assess functionality for species (i.e., the degree to which a species is performing its role as an integral part of the ecosystem in which it is embedded) into a restoration context. Integrating multiple lines of evidence with respect to the animal community can provide more nuanced insights for predicting outcomes and refining methodologies.

(3) Correlate animal responses to the success of habitat-forming species to better understand these relationships. Such knowledge is useful for guiding future restoration, including the growing interest in, and application of, manipulating animals within restored sites to benefit from positive species interactions between habitat-forming species and animals (e.g., Derksen-Hooijberg et al. and Zhang et al.[79,80]).

EXPERIMENTAL PROCEDURES

Resource availability

Material availability

This study did not generate new unique materials.

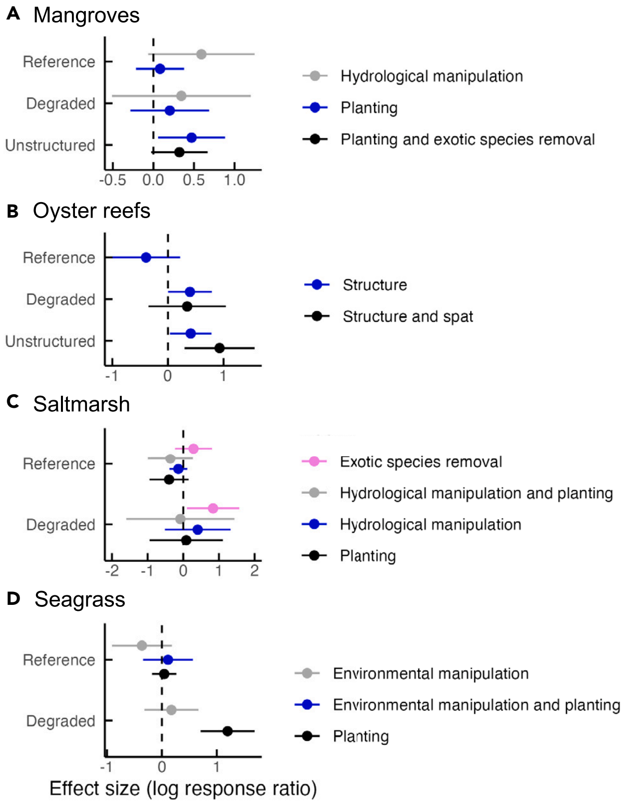

Figure 7. Animal responses to different restoration methodologies

Forest plots of response ratios (and 95% CI) for population-level metrics for the primary restoration method (>10 response ratios) for (A) mangroves, (B) oyster reefs, (C) saltmarsh, and (D) seagrass. Numbers represent the number of response ratios. All mixed models contained study ID and site ID as random factors. All mixed models contained study ID and site ID as random factors. Positive effect sizes mean the value for that metric was higher in restored sites, whereas negative values mean the value was lower in restored sites.

Data and code availability

This paper analyses existing, publicly available data (see Table S1 in supplemental information for a full list of the studies data were extracted from). Original code has been deposited at Zenodo under https://doi.org/10.5281/zenodo.10668821 and is publicly available as of the date of publication. Any additional information required to reanalyze the data reported in this paper is available from the corresponding author upon request.

Literature search

A literature search was performed on 3 December 2021 using ISI Web of Science and Scopus and the following term: TITLE (coast* OR reef OR coral OR oyster OR shellfish OR kelp OR alga* OR seaweed OR saltmarsh OR "salt marsh" OR "tidal marsh" OR eelgrass OR seagrass* OR "sea grass" OR mangrove* or mangal*) AND (restor* OR rehab*). Reference lists and databases from reviews were examined for additional studies. Excluding duplicates, 3,227 potentially relevant studies were assessed for inclusion (see Figure S11 for PRISMA flow diagram).

Data extraction, classification, and effect size calculation

To be included, a study had to (1) study saltmarsh, mangrove, seagrass, macroalgae forest, coral reef, or oyster reef ecosystems; (2) focus on actions directed toward the habitat-forming species, such as planting, translocations, deploying structure to explicitly attract habitat formers, exotic species removal, or restoring tidal flow to allow natural processes to reinitiate with respect to vegetation; (3) measure non-habitat-forming animal responses; and (4) compare animal responses to a comparative habitat, such as a natural reference site, a degraded control site, or an unstructured (e.g., bare sand) control site. Studies on creating protected areas, mitigating degrading factors such as contaminants, or deploying artificial structures without a direct intention of attracting the focal habitat-forming species were not included.

A suite of descriptors was extracted from each study, including publication details (journal, year published), study location (continent, country, latitude, longitude), year of the study, restored ecosystem type, restoration technique (e.g., planting, hydrological manipulation, exotic species removal), focal habitat-forming species restored, taxonomic information of the animal being monitored, response type measured (see Table S4), method used to monitor the animal, control habitat type (reference [i.e., natural], degraded, or unstructured), experimental design (e.g., control impact, before and after [BA]), TSR action in years, and the size of the restored habitat (ordinal categories: <1 ha, 1–10 ha, 10–100 ha, etc.). Several types of studies were not included due to an inability to calculate response ratios from the data, including those looking at stable isotopes, conducting only multivariate analyses of community composition, reporting responses as percentages, and studies that directly manipulated animals to examine ecosystem responses.

We extracted data from restored (impact) and control/reference sites from the text, tables, and figures using open-source graphical digitizer software[81] to calculate log response ratios (lnRRs). Where possible, species-specific data were extracted, otherwise taxonomic means (e.g., all fish) were extracted (lnRR showed no biases between these two; Figure S12). For BA and control/impact studies:

$$\ln[RR] = \ln[B \text{ or } R] - \ln[A \text{ or } C] \qquad \text{(Equation 1)}$$

and for BA–control/impact (BACI) studies:

$$\ln[RR] = \ln[R_A / C_A] - \ln R_B / C_B \qquad \text{(Equation 2)}$$

where R is the restored site mean, C is the control site mean, A is the after mean, and B is the before mean.[82,83] For studies with multiple, unpaired control sites, we averaged raw data from control sites and calculated an lnRR for each restored site. Since an lnRR cannot be defined for situations when one of the components (i.e., control or restored site value) is zero, and adding a constant to these values can lead to significant bias, we took the more conservative approach of excluding these data from further analysis. Where BACI designs had zeros for any of the four components, we decomposed these into control/impact or BA data in order to still calculate an RR, where possible. In total, 28% of the lnRRs were excluded from the main analyses, but these were not biased toward the zero value being associated with the restored site (44.4%) or the control site (56.6%).

Statistical analysis

Not all combinations of ecosystem type, taxonomic group, and response measured were exposed to restoration action, precluding the exploration of complex interactions. Instead, we examined taxon- and ecosystem-specific individual-, population-, and community-level responses to each driver independently. For these, we constructed a generalized linear mixed-effects model with the variable of interest (e.g., taxa) fitted as a fixed effect, and RefID (i.e., the study) and SiteID (i.e., the restoration site) fitted as random effects.[84] Site accounted for any correlation among observations at a given site and for common local environmental or contextual effects. The study random effect accounted for any systematic differences due to common regional environmental conditions or study-specific methodologies or biases. Our model structure therefore allowed us to analyze the multiple RRs from within a given study rather than having to aggregate data to a single mean value per study, and it ultimately accounted for non-independence of multiple entries extracted from the same study and multiple studies conducted at the same site (e.g., Krist and Davidson et al.[85,86]). While we did not weight our estimates due to issues with data availability and interpretation (see Note S1 for further justification), the random effects model automatically weights by the uncertainty of the estimates, since the regression analyses, and the variation in the regression estimates, were included as part of the model.[84] We produced unbiased parameter estimates and 95% CIs using restricted maximum-likelihood estimation (REML) and suppressed intercepts. We performed analyses using the lmerTest package[87] in R v.4.1.2[88] to build models and extract least-squares means and confidence intervals.[89]

To calculate response trajectories through time, we focused only on studies with multiple years of data from the same site(s) (N = 54 studies). We created a series of hierarchical generalized additive models (GAMs)[90] to predict trajectories for each response type, and each response type was fitted with the same model formula. We modeled the lnRR as a Gaussian response. We modeled change in the LRR over time with thin plate splines applied to the square root of TSR. We took the square root to reduce the influence of a few very high TSRs. The hierarchical component was structured to allow for different TSR trends by control types, then for the splines to vary by combinations of control type and habitat, and control type and taxa (i.e., two-way interactions between control type and taxa, and control type and habitat). Finally, we allowed for random intercepts by study. Degrees of freedom for the splines were adjusted to ensure the model was identifiable. Predictions and credible intervals were estimated using the empirical Bayesian approach, with study random effects set to zero, so predictions represent an average study.[91] Model formulas are available in Note S2.

After observing high variability in trajectories as restored sites mature (i.e., TSR), we decided to examine the influence of how we calculated our lnRR by running analyses using an addition two variations of the dataset: (1) all data with a value for TSR (N = 147 studies), and (2) the 54 studies with multiple years of data from the same site(s) but where single-species data for a site are combined to provide a mean value for each taxon.

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.oneear.2024.02.013.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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