Check for updates



ECOLOGY

# Legacies of foundation species shape life after death

**Kai L. Kopecky[1,2]*, Max C. N. Castorani[3], Ty Tuff[1,2], Audrey Barker Plotkin[4], David M. Bell[5], Jill F. Johnstone[6], John S. Kominoski[7], Jesse B. Nippert[8], Christopher J. Nytch[9], Steven C. Pennings[10], Daniel C. Reed[11], Aaron B. Shiels[9]†, Katharine N. Suding[12,13]**

Copyright © 2026 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).

**Ecosystems carry memory through the material remains of organisms. Foundation species—trees, grasses, corals, and oysters—while alive are central to ecosystem structure, and the remains of these organisms continue to influence ecological processes after death. We conducted, to our knowldge, the first continental-scale exploration of how dead foundation species influence living conspecifics, leveraging long-term experiments and observations (2 to 32 years) from 10 ecosystems (five terrestrial and five marine) across the US Long Term Ecological Research Network. We found that material legacies commonly alter demographic processes, ranging from a 50% reduction to a 12-fold increase. The ubiquity of these postmortem effects reveals an underappreciated dimension of ecological memory that shapes pathways of ecosystem resilience, reorganization, and collapse, providing a critical management tool in an era of increasing disturbance- and climate-driven mortality events.**

## INTRODUCTION

An ecosystem is comprised not only of its current inhabitants but also of the remains of those from the past. Ecological memory, or the influence of historical events on present ecological conditions (*1*), plays a central role in shaping how ecological systems respond and adapt to disturbance (*2*–*5*). One component of ecological memory arises from material legacies—structural or resource remnants of organisms that persist after death (*6*). Material legacies can have strong, immediate, and long-lived effects on ecological processes that shape patterns of community assembly (*7*) and properties of ecosystem resilience (*3*, *8*, *9*). Whether material legacies tend to elicit beneficial or detrimental, weak or strong responses across distinct ecosystems remains poorly resolved, limiting a generalized understanding of their ecological importance.

The loss of living foundation species (e.g., certain species of trees, corals, grasses, and oysters) (*10*) can have enduring effects on ecosystem function and resilience (*11*, *12*) but so too can the loss, decomposition, or retention of their dead biogenic structures (*3*, *8*, *9*, *13*, *14*). Foundation species typically have three general, defining characteristics (*11*, *15*, *16*): (i) dominance in abundance and/or biomass; (ii) presence at or near the base of directional interaction networks (i.e., occupy low trophic levels); and (iii) strong influence through nontrophic and/or mutualistic interactions with other species (e.g., habitat provisioning and nutrient cycling). Through their numerous and diverse interactions with other organisms, foundation species strongly influence ecosystem structure and processes (*16*). Because of their abundance, foundation species often leave behind substantial material legacies after they die. These legacies vary in their retention within an ecosystem and in their effects on organisms, including the demographic rates (e.g., recruitment, growth, and survival) of the foundation species themselves. Thus, we expect the strength of postmortem feedbacks between foundation species and the material legacies they leave behind to influence the capacity for ecosystems to recover to a similar state after a disturbance.

Although ecologists have pieced together the importance of postmortem effects in specific ecosystems (e.g., coral reefs, grasslands, and forests) (*17*–*20*), general inference regarding the strength and nature of these influences is limited by lack of a broad synthesis across disparate environments. The strength of postmortem effects found in these representative examples, however, provides a compelling argument that the ecological roles of dead organisms may be underappreciated in other ecosystems. Efforts to understand the breadth of postmortem effects in nature—including cases where they are subtle—will lead to deeper insights into how dead organisms generally shape ecological processes and pathways, including the resilience of foundation species and the ecosystems they define. Furthermore, the prevalence of dead organisms is expected to increase in many ecosystems, as disturbances intensify under global change (*2*, *3*, *8*). Postmortem effects may therefore strengthen in the future, underscoring the value of understanding their ecological importance across a wide range of ecosystems, regardless of how weak or strong these effects are currently.

To move toward a generalized understanding of material legacy effects on population dynamics of foundation species, we used data from the US Long Term Ecological Research (LTER) Network—a multidecadal investment by the US National Science Foundation to understand the long-term dynamics of (primarily North American) ecosystems—to conduct, to our knowledge, the first continental-scale assessment of how live foundation species are influenced by their dead counterparts. All LTER sites include a focus on how disturbance affects population demography (often of foundation species) and organic material (often the material legacies of foundation species) through long-term experiments and observations. Hence, LTER data provide a robust framework for this synthesis by capturing the dynamics of live and dead foundation species across a diversity of

[1]Cooperative Institute for Research in Environmental Sciences, University of Colorado Boulder, Boulder, CO 80309, USA. [2]Environmental Data Science Innovation & Impact Lab, University of Colorado Boulder, Boulder, CO 80309, USA. [3]Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA. [4]Harvard Forest, Harvard University, 324 N. Main St., Petersham, MA 01366, USA. [5]Pacific Northwest Research Station, USDA Forest Service, Corvallis, OR 97331, USA. [6]Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA. [7]Institute of Environment & Department of Biological Sciences, Florida International University, Miami, FL 33199, USA. [8]Division of Biology, Kansas State University, Manhattan, KS 66506, USA. [9]Department of Environmental Sciences, University of Puerto Rico-Río Piedras, San Juan, PR 00925, USA. [10]Department of Biology and Biochemistry, University of Houston, Houston, TX 77204 USA. [11]Marine Science Institute, University of California, Santa Barbara, CA 93106, USA. [12]Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO 80309, USA. [13]Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, CO 80309, USA.
*Corresponding author. Email: kai.kopecky@colorado.edu
†Present address: USDA APHIS National Wildlife Research Center, Fort Collins, CO 80521, USA.

Downloaded from https://www.science.org on June 13, 2026

biomes and over multiple cycles of loss and recovery (here, 2 to 32 years; mean = 16 years). We note that the locations of LTER sites were chosen without a priori expectation that material legacies would be important when the sites were established, thus minimizing study bias in this context.

We examined how legacies of dead foundation species (hereafter, material legacies; Fig. 1) influence the demography of living conspecific or congeneric foundation species across an array of 10 ecosystems (five marine and five terrestrial) that span the tropics to the boreal North (Fig. 2 and table S1). For each ecosystem, we identified an important (but not necessarily the only) demographic process directly affected by legacies (Table 1), quantified the magnitude and direction of the demographic response, and standardized outcomes to enable cross-system comparison. We chose to focus on these specific processes based both on expert opinion that these represent important pathways for legacy effects to directly manifest in each ecosystem and that these pathways are suitable for comparison across ecosystems with available data from each LTER site. We describe a set of general mechanisms that link legacies to demography and outline a conceptual framework to broadly categorize legacy-demography relationships based on their potential to structure communities and ecosystem processes.

## RESULTS

The material legacies of dead foundation species significantly altered demographic processes of living conspecifics/congenerics in 9 of the 10 ecosystems we studied ($P < 0.05$; Fig. 3). We analyzed each legacy-demography relationship with a generalized linear mixed-effects model (GLMM) tailored to the structure of the available dataset (Table 1 and tables S2 and S3). Significant legacy effects ranged from a reduction of about 50% to more than a 12-fold increase in the demographic response, influencing establishment, growth, and survival of living foundation species across biomes from tropical to subpolar latitudes and from the ocean to the mountains (Fig. 3).

Five ecosystems exhibited facilitative effects of legacies on demographic processes in live foundation species (Fig. 3, A to E). The presence of standing dead hemlock trees in temperate forests and larger amounts of dead oyster shells on oyster reefs supported higher densities of colonizing conspecifics ($P < 0.001$ for both). In subtropical mangrove forests, higher litterfall inputs following a hurricane enhanced fine root production (a proxy for growth) in surviving mangroves ($P < 0.001$). In boreal forests, more standing burned trees after wildfire led to higher densities of seeds released into surrounding soils ($P = 0.015$). In temperate rainforests, higher biomass of downed deadwood led to faster growth rates in living individuals

**Fig. 1. Examples of dead foundation species (material legacies) in various ecosystems.** Material legacies of foundation species within different ecosystem types (clockwise from top-left image): dead oyster shells, standing dead coral skeletons, standing burned trees, and dead grass litter. Photo credits: J. E. Byers, University of Georgia (top-left image); K. L. Kopecky, Environmental Data Science Innovation and Impact Lab (top-right and bottom images).

Downloaded from https://www.science.org on June 13, 2026

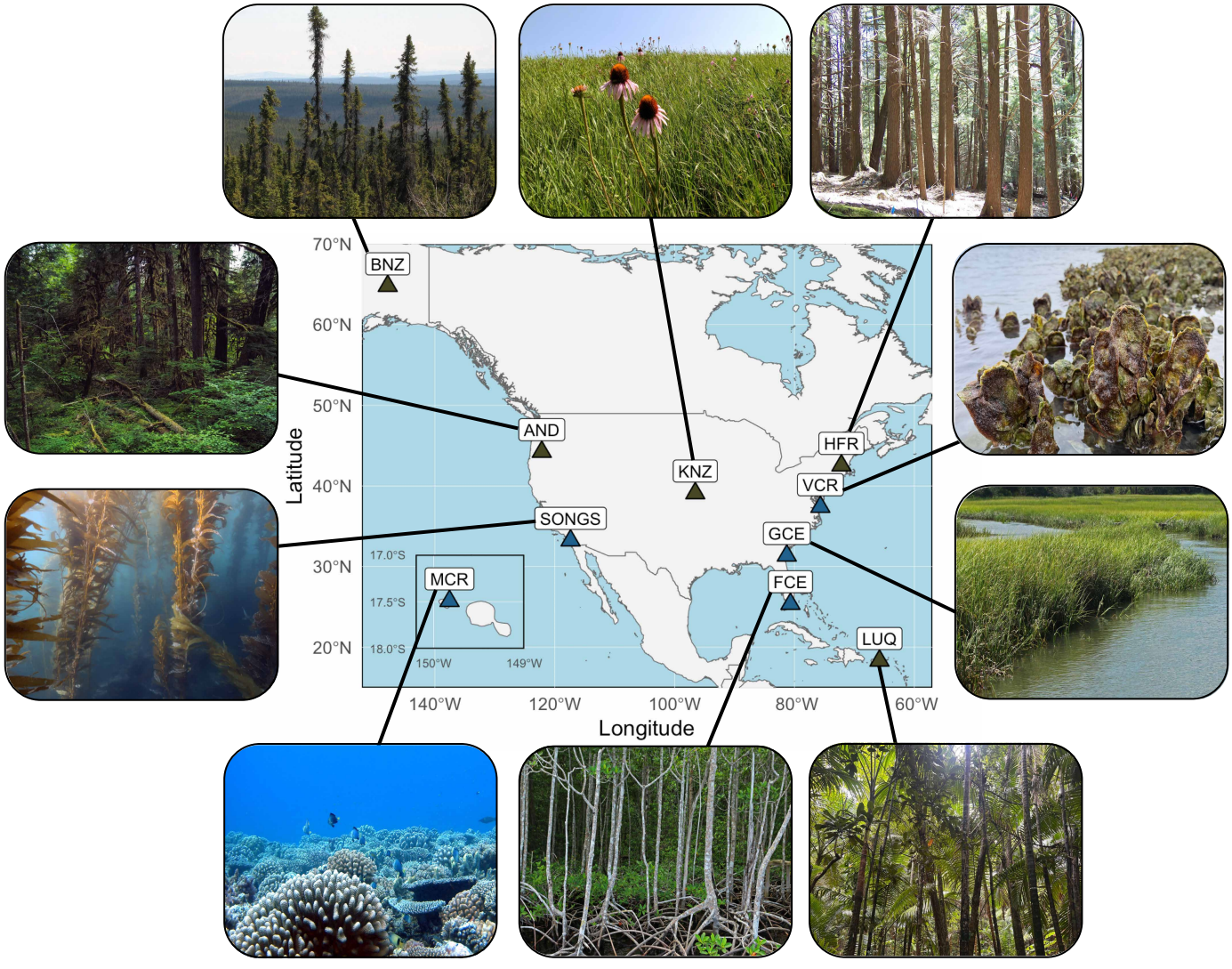


**Fig. 2. Map and images of study sites.** Clockwise from top-left image: Bonanza Creek (BNZ), Konza Prairie (KNZ), Harvard Forest (HFR), Virginia Coast Reserve (VCR), Georgia Coastal Ecosystems (GCE), Luquillo (LUQ), Florida Coastal Everglades (FCE), Moorea Coral Reef (MCR), San Onofre Nuclear Generating Station (SONGS) Mitigation Monitoring Program, and H. J. Andrews Experimental Forest (AND). Blue triangles represent marine ecosystem sites; green triangles represent terrestrial ecosystem sites. Photo credits (in same order): J. F. Johnstone, University of Alaska Fairbanks; J. B. Nippert Kansas State University; A. Barker Plotkin, Harvard University; M. C. N. Castorani, University of Virginia; S. C. Pennings, University of Houston; R. Baran, University of Puerto Rico; E. Zambello, Florida International University; R. J. Schmitt, University of California Santa Barbara; Santa Barbara Coastal LTER; G. De La Rosa, LTER Network Office.

of Douglas fir (*Pseudotsuga menziesii*), the predominant conifer species ($P = 0.004$).

In contrast, four systems showed inhibitory effects of legacies on demographic processes in live conspecific/congeneric foundation species (Fig. 3, G to J): In tropical montane forests, hurricane canopy detritus suppressed seedling survival ($P < 0.001$); on tropical coral reefs, dead branching coral skeletons left after a marine heatwave accelerated live coral decline ($P < 0.001$); in tallgrass prairies, the accumulation of unburned litter limited clonal regrowth from belowground biomass compared to burned sites ($P < 0.001$); in salt marshes, disturbance by floating mats of detrital marsh plants (wrack) sharply reduced live marsh grass biomass ($P < 0.001$). Only in kelp forests was the relationship nonsignificant between the material legacy predictor (cover of dead kelp holdfasts attached to the seafloor) and the demographic response (giant kelp recruitment; $P = 0.278$). See table S3 for slope estimates and confidence intervals of each relationship described above.

To compare relationships across ecosystems, we built standardized models with predictors and responses scaled to $z$-scores (units of SDs), allowing effect sizes to be compared on a common scale (Fig. 4, fig. S1, table S4, and the Supplementary Materials). Results of these analyses were largely consistent with our original models, confirming that legacy effects were rarely neutral: 9 of 10 ecosystems had significant or near-significant ($P < 0.1$) $z$-score responses (Fig. 4 and table S4). Facilitative (positive) and inhibitory (negative) effects were equally common (five versus four, respectively) and spanned a similar range in magnitude (Fig. 4A). Where legacies enhanced demographic processes, effects ranged from weakly to strongly positive (+0.1 to

Downloaded from https://www.science.org on June 13, 2026

**Table 1. Material legacies and demographic responses.** Table displaying the ecosystem type (and associated LTER/long term site), representative foundation species, material legacy, identified demographic response, and the duration and type of each dataset used in our study.

| Ecosystem type (site) | Foundation species | Material legacy | Demographic response | Duration of dataset (data type) |
|---|---|---|---|---|
| Temperate forest (HFR) | Eastern hemlock | Standing dead trees | Hemlock sapling recruitment | 18 years (experimental) |
| Mangrove forest (FCE) | Mangrove trees | Leaf litter | Mangrove root production | 2 years (observational) |
| Oyster reef (VCR) | Oysters | Dead shells | Oyster settlement | 15 years (observational) |
| Temperate rainforest (AND) | Douglas fir | Downed deadwood | Growth of Douglas fir trees | 29 years (observational) |
| Boreal forest (BNZ) | Black spruce | Standing burned trees | Seed release | 3 years (observational) |
| Kelp forest (SONGS) | Giant kelp | Dead holdfasts | Giant kelp recruitment | 23 years (observational) |
| Saltmarsh (GCE) | Marsh grass | Mats of dead plants | Marsh grass productivity | 25 years (observational) |
| Coral reef (MCR) | Branching coral | Branching coral skeletons | Branching coral growth and survival | 5 years (experimental) |
| Tropical montane forest (LUQ) | Tabonuco forest trees | Canopy debris | Tree seedling establishment | 9 years (experimental) |
| Tallgrass prairie (KNZ) | Perennial grasses | Perennial grass litter | Clonal regrowth of grass | 32 years (experimental) |

+1.2 SD), and where they suppressed demography, effects ranged from moderately to strongly negative (−0.4 to −1.2 SD). The strongest effects occurred in terrestrial ecosystems (absolute value: 0.3 to 1.2 SD), whereas effects in marine systems were comparatively more moderate (absolute value: 0.1 to 0.8 SD; Fig. 4B).

Last, ancillary partial regression analyses of observational time series (see the Supplementary Materials) showed relationships that aligned in direction with those identified in our primary analyses; three of the four were statistically significant: oyster reefs ($P = 0.003$; fig. S2), temperate rainforests ($P < 0.001$; fig. S3), and mangrove forests ($P = 0.042$; fig. S4). For boreal forests, we found the same positive relationship observed in the primary analysis, although the partial regression result was not statistically significant ($P = 0.24$; fig. S5). The consistency in the direction found in this more conservative analysis with those from our primary analysis strengthens support for our conclusions drawn from the observational datasets.

## DISCUSSION

Our study provides strong evidence that material legacies of foundation species can shape ecological processes that underlie community assembly and ecosystem resilience across marine and terrestrial environments. Three points of understanding emerge from our synthesis: (i) effects of material legacies on the demographic processes of foundation species were common across a wide variety of ecosystems and often large in magnitude; (ii) facilitative (positive) and inhibitive (negative) legacy effects were equally common, both across and within marine and terrestrial ecosystem types; and (iii) our comparative framework identified coherent mechanisms driving variation in the direction and magnitude of legacy effects, opening the doorway to further analyses to increase our understanding of general processes operating across marine and terrestrial ecosystems. Together, our findings suggest that material legacies rarely serve as passive debris but instead routinely shape population dynamics of foundation species and, by extension, the structures of communities and processes of ecosystems. The occurrence of these postmortem influences in 9 of the 10 ecosystems that we studied suggests that they are likely present, consequential, and underappreciated in other ecosystems where legacy effects have not been directly studied.

We note that three of the four negative relationships came from long-term experimental datasets, while five of the six positive relationships were from long-term observational records. However, the sign of the relationship was not merely an artifact of the study type, as each pattern aligned with documented ecological mechanisms (described below). Moreover, ancillary partial regressions on the observational time series further support our conclusions, as the trends we found in these more conservative analyses were directionally consistent with those from our primary analyses. Together, these findings suggest that positive and negative demographic responses to material legacies reflect real ecological differences among systems rather than arising solely from the study design.

### Mechanisms linking legacies to demography

A diversity of legacy effects reflects the multiple pathways by which material legacies alter establishment, growth, and survival of foundation species. Below, we describe mechanisms underlying the legacy effects we observed in each of the environments we evaluated. We assign these mechanisms to two general classes, resource effects or structural effects, which influence demographic processes to either promote or hinder recovery of foundation species populations.

#### *Resource effects*

Material legacies can affect the availability of resources to either enhance or suppress demographic processes. In some of the systems we evaluated, legacies subsidize regeneration of foundation species by storing and releasing nutrients or propagules that fuel growth or drive reestablishment: Hurricane litterfall increases nutrient inputs that stimulate root production in mangrove trees (*21*), downed deadwood slowly releases nutrients (*22*) that could contribute to faster tree growth in temperate rainforests, and standing burned trees drop copious seeds that regenerate boreal forests (*23*). In other cases, legacies such as accumulated grass litter and canopy detritus block light resources, delaying clonal regrowth of prairie grasses from belowground biomass (*19*) and limiting survival of seedlings in tropical montane forests (*24*).

#### *Structural effects*

Material legacies can also change the physical environments in which live foundation (and other) species establish, grow, and survive. Standing dead hemlocks mediate the understory micro-climate in

Downloaded from https://www.science.org on June 13, 2026

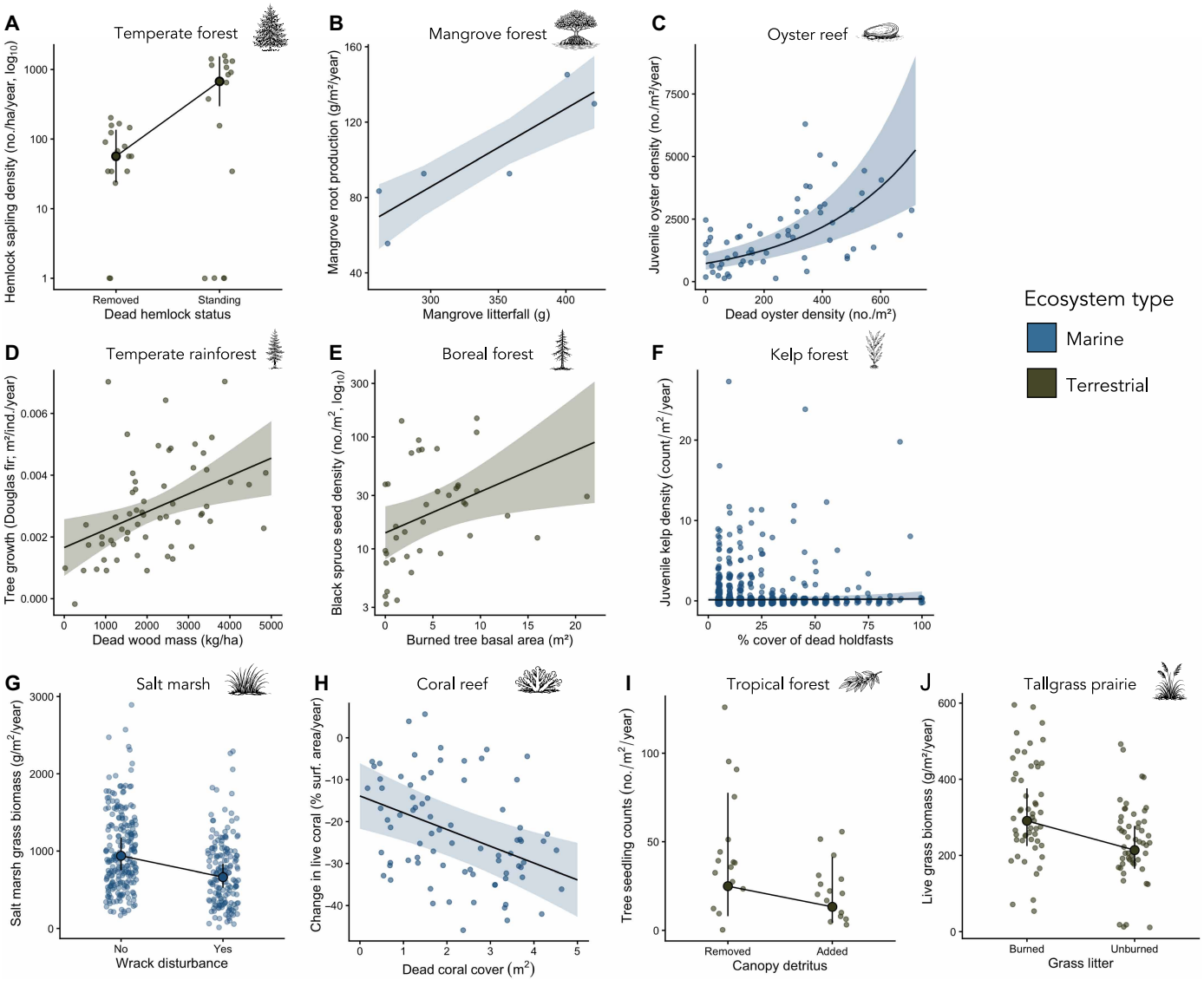


**Fig. 3. Material legacies of foundation species influence demographic responses across a wide range of ecosystems, with varying positive, null, and negative effects.** Each panel displays the output from a GLMM tailored to the structure of the dataset used from each site/system. Means ± 95% confidence intervals (CIs) are displayed as large dots with error bars for categorical predictors and as lines with ribbons for continuous predictors. For all panels, small transparent dots represent replicate-level values from which mean relationships were modeled. Some response variables are represented on a log (base 10) scale for visualization purposes. (**A**) Temperate forest; (**B**) mangrove forest; (**C**) oyster reef; (**D**) temperate rainforest; (**E**) boreal forest; (**F**) kelp forest; (**G**) salt marsh; (**H**) coral reef; (**I**) tropical forest; (**J**) tallgrass prairie. ind., individual. surf., surface. Illustration credit: M. Whalen.

temperate forests and favor establishment of conspecific saplings (*20*, *25*), while dead oyster shells act as settlement substrate for incoming larval oysters on intertidal flats (*26*). Conversely, floating wrack in salt marshes mechanically damages and suppresses productivity in live marsh grasses (*27*), and dead branching coral skeletons provide structurally complex habitat that facilitates competitors (macroalgae), which reduce the recruitment, growth, and survival of live coral (*17*, *18*).

## Conceptual framework for how legacies shape community structure

Through the various mechanisms described above, material legacies act directly on demographic processes of foundation species (Fig. 5, top), which strongly influence how ecosystems and biodiversity are structured (*11*, *16*). In turn, material legacies hold the potential to influence whether ecological communities maintain their structure, reorganize or shift to an alternative state, or even collapse into degradation after disturbance (Fig. 5, bottom). Specifically, legacies that facilitate establishment, growth, and/or survival of living foundation species promote the return or persistence of conspecific or congeneric foundation species. This, in turn, helps rebuild the communities that depend (directly or indirectly) on those foundation species, ultimately supporting resilience by maintaining the community structure that a system held before disturbance (*16*). By contrast, legacies that inhibit demographic processes slow or prevent the return of foundation species, which can result in cascading declines or

Downloaded from https://www.science.org on June 13, 2026

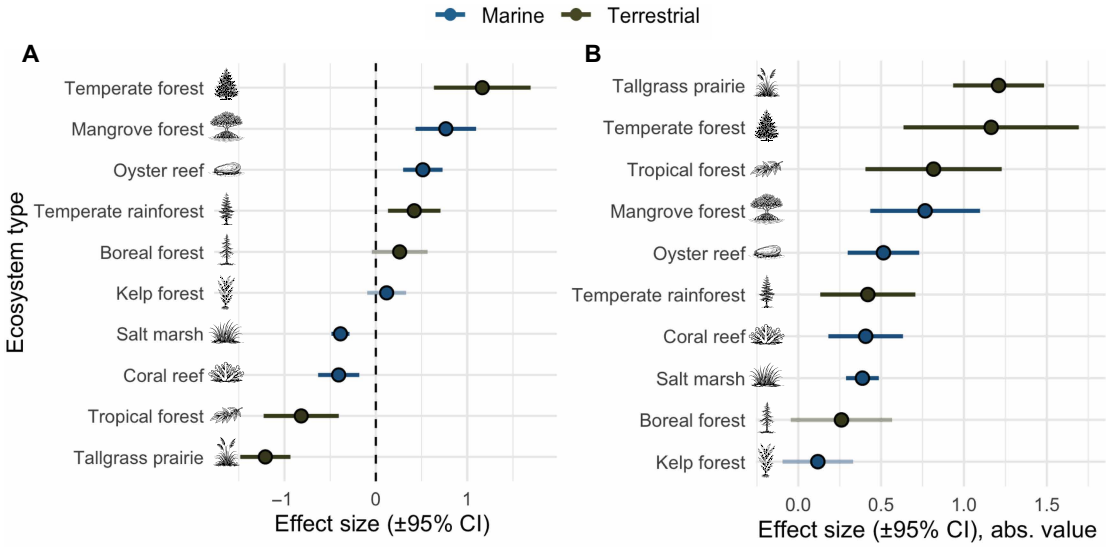


**Fig. 4. Standardized effect sizes of the relationships between material legacy predictors and demographic responses.** (**A**) Standardized effect sizes (±95% CIs) extracted from GLMMs for each ecosystem, where predictors and responses were scaled to *z*-scores (units of SDs). (**B**) Effect sizes from (A) displayed as absolute values to allow for more direct comparisons of their magnitudes. Transparent error bars indicate nonsignificant relationships (in standardized models only). abs., absolute. Illustration credit: M. Whalen.

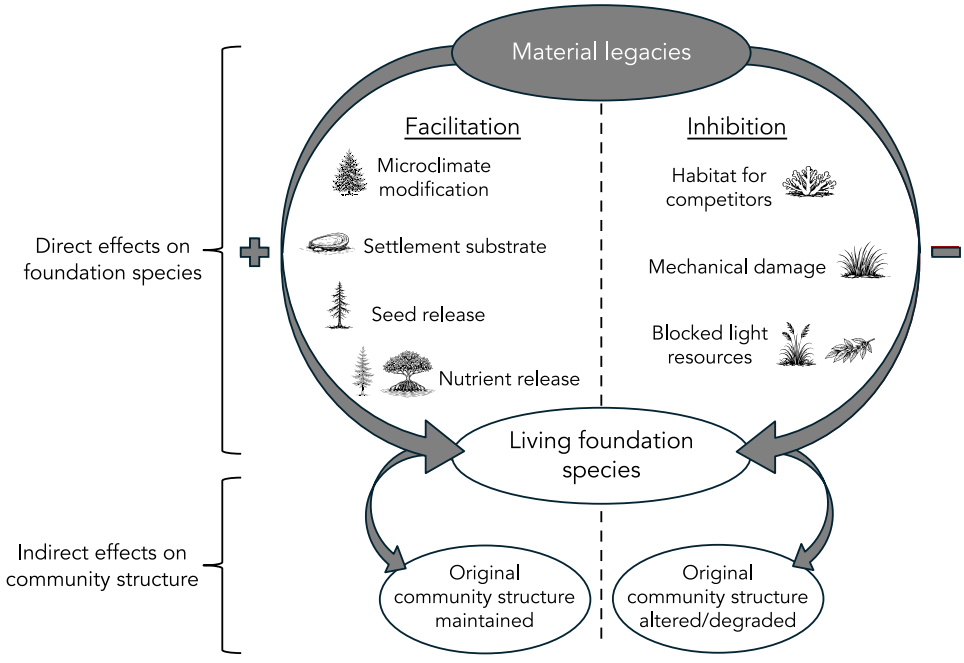


**Fig. 5. Consequences of positive versus negative effects of material legacies for ecological community structure.** Material legacies that positively affect demographic processes in live foundation species support establishment and growth of living conspecifics ("facilitation") and thereby stabilize or promote return to the original community composition that existed before disturbance/mortality. Material legacies that negatively influence foundation species demographic processes may prevent return to predisturbance/mortality community composition by suppressing conspecific establishment, growth, and/or survival ("inhibition"), ultimately leading to a departure from the original community to an altered or degraded community via decline or loss of taxa that depend on the foundation species. Icons signify ecosystems (and the associated legacies) that we evaluated as either facilitative (i.e., positive) or inhibitive (i.e., negative) with respect to foundation-species demographic processes, while the accompanying phrases refer to the documented mechanism underlying each effect. Illustration credit: M. Whalen.

Downloaded from https://www.science.org on June 13, 2026

losses of other dependent species (*11*). Inhibitory legacies may therefore block a system from regaining its original community structure and instead veer it toward reorganization or potentially collapse (Fig. 5).

### Complex dynamics involving legacy effects

While we focus on comparing legacies across systems, we also expect that these processes produce complex dynamics within a system over time. For instance, legacies may affect early and late life stages of foundation species differently. Specifically, a facilitative effect at one life stage may reduce, cancel out, or override an inhibitive effect at another life stage (or vice versa), depending on the relative strengths of the effects at each stage. In the case of tropical montane forests, hurricane-deposited canopy detritus can both kill existing woody seedlings and provide a mechanical barrier that suppresses seedling recruitment (*28*) while simultaneously contributing to small increases in basal area (*29*) and aboveground carbon (*30*) of adult trees that persist for several years. Conversely, if the nature of a legacy effect is the same for different life stages (i.e., positive or negative for both early and late stages), the overall strength of the effect would be greater than we report here. In our coral reef example, we report a negative effect for growth and survival of late–life stage coral colonies, but dead coral skeletons—both while standing and when broken down into unconsolidated rubble—have been reported to hamper survival of juvenile, recruiting corals as well (*17*, *31*).

Material legacy impacts could also occur many years after their production—including across generations of a foundation species—if feedbacks further amplify or reinforce demographic change. For instance, accumulation of dead oyster shells over several years may increase reef elevation and structural complexity, enhancing juvenile recruitment (*32*, *33*). Climate variation that influences the occurrence of mortality events could also affect recruitment conditions. Estimating such causal effects requires careful manipulation or detailed observational time series that are rarely available, restricting cross-system comparisons. While more work is needed on this front, we nonetheless expect that our findings based on relationships within a single timestep and at a single life stage are conservative estimates of material legacy effects that may compound over time through feedbacks.

Material legacies also play diverse and nuanced roles within the ecosystems they occupy that extend beyond those we have described here. For example, in addition to the inhibitory and facilitative effects of canopy detritus on woody vegetation dynamics in the tropical montane forest mentioned above, this same legacy was reported to spur increases in coquí frog (*Eleutherodactylus coqui*) density following a major hurricane (*34*). Further, material legacies alter environments in ways that tip the balances between competing species—dead branching coral skeletons favor proliferation of macroalgae that can outcompete and replace reef-building corals (*9*, *18*). Thus, the same legacy can simultaneously aid some taxa while harming others. We therefore recommend considering the full breadth of influences before removal, addition, or other manipulations of material legacies for desired management outcomes.

### Emergent questions and directions

In our synthesis, we found wide variation in the strength of legacy effects across (and in some cases, within) ecosystems. The diversity of these effects and their mechanisms are reflective of the disparate foundation species represented in the marine and terrestrial ecosystems we studied. These findings gave rise to several emergent questions, including the following: (i) Why are legacy effects stronger in some systems than in others? On the basis of the environments represented in our analysis, legacy effects may be stronger in terrestrial ecosystems and more moderate (or even neutral) in marine ecosystems, but additional analyses that include more examples of each ecosystem type would be required to resolve this. (ii) How does the input rate of legacies into ecosystems shape their effects on living organisms? Whether legacies accumulate gradually through background mortality of organisms or rapidly through pulse disturbance may affect the strength of their effects. (iii) How does the residence time of a legacy within an ecosystem influence the strength and duration of its effect? Material legacies are removed from the environment in a variety of ways (e.g., decomposition, erosion, burial, burning, and lateral transport); how quickly or slowly this occurs may constrain the strength and duration of the effect. (iv) How does the spatial extent of a legacy within a landscape interact with the spatial scale of the affected demographic rate to influence the legacy's overall effect on population and community dynamics? A legacy that has a strong effect but a small spatial footprint may have overall weaker effects than a more spatially pervasive legacy with a moderate or weak effect (*7*, *35*). These temporal and spatial attributes of material legacies likely determine the importance of legacy effects more broadly and thus warrant explicit investigation, especially considering that changing global conditions will likely alter both attributes.

As global change intensifies events that cause mortality—from pest outbreaks and megafires to heatwaves and storms that cause widespread die-offs of terrestrial and marine foundation species—the prevalence and dynamics of material legacies will change. In this era of accelerating species losses and die-offs (*36*–*38*), managing and understanding the legacies of the dead will become more important than ever for managing the living. In some cases, material legacies are already recognized as levers for management and restoration: retention of deadwood in forests (*14*), prescribed burns in grasslands (*39*), and addition of shells to oyster reefs (*26*) are all strategies implemented to support biodiversity or stimulate foundation-species recovery in degraded ecosystems. While compelling, these examples are few, yet they highlight the need for integration of the dead's influence on the living as a core concept in ecology. The remains of foundation species are not merely ecological "background," but agents with strong potential to modify the structure, function, and resilience of ecosystems. Our synthesis provides an important step toward achieving a generalizable understanding of how material legacies interact with living organisms to shape ecological memory and the fates of Earth's ecosystems.

## MATERIALS AND METHODS

### Description of data sources

We identified 10 sites (five marine and five terrestrial) within the National Science Foundation LTER Network that span the tropics to the boreal North (Fig. 2). Each LTER site represents a distinct ecosystem type: Bonanza Creek (BNZ; boreal forest), Harvard Forest (HFR; temperate hemlock forest), H. J. Andrews Experimental Forest (AND; temperate rainforest), Konza Prairie (KNZ; tallgrass prairie), Luquillo (LUQ; tropical montane tabonuco forest), Moorea Coral Reef (MCR; coral reef), Virginia Coast Reserve (VCR; oyster reef), Georgia Coastal Ecosystems (GCE; salt marsh), and Florida Coastal Everglades (FCE; mangrove forest). Because of logistical constraints associated with the structure of available data at the kelp forest LTER site (Santa Barbara Coastal), we used kelp forest data

Downloaded from https://www.science.org on June 13, 2026

from the San Onofre Nuclear Generating Station (SONGS) Mitigation Monitoring Program, which is a collaborative partner of the Santa Barbara Coastal LTER. In some cases, we used data from observational time series, while in others, we extracted data from long-term experiments where material legacies were manipulated (see table S1 for dataset descriptions and links to source files). Regardless, each dataset captured the abundance, cover, biomass, or presence of dead foundation species and a corresponding demographic response metric of live conspecifics or congenerics (e.g., recruitment, growth, and survival). See the Supplementary Materials for descriptions of datasets, model structures, diagnostics for each individual ecosystem/site, and ancillary partial regression analyses that strengthen evidence for the relationships found in our primary analysis of observational time series.

### Analytical approach

For each ecosystem type, we identified a material legacy predictor–demographic response relationship that represented an important pathway for legacy effects to directly manifest (based on expert opinion) and that could be consistently assessed using available data. We then constructed GLMMs tailored to each dataset in R using the glmmTMB package (*40*). The response variable in each model represented an annual rate of a key demographic attribute of the live foundation species—e.g., colonization/recruitment or changes in density, biomass, cover, etc. indicative of growth or mortality. The predictor variable (fixed effect) represented the abundance, biomass, density, or presence/absence of dead conspecific/congeneric material—e.g., litterfall, dead coral cover, and burned basal area of trees—at the same point in time that the demographic response was measured. In some cases, predictors were continuous measurements of a material legacy, while in others, they were categorical variables representing the presence/absence or removal/addition of material legacies. Random intercept terms were included to account for spatial nesting or nonindependence of sampling units (e.g., site, plot, and transect) and repeated measurements through time (year of observation). Appropriate model distributions (families) and link functions were selected on the basis of the distributional properties of each response variable (Gaussian, Tweedie, and negative binomial) and whether the data were zero inflated. See the Supplementary Materials ("System-specific analyses and model structures" section and table S2) for details on the specific model structure used for each ecosystem type.

To allow for direct comparisons of effect sizes across ecosystem types, we built standardized versions of each model where predictors and/or responses were centered and scaled to their $z$-scores (units of SDs) before model fitting. Where predictor variables were categorical, we scaled only the response variable (except for one case where we scaled only the predictor; rationale described in subsection Kelp forest of the Supplementary Materials). Effect sizes and their 95% confidence intervals were then extracted from outputs of the standardized models using the tidyr() function in the "broom.mixed" R package (*41*) to compare the magnitude and direction of material legacy effects across systems.

We evaluated model assumptions using the simulateResiduals() function in the "DHARMa" R package (*42*), which compares simulated and observed residuals to test for model fit. This includes a Kolmogorov-Smirnov test for uniformity, an outlier test for excess extreme values, and a dispersion test for over- or underdispersion. Model predictions were extracted using the ggpredict() function in the "ggeffects" R package (*43*), and visualizations were created using the "ggplot2" R package (*44*). All data cleaning, wrangling, analysis, and visualization were conducted using R (*45*) and RStudio (*46*).

## Supplementary Materials

**This PDF file includes:**

Supplementary Methods and Analysis
Figs. S1 to S5
Tables S1 to S4
References

## REFERENCES


1. G. D. Peterson, Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* **5**, 329–338 (2002).
2. T. P. Hughes, J. T. Kerry, S. R. Connolly, A. H. Baird, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, M. Jacobson, G. Liu, M. S. Pratchett, W. Skirving, G. Torda, Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nat. Clim. Change* **9**, 40–43 (2019).
3. J. F. Johnstone, C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, M. G. Turner, Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* **14**, 369–378 (2016).
4. K. Ogle, J. J. Barber, G. A. Barron-Gafford, L. P. Bentley, J. M. Young, T. E. Huxman, M. E. Loik, D. T. Tissue, Quantifying ecological memory in plant and ecosystem processes. *Ecol. Lett.* **18**, 221–235 (2015).
5. M. Khalighi, G. Sommeria-Klein, D. Gonze, K. Faust, L. Lahti, Quantifying the impact of ecological memory on the dynamics of interacting communities. *PLOS Comput. Biol.* **18**, e1009396 (2022).
6. J. F. Franklin, D. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, D. Foster, Threads of continuity: There are immense differences between even-aged silvicultural disturbances (especially clearcutting) and natural disturbances, such as windthrow, wildfire, and even volcanic eruptions. *Conserv. Pract.* **1**, 8–17 (2000).
7. L. K. Albertson, L. S. Sklar, B. B. Tumolo, W. F. Cross, S. F. Collins, H. A. Woods, The ghosts of ecosystem engineers: Legacy effects of biogenic modifications. *Funct. Ecol.* **38**, 52–72 (2024).
8. P. H. Saldaña, C. Angelini, M. D. Bertness, A. H. Altieri, Dead foundation species drive ecosystem dynamics. *Trends Ecol. Evol.* **39**, 294–305 (2024).
9. K. L. Kopecky, A. C. Stier, R. J. Schmitt, S. J. Holbrook, H. V. Moeller, Material legacies can degrade resilience: Structure-retaining disturbances promote regime shifts on coral reefs. *Ecology* **104**, e4006 (2023).
10. P. Dayton, "Toward an understanding of community resilience and the potential effects of enrichment to the benthos at McMurdo Sound, Antarctica," in *Proceedings of the Colloquium on Conservation Problems in Antarctica*, B. C. Parker, Ed. (Allen Press, 1972), pp. 81–96.
11. A. M. Ellison, M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, J. R. Webster, Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**, 479–486 (2005).
12. M. C. N. Castorani, D. C. Reed, R. J. Miller, Loss of foundation species: Disturbance frequency outweighs severity in structuring kelp forest communities. *Ecology* **99**, 2441–2454 (2018).
13. S. E. Hobbie, Effects of plant species on nutrient cycling. *Trends Ecol. Evol.* **7**, 336–339 (1992).
14. M. E. Swanson, J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, F. J. Swanson, The forgotten stage of forest succession: Early-successional ecosystems on forest sites. *Front. Ecol. Environ.* **9**, 117–125 (2011).
15. B. Baiser, N. Whitaker, A. M. Ellison, Modeling foundation species in food webs. *Ecosphere* **4**, 1–14 (2013).
16. A. M. Ellison, Foundation species, non-trophic interactions, and the value of being common. *iScience* **13**, 254–268 (2019).
17. K. L. Kopecky, S. J. Holbrook, E. Partlow, M. Cunningham, R. J. Schmitt, Changing disturbance regimes, material legacies, and stabilizing feedbacks: Dead coral skeletons impair key recovery processes following coral bleaching. *Glob. Change Biol.* **30**, e17504 (2024).
18. K. L. Kopecky, G. Pavoni, M. Corsini, A. J. Brooks, B. P. DiFiore, F. Menna, E. Nocerino, Removing dead coral after marine heatwaves can mitigate coral–algae competition and increase viable coral recruitment. *Ecol. Appl.* **35**, e70077 (2025).
19. A. K. Knapp, T. R. Seastedt, Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* **36**, 662–668 (1986).


Downloaded from https://www.science.org on June 13, 2026

20. M. N. Lustenhouwer, L. Nicoll, A. M. Ellison, Microclimatic effects of the loss of a foundation species from New England forests. *Ecosphere* **3**, 1–16 (2012).
21. E. Castañeda-Moya, V. H. Rivera-Monroy, R. M. Chambers, X. Zhao, L. Lamb-Wotton, A. Gorsky, E. E. Gaiser, T. G. Troxler, J. S. Kominoski, M. Hiatt, Hurricanes fertilize mangrove forests in the Gulf of Mexico (Florida Everglades, USA). *Proc. Natl. Acad. Sci. U.S.A.* **117**, 4831–4841 (2020).
22. M. E. Harmon, The role of woody detritus in biogeochemical cycles: Past, present, and future. *Biogeochemistry* **154**, 349–369 (2021).
23. J. Johnstone, L. Boby, E. Tissier, M. Mack, D. Verbyla, X. Walker, Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Can. J. For. Res.* **39**, 1575–1588 (2009).
24. A. B. Shiels, G. González, Understanding the key mechanisms of tropical forest responses to canopy loss and biomass deposition from experimental hurricane effects. *For. Ecol. Manage.* **332**, 1–10 (2014).
25. D. L. Goerlich, R. D. Nyland, "Natural regeneration of eastern hemlock: A review," in *Proceedings: Symposium on sustainable management of hemlock ecosystems in eastern North America*, K. A. McManus, K. S. Shields, D. R. Souto, Eds. (US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 2000), pp. 14–22.
26. R. S. Smith, S. L. Cheng, M. C. N. Castorani, Meta-analysis of ecosystem services associated with oyster restoration. *Conserv. Biol.* **37**, e13966 (2023).
27. S. Li, S. C. Pennings, Disturbance in Georgia salt marshes: Variation across space and time. *Ecosphere* **7**, e01487 (2016).
28. A. B. Shiels, J. K. Zimmerman, D. C. García-Montiel, I. Jonckheere, J. Holm, D. Horton, N. Brokaw, Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *J. Ecol.* **98**, 659–673 (2010).
29. J. K. Zimmerman, J. A. Hogan, A. B. Shiels, J. E. Bithorn, S. M. Carmona, N. Brokaw, Seven-year responses of trees to experimental hurricane effects in a tropical rainforest. Puerto Rico. *For. Ecol. Manage.* **332**, 64–74 (2014).
30. H. Chevalier, N. V. L. Brokaw, S. E. Ward, J. K. Zimmerman, A. B. Shiels, J. Bithorn, S. Matta Carmona, Aboveground carbon responses to experimental and natural hurricane impacts in a subtropical wet forest in Puerto Rico. *Ecosphere* **13**, e4041 (2022).
31. T. M. Kenyon, C. Doropoulos, K. Wolfe, G. E. Webb, S. Dove, D. Harris, P. J. Mumby, Coral rubble dynamics in the Anthropocene and implications for reef recovery. *Limnol. Oceanogr.* **68**, 110–147 (2023).
32. K. N. Tedford-Callahan, R. S. Smith, B. W. Lusk, M. C. N. Castorani, Hydrodynamics, elevation, and restoration history structure intertidal oyster recruitment. *Landsc. Ecol.* **40**, 114 (2025).
33. J. R. Esquivel-Muelbert, L. Fontoura, K. Zawada, K. Erickson, W. Figueira, J. S. Madin, M. J. Bishop, The natural architecture of oyster reefs maximizes recruit survival. *Nature* **652**, 393–397 (2026).
34. L. L. Woolbright, The impact of hurricane hugo on forest frogs in Puerto Rico. *Biotropica* **23**, 462–467 (1991).
35. S. A. Levin, The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology* **73**, 1943–1967 (1992).
36. H. Hartmann, A. Bastos, A. J. Das, A. Esquivel-Muelbert, W. M. Hammond, J. Martínez-Vilalta, N. G. McDowell, J. S. Powers, T. A. M. Pugh, K. X. Ruthrof, C. D. Allen, Climate change risks to global forest health: Emergence of unexpected events of elevated tree mortality worldwide. *Annu. Rev. Plant Biol.* **73**, 673–702 (2022).
37. C. D. Allen, D. D. Breshears, N. G. McDowell, On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* **6**, 1–55 (2015).
38. S. B. Fey, A. M. Siepielski, S. Nusslé, K. Cervantes-Yoshida, J. L. Hwan, E. R. Huber, M. J. Fey, A. Catenazzi, S. M. Carlson, Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1083–1088 (2015).
39. O. Valkó, B. Deák, T. Magura, P. Török, A. Kelemen, K. Tóth, R. Horváth, D. D. Nagy, Z. Debnár, G. Zsigrai, I. Kapocsi, B. Tóthmérész, Supporting biodiversity by prescribed burning in grasslands — A multi-taxa approach. *Sci. Total Environ.* **572**, 1377–1384 (2016).
40. M. E. Brooks, K. Kristensen, K. J. van Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Machler, B. M. Bolker, glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* **9**, 378–400 (2017).
41. B. Bolker, D. Robinson, D. Menne, J. Gabry, P. Buerkner, C. Hua, W. Petry, J. Wiley, P. Kennedy, E. Szöcs, I. Patil, V. Arel-Bundock, B. Denney, C. Brunson, J. Wasserman, A. Stukalov, M. Bruneaux, broom.mixed: Tidying methods for mixed models, version 0.2.9.6 (2024); https://cran.r-project.org/web/packages/broom.mixed/index.html.
42. F. Hartig, L. Lohse, M. de S. leite, DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models, version 0.4.7 (2024); https://cran.r-project.org/web/packages/DHARMa/index.html.
43. D. Lüdecke, F. Aust, S. Crawley, M. S. Ben-Shachar, S. C. Anderson, ggeffects: Create tidy data frames of marginal effects for "ggplot" from model outputs, version 2.3.0 (2025); https://cran.r-project.org/web/packages/ggeffects/index.html.
44. H. Wickham, W. Chang, L. Henry, T. L. Pedersen, K. Takahashi, C. Wilke, K. Woo, H. Yutani, D. Dunnington, T. van den Brand, Posit, PBC, ggplot2: Create elegant data visualisations using the grammar of graphics, version 3.5.2 (2025); https://cran.r-project.org/web/packages/ggplot2/index.html.
45. R Core Team, R: A language and environment for statistical computing, version 4.2.3 (R Foundation for Statistical Computing, 2023); www.R-project.org/.
46. Posit team, RStudio: Integrated development environment for R, version 2023.12.1.402 (Posit Software, PBC, 2024); www.posit.co/.
47. S. C. Pennings, W. Sheldon, A. Sapp, S. Li, Long-term plant biomass monitoring data from the Georgia Coastal Ecosystems LTER Project on Sapelo Island, Georgia, Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/935872AE9B32D59D2C59B26856F0EA95.
48. Georgia Coastal Ecosystems LTER Project, S. C. Pennings, Disturbance to permanent monitoring plots at GCE sites 1-10, from 2001 to 2024, Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/87B61D3EF631D3BFB94A06DFE2D6E159.
49. B. Lusk, R. Smith, M. C. N. Castorani, Oyster and associated fauna counts and lengths from restored and reference reefs in the coastal bays of Virginia, 2005-2019, Environmental Data Initiative (2024); https://doi.org/10.6073/PASTA/18231A2EECFCE87CDBBBDA3A678689CA.
50. J. Zimmerman, Canopy Trimming Experiment (CTE) plant seedling measurements, Environmental Data Initiative (2024); https://doi.org/10.6073/PASTA/D47F3C02EA494B2D24864AFD4C02D066.
51. J. K. Zimmerman, Canopy Trimming Experiment (CTE) plot treatments, Environmental Data Initiative (2023); https://doi.org/10.6073/PASTA/26B0315DA71F5B43DC16FE9B266A1BDD.
52. E. Castañeda-Moya, E. Solohin, J. Kominoski, Patterns of root biomass, productivity, turnover, and decomposition in riverine mangroves in the Everglades, Florida, USA, post-Irma, 2018-2019, Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/2EA2D47E2DE9DE450A9FA270C67733BF.
53. K. Kopecky, G. Pavoni, M. Corsini, Dead-coral-removal-experiment, version 1.0 (Zenodo, 2025); https://doi.org/10.5281/zenodo.15595348.
54. K. L. Kopecky, G. Pavoni, E. Nocerino, A. J. Brooks, M. Corsini, F. Menna, J. P. Gallagher, A. Capra, C. Castagnetti, P. Rossi, A. Gruen, F. Neyer, A. Muntoni, F. Ponchio, P. Cignoni, M. Troyer, S. J. Holbrook, R. J. Schmitt, Quantifying the loss of coral from a bleaching event using underwater photogrammetry and AI-assisted image segmentation. *Remote Sens.* **15**, 4077 (2023).
55. J. Blair, J. Nippert, PAB01 Aboveground net primary productivity of tallgrass prairie based on accumulated plant biomass on core LTER watersheds (001d, 004b, 020b), Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/38206EA12B42BBD77AD97E1C0747353D.
56. J. Nippert, PAB04 Aboveground primary productivity of tallgrass prairie based on accumulated plant biomass on miscellaneous LTER watersheds, Environmental Data Initiative (2024); https://doi.org/10.6073/PASTA/5A198CF7BEE61EC7AD7854E4AC44EA4E.
57. J. Blair, P. O'Neal, KFH01 Konza prairie fire history, Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/4062CF9E699B742DC6D400CEB8E3FED6.
58. A. Ellison, A. B. Plotkin, Coarse woody debris in hemlock removal experiment at harvard forest since 2005, environmental data initiative (2023); https://doi.org/10.6073/pasta/78bd1db933d302665f65ea10c1830d82.
59. A. Ellison, A. B. Plotkin, Understory vegetation in hemlock removal experiment at Harvard Forest since 2003, Environmental Data Initiative (2024); https://doi.org/10.6073/PASTA/2C64E2AFD4FAA2C0B57582D675D9CB51.
60. M. E. Harmon, Dimensions, cover, volumes, mass and nutrient stores of coarse woody debris (bark and wood from logs, snags, and stumps) from forests plots in the western United States and Mexico, 1977 to 2005, Environmental Data Initiative (2016); https://doi.org/10.6073/PASTA/E683B01F0AB3B1E4B4566471072BCEDF.
61. J. F. Franklin, D. M. Bell, S. M. Remillard, R. J. Pabst, A. Bluhm, Long-term growth, mortality and regeneration of trees in permanent vegetation plots in the Pacific Northwest, 1910 to present, Environmental Data Initiative (2025); https://doi.org/10.6073/PASTA/DC4BE3DB15934E0E5EB4820F56E5D569.
62. J. Johnstone, Bonanza Creek LTER, Black spruce seed counts from seed rain traps in the 2004 burns off the Steese, Taylor, and Dalton Highways, collected in 2005-2007, Environmental Data Initiative (2016); https://doi.org/10.6073/PASTA/89B6B0750C86CF9B8B73D769106555E1.
63. D. C. Reed, S. C. Schroeter, H. M. Page, K. M. Beheshti, R. S. Smith, D. Y. Huang, SONGS Mitigation Monitoring, UCSB SONGS mitigation monitoring: Reef process study - Density of giant kelp recruits and cover of dead holdfasts ver 1, Environmental Data Initiative (2025); https://doi.org/10.6073/pasta/2ee6027881f465f260a6e37ab1863449.


**Acknowledgments:** We thank the National Science Foundation (NSF) LTER Network for support in enabling the creation of the datasets used in this study. This is contribution #2124 from the Institute of Environment at Florida International University. We are also grateful for insights on crafting this study from members of ESIIL, the Earth Lab, and the Suding Lab. Last, we thank M. Whalen for development of graphics. **Funding:** This work was funded by the Florida Coastal Everglades LTER: DEB-2424122 (NSF) and DEB-2025954 (NSF), awarded to J.S.K.; the Konza Prairie LTER: DEB-2025849 (NSF), awarded to J.B.N.; OCE-2337532 (NSF), awarded to M.C.N.C. The SONGS Mitigation Monitoring Program: Southern California Edison funded this project as required by the California Coastal Commission (CDP 6-81-330-A.). Publication of this article was funded by the University of Colorado Boulder Libraries Open Access Fund and the Environmental Data Science Innovation and Impact Lab (ESIIL). We thank the Long Term

Downloaded from https://www.science.org on June 13, 2026

Ecological Research Network Office (LNO) (NSF award numbers 1929393 and 2419138) for facilitating this project. Data used in this study received funding from the Bonanza Creek LTER: DEB-1636476 (NSF), awarded to M. Mack (PI), and the USDA Forest Service Pacific Northwest Research Station, Agreement #RJVA-PNW-20-JV-11261932-018; the Environmental Data Science Innovation & Impact Lab: DBI-2153040 (NSF), awarded to J. K. Balch (PI); the Florida Coastal Everglades LTER: DEB-1801244 (NSF), awarded to E. E. Gaiser (PI); the Georgia Coastal Ecosystems LTER: OCE-1832178 (NSF), awarded to M. L. Alber (PI); the Harvard Forest LTER: DEB-0620443 (NSF) and DEB-1237491 (NSF), awarded to D. R. Foster (PI), and DEB-1832210 (NSF), awarded to J. R. Thompson (PI); the H. J. Andrews Experimental Forest LTER: DEB-2025755 (NSF), awarded to M. G. Betts (PI), and the USDA Forest Service Pacific Northwest Research Station; the Luquillo LTER: DEB-0080538, DEB-0218039, and DEB-0620910 (NSF), awarded to N. V. Brokaw (PI), and DEB-1239764 (NSF), awarded to J. K. Zimmerman (PI); the Moorea Coral Reef LTER: OCE-1637396 (NSF), awarded to R. J. Schmitt (PI); and the Niwot Ridge LTER: DEB-2224439 (NSF), awarded to N. C. Emery (PI). Additional support was provided through the Santa Barbara Coastal LTER: OCE-1831937 (NSF) and OCE-2425417 (NSF), awarded to R. J. Miller (PI); and the Virginia Coast Reserve LTER: DEB-1832221 (NSF) and DEB-2425178 (NSF), awarded to K. J. McGlathery (PI). **Author contributions:** Conceptualization: K.L.K., K.N.S., J.F.J., T.T., J.S.K., and A.B.P. Methodology: K.L.K., M.C.N.C., T.T., J.S.K., and A.B.P. Investigation: K.L.K., M.C.N.C., A.B.P., J.F.J., J.S.K., J.B.N., C.J.N., S.C.P., D.C.R., A.B.S., T.T., and K.N.S. Data curation: K.L.K., M.C.N.C., D.C.R., J.S.K., A.B.P., J.F.J., S.C.P., and D.M.B. Formal analysis: K.L.K., M.C.N.C., and D.M.B. Resources: K.L.K., M.C.N.C., T.T., D.C.R., and J.S.K. Visualization: K.L.K. and M.C.N.C. Project administration: K.L.K., T.T., and J.S.K. Funding acquisition: T.T., D.C.R., J.S.K., K.N.S., J.F.J., S.C.P., and J.B.N. Supervision: K.N.S., M.C.N.C., and T.T. Software: K.L.K., M.C.N.C., and T.T. Validation: K.L.K., M.C.N.C., T.T., D.C.R., J.S.K., and J.F.J. Writing—original draft: K.L.K. and T.T. Writing—review and editing: K.L.K., M.C.N.C., A.B.P., D.M.B., J.F.J., J.S.K., J.B.N., C.J.N., S.C.P., D.C.R., A.B.S., T.T., and K.N.S. **Competing interests:** The authors declare that they have no competing interests. **Data, code, and materials availability:** This study did not generate new materials (data). All data used in this study are available with metadata via the Environmental Data Initiative (descriptions of each dataset used and hyperlinks to access them are available in table S1). The data are also compiled, along with code used to run the analyses and create visualizations, in the following Zenodo repository: https://doi.org/10.5281/zenodo.19208027. The same code can also be obtained from the following publicly accessible GitHub repository: https://github.com/kkopecky711/LTER-material-legacies. All data and code needed to evaluate and reproduce the results in the paper are present in the paper and/or the Supplementary Materials.

Submitted 30 January 2026
Accepted 4 May 2026
Published 10 June 2026
10.1126/sciadv.aef9983

Downloaded from https://www.science.org on June 13, 2026

ScienceAdvances

# Legacies of foundation species shape life after death

Kai L. Kopecky, Max C. N. Castorani, Ty Tuff, Audrey Barker Plotkin, David M. Bell, Jill F. Johnstone, John S. Kominoski, Jesse B. Nippert, Christopher J. Nytch, Steven C. Pennings, Daniel C. Reed, Aaron B. Shiels, and Katharine N. Suding

*Sci. Adv.* **12** (24), eaef9983. DOI: 10.1126/sciadv.aef9983

**View the article online**
https://www.science.org/doi/10.1126/sciadv.aef9983
**Permissions**
https://www.science.org/help/reprints-and-permissions

Downloaded from https://www.science.org on June 13, 2026

Use of this article is subject to the Terms of service

*Science Advances* (ISSN 2375-2548) is published by the American Association for the Advancement of Science. 1200 New York Avenue NW, Washington, DC 20005. The title *Science Advances* is a registered trademark of AAAS.

Copyright © 2026 The Authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original U.S. Government Works. Distributed under a Creative Commons Attribution NonCommercial License 4.0 (CC BY-NC).