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CONCEPTS & THEORY

Loss of foundation species revisited: conceptual framework with lessons learned from eastern hemlock and whitebark pine

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Abstract. Ecologists and conservation biologists often prioritize the study of species that are declining, threatened, or endangered over species that are abundant and ecologically important, such as foundation species (FS). Because entire ecosystems and their biodiversity depend on FS, we argue that they have high conservation priority. A citation analysis reveals that FS are studied, but often are characterized ambiguously. More effort is needed to identify FS before they, and the ecosystems they define, are at risk of decline or loss. We suggest a new conceptual framework that includes: informed identification of FS in ecosystems; documentation of ecosystem services provided by FS; a long-term monitoring strategy to detect threats to FS within specified ecosystems; and, if threats are identified, a comprehensive conservation and adaptive management strategy for FS. We use two widely distributed, rapidly declining North American foundation tree species (*Tsuga canadensis* [eastern hemlock] and *Pinus albicaulis* [whitebark pine]) to illustrate this framework. These species exemplify the importance of identifying FS early and conserving or restoring them when they are threatened.

Key words: citation analysis; conceptual conservation framework; conservation; nonnative species; *Pinus albicaulis; Tsuga canadensis.*

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INTRODUCTION

Species that are dominant, abundant, or not in immediate danger of population loss are studied less frequently by ecologists and conservation biologists than are rare or threatened species (Gaston and Fuller 2007, Baker et al. 2019). Abundant species typically are excluded from conservation planning until threats to their populations emerge, by which time research to understand their life history, roles, and functions in their ecosystem is akin to emergency triage (Gerber 2016, Cornwall 2018). However, the assumption that dominant or abundant species should not be a priority for conservation is unfounded, because commonness itself is rare (Gaston and Fuller 2007), and common species often are ecologically important as structural, dominant, or foundation species (Ellison et al. 2005, Ellison 2019). We strongly warn against assuming that common species have little conservation value. For example, several species of ash trees (*Fraxinus* spp.) have recently declined dramatically. Although there are still $>8 \times 10^9$ individual living trees globally, they are now considered critically endangered (IUCN). Further, if common species that also are foundation species are understudied or ignored by conservation biologists until they become rare and no longer function in their foundational roles, it is more likely that their ecological importance may be underestimated or misinterpreted, and it may be impossible to recover either their populations or their functionality in the ecosystems they otherwise define.

Dayton (1972), working in the marine benthos of Antarctica, described a foundation species (FS) as, “a single species that defines much of the structure of a community by creating locally stable conditions for other species and by modulating and stabilizing fundamental ecosystem processes.” This concept was extended to terrestrial ecosystems by Ellison et al. (2005) who delineated the common characteristics of terrestrial FS—especially that many are primary producers. Ellison (2019) expanded the definition of a FS to include functional groups linked by key traits and explained more clearly the meaning of structure of a community: “a foundation species can be defined as a species (or group of functionally similar taxa) that dominates an assemblage numerically and in overall size (usually mass), determines the diversity of associated taxa through non-trophic interactions, and modulates fluxes of nutrients and energy at multiple control points in the ecosystem it defines.” Although Ellison et al. (2005) have been cited extensively (>800 citations listed in Web of Science as of 3 April 2019), a citation analysis through 2017 (results below) illustrates that neither Dayton’s nor Ellison et al.’s concept of an FS is used accurately in basic research or consistently in conservation practice (Ellison and Degrassi 2017).

Here, we present a framework to reify the FS concept and guide its useful application in ecological research and conservation practice (Fig. 1). Our framework includes three components: (1) reliable and consistent definition and identification of FS for different ecosystems, illuminated through citation analysis; (2) assessment and documentation of ecosystem services provided by FS in these ecosystems; and (3) comprehensive monitoring strategies to detect threats to FS and, if threats are identified, the implementation of conservation and adaptive management strategies for FS (Holling 1973) that reflect and inform primary research. Our framework could assist in forecasting the cascading effects of FS loss and encourage timely implementation of conservation strategies to ameliorate those consequences.

The importance of FS also challenges many assumptions held about conservation and assigning species conservation status. If a once-abundant FS declines or is (functionally) extirpated, the ecosystem it defines deteriorates and the other species that depend on it are more likely to decline or disappear. Given that we cannot easily predict the next existential threat to a FS, identification, ongoing monitoring and surveillance for threats are crucial. Because FS are often abundant, large-scale efforts are likely to be needed to conserve, manage, or restore them. We suggest that it is ecologically sensible and cost-effective to protect a FS proactively rather than engage in *post hoc*, costly, and often untested efforts to restore a once-abundant and widespread species. We use information on two declining FS—*Tsuga canadensis* (L.) Carr. (eastern hemlock) and *Pinus albicaulis* Engelm. (whitebark pine)—to illustrate the application of this framework. Both tree species, now understood to be foundation species, were identified as ecologically important long before the FS concept was applied to terrestrial ecosystems.

An Integrated Framework for Research, Conservation, and Management of Foundation Species

Identifying and distinguishing foundation species

The first component of our framework is to carefully and consistently define FS (Dayton 1972, Ellison 2019) so that they can be identified and differentiated reliably from other important

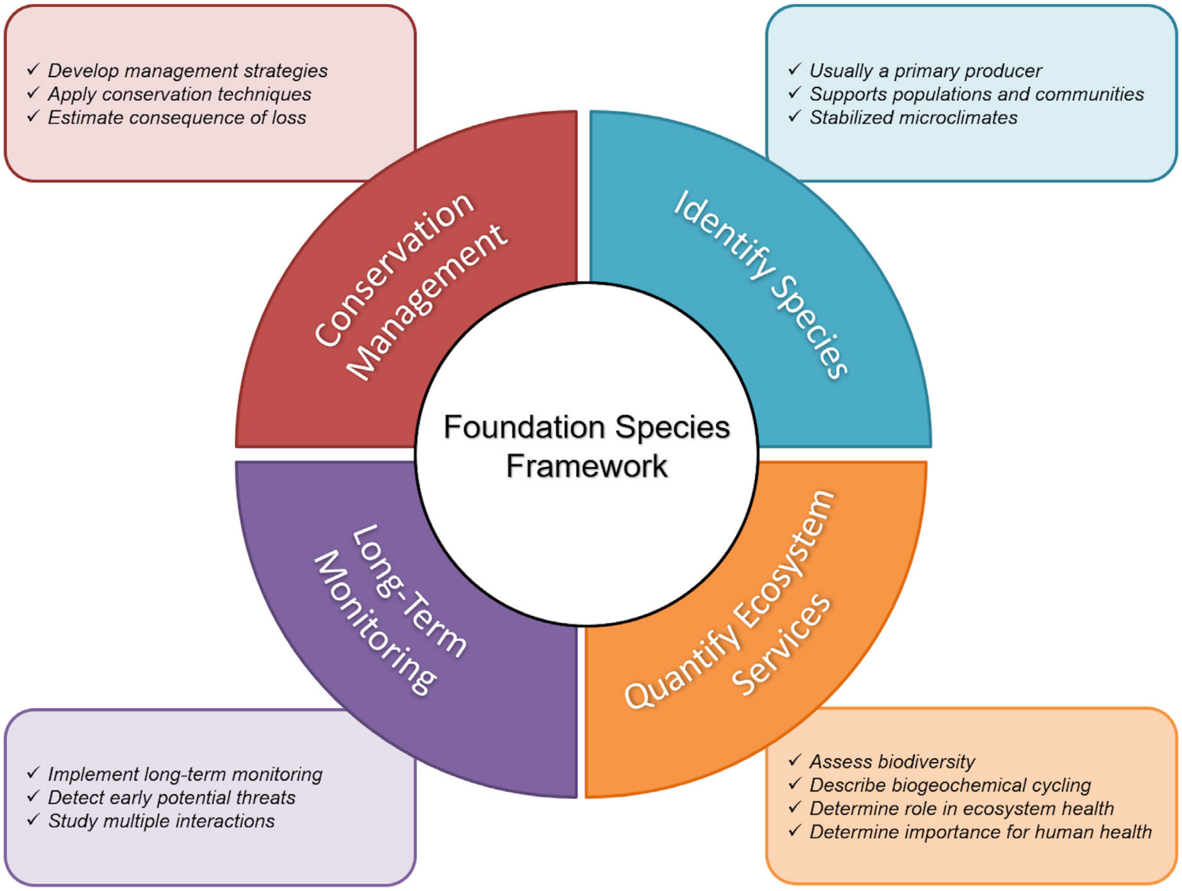

Fig. 1. Suggested framework for research, monitoring, management, and conservation of foundation species.

species types (Ellison and Degrassi 2017; see also Box 1 in Ellison 2019). A citation analysis illustrates that the concept of a FS still is not fully understood or widely embraced by terrestrial ecologists or natural resource managers.

We used Web of Science to identify literature citing Ellison et al. (2005) through December 2017. We focused our literature review on the 630 papers recovered in Web of Science because it was most inclusive of citation type and did not yield as many misleading results. (For example, the number of citations to Ellison et al. (2005) was nearly 20% greater in Google Scholar, which included non-peer-reviewed papers and conference abstracts. However, the Google Scholar search also inexplicably returned citations to Ellison et al. (2005) that were published before 2005.) Of the set of 630 papers, we excluded from our analysis 77 secondary or tertiary reviews and commentaries related to the concept and definition of FS presented by Ellison et al. (2005). For the remaining 553 primary research papers, we identified the focus of the original research described by the authors. We then asked whether the authors:

1. Precisely or accurately defined FS, or if not, what or whose definition was used?
2. Explicitly studied a FS?
3. Characterized the main ecological role of the FS being studied?
4. Identified the main threats to the FS?

The raw data from our search are available from the Harvard Forest Data Archive (Degrassi and Brantley 2017), and we used R version 3.4.1 (R Core Team 2017) for all analyses.

Our analyses indicated that the FS concept was not defined or mentioned in 40% of the papers (Table 1). Ellison et al.'s (2005) definition was cited in 47% of the papers, whereas Dayton's original paper was cited in 3%. Dayton (1972) and Ellison et al. (2005) were cited together in 4% of the papers. The remaining 6% either defined a FS differently from Dayton or Ellison et al.; inaccurately equated it with an ecosystem engineer, keystone species, or framework species (among others); or attributed the FS concept to other authors (Table 1). We conclude that many researchers may not be aware of the FS concept as an entity distinct from other functional ecological terms for species that are important in ecosystems (Ellison and Degrassi 2017). Alternatively, despite efforts of ecologists to clearly distinguish different types of important species (Ellison et al. 2005, Valls et al. 2015, Ellison 2019), researchers do not agree on and use a single definition of FS or any other important species.

Study organisms were identified as a FS in 53% of the reviewed papers; however, only 77% were identified to species (Appendix S1: Table S1). The other 23% were identified to genus (7%; Appendix S2: Table S1) or were identified to a group only (16%, e.g., trees, cushion plants, oysters; Appendix S2: Table S1). Among studies that identified FS, 34% studied only their role in community interactions, 17% studied ecosystem processes alone, 21% studied ecosystem processes and impact on community interactions, and 28% did not specify an ecological role (Table 1). These data suggest that the foundation species concept is used more in the context of biotic interactions than in the context of biogeochemistry or other ecosystem processes.

Most of the papers (83%) identified the FS during or after a population decline, and the most frequent threats identified were nonnative species (24%) and climate change (17%; Table 1).

Table 1. Summary and interpretation of general trends in the study of foundation species based on the results of the Ellison et al. 2005 study.

Questions	Studies (*n*)	%	Conclusion
Was foundation species defined and how was it defined?			Defining the foundation species (FS) concept accurately did not appear to be a major priority for these papers as the term was not defined in ~40% of the papers. Other definitions included *keystone, dominant,* and *ecosystem engineers*
Ellison et al. (2005)	258	46.7	
Not defined	220	39.8	
Other	35	6.3	
Ellison et al. (2005) and Dayton (1972)	23	4.1	
Dayton (1972)	16	2.8	
What was the main topic of the p aper or the main role of the foundation species?			Foundation species roles (either support for other organisms or abiotic ecosystem functions) are being studied. Most papers studied the importance of FS to other organisms, and the minority of papers studied the role of FS in ecosystem functions
Community	180	33.5	
Ecosystem and community	112	20.8	
Ecosystem	94	17.5	
Not identified	150	27.9	
Did the study identify a threat to foundation species, and what is the major threat?			Threats to FS are being identified. Most studies identified nonnative species and pathogens as threats. Studies also identified habitat degradation and climate change as threats. Ellison et al. (2005) suggested that ecologists study FS before a threat occurs, but these data suggest that FS are being studied only during or after a threat has been identified
Nonnative species	221	24.4	
Climate change	145	16.8	
Disease or pathogen	142	16.4	
No threat identified	122	14.1	
Exploitation	108	12.5	
Habitat degradation	107	12.3	
Other	28	3.2	

These data illustrate a failure of researchers to study FS before they decline. This failure may be a result of long-term population declines that pre-date discussion of FS; lack of awareness of the FS concept when planning research programs (Ellison and Degrassi 2017); or lack of research or conservation attention to abundant species (Gaston and Fuller 2007, Baker et al. 2019).

Documenting foundation species and the ecosystem services they provide

The second component of our framework is to assess and communicate the importance of FS through research and discussion of the ecosystem functions and services they provide. We illustrate some of the functions and services provided by FS using examples drawn from two canonical FS—*Tsuga canadensis* and *Pinus albicaulis*. Both species were discussed by Ellison et al. (2005), and both are declining primarily because of nonnative species (the hemlock woolly adelgid, *Adelges tsugae* Annand, and the fungal pathogen causing white pine blister rust, *Cronartium ribicola* (J. C. Fisch.), respectively). Regional extirpation or functional extinction of FS will lead to major shifts in biodiversity and loss of important ecosystem services.

Tsuga canadensis.—*Tsuga canadensis* has a historic range in eastern North America that covers >10,000 km^2 from northern Georgia (USA) to southern Canada, and west into Michigan and Wisconsin. Throughout much of its range, *T. canadensis* historically comprised >50% of the total basal area in any given forest stand (Smith et al. 2009), and it is the dominant component of 14 forest associations—more than any other tree species in North America (FGDC 2008).

Tsuga canadensis is a late-successional, shade-tolerant species that exerts strong local control on rates and seasonality of biogeochemical and biophysical processes, including microclimate (Lustenhouwer et al. 2012), soil moisture and stream flow (Brantley et al. 2013), and carbon storage (Krebs et al. 2017). Further, it is the only shade-tolerant coniferous species within its range, so its role for winter-time ecosystem process likely will be particularly impacted by its extirpation and replacement by deciduous trees. Together, these critical processes create habitat conditions and resources that support unique communities of ants (Record et al. 2018), birds (Tingley et al. 2002), small mammals (Degrassi 2018), and freshwater fauna (Snyder et al. 2002). There also are unexpected interactions between some organisms supported by *T. canadensis* and ecosystem processes including nutrient cycling and decomposition that further illustrate the irreplaceable role of this FS and the ecosystem services that it provides (Kendrick et al. 2015).

Research on the ecological role of *T. canadensis* has been site-specific (Foster 2014), and its identity as a FS has been supported through long-term observations and experiments on physiological, population, community, and ecosystem ecology (Ellison 2014). Although its ecological role overlaps with dominant species, structural species, and ecosystem engineers, its combination of life-history characteristics, functional traits, and defining effects on stand-level ecosystem processes distinguish it from these other types of important species (Ellison et al. 2005, Ellison 2014).

Tsuga canadensis has been a conspicuous component of eastern North American forests since the end of the Holocene glacial retreat. It declined precipitously in abundance ≈5400 yr ago—most likely because of a combination of climate change and defoliation by a native insect—but it recovered its former abundance after ~1000 yr (Foster et al. 2006). During the 17th–19th centuries, European colonists cut *T. canadensis* to clear land for pasture and to extract tannins from its bark; again, natural regeneration led to the recovery of *T. canadensis* to approximate pre-colonization abundances (Foster 2014). Now, *T. canadensis* populations are declining again as the species is host to the rapidly spreading nonnative hemlock woolly adelgid, *Adelges tsugae* (Domec et al. 2013). Trees normally die within 2–10 yr of infestation, and resistance is uncommon (Vose et al. 2013). Regardless of differences in the time required for trees to succumb, the result is the same: a ghost-like, dead forest and a homogeneous understory of hardwood vegetation. Because the adelgid feeds on and kills all size and age classes of *T. canadensis*, and its seeds do not persist in the seed bank, it is unlikely that natural regeneration will lead to recovery of this tree to its former range or abundance (Farnsworth et al. 2012).

Pinus albicaulis.—*Pinus albicaulis* ranges from about 37°–55° N latitude and grows in upper subalpine and treeline zones, from ~900 to 3660 m a.s.l.— to higher latitudes than other North American white pines (*Pinus* subgen. *Strobus*; Tomback and Achuff 2010). Within its western distribution, it occurs from the southern Sierra Nevada north through the coastal ranges of British Columbia. In the Rocky Mountains, it grows from western Wyoming north through the Canadian Rocky Mountains. On sheltered, productive sites in the subalpine zone, *P. albicaulis* pioneers after wildfire and persists as a long-lived minor or major seral species late into succession, whereas on harsh, exposed sites, *P. albicaulis* forms self-replacing communities (Tomback and Achuff 2010). In the drier regions throughout its range, *P. albicaulis* is a major component of treeline communities, growing both as a solitary tree and within tree islands (Tomback et al. 2016; Fig. 2C, D). In the United States alone, *P. albicaulis* communities are estimated to cover ~57,000 km^2, with nearly 40% in designated wilderness (Keane et al. 2012) and more than 4×10^6 ha if all community types are considered together (Goeking and Izlar 2018). Seven recognized forest cover types include *P. albicaulis* growing with one or more other conifers (Tomback and Achuff 2010).

The large, calorie-rich seeds of *P. albicaulis* are obligately dispersed by Clark's nutcrackers (*Nucifraga columbiana* (Wilson)), which bury them in caches for later consumption (Tomback 1978, Tomback et al. 2011). This mutualism has shaped the ecology, distribution, and multi-scale genetic structure of *P. albicaulis* populations. The seeds are also an important food source for many other granivorous birds, small mammals, grizzly bears (*Ursus arctos* L.), and black bears (*Ursus americanus* Pallas; Tomback and Kendall 2001). Many western North American indigenous peoples used its nutritious seeds and inner bark as seasonal foods (Tomback et al. 2011).

The foundational role of *P. albicaulis* also is expressed through ecosystem processes based on its extreme hardiness and effective seed dispersal (Tomback et al. 2011). As a post-disturbance pioneer, it appears early in succession across a range of aspects and topography, mitigating harsh conditions by providing shade, shelter, and moisture (Tomback et al. 2001). On exposed sites and ridgelines, less hardy conifers establish and grow faster under its shelter (Callaway 1998). At treeline on the harsh eastern Rocky Mountain Front and other cold, arid regions, *P. albicaulis* is the most abundant krummholz conifer and initiator of tree islands (Tomback et al. 2016). *Pinus albicaulis* forest stands and treeline communities redistribute and retain snow, which persists into summer months and leads to continuous downstream flow during the growing season (Fig. 2).

Multiple factors threaten *P. albicaulis*, including outbreaks of the native mountain pine beetle (*Dendroctonus ponderosae*), altered fire regimes, and distributional changes effected by climate change (Tomback and Achuff 2010). However, the most pervasive threat is the nonnative pathogen *Cronartium ribicola*, which causes white pine blister rust. *Cronartium ribicola* now occurs at various infection levels within the *P. albicaulis* range and potentially infects all age classes. Branch infections damage tree canopies and reduce cone production, and stem infections kill trees. Some *P. albicaulis* populations are nearly 100% infected, and most have low genetic resistance to the disease (Tomback and Achuff 2010). A recent assessment using national forest inventory plots indicates that 51% of all whitebark pine trees are dead (Goeking and Izlar 2018).

Adaptive conservation and management of foundation species

The third component of our framework is to conserve and manage FS using strategies that retain or restore key interactions, functions, and ecosystem services (Fig. 1). The decline of both *T. canadensis* and *P. albicaulis* continues to result in functional loss of regional ecosystems and shifts (and some losses) in the diversity of their associated species. The ecological importance of our exemplar FS (*T. canadensis* and *P. albicaulis)* and consequences of their decline were not well understood when threats to them were first detected. The continuing losses of these FS represent a failure of the current system to assign recognized FS and assign them conservation priority (see also Gerber 2016).

Neither eastern hemlock nor whitebark pine are currently listed as endangered in the United States, although whitebark pine is listed in Canada and being evaluated for U.S. listing (Table 2). Both FS, however, are recognized as species of importance to forest communities and have inspired the formation of several advocacy

Fig. 2. (A) Eastern hemlock retaining snow fall in Harvard Forest Petersham, Massachusetts. (B) Old-growth eastern hemlock forest, Harvard Forest Petersham, Massachusetts. (C) Whitebark pine growing along a ridgeline in Grand Teton National Park, Wyoming, resulting in snow retention. (D) Whitebark pine tree island community, Divide Mountain, Blackfeet Reservation, Montana, July, illustrating snow redistribution and retention. Photo credits for eastern hemlocks: AM Ellison, and for whitebark pine: DF Tomback.

groups (Table 2). Restoration efforts to date have been funded primarily by the U.S. Forest Service and other federal agencies, but the non-profit organizations have raised awareness and contributed financially and logistically to conservation and restoration efforts (Table 2).

Although there is no central coordination of efforts to conserve *T. canadensis*, multiple state and federal agencies, numerous universities, and non-governmental organizations are involved in relevant conservation and management activities (Table 2). Chemical control of the adelgid is cost-prohibitive and impractical in large forest stands (Vose et al. 2013). Introductions of predatory beetles, such as *Laricobius nigrinus* (Fender) and *L. rubidus* (LeConte), for biological control are underway (Mausel et al. 2012), but results to date are mixed (Vose et al. 2013). Genotypes of *T. canadensis* with some resistance to the adelgid have been identified and are being propagated (Ingwell and Preisser 2011, McKenzie et al. 2014). Finally, the international tree breeding conservation program at North Carolina State University Department of Forestry and Environmental Resources and the U.S. Forest Service have been collecting seeds of both *T. canadensis* and the narrow endemic *Tsuga caroliniana* Engelm. (Carolina hemlock) since 2003. This program prioritizes genetic diversity and long-term storage of seeds to provide material for future breeding for resistance (Hastings et al. 2017).

The fundamental approach to restoring *P. albicaulis* consists of speeding up natural selection by planting seedlings with genetic resistance to *C. ribicola* (Table 2). Determining genetic resistance in *P. albicaulis* follows a protocol whereby seedlings grown from candidate trees are exposed to high densities of *C. ribicola* spores under controlled conditions and then followed over time to determine whether they develop

Table 2. Comparison between eastern hemlock and whitebark pine in distribution, foundational functions, conservation status, advocacy groups, restoration plans, and source of funding for conservation and restoration.

Comparison	Eastern hemlock	Whitebark pine
Status	Not currently listed, but the Carolina hemlock is under review for U.S. E.S.A. listing	Candidate for U.S. E.S.A. listing; listed as endangered under S.A.R.A. in Canada
Advocacy	Saving hemlocks—private group, Hemlock Restoration Initiative, Forest Restoration Alliance	Whitebark Pine Ecosystem Foundation (and WPEF-Canada), American Forests, Natural Resources Defense Council
Restoration plans drafted or in progress	Camcore, U.S. Forest Service, North Carolina Forest Service, Grandfather Restoration Project	Regional plans from U.S. Forest Service and Greater Yellowstone; Crown of the Continent; Bureau of Land Management; S.A.R.A., Canada Recovery Plan; U.S. National Whitebark Pine Restoration Plan; Keane et al. (2012)
Funding for conservation and restoration	U.S. Forest Service, National Park Service, State forestry agencies	U.S. Forest Service, National Park Service, Bureau of Land Management; American Forests and National Arbor Day

Note: Camcore, Central American and Mexico Coniferous Resources Cooperative; E.S.A., Endangered Species Act; S.A.R.A., Species at Risk Act.

blister rust symptoms or show resistance (Sniezko et al. 2011). The frequency of resistance is highly variable among populations, with most showing from zero to <10% resistance among seed parents. Other management actions include developing regional seed orchards for seed production from genetically resistant trees while maintaining high genetic diversity, protecting putative and confirmed resistant trees from mountain pine beetle attack, and resetting successional processes using prescribed fire and silvicultural techniques (Tomback and Achuff 2010, Keane et al. 2012; Table 2).

SYNTHESIS

Foundation species such as *T. canadensis* and *P. albicaulis* define the structure of an ecological community, control local biodiversity, and stabilize and modulate core ecosystem processes (Dayton 1972, Ellison et al. 2005). Foundation species differ in significant ways from other important species (Ellison et al. 2005, Ellison 2019). Unlike keystone species, FS are common and do more than increase local biodiversity. Unlike dominant species, the effects of FS on ecosystem processes are disproportionate (e.g., nonlinearly related) to their abundance. Unlike ecosystem engineers, FS do more than create novel habitats through their activities. And most species are not FS. Given their critical community functions, we need to be consistent in defining FS, rigorous in identifying them, and as certain as possible in characterizing their foundational traits.

Non-recognition of FS also could be detrimental to conservation efforts. For example, if a species is incorrectly classified as something other than a FS, such as a dominant species, projections of loss and impact on the community will be modeled as linear, while, in fact, the impact to greater community and ecosystem function will be greatly underestimated. Therefore, the species in question may not receive the proper attention and funding needed to protect that system. Ellison and Degrassi (2017) suggested that researchers consider studying common species, spend more time reading scientific literature, and also read place-based poetry and literature to discover and study new FS before populations become threatened. Any outcomes and management decisions should be the product of careful observation and long-term studies.

These case studies of *Tsuga canadensis* and *Pinus albicaulis* illuminate key traits of FS, identify important threats and consequences to the ecosystems they define, and highlight different strategies to manage and conserve them. Future research and successful conservation of FS and the ecosystems they define depend on precise identification, according them conservation status, and monitoring and surveilling them to identify emerging threats.

Our suggested integrated framework (Fig. 1) tracks basic and applied work on FS from definition and scoping through conservation and management. We propose this framework both to improve the recognition of FS and to provide a general workflow for prioritizing research and conservation tailored to the threats experienced by a FS. Because one of the more interesting take-home messages from our citation analysis was that FS were not consistently identified as such, we encourage researchers to distinguish FS from other important species so that our understanding of the key roles of any species can be accurately evaluated and communicated.

We also think our framework will be useful for ecosystem and community ecologists studying species for which threats have yet to be identified. Ecosystem science tends to work at larger scales of space, time, and biological organization, and focuses on total system fluxes and, by necessity, simplifying ecosystems using system-wide parameters (e.g., NDVI or leaf area index of forests) regardless of the ecological roles of individual species. In such cases, the system is treated as the subject, even when the magnitude or flux of system-wide processes may depend on species composition and relative abundance. Elucidating the unique contributions of FS to ecosystem structure and function, especially under relatively undisturbed conditions, may determine the characteristics that make ecosystems either vulnerable or resilient to change.

Lastly, our framework could help conservation biologists and land managers discover commonalities between their species of interest and FS. These commonalities might include threats to ecosystems of interest or the effectiveness of specific management techniques applied to specific situations. These parallels could be especially useful for conservationists who are looking for case studies of restoration to use as examples for species that are becoming more vulnerable as disturbances increase. For restoration ecologists, these studies could provide insights into the possible desired future conditions of other ecosystems being considered for restoration.

We do not suggest that we have identified all potential FS through our citation analysis. Nor are we suggesting that scientists are unaware that they are studying important species. On the contrary, all species have value, and it is incumbent on researchers, conservation biologists, and land managers to communicate the importance of each species they study and care about. At the same time, it is not enough to simply assert that an apparently important species is a FS. Rather, that a species plays a foundational role should be regarded as a hypothesis to be tested; observations or experiments to support or reject the hypothesis that a species is an FS can take decades or longer (Ellison 2014, Foster 2014). We hope that FS in global communities will be recognized, described, and studied whenever appropriate so that we can coordinate efforts to understand, conserve, and manage them. Preserving foundation species proactively (i.e., before threats are present) will prove to be a more strategic and efficient means of conserving communities and the biodiversity that they harbor rather than attempting to restore some semblance of these communities at some future time through triage when population are dwindling.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2917/full