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ECOLOGY

Legacies of foundation species shape life after death

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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

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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).

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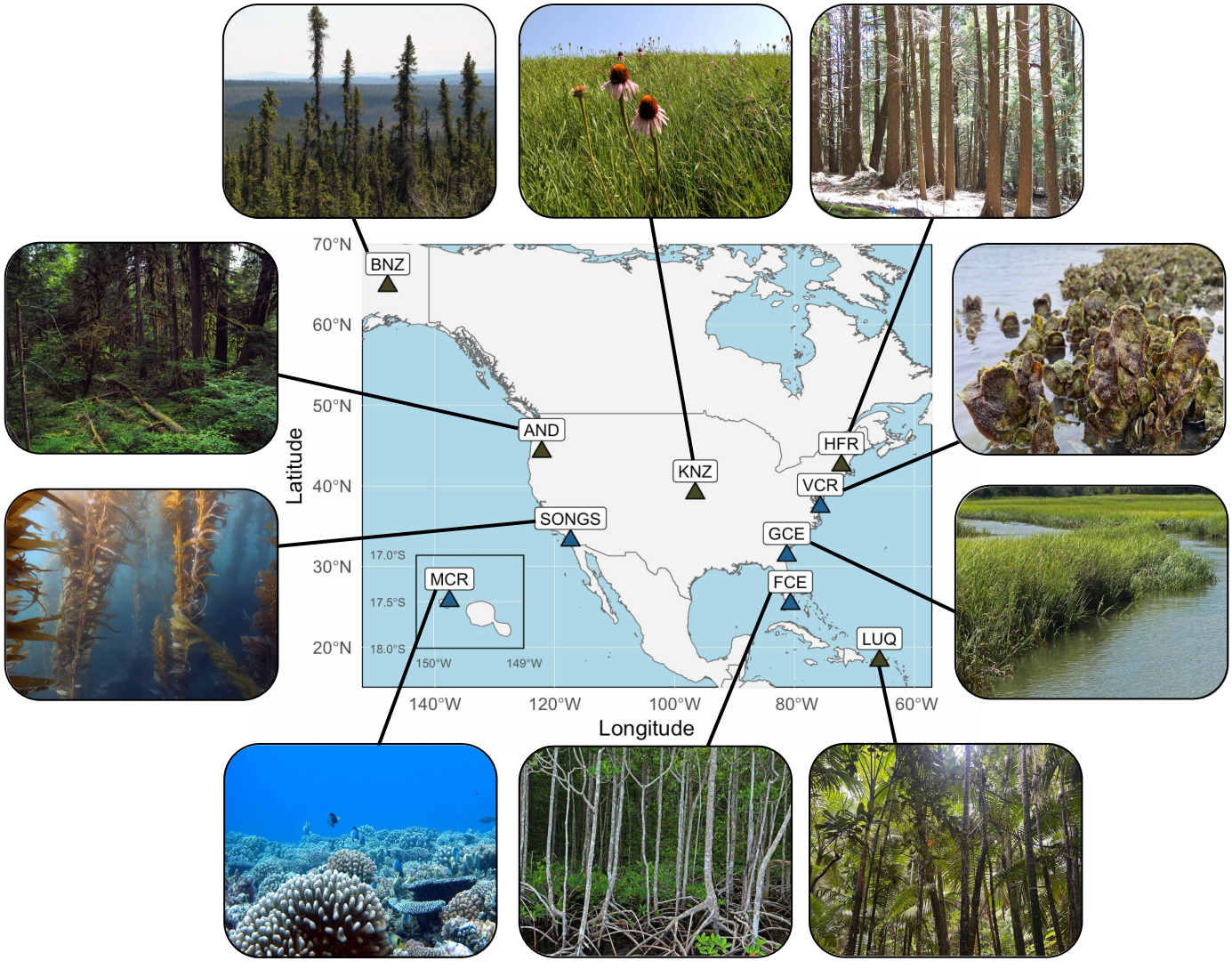

Fig. 2. Map and images of study sites. Clockwise from top-left image: Bonanza Creek (BNZ), Konza Prairie (KNZ), Harvard Forest (HFR), Virginia Coast Reserve (VCR), Georgia Coastal Ecosystems (GCE), Luquillo (LUQ), Florida Coastal Everglades (FCE), Moorea Coral Reef (MCR), San Onofre Nuclear Generating 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

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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

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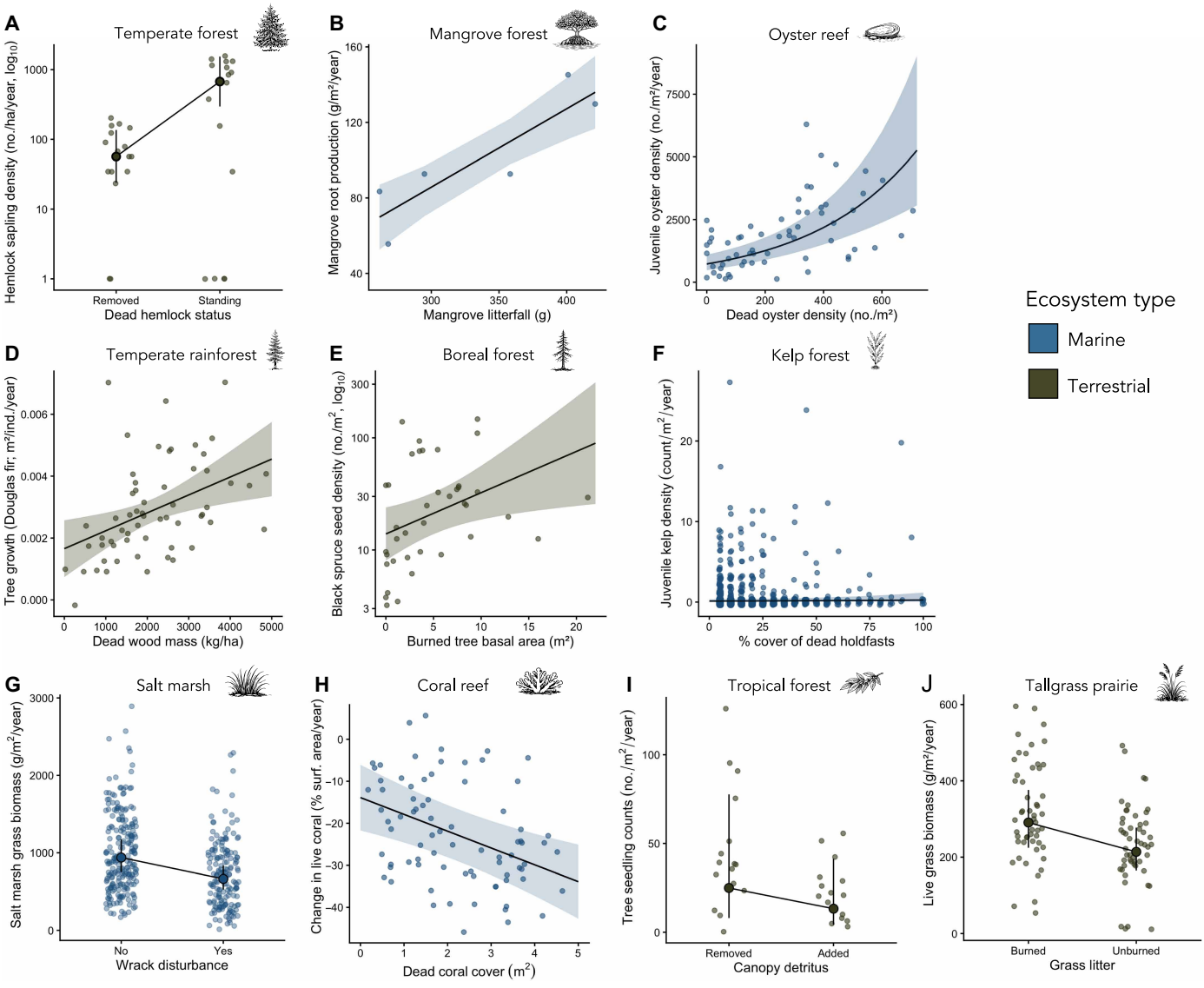

Fig. 3. Material legacies of foundation species influence demographic responses across a wide range of ecosystems, with varying positive, null, and negative effects. Each panel displays the output from a GLMM tailored to the structure of the dataset used from each site/system. Means ± 95% confidence 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

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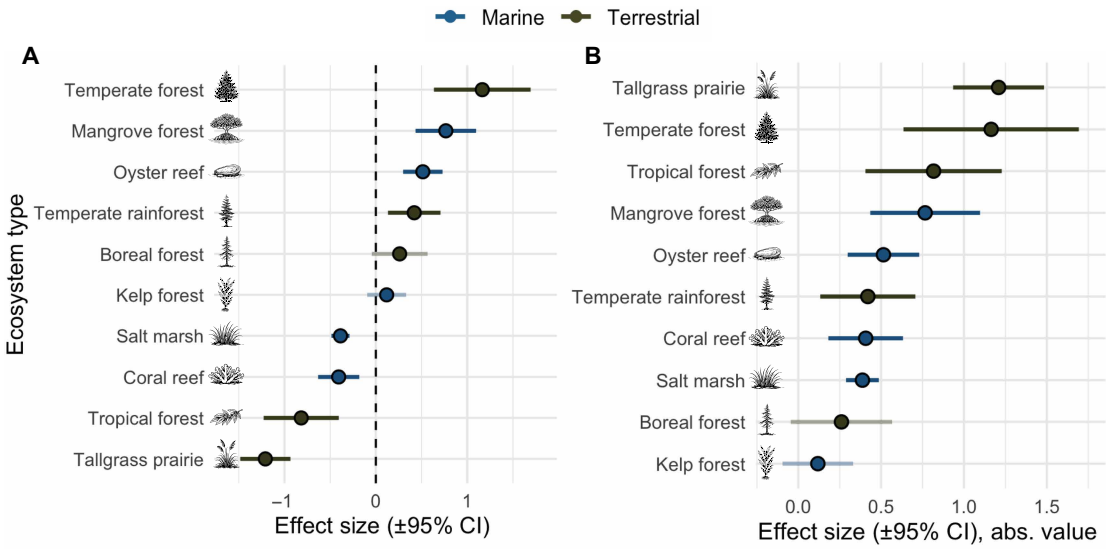

Fig. 4. Standardized effect sizes of the relationships between material legacy predictors and demographic responses. (**A**) Standardized effect sizes (±95% CIs) extracted from GLMMs for each ecosystem, where predictors and responses were scaled to *z*-scores (units of SDs). (**B**) Effect sizes from (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.

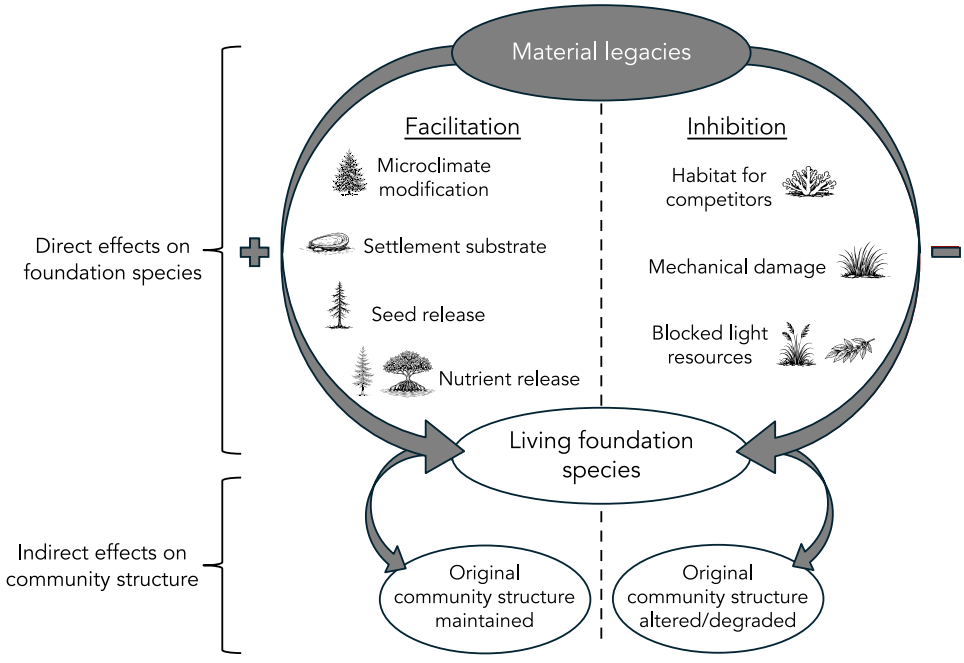

Fig. 5. Consequences of positive versus negative effects of material legacies for ecological community structure. Material legacies that positively affect demographic processes in live foundation species support establishment and growth of living conspecifics ("facilitation") and thereby stabilize or 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.

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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

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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

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