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From the early Anisian onward, three successive diversity cycles are evident: Early Anisian–Early Carnian, Early Carnian–Early Norian, and Early Norian–Rhaetian (Figs. 2 and 3). The last cycle ends with a marked diversity decline through the Late Norian and Rhaetian, corresponding to the Triassic-Jurassic mass extinction (*19*).

Unlike in the Permian, where genera show uncorrelated to weakly correlated origination and extinction dynamics (Fig. 3 and table S2) [linear association between $\log(N_{Ori}^{t+1}/N_{Ori}^{t})$ and $\log(N_{Ext}^{t+1}/N_{Ext}^{t})$: $R^2 = 0.060$, $P = 0.56$ for Goniat; $R^2 = 0.536$, $P = 0.025$ for Ammon], Triassic ammonoids show highly coupled dynamics ($R^2 = 0.978$, $P = 1.2 \times 10^{-9}$) because of the large average proportion of sampled singletons [71% versus 19% (Goniat) to 53% (Ammon) before the PTB]. We investigated the Triassic ammonoid diversity dynamics through diversification models directly derived from the empirical origination and extinction rates (Fig. 4). Based on the overall geometry of the sampled time series (excluding the Late Norian and Rhaetian time bins, which correspond to the end-Triassic mass extinction), we selected two diversity-dependent constrained diversification models: the (evolutionary-based) logistic (*27*) and (population dynamics–based) hierarchical (*28*) ones. These models basically differ in the way origination and extinction rates linearly (logistic) or exponentially (hierarchical) relate to taxonomic richness, ultimately leading to a sigmoidal-shaped curve of richness changing through time modeled as a two-parameter logistic function or a three-parameter Gompertz function, respectively. All computations were done based on Maurer's per-taxon per-My origination and extinction rates (*28*) computed with or without singletons (*10*). These rates share the same statistical behavior as Foote's estimated per-capita per-My rates (*29*), with which they highly correlate (table S3). We selected Maurer's rather than Foote's rates because the later cannot be calculated for three of the four Early Triassic time bins, that is, when ammonoids actually recovered (table S2).

Model comparison using evidence ratios calculated from corrected Akaike information criterion values favors the hierarchical diversification model over the logistic one (table S5). Indeed, even if both models converge toward the same steady-state richness values (~70 sampled genera) (Fig. 4), the logistic model clearly fails to capture the Early Triassic nondelayed recovery dynamics, contrary to the hierarchical one. In addition, the empirical (log) richness-rates relationships (table S4) illustrate a possible niche incumbency effect (*30*). This hypothesis, which predicts that richness and extinction rates are independent, allows the estimate of an average steady-state generic niche saturation level of ~85% under the hierarchical model, compatible with species niche saturation levels previously published for various clades of marine organisms (*30*).

Numerous Lazarus taxa among benthic and pelagic mollusks reappear during the Smithian (e.g., *6, 31*). Coupled with the Triassic ammonoid

nondelayed diversity dynamics evidenced here, this suggests that complex trophic webs based on abundant and diversified primary producers were already functioning less than 2 My after the PTB and opens the possibility that heterotrophic taxa other than ammonoids also rapidly recovered. The end-Smithian global event, possibly linked to a late eruptive phase of the Siberian traps, initiated the conodont demise and corresponds to a major global change in the carbon cycle and climate (*8, 18, 20, 21*) but did not markedly delay the explosive recovery of Ceratitid ammonoids. This phased scenario for the Triassic biotic recovery accounts well for its generally accepted delayed character, which may reflect still inadequate sampling and time resolution and/or biased diversity estimates due to the lack of sampling standardization in the first million years after the PTB (*32, 33*). Recoveries obviously show environment- and clade-specific dynamics. Nevertheless, our results indicate that the time duration of the post-PTB recovery is likely overestimated, at least for some marine taxa.

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Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis

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Ecological restoration is widely used to reverse the environmental degradation caused by human activities. However, the effectiveness of restoration actions in increasing provision of both biodiversity and ecosystem services has not been evaluated systematically. A meta-analysis of 89 restoration assessments in a wide range of ecosystem types across the globe indicates that ecological restoration increased provision of biodiversity and ecosystem services by 44 and 25%, respectively. However, values of both remained lower in restored versus intact reference ecosystems. Increases in biodiversity and ecosystem service measures after restoration were positively correlated. Results indicate that restoration actions focused on enhancing biodiversity should support increased provision of ecosystem services, particularly in tropical terrestrial biomes.

Ecological restoration involves assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed, typically as a result of human activities (*1*). Restoration actions are increasingly being implemented throughout the world (*2*), supported by global policy commitments such as the Convention on Biological Diversity [article 8(f), (*3*)]. A major

goal of ecological restoration is the reestablishment of the characteristics of an ecosystem, such as biodiversity and ecological function, that were prevalent before degradation (4). Increasing attention is being given to the value of ecosystems in providing ecosystem services [i.e., "the benefits people obtain from ecosystems" (5)]. There is a widespread assumption that ecological restoration will increase provision of ecosystem services (6, 7), but this has not yet been systematically tested.

Ecosystem services with high value for supporting human livelihoods include carbon storage, regulation of climate and water flow, provision of clean water, and maintenance of soil fertility (5, 8). A lack of scientific understanding of the factors influencing provision of ecosystem services and of their economic benefits limits their incorporation into land-use planning and decision-making (9). Many restoration actions are undertaken with the aim of increasing biodiversity (4). However, despite being the focus of major research attention, the relation between biodiversity and provision of ecosystem services remains uncertain (10). Restoration actions can provide insights into the dynamics and functioning of ecological systems as they constitute a form of experimental manipulation (4). Consequently, examination of the effects of restoration actions could provide insights into whether increases in biodiversity are likely to be associated with greater provision of ecosystem services.

Here, we describe a meta-analysis of 89 published scientific assessments of the outcomes of restoration actions undertaken in a variety of ecosystems from all continents except Antarctica. We used a standardized procedure to select restoration studies from scientific bibliographic databases on the basis of the comparators used and the measures made (11). In these studies, ecosystems had been degraded by a wide variety of processes (Table 1). Restoration actions generally included the removal or amelioration of the factor causing environmental degradation and/or the reestablishment of key ecosystem components to influence the rate and direction of recovery. The simplest approach was to cease the damaging activity—for example, the abandonment of agricultural land ["passive restoration" (12)]. Active restoration approaches are summarized in Table 1.

Assessment of the impacts of restoration actions typically involved field-based comparisons of different intervention treatments (11). Time scales of the restorations ranged from <5

to 300 years. To ensure suitable baselines (13) for examination of restoration success, we restricted our analysis to those studies that compared restored (Rest), reference (Ref), and degraded (Deg) ecosystems within the same assessment. We define reference ecosystems as those not subjected to the environmental degradation that the restoration was intended to redress. The degraded system therefore represented the starting point of the restoration and the reference system represented the desired end point.

From the 89 studies, we extracted 526 quantitative measures of variables relating to biodiversity and ecosystem services, which were incorporated into a database. The ecosystem services were classified according to the scheme developed by the Millennium Ecosystem Assessment (5), which distinguishes four categories: (i) supporting (e.g., nutrient cycling and primary production), (ii) provisioning (e.g., timber, fish, food crops), (iii) regulating (e.g., of climate, water supply, and soil characteristics), and (iv) cultural (e.g., aesthetic value). We examined only the first three services, because cultural services were not measured explicitly in any of the studies that we analyzed. Measures of biodiversity were related to the abundance, species richness, diversity, growth, or biomass of organisms present. We calculated response ratios (14) of the restored ecosystems compared with both the reference [ln(Rest/Ref)] and degraded [ln(Rest/Deg)] ecosystems for each measure of biodiversity and ecosystem services. The individual studies were classified into four broad biome types, according to whether they were aquatic or terrestrial and whether they were located in tropical or temperate regions (11) (table S1).

Using Wilcoxon signed rank tests, we examined whether the response ratios were different from zero to ascertain whether restoration affected biodiversity and the provision of ecosystem services. We also tested whether response ratios differed among ecosystem service categories and among biome types with the use of Kruskal-Wallis tests. Our results indicate that measures of supporting and regulating ecosystem services and biodiversity across the whole data set were higher in restored than in degraded systems (response ratio > 0, Fig. 1A) but lower than in reference systems (ratio < 0, Fig. 1B). Provisioning services showed no effect of restoration, but the sample size for this type of service was low. Our data indicate that supporting services, which provide the basis for provision of other services, were restored more effectively than other service types.

It is sometimes questioned whether restoration actions can be effective in enabling degraded ecosystems to acquire the characteristics of reference systems (13). Median values of response ratios showed that biodiversity and ecosystem services (all three types combined) in degraded systems were only 51 and 59%, respectively, of those in reference systems. Median response ratios of restored systems were sub-

stantially higher than those of degraded systems, with values of 144% for biodiversity and 125% for ecosystem services. However, the restored systems were not fully rehabilitated, as median response ratios for biodiversity and combined ecosystem services were 86 and 80%, respectively, of those in reference systems.

Biodiversity and provision of ecosystem services in restored ecosystems were more similar to degraded or reference ecosystems in aquatic than in terrestrial biomes and in temperate than in tropical biomes (Fig. 2). Response ratios were not significantly different from zero in tropical aquatic systems, probably because this biome had low sample size. The temperate aquatic biome showed significant effects of restoration only on biodiversity. When compared with degraded ecosystems, restoration was associated with the largest increases in ecosystem services and biodiversity in tropical terrestrial ecosystems (Fig. 2).

Theoretical and empirical work has identified a variety of linkages between changes in biodiversity and the way ecosystems function (15). We tested the hypothesis that a change in biodiversity is positively associated with altered provision of ecosystem services by correlating biodiversity and ecosystem service response ratios across studies. Treating each study as an

Table 1. Summary of the types of human activity that resulted in degraded ecosystems and the forms of restoration action undertaken in the 89 studies included in the meta-analysis.

| Action	Number of studies
Degrading action	
Cessation of prescribed burning	3
Cultivation and cropping	13
Disturbance, excavation, or burial of substrate	15
Eutrophication	3
Hydrological disruption	21
Invasion by non-native species	4
Logging of trees	16
Over-grazing	5
Removal of carnivores or herbivores	3
Soil contamination	6
Restoration action	
Cessation of degrading action only (passive restoration)	13
Extirpation of damaging species (including non-natives)	8
Nutrient removal	3
Planting of forbs or grasses	12
Planting of trees	16
Reinstatement of burning	3
Reintroduction of herbivores or carnivores	3
Remodeling of topography	25
Soil amendments (to bind or dilute contaminants or restore fertility)	6

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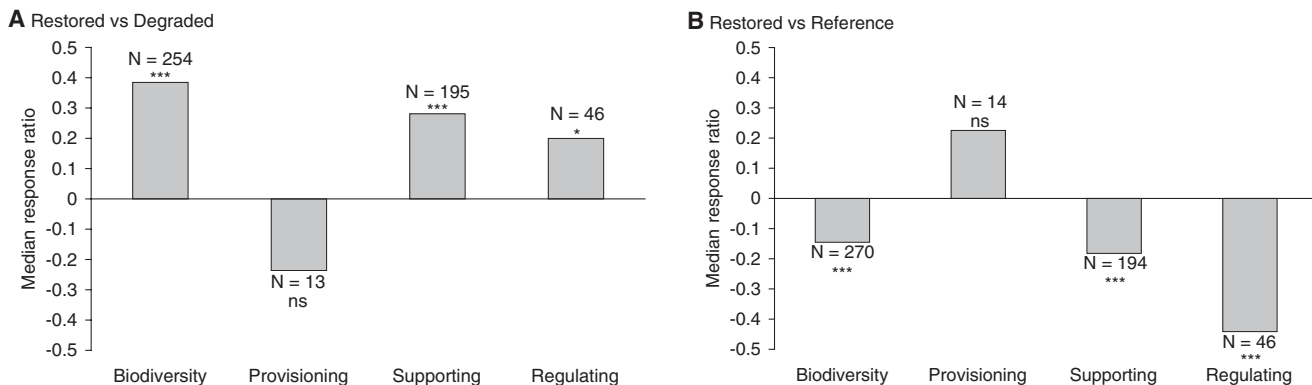
Fig. 1. Response ratios of biodiversity and ecosystem services in (**A**) restored compared with degraded ecosystems and (**B**) restored compared with reference ecosystems. All response ratios differed significantly from zero (Wilcoxon signed rank tests, ***$P < 0.001$, *$P < 0.05$), except those for provisioning services [not significant (ns) $P > 0.05$]. Significant differences were found between the response ratios for biodiversity and the three ecosystem service categories with the use of Kruskal-Wallis tests [restored versus degraded: H (the K-W test statistic) = 11, N (sample size) = 508, $P < 0.05$; restored versus reference: $H = 15$, $N = 524$, $P < 0.01$].
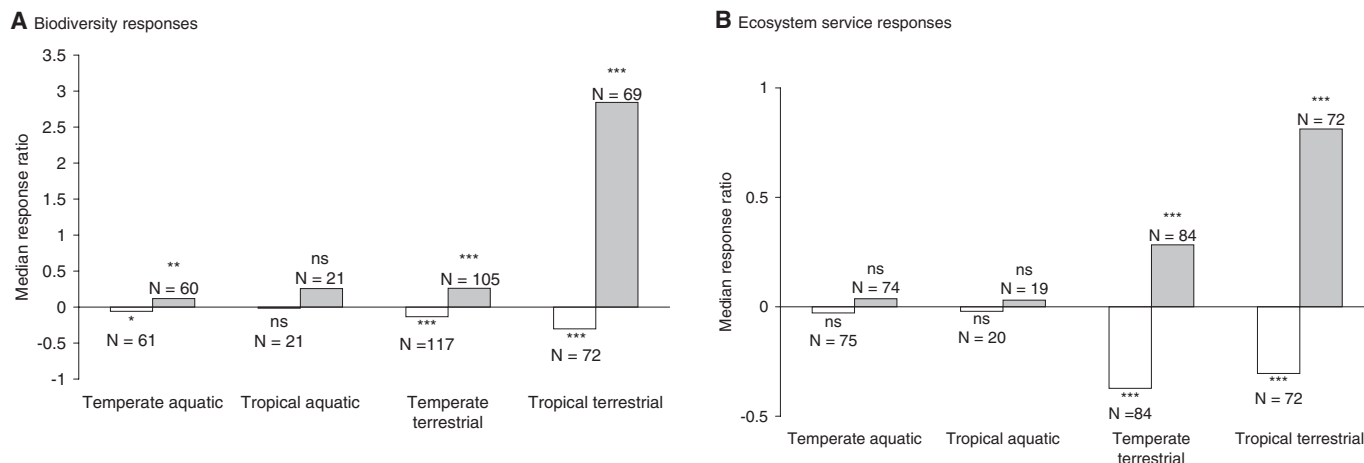
Fig. 2. Response ratios of (**A**) biodiversity and (**B**) amalgamated measures of ecosystem services in restored versus reference ecosystems and restored versus degraded ecosystems classified according to broad biome types. Except for biodiversity in the tropical aquatic biome and for ecosystem services in both temperate and tropical aquatic biomes, response ratios were significantly different from zero (Wilcoxon signed rank tests, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns $P > 0.05$) in each biome type. Kruskal Wallis tests showed significant differences among the biomes in the response ratios for biodiversity (restored versus reference: $H = 11$, $N = 271$, $P < 0.05$; restored versus degraded: $H = 61$, $N = 255$, $P < 0.001$) and ecosystem services (restored versus reference: $H = 25$, $N = 253$, $P < 0.001$; restored versus degraded: $H = 46$, $N = 251$, $P < 0.001$).
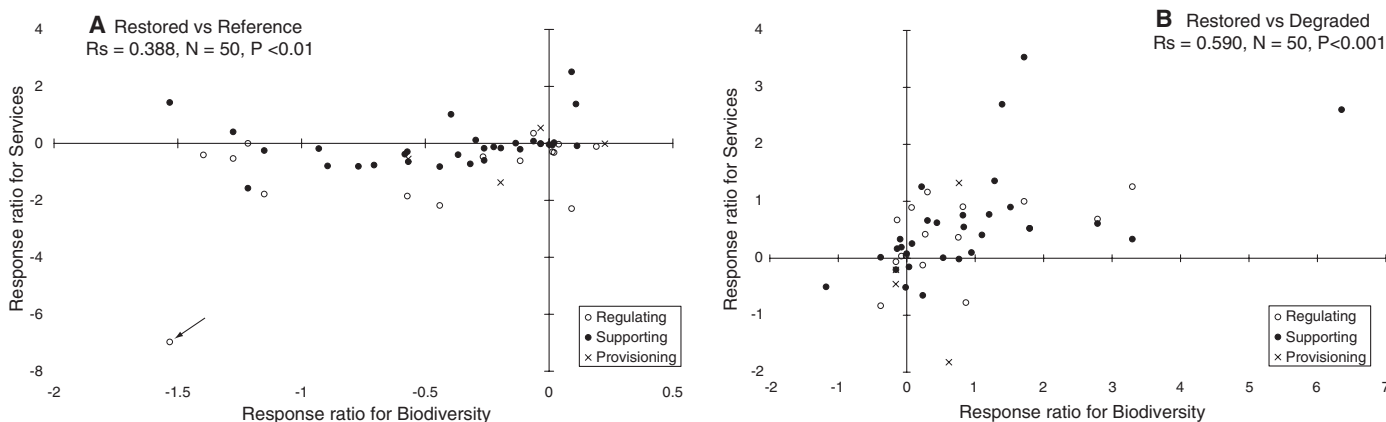
Fig. 3. Spearman rank (Rs) correlations between response ratios for biodiversity and for provision of ecosystem services in (**A**) restored versus reference ecosystems and (**B**) restored versus degraded ecosystems. The restored versus reference correlation remained significant after removing the outlier (indicated with an arrow) ($Rs = 0.353$, $P < 0.05$). Where multiple measures of biodiversity or of a service were made in a study, pseudo-replication was avoided by averaging the response ratios to provide a single pair of values for biodiversity and each ecosystem service for analysis. To achieve a reasonable sample size, the different service types were combined, but here they are indicated by different symbols to illustrate the lack of systematic differences among them.

independent sample unit, Spearman rank correlation analysis showed that biodiversity and ecosystem service response ratios were positively correlated for both restored versus degraded and restored versus reference comparisons (Fig. 3). The relation was much stronger in the former comparison. This difference in the observed relations may be linked to an asymptotic relation between biodiversity and ecosystem function (*15*), whereby increasing biodiversity from low values has relatively strong impacts on individual ecosystem functions, but the relation plateaus at relatively high biodiversity values. Experimental investigations of the biodiversity-ecosystem function relation have generally been laboratory based or have employed small field plots (<100 m^2), which arguably have little relevance to the larger scales (hectares to square kilometers) at which land management decisions are made (*16*). The current results support suggestions that when studies undertaken at a range of scales are combined, biodiversity is positively related to the ecological functions that underpin the provision of ecosystem services.

The relation between biodiversity and provision of ecosystem services is still poorly defined (*10, 17*). Preliminary mapping efforts at the global scale have shown that areas targeted for biodiversity conservation do not necessarily coincide with areas of relatively high provision of ecosystem services (*10*). However, conservation actions and investments typically occur at national, regional, and local scales. Our results suggest that, at such scales, ecological restoration is likely to lead to large increases in biodiversity and provision of ecosystem services, offering the potential of a win-win solution in terms of combining biodiversity conservation with socio-economic development objectives. Because ecological restoration can be effective in restoring natural capital, it should be implemented in areas that have undergone environmental degradation (*18*). The impacts of environmental degradation on human communities have been felt particularly heavily in tropical countries (*19*), where biodiversity loss and poverty are often associated (*20*). The meta-analysis showed the greatest impact of restoration in tropical terrestrial ecosystems, supporting the view that such management interventions could benefit human livelihoods in tropical regions (*2*).

Restoration actions cannot be implemented without incurring costs, and therefore, financial incentives will need to be provided for ecological restoration to be widely implemented (*21*). Potential approaches include improved markets and payment schemes for ecosystem services (*22*) and the Clean Development Mechanism developed under the Kyoto protocol. Cost-benefit analyses incorporating the values of biodiversity and associated ecosystem services and analysis of economic pathways are required to maximize return on investments in restoration (*18*). Restoration does not necessarily achieve the values of biodiversity or ecosystem services found in intact ecosystems, at least in the decadal time scales

adopted in the studies analyzed here, and this highlights the primary need to conserve wild nature and avoid environmental degradation wherever possible (*23, 24*). There is also a need to improve techniques for rehabilitating degraded ecosystems that will increase biodiversity and the provision of associated benefits to human society (*12*). Such techniques include improved monitoring of both biodiversity and ecosystem service outcomes of restoration actions.

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Unprecedented Restoration of a Native Oyster Metapopulation

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Native oyster species were once vital ecosystem engineers, but their populations have collapsed worldwide because of overfishing and habitat destruction. In 2004, we initiated a vast (35-hectare) field experiment by constructing native oyster reefs of three types (high-relief, low-relief, and unrestored) in nine protected sanctuaries throughout the Great Wicomico River in Virginia, United States. Upon sampling in 2007 and 2009, we found a thriving metapopulation comprising 185 million oysters of various age classes. Oyster density was fourfold greater on high-relief than on low-relief reefs, explaining the failure of past attempts. Juvenile recruitment and reef accretion correlated with oyster density, facilitating reef development and population persistence. This reestablished metapopulation is the largest of any native oyster worldwide and validates ecological restoration of native oyster species.

Along North American, European, and Australian coastlines, native oyster populations have been devastated to less than 10% of their historical abundance by overfishing and oyster reef destruction (*1–3*). These vital ecosystem engineers influence nutrient cycling, water filtration, habitat structure, biodiversity, and food web dynamics (*3, 4*). The widespread decline of these dominant suspension feeders was a leading cause of eutrophication in estuarine

ecosystems, owing to the shift from benthic to planktonic primary production and the accompanying hypoxia resulting from microbial decomposition (*3*). This phenomenon remains a major

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