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Trends in
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Review

Dead foundation species drive ecosystem dynamics

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Foundation species facilitate communities, modulate energy flow, and define ecosystems, but their ecological roles after death are frequently overlooked. Here, we reveal the widespread importance of their dead structures as unique, interacting components of ecosystems that are vulnerable to global change. Key metabolic activity, mobility, and morphology traits of foundation species either change or persist after death with important consequences for ecosystem functions, biodiversity, and subsidy dynamics. Dead foundation species frequently mediate ecosystem stability, resilience, and transitions, often through feedbacks, and harnessing their structural and trophic roles can improve restoration outcomes. Enhanced recognition of dead foundation species and their incorporation into habitat monitoring, ecological theory, and ecosystem forecasting can help solve the escalating conservation challenges of the Anthropocene.

What are dead foundation species?

Foundation species (FS) (see Glossary) create living, growing, biogenic structures that define ecosystems and enhance their stability [1–4]. Like every other organism, they also die, and their dead structures constitute an immense quantity of biogenic material in terrestrial, aquatic, and marine ecosystems. For example, tree death generates up to 30 Mg ha^{-1} $year^{-1}$ of dead wood in terrestrial forests [5]. Dead kelp, seagrass, and mangrove wood contribute beach wrack, which can amount to 325 kg m^{-1} of coastline [6], and calcifying organisms generate dead shell mounds, reefs, and bioherms that can span up to thousands of km^2 on the ocean floor [7–9]. Although it is now recognized that these structures provide important habitat, trophic, and biogeochemical roles within a variety of ecosystems [6,10,11], a broad synthesis of the interactions involving the remains of FS and their significance for ecosystem dynamics is lacking.

We define dead foundation species (DFS) as dead organisms that play foundational roles both before and after they die (type I), only after they die (type II), and only before they die (type III) (Figure 1). Because FS often exhibit **traits** (high biomass, group-living, complex structures) of potent **ecosystem engineers (EE)**, they have the potential to leave strong **legacy effects**, or environmental modifications that remain after the death and disappearance of the EE from a system [12,13]. Given that DFS can persist as interacting components within and across environments [6,7,14], their engineering effects do not necessarily taper after death and can in fact exceed or rival those of living FS. Here we reveal the widespread importance of DFS for ecosystem dynamics and how the change or persistence of FS traits following death can predict environmental modifications. We discuss the relevance of these modifications for feedbacks underlying system resilience and restoration efforts, and stress the need for broad recognition of DFS as interacting components of ecosystems given their shifting dynamics and vulnerability to global change.

Highlights

The powerful community-structuring roles of foundation species (FS) are well recognized; however, ecological interactions involving their dead structures have yet to be broadly integrated within ecological theory or ecosystem management.

As interacting components of ecosystems, dead foundation species (DFS) modify environments and mediate feedbacks underpinning ecosystem resilience.

DFS are vulnerable to global change and often respond differently than living FS.

Changes in DFS quantity, composition, and frequency of occurrence influence habitat heterogeneity within systems and subsidy dynamics across systems, provoking far-reaching effects on biodiversity and ecosystem functions.

Enhanced recognition of DFS traits and ecological roles will improve restoration outcomes, inform ecological forecasts, and guide conservation of ecosystems challenged by global change.

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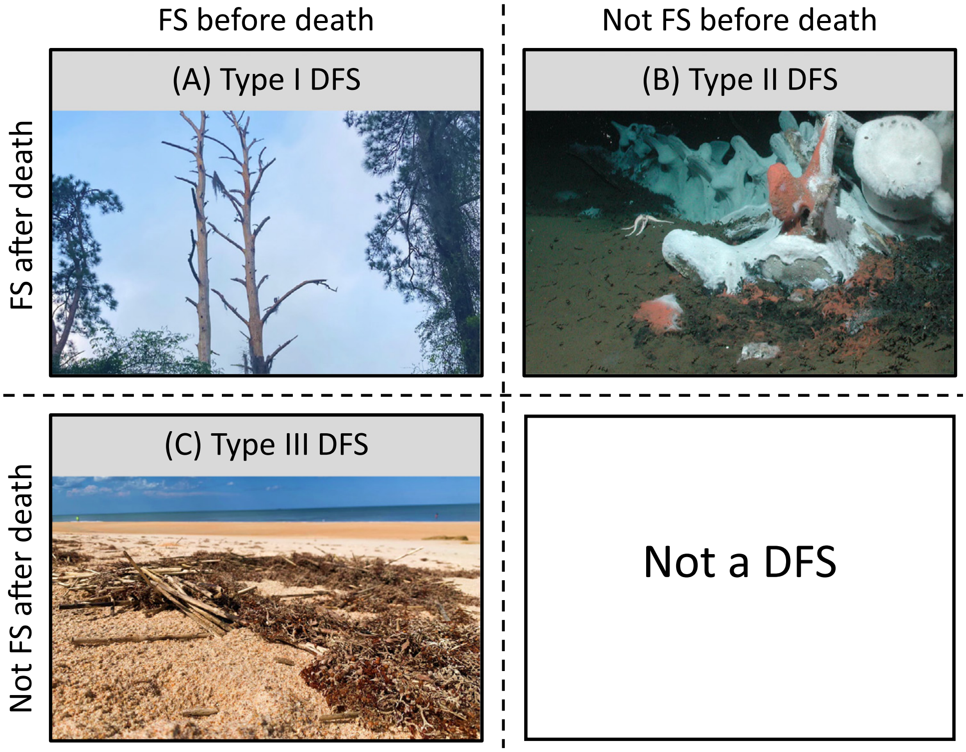

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Figure 1. The types of dead foundation species (DFS) with illustrative examples. (A) Type I DFS: a species that acts as a foundation species both before and after death, such as a tree that continues to provide habitat for birds after it dies. (B) Type II DFS: a species that provides foundational roles only after death, such as a whale skeleton on the deep-sea floor represents a foundational habitat for benthic communities of invertebrates and fishes. (C) Type III DFS: a foundation species before death that may provide an important trophic subsidy after death but may not offer the habitat role of a foundation species, such as seaweed detritus on a beach. Photo credits: (A) Patrick H. Saldaña, (B) Craig R. Smith, (C) Britney K. Hay.

Glossary

Driftcretions: driftwood concentrations that engineer shoreline geomorphology, provide habitat, increase productivity, sequester carbon, and provide shoreline protection.

Ecosystem engineers (EE): organisms that create or modify habitat and mediate resource availability in associated communities. These include: (i) allogenic engineers, such as beavers, that transform raw materials to an engineered state; and (ii) autogenic engineers, such as corals and trees, that modify environmental conditions through their own growth.

Ecosystem functions: processes that determine the flow and transfer of energy, matter, and information throughout ecosystems.

Facilitation cascade: a hiearchical interaction in which a primary species facilitates a secondary species, which in turn facilitates other associated species.

Foundation species (FS): organisms or groups of organisms that define community structure by creating living, growing, biogenic structures. They are generally abundant, near the base of food webs, and modulate habitat and energy flow through primarily non-trophic interactions.

Habitat heterogeneity: a highly variable term in ecology that depends on the scale of observation. Here we use it to broadly refer to variation in the amount, trophic function, and morphology of habitats within an ecosystem.

Keystone structures: distinct spatial structures that provide resources, habitat, and other goods and services to other species. They are not necessarily of biogenic origin.

Legacy effects: any long-lasting impact of organisms and their ecological interactions, including transformation of the environment by ecosystem engineers, that persist after the disappearance of the engineer.

Snag: a dead, standing tree.

Trait: any measurable feature of an individual organism without reference to its environment. Traits can be morphological, taxonomic, and phenological and can serve as useful tools for identifying patterns in biodiversity and generating causal relationships with ecological processes.

Traits and environmental effects of dead foundation species

Many DFS structures engineer their environment after death, sometimes with effects that are redundant to their live counterparts, and other times unique [15–17]. In marine systems, recently dead coral skeletons, tubeworm tests, and bivalve shells continue to provision habitat to associated communities [17–19]. Dead oysters continue to ameliorate high temperatures in estuaries by providing shade [20], dead shrubs continue to provide labile carbon sources that support vegetative growth [16], and dead seagrass mats persist as biogeochemical sinks that continue to sequester nutrients and heavy metals [21]. Because some DFS play roles that are redundant to their living counterparts, the persistence of DFS can maintain ecosystem services and support self-facilitating feedbacks that increase resilience [16,21,22] (see ‘Feedbacks and system transitions’). In other cases, the traits of FS change after death, with ecologically important environmental consequences of their own. Traits that may persist or change with death of a FS fall into three general categories: metabolism, mobility, and morphology (Figure 2).

FS death and resulting loss in metabolic activity represents a trait change that can alter biogeochemical processes and **ecosystem functions**. Widespread oyster mortality results in lowered denitrification rates in estuaries as oysters stop filtering water [23], and cessation of carbon and gas translocation from leaves and pneumatophores to roots and rhizomes of terrestrial and aquatic plants following death can affect microbial biogeochemical cycling and either reduce or

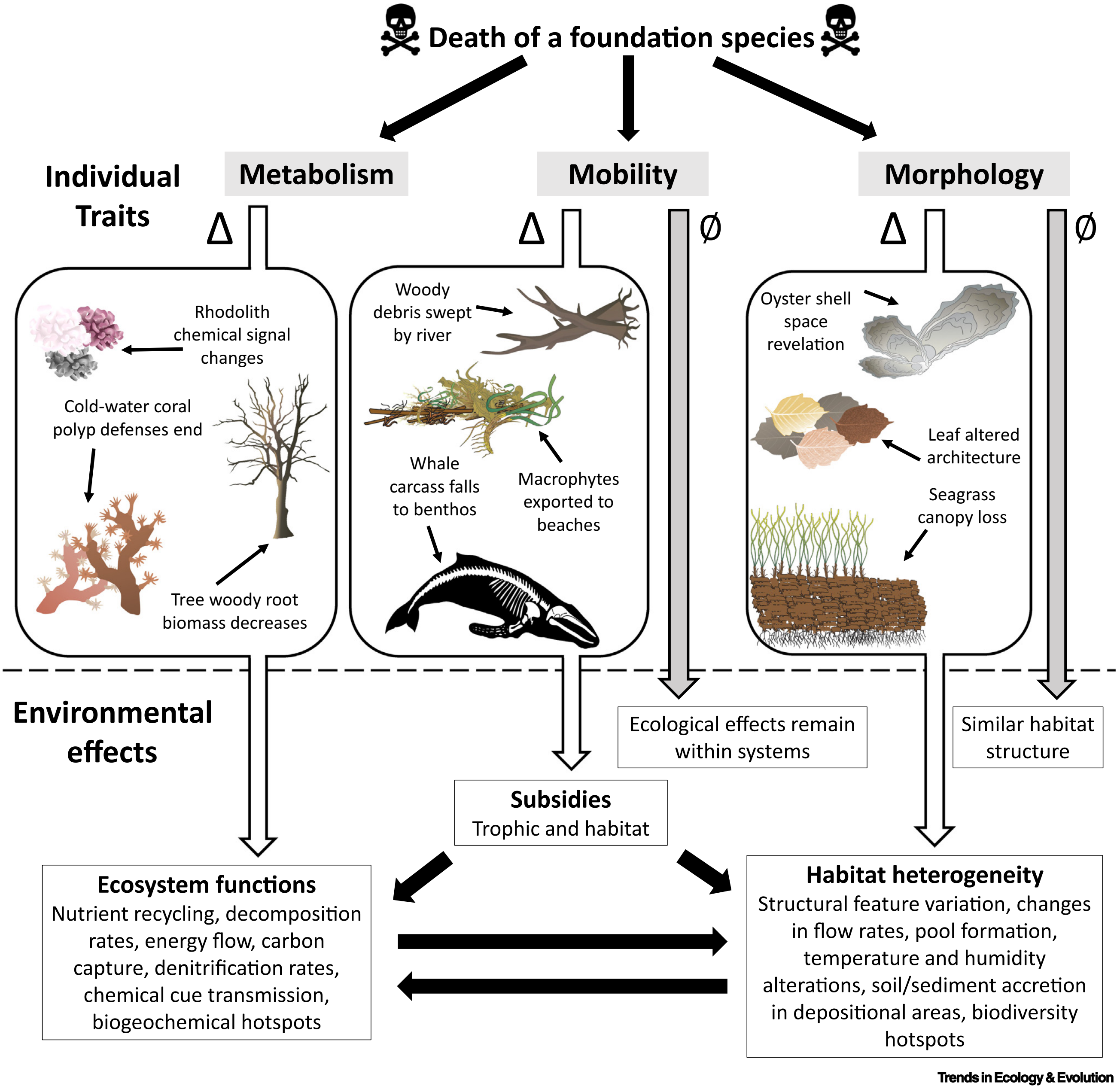
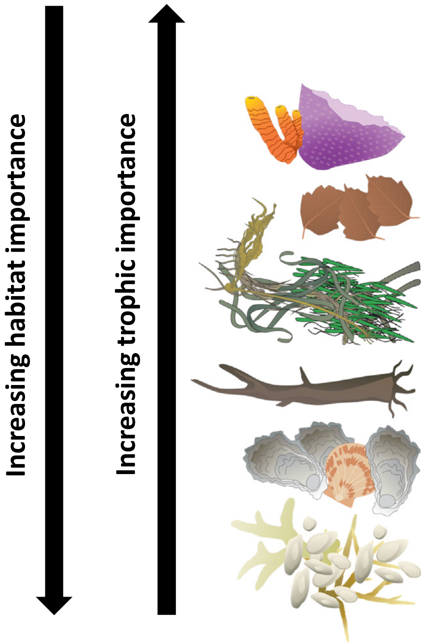


Figure 2. Environmental effects of trait changes and persistence after foundation species' (FS) death. The change and/or persistence of FS traits, including metabolic activity, mobility, and morphology after death, can have widespread environmental effects. The dashed horizontal line represents a change in scale from the individual traits to the environmental effects. The delta (Δ) and empty set (Ø) symbols represent change or persistence in traits, respectively. White arrows with expanded illustrations of examples of FS trait changes connect traits to their environmental effects that include altered ecosystem functions, provisioning of subsidies, and contributions to habitat heterogeneity. Gray arrows connect the persistence of traits with their respective environmental effects. Black arrows represent causal relationships within individual or ecosystem scales.

enhance mineralization of soil organic carbon [24–26]. Such functions directly driven by FS metabolic activity will cease where mortality occurs, but FS death also represents a natural process that can support ecosystem productivity. In the nutrient-limited deep sea, for example, dead coral frameworks passively retain phytodetritus and support endo- and epilithic communities that recycle nutrients and boost reef metabolic activity [27]. By enhancing resource retention, these dead components of reefs play crucial roles in sustaining food webs and deep-sea biodiversity hotspots [27].

FS death can also result in mobility trait changes that drive vertical and horizontal export of DFS as trophic and habitat subsidies across systems (Figure 3). In some cases, a resulting loss of mobility can initiate organisms' foundational roles (i.e., type II DFS), such as whale carcasses that fall to the ocean floor and become habitat and food resources for multiple successional stages of organisms (Figure 1B) [28]. By contrast, dead soft-bodied plants and seaweeds experience increases in mobility that may decrease or end their foundational roles (i.e., type III DFS, Figure 1C), or initiate their provisioning of important subsidies to sandy beaches and deep sea ecosystems [6,29]. Recent work has reviewed the context dependency of animal subsidy effects across ecosystems [30–32], but more work is needed on how changing amounts, frequency of occurrence, and composition of DFS will affect cross-ecosystem exchange (Box 1). We predict that generally, the durability of the DFS will impact its relative structural and trophic importance as a subsidy, as longer lasting materials such as bivalve shells, dead coral, and large woody debris subsidize structures such as atolls, reef slopes, and **driftcretions** [14,33,34], and less durable structures will mostly play a trophic subsidy role (Figure 3). However, emerging evidence suggests that ephemeral DFS can also provide important habitats. Dead seagrass rafts provide roosting structures for shorebirds and seaweed wrack piles offer refuge for sandy beach fauna [6,35]. Thus, even relatively short-lived DFS may represent important, although pulsed, structural features of **habitat heterogeneity** that support populations and communities.

Death also initiates changes in FS morphological traits via three primary pathways that impact DFS habitat roles. First, FS death can create newly available habitat for organisms. Examples



Dead foundation species	Donor system(s)	Recipient system(s)
Sponges	Submarine cliffs	Benthic soft sediment [98]
Leaf litter	Terrestrial/mangrove forest canopy	Forest floor, lotic/lentic/benthic systems, sandy beaches [61]
Macrophyte wrack/ detritus	Kelp forest, seagrass bed	Deep sea benthos, sandy beaches, dunes [6,29]
Large woody debris	Terrestrial forests, mangrove forests, riverine systems	Lentic/lotic systems, mangrove ponds, shorelines, deep sea benthos [5,44,100]
Bivalve shells	Bivalve reefs, subtidal walls	Benthic shell beds, coquina reefs, shell ridges [8,34]
Coral skeletons, rubble	Coral reefs	Atolls, reef rubble fields, adjacent reef slopes [33]

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Figure 3. Dead foundation species as subsidies across systems. Examples of cross-system exchange of trophic and habitat subsidies provided by dead foundation species (DFS) in terrestrial and marine systems. DFS can contribute substantial subsidies to recipient ecosystems, although the temporal and spatial scale of the exchange may depend on DFS traits related to its persistence and mobility. As the structural persistence of the DFS goes up, its role as a trophic subsidy relative to its role as a habitat subsidy is predicted to decrease. See [5,6,8,29,33,34,44,61,98,100].

Box 1. Anthropogenic changes in the frequency, production, and composition of dead foundation species across ecosystems

DFS provide important trophic and habitat subsidies to recipient systems [28,98,99] (Figure 3), but their ecological impacts are likely changing due to human-induced alterations to their transport. Habitat loss, altered river flow dynamics, and changing weather patterns represent just a few factors influencing the frequency of occurrence of DFS subsidies across systems [6,14,100,101], which will have consequences for recipient systems. For example, damming, riparian vegetation removal, and wood stabilization have driven reductions in woody debris movement and distribution that affect geomorphological processes, biodiversity, and nutrient fluxes in fluvial channels, beach dunes, and the deep-sea benthos [14,44,100].

Human impacts have also driven changes in foundation species' (FS) production that can have cross-system consequences. For example, increased nutrient inputs are thought to be fueling record-breaking amounts of floating pelagic *Sargassum* seaweed [102]. Although this FS provides habitat and foraging grounds for associated fauna, the stranding and decay of large accumulations of *Sargassum* have re-engineered sandy beaches and coastal systems by increasing hypoxia, hydrogen sulfide concentrations, and faunal mortality rates [103]. Thus, changes in FS production can have strong cascading effects via their dead biomass that moves, or discontinues moving, across systems.

Compositional changes in FS have restructured ecosystems globally, especially in the context of non-native and range-expanding FS [104,105]. Largely overlooked, however, are the roles of such novel FS across systems after they die. Due to the diversity of traits DFS exhibit (e.g., chemical composition, decay rate, morphology, etc.) [44,106,107], their roles extend beyond provisioning of structures, and ignoring changes in DFS subsidy identity represents an oversight in understanding global change effects on the dynamics of coupled ecosystems. Consider the notoriously invasive alga, *Caulerpa taxifolia*, that has opportunistically occupied many seagrass beds outside its native range. Widely recognized for restructuring systems that it colonizes, its detritus also represents a non-native subsidy that decreases the abundances of invertebrates inhabiting nearby mudflat habitats that receive allochthonous inputs of native detritus [108]. Even in cases where non-native living FS provide redundant roles to native FS, their dead structures may differentially structure communities [107] and we suggest that a stronger recognition of DFS traits and roles is needed for predicting the impacts of non-native species. More generally, it will be difficult to predict the trajectories of recipient systems without clearer understanding of how the composition, amount, and frequency of occurrence of DFS is changing both within and across ecosystems.

include bivalves that emerge from sediment and/or open after death to reveal shell surfaces and crevice spaces for epibionts [19,36], and trees that drop their leaves after death and provide canopy gap habitats that increase bird abundance and diversity [37]. Second, abiotic factors can alter DFS habitat physical complexity, such as when desiccation increases dead leaf architectural complexity, creating favorable habitat for predatory arthropods [38]. Third, biotic interactions can modify and enhance DFS structural complexity, such as when shipworms bore through fallen mangrove branches and create microhabitats for communities of mobile organisms [39]. Because time since death can affect DFS traits and roles [27,40], FS death may initiate gradual ecological changes rather than an abrupt shift in diversity or ecosystem function, as the DFS continues to interact, modify, and degrade within its environment.

DFS can augment heterogeneity that directly and indirectly mediates biodiversity (Figure 4), similar to living FS [41–43]. Dead glass sponges, whale carcasses, and **snags** directly provide habitat and represent **keystone structures** (Figure 4A), as the loss of these DFS decreases habitat heterogeneity and biodiversity [7,42,44]. Some DFS structures also provide primary substratum in **facilitation cascades**, thereby indirectly mediating biodiversity [43] (Figure 4B). For example, dead bivalve shells support barnacle colonization, which then supports tertiary FS in a hierarchical facilitation that promotes habitat heterogeneity and increases epibiont diversity [45].

Moreover, DFS also often exist in mixed FS assemblages where they can increase habitat heterogeneity and directly enhance biodiversity in three ways (Figure 4C). First, DFS can represent unique structures within assemblages that also include living FS. Trees, corals, and oysters are often found with live and dead individuals of a given species intermixed, with the DFS contributing metabolically inactive and morphologically unique habitat for associated assemblages [37,46,47] (Figure 4Ci). Second, a mixture of structures created by DFS of different species can increase

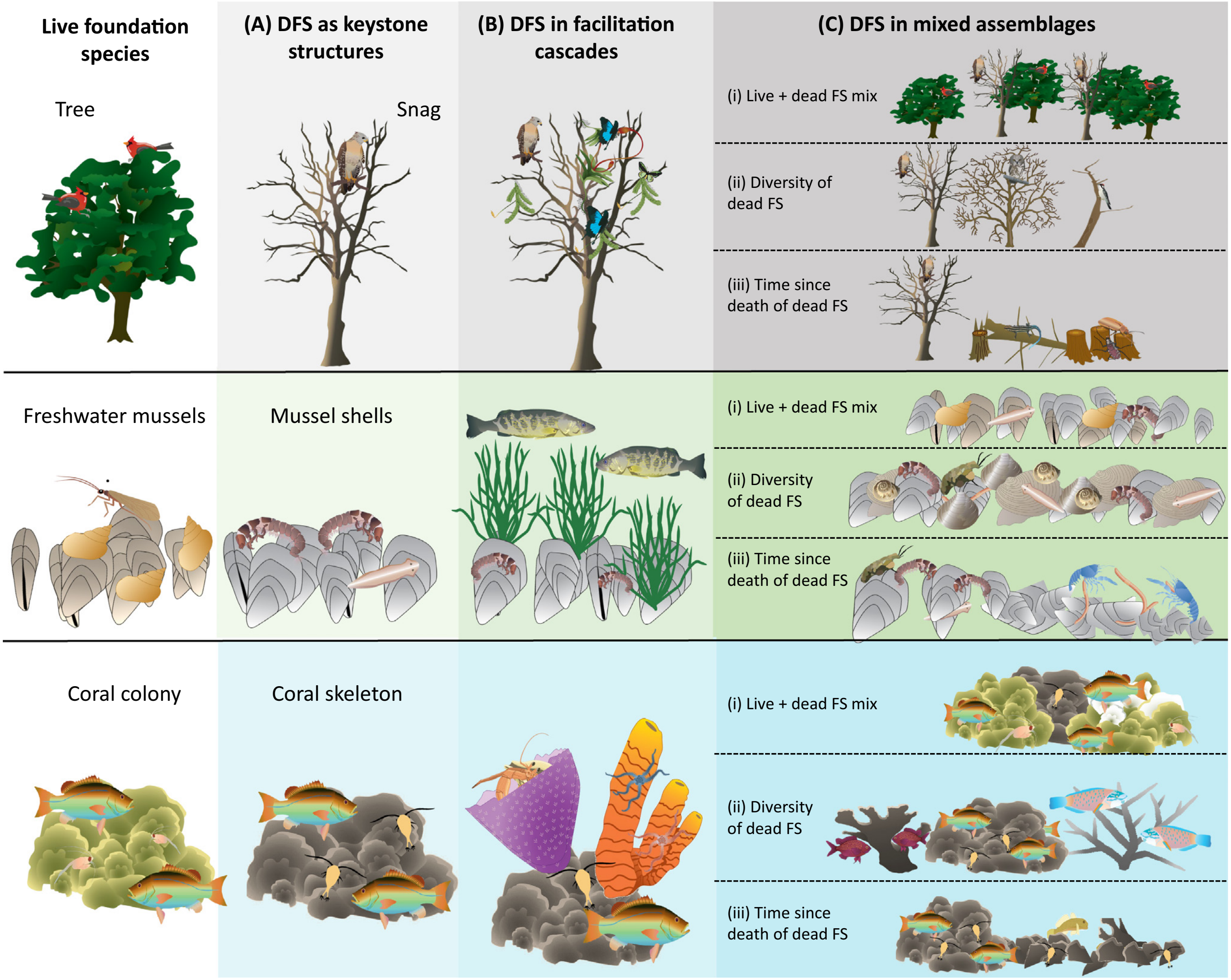

Figure 4. Dead foundation species (DFS) as components of habitat heterogeneity. Terrestrial forest (top), freshwater bivalve (middle), and marine coral reef (bottom) examples of how DFS create heterogeneity in land- and seascapes that mediates community structure. (A) DFS can directly support biodiversity as keystone structures that represent distinct spatial features. The presence of snags, shells, and coral skeletons increase available habitat and niche space for organisms. (B) DFS also indirectly facilitate secondary foundation species (FS) that increase habitat heterogeneity hierarchically in facilitation cascades that support unique communities. Dead trees provide primary habitat for secondary epiphytic plant FS, mussel shells provide substratum for secondary macrophyte FS, and coral skeletons provide substratum for secondary habitat space-holders such as sponges. Each of these secondary FS facilitate different organisms than the dead primary FS. (C) DFS also increase heterogeneity in mixed assemblages of FS such as snags, mussel shells, and coral skeletons that can co-occur with (i) their live counterparts, (ii) with different species of DFS, and (iii) with DFS at different stages of degradation, or any combination of these.

beta diversity, as when different species of dead trees each host unique fungal communities [48] (Figure 4Cii). Third, an assemblage of DFS that varies in time since death will offer greater trait heterogeneity that likely results in greater associated biodiversity than a stand of DFS of the same age (Figure 4Ciii), as revealed by increases in biodiversity that occur along gradients of DFS at different decay states in coral reefs and terrestrial forests [40,49]. Awareness of the links between DFS, habitat heterogeneity, and biodiversity can directly inform conservation management on best practices for increasing biodiversity (i.e., increasing dead wood heterogeneity over increasing dead wood quantity) [50], and characterization of biodiversity drivers should include DFS to capture their functional importance in assemblages.

Feedbacks and system transitions

FS often support their own persistence through self-facilitative feedbacks, as recognized in research involving system transitions and alternate states [51,52]. DFS can also play an important role in these feedbacks, although this has received far less attention to date in the scientific literature. A widespread mechanism, however, involves the structures of DFS as substratum for recolonization. Downed, dead trees provide structural foundations for plant regrowth, dead seagrass mats provide consolidated substrata for seedling attachment, and marine hard-bodied FS such as dead corals and bivalves provide the necessary substratum for larval settlement of conspecifics [53–56]. The persistence of these structures is crucial for the self-facilitative regeneration of the FS.

DFS can mediate stability within systems by providing nutrients and trophic resources in several ways. First, DFS can promote resilience, such as flood-redistributed large woody debris that elevate soil nutrient (N and P) and moisture levels in riverine systems that then facilitate riparian vegetation growth [57]. Second, DFS may enhance community persistence by fueling secondary production, such as dead corals that support epifaunal invertebrate assemblages critical for reef food webs [58,59]. Third, DFS may facilitate community successional stages. Vicente and colleagues hypothesized that detritus of pioneering sponge species in tropical reefs fuel community development during ecological succession by providing particulate organic matter to detritivores [60]. Although trait-based approaches have been proposed to better conceptualize how leaf litter and dead wood quality affects energy flow, stability, and forest regeneration [5,54,61], the mechanisms by which resource provisioning involving DFS drives recovery processes in marine systems remains understudied, despite recognition of feedbacks as important contributors to system transitions [52]. Relationships between DFS and successional processes deserve additional investigation as they may determine whether systems return to FS-characterized states following disturbance events.

DFS may also play a pivotal role in destabilizing feedbacks that amplify FS mortality and/or contribute to system transitions to alternate states. In seagrass beds, the mortality of seagrass and other macrophytes can drive pulses of organic matter that fuels turbidity, hypoxia, and toxic sulfides, further amplifying seagrass mortality rates and accelerating transitions to unvegetated states through a positive feedback [62]. In such cases, the traits (e.g., lability) of decaying macrophyte material can affect the strength of these feedbacks by controlling benthic respiration rates and associated oxygen depletion [63]. Therefore, DFS identity, in addition to its abundance, can mediate system resilience by controlling recovery rates and/or transitions to alternate states following mass mortality events.

Many DFS host unique communities compared with their live counterparts [37,46,47], and the cascading effects of DFS-associated communities on system transitions are poorly understood but could contribute to whether DFS lead to stabilizing or destabilizing ecosystem effects. For example, the various fungal communities of decaying wood (e.g., white, brown, and soft-rot) can differentially affect seedling regrowth and saproxylic communities, but interactive effects of saproxylic communities and wood decay type on seedling regeneration are largely unknown, especially across large biogeographic scales [54]. In coral reefs, dead as opposed to live corals may promote herbivore communities that aid coral recovery [64], or attract bioeroders that accelerate reef degradation [65]. The role of DFS-associated communities on system feedbacks and transitions is an area ripe for research and has broad relevance for restoration, which may require incorporation of these roles to facilitate FS recovery.

Degradation of DFS in the Anthropocene

Global change and human impacts are affecting DFS degradation dynamics, which in turn can have dramatic effects on their role in the environment. Unregulated harvesting of dead wood, trawling of hard-bottomed marine benthic structures, and the removal of macroalgal wrack from sandy beaches are examples of direct threats to DFS persistence that can drive substantial losses in biodiversity, ecosystem function, and services that benefit human welfare and economies [6,10,66]. For instance, the C sequestered in seagrass mats and large woody debris escapes back into the atmosphere when these DFS are eroded or combusted [67,68]. We emphasize the urgency in minimizing human activities that damage and/or destroy DFS without first understanding their functional roles and increasing efforts to understand how changing environmental conditions will affect their persistence.

Although global change factors can impact DFS degradation rates, the effects often differ from live FS. Morphological trait changes in DFS may be more drastic than in living FS following abiotic disturbances. In forests, standing dead trees experience more structural damage than live trees from fires [69], and in deep sea environments, the weakening of dead coral frameworks due to ocean acidification has been attributed to the ‘crumbling’ of reefs and loss of structural complexity, despite persistence of live coral cover [70]. In some cases, dead and living FS may have different directional responses, as with warming temperatures, which can benefit some living autotrophic FS by enhancing productivity [71], while increasing decay rates of dead autotrophs, threatening the habitat and carbon storage function provided by these materials [72,73]. The effects of global change on FS-characterized systems will depend on the responses of DFS, as well as the responses of living FS and their likelihood of mortality and transition to DFS.

The response of DFS persistence to anthropogenic impacts can be non-linear due to interactions between biotic and abiotic factors. For example, accelerated decomposition rates of dead wood in tropical forests will likely result from increasing temperatures triggering higher insect consumption rates [73], and heatwaves that drive coral mortality events also increase microbial metabolic activity that amplifies dissolution of the newly dead coral [74]. Bioerosion of these hard structures may also increase due to overexploitation that releases bioeroding organisms (e.g., urchins, insects, worms) from top-down control, as well as eutrophication that increases food quality for bioeroders [65,75]. Synergistic effects of biotic and abiotic factors on DFS persistence are thus a result of changes in both the intensity of degradation factors and susceptibility of DFS to those factors [65,76].

We encourage increased investigation into how DFS traits will affect their persistence in the Anthropocene. The morphologies, chemical properties, material densities, and mobility potential of DFS may predict their expected responses to global change and their impacts on ecosystem trajectories. Trait-based frameworks have revealed how types of dead wood can vary in their susceptibility to agents of degradation, such as microbial decomposition, fire, storm-driven fragmentation, and insect consumption [5,76]. We suggest this trait-based framework, which has been broadly applied to living FS [77–79], should be applied to DFS given that the strength of their influence on ecosystem dynamics and the variability in their traits can rival live FS.

Implications for restoration

Recognition of DFS traits and ecological roles has potential to inform and enhance restoration and ecological engineering efforts (e.g., living shorelines, nature-based solutions) designed to counteract human impacts on ecosystems and promote services such as coastal defense, flood mitigation, and blue carbon sequestration [80–82]. As EE, DFS can provide habitat for other species, mediate biogeochemical processes, and drive feedbacks that lead to ecological shifts or reinforce persistence of their live counterparts. Although living EE are now recognized as important components of restoration [83], there is a need to identify the contexts in which engineering effects of DFS via deployment, manipulation, or removal should be integrated into restoration strategies to initiate shifts towards desired ecosystem states.

When DFS contribute to feedbacks supporting system resilience, their deployment can initiate FS recovery. For example, many hard-bodied DFS provide substrate favored by conspecifics and this is widely acknowledged in oyster reef restoration, where the addition of dead shells as prerequisite substratum for oyster recruitment initiates living reef development [84]. Similar techniques may be useful in other systems, such as coral reefs, where the large dead colonies can be 'reskinned' with outplanted fragments to achieve a large living colony far more rapidly than growing a large colony *de novo* [85]. The natural process of DFS decay may also create facilitative abiotic conditions for FS recovery, such as in deserts where dead plants maintain favorable soil conditions for plant regeneration, and deploying DFS to engineer landscapes that facilitate living FS may provide relatively cost-effective methods for restoration as opposed to directly outplanting living FS [86].

DFS can exhibit a wide variety of traits and more research on the links between their traits and facilitative roles is needed to inform key aspects of restoration, including the selection of suitable DFS and the quantity and configuration for their deployment. For example, the trait-based ecological characterization of large woody debris and its use in riverine system restoration demonstrates how the incorporation of DFS into ecological theory benefits applied ecological objectives [5,57]. Dead wood and leaf litter traits, such as decay rate, C:N ratios, and diameter at breast height, represent important metrics in the application of DFS in restoration [76,87], but the configuration of such material can also modify ecosystem and community responses [88]. For example, dead wood placed in sunny forest areas can exhibit greater microclimate heterogeneity and thus increase saproxylic insect diversity more than in shaded areas [89]. Oyster reef restoration success can depend on dead shell reef height, making reef elevation an important metric to consider in the design of restored reefs [22]. In addition, planting *Posidonia* seagrass in areas containing dense root mats of dead grass enhances seedling survival rates relative to planting in less consolidated sediment [55]. The high density of dead rhizomes allows the mat to persist for several years after death, and continue to both retain and accumulate carbon, and so restoring the dead mat also preserves the service of carbon sequestration [21,55]. There are clear benefits from applying DFS into restoration strategies and we suggest that the field evolve past the trial-and-error approach to a more systematic one based on how DFS traits are linked to desired ecological effects to optimize the types, amounts, and configurations of DFS to meet restoration goals.

Where DFS are not readily available for large-scale restoration projects, knowledge of their roles based on insight of their traits can inform the development of mimics as DFS substitutes. For example, in sandy beach ecosystems, wheat straw exhibits physical traits and nutrient concentrations similar to beach-cast wrack and has been successfully deployed to facilitate the growth of grasses necessary for dune persistence [90]. In addition, 3D printing has proven a promising new tool for the construction of dead coral colony mimics that incorporates characteristic ridges, bumps, and interstitial spaces to jump-start reef creation [91,92]. However, additional research that identifies required DFS traits and configurations for driving desired outcomes will benefit such applications, as artificial mimics can fail at meeting restoration goals even when formed from naturally occurring materials within systems [93].

In some cases, DFS can inhibit recovery, and so ecosystem restoration through their removal may be necessary to establish favorable conditions for desired species (including other FS) and ecosystem function. For example, in a salt marsh dominated by native rushes and forbs, the dead litter at the advancing front of an invasive reed kills native plants and conditions the marsh for clonal invasion of the living reed [94]. In such an instance, restoration efforts may consider DFS removal to facilitate native marsh revegetation. However, careful study is needed to decipher whether DFS effects are facilitative or inhibitory. The northward expansion of mangroves represents a concern for historically cordgrass-dominated salt marshes in some sites of the North American ecotone, and mangrove encroachment was initially considered to be facilitated by dead cordgrass litter, which created favorable moisture levels and environmental modifications for propagule growth [95,96]. However, subsequent experiments showed that dead cordgrass negatively affected mangrove establishment by smothering seedlings and attracting herbivores that graze on propagules [95]. These examples further reveal the magnitude of influence that DFS can have on ecosystem change and the importance of measuring multiple response variables at different timescales, ideally through experimentation, to fully grasp the functional roles of DFS in driving system transitions.

Concluding remarks

Although the importance of DFS has been recognized independently in some systems, such as terrestrial forests, this synthesis illuminates their general, global significance across ecosystem types. We hope this review encourages their incorporation into ecological theory and increases public recognition of DFS as important interacting components of ecological systems. Because habitats dominated by DFS are often assumed to be degraded or defunct (if they are considered at all), they are commonly undervalued and so may be especially vulnerable to anthropogenic degradation and removal [6,7,10]. Yet, interactions involving DFS can drive ecosystem dynamics and enhance ecosystem productivity, even over thousands of years [97]. The amounts, composition, and timing of occurrence of DFS should be included in monitoring programs to better assess their persistence across land and seascapes and into management plans to incorporate their engineering effects into restoration and provide protective measures where necessary. DFS are ubiquitous, interacting components of ecosystems that are vulnerable to global change. They often mediate biodiversity, ecosystem function, and resilience, and further research and recognition of their ecological roles (see Outstanding questions) holds promise in improving ecosystem management, restoration, and forecasts of ecosystem trajectories.

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Declaration of interests

No interests are declared.

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Outstanding questions

How do ratios of live to dead foundation species (FS) mediate system transitions and stability within systems? Both live and dead FS provide essential functions, and dramatic changes in their relative abundances can affect habitat availability, energy flow, and biogeochemical processes. Increasing proportions of dead foundation species (DFS) can have non-linear effects on ecosystem dynamics, and live to dead FS ratios may represent tipping points for system transitions.

What are the functional roles of DFS-associated communities and do they facilitate recovery of live FS? Because community composition frequently differs between live and dead FS, FS death may initiate new networks of species interactions that have differential effects on FS persistence than communities associated with living FS.

How will DFS degradation rates be affected by global change? Since DFS often differentially respond to global change factors than their living counterparts, additional research on this topic remains crucial for predicting DFS' structural persistence, biogeochemical changes, and the stability of FS-characterized ecosystems.

What traits of DFS maintain ecosystem functions related to system resilience and/or initiate feedbacks that support recovery? Answers to this question will help guide the construction of DFS mimics to accelerate ecosystem restoration and the initiation of self-facilitating feedbacks.

How will global change affect the amounts, composition, and/or timing of occurrence of DFS as subsidies across systems and what are the implications of this for recipient system dynamics? Habitat modification, non-native species, and environmental changes that affect DFS transport (i.e., currents, storm frequency) may independently and synergistically impact both source systems and recipient systems that depend on DFS subsidies.

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