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 rather than abundant and ecologically important ones (e.g., foundation species). Because entire ecosystems and their biodiversity depend on foundation species, we argue that these species deserve high conservation priority. A citation analysis reveals that foundation species are studied, but they are often ambiguously characterized. More effort is needed to identify foundation species before they, and the ecosystems they define, are at risk of decline or disappearance. We suggest a new conceptual framework linking identification of foundation species with research on their functional roles and monitoring them for emerging threats that can trigger formulation of management plans. We use two widely-distributed, rapidly declining North American tree species (*Tsuga canadensis* [eastern hemlock] and *Pinus albicaulis* [whitebark pine]) to illustrate this framework. These species exemplify the importance of identifying foundation species early and conserving or restoring them when they are threatened.

Key Words

Citation analysis; conceptual conservation framework; conservation; invasive species; *Pinus albicaulis; Tsuga canadensis*
Species that are dominant, abundant, or not in immediate danger of population loss are studied less frequently by ecologists or 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 and their 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 unwarranted as 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 this attitude and find support in our argument with several species of recently critically endangered ash trees (*Fraxinus* spp.), of which there remain alive globally more than eight billion trees (IUCN, accessed 05 Nov 2018). 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 functional roles may be unappreciated 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) and delineated the common characteristics of FS—especially that many are primary producers. Ellison (2019) expanded the definition of a foundation species to include functional
groups linked by key traits and specified more clearly a 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) has been cited extensively (>800 citations listed in Web of Science as of 3 April 2019), a citation analysis though 2017 (results below) illustrates that neither Dayton’s nor Ellison et al.’s conception of an FS is used accurately in basic research or applied 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 illuminated through citation analysis; [2] assessment and documentation of ecosystem services provided by FS; and [3] comprehensive adaptive conservation and management (Holling 1973) of FS that reflects and informs primary research about FS. Our framework could assist in forecasting cascading effects of FS loss and encourage timely implementation of strategies to ameliorate those consequences.

The importance of FS 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 decline or disappear. Given that we cannot easily predict the next catastrophic threat to FS, identification, ongoing monitoring, and surveillance for threats is 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” species types (Ellison and Degrassi 2017; see also Box 1 in Ellison 2019). A citation analysis illustrates that the concept of a FS is still 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, while noting that the number of citations was nearly 20% larger in Google Scholar, which included non-peer reviewed papers and conference abstracts. 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, Google Scholar search returned citations to Ellison et al. (2005) that were published before 2005. For each of these papers, we identified the focus of the original research described by the authors (n = 553 primary research papers; 77 secondary or tertiary reviews and commentaries were excluded from our
analysis) and its relationship to the concept and definition of FS presented by Ellison et al. (2005). Specifically, we 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 studies citing Ellison et al. (2005). 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 (e.g., Ellison et al. 2005, Valls et al. 2015, Ellison 2019), researchers do not agree on and use a single definition of FS.

Study organisms were identified as a FS in 53% of the reviewed papers. Among studies that identified FS, 34% studied 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 ecosystem processes or biogeochemistry.

Most of the papers (83%) identified the FS during or after a population decline, and the most frequent threats identified were invasive species (24%) and climate change (17%, Table 1). These data illustrate a failure of researchers to study FS before they decline, as advocated in Ellison et al. (2005). 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 foundation species will lead to major shifts in biodiversity and loss of important ecosystem services.

*Tsuga canadensis*
Tsuga canadensis has an historic range in eastern North America that covers >10,000 km² from northern Georgia (USA) to southern Canada, and west into Michigan and Wisconsin (Fig. 2). 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 evergreen species within its range, so its role for wintertime ecosystem process will likely be particularly impacted with 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, nutrient cycling, and decomposition that further illustrate the irreplaceable role of this foundation species and the ecosystem services that it provides (Kendrick et al. 2015).

Research on the ecological role of T. canadensis has been site-specific (e.g., 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

*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 years
ago, most likely because of a combination of climate change and defoliation by a native insect; it
recovered its former abundance after ~1000 years (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 exotic *Adelges tsugae* (Domec et al. 2013). Trees
normally die within 2–10 years 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 – 3660 m a.s.l.—more broadly and to higher latitudes than other North
American white pines (subgen. *Strobus*) (Tomback and Achuff 2010; (Fig. 2). 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. 3 C&D). In the U.S. 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 million ha if all community types are considered (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*), which bury them in caches for later consumption (eg, 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*), and black bears (*Ursus americanus*) (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* 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 (e.g., 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. 3).

Multiple factors threaten declining populations of *P. albicaulis*, including outbreaks by mountain pine beetles (*Dendroctonus ponderosae*), fire exclusion, and climate change (Tomback and Achuff 2010). However, the most pervasive threat is the non-native pathogen *Cronartium ribicola*, which causes white pine blister rust. The *C. ribicola* invasions cover nearly the entire range of *P. albicaulis* and 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 in ways that reflect and feed back to the primary research about them. The decline of both *T. canadensis* and *P. albicaulis* continues to result in functional loss of entire ecosystems and shifts (and some losses), in the diversity of their associated species. The ecological importance of these two FS (*T. canadensis* and *P. albicaulis*) and consequences of decline were not well understood when threats to them were first detected. The ongoing decline of these FS represents a failure of the current system of assigning conservation priority to specific species (see also Gerber 2016).
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 non-native 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. albiculis* consists of speeding up natural selection by planting seedlings with genetic resistance to *C. ribicola*. Determining genetic resistance in *P. albiculis* 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 if they develop 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 individuals. 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). Restoration efforts to date have been funded and encouraged primarily by the U.S. Forest Service and other federal agencies, but non-profit organizations also have been important advocates and contributed financially and logistically to this effort (Table 2).

Synthesis

Foundation species like *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. These outcomes should be the product of careful observation and long-term studies.

These case studies of *Tsuga canadensis* and *Pinus albicaulis* illuminate key traits of foundation species, 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 foundation species 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 intend this framework both to improve the recognition of FS and provide a general workflow for prioritizing research and conservation tailored to the threats experienced by a focal. Because one of the more interesting take-home messages from our citation analysis was that FS rarely were reliably identified as such, we encourage researchers to distinguish “foundation species” from other categories of “important species” so that our understanding of the key roles of FS and other important 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 higher scales, focusing 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 the ecosystems, 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.
At the same time, we are not 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 we
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 (e.g., Ellison 2014, Foster 2014). We hope that in the
future 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 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.

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LITERATURE CITED


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Farnsworth, E. J., A. A. Barker-Plotkin, and A. M. Ellison. 2012. The relative contributions of seed bank, seed rain, and understory vegetation dynamics to the reorganization of *Tsuga canadensis* forests after loss due to logging or simulated attack by *Adelges tsugae*. Canadian Journal of Forest Research 42: 2090–2105.


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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.

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. Abbreviations: Endangered Species Act (E.S.A.); Species at Risk Act (S.A.R.A.).

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

Figure 2. Species distribution map of eastern hemlock (blue) and whitebark pine (orange) in North America.

Table 1.

<table>
<thead>
<tr>
<th>Questions</th>
<th>Studies</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Was foundation species defined and how was it defined?</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ellison et al. 2005</td>
<td>258</td>
<td>Defining the foundation species concept did not appear to be a major priority within this dataset. There were almost as many definitions as non-definitions.</td>
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<tr>
<td>Not Defined</td>
<td>220</td>
<td></td>
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<tr>
<td>Other</td>
<td>35</td>
<td>The other definitions included keystone, dominant, and ecosystem engineer species concepts.</td>
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<td>Ellison 2005 &amp; Dayton 1972</td>
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<td></td>
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<td>Dayton 1972</td>
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<td><strong>What was the main topic of the paper or the main role of the foundation species?</strong></td>
<td></td>
<td></td>
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<tr>
<td>Community</td>
<td>180</td>
<td>Foundation species roles (either support for other organisms or abiotic ecosystem functions) are being studied.</td>
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<tr>
<td>Ecosystem and Community</td>
<td>112</td>
<td>The majority of papers studied the effect of foundation species on other organisms and the minority of papers studied effects of foundation species on ecosystem functions.</td>
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<tr>
<td>Ecosystem Function</td>
<td>94</td>
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<td>Not Identified</td>
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<td><strong>Did the study identify a threat to foundation species and what is the major threat?</strong></td>
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<td>Invasive Species</td>
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<td>Threats to foundation species are being identified. The majority of studies identified invasive species as a threat.</td>
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<tr>
<td>Climate Change</td>
<td>145</td>
<td>The minority of studies identified habitat degradation as a threat. Ellison et al. (2005) suggested that ecologists</td>
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<td>Disease or Pathogen</td>
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<td>No Threat Identified</td>
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<td>study foundation species before threat</td>
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<td>Comparison</td>
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<td>Whitebark pine</td>
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<tr>
<td>-----------------------------</td>
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<td>--------------------------------------------------------------------------------</td>
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<tr>
<td>Foundational function</td>
<td>Forms dense canopies that tightly regulate cycling of water and nutrients; important for local snow retention in northern range and hydrology of headwater catchments in southern watersheds</td>
<td>Fosters community development through facilitation; important for watershed-scale snow retention and hydrology; seeds are important wildlife food</td>
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<td>Status</td>
<td>Not currently listed, but the Carolina Hemlock is under review for U.S. E.S.A. listing</td>
<td>Candidate for U.S. E.S.A. listing; listed as endangered under S.A.R.A. in Canada</td>
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<td>Advocacy</td>
<td>Saving Hemlocks – private group, Hemlock Restoration Initiative, Forest Restoration Alliance</td>
<td>Whitebark Pine Ecosystem Foundation (and WPEF-Canada), American Forests, Natural Resources Defense Council</td>
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<td>Funding for conservation and restoration</td>
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<td>U.S. Forest Service, National Park Service, Bureau of Land Management; American Forests and National Arbor Day</td>
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Figure 1.
Figure 2.

Figure 3.