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COMMENTARY

All species are important, but some species are more important than others

Aaron M. Ellison & Allyson L. Degrassi

Ellison, A.M. (corresponding author, aellison@fas.harvard.edu)[1],
Degrassi, A.L. (Allyson.Degrassi@unh.edu)[2]

[1]Harvard Forest, Harvard University, Petersham, MA 01368, USA;
[2]Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA

Abstract

Foundation species control biodiversity and ecosystem processes, but are difficult to identify. In this issue of the *Journal of Vegetation Science*, Elumeeva et al. show that *Festuca varia* and *Nardus stricta* act as foundation species in the Caucasus' alpine. This paper augments the piecemeal literature on foundation species while highlighting the need for more comprehensive approaches to their identification and conservation.

Foundation species fundamentally shape the structure of ecological assemblages and modulate ecosystem processes (Dayton 1972; Ellison et al. 2005). Where they occur, foundation species are primary producers or occupy low trophic levels; are locally abundant and regionally common; create habitat conditions that support dependent, often specialized, species; and through a variety of physical and chemical means, regulate many biogeochemical stocks and fluxes (Ellison et al. 2005; Baiser et al. 2013). Several other "important" types of species share characteristics with foundation species: dominant species (Grime 1984), structural species (Huston 1994), core species (Hanski 1982), keystone species (Paine 1966) and ecosystem engineers (Jones et al. 2010; Fig. 1a). However, foundation species have functionally irreplaceable, unique combinations of traits (Ellison et al. 2005).

Identifying foundation species is critical for at least three reasons. First, species that control biodiversity and ecosystem function are targets for basic research on habitat availability, population regulation, trophic dynamics or fluxes of nutrients and energy. Second, careful management of foundation species alone can result in sustaining an entire ecosystem. However, as foundation species often are common, they have attracted less attention from conservation biologists than have threatened or rare species (Gaston & Fuller 2007). Third, people intuitively understand and care about foundation species because they often "name the system" (e.g. redwood [*Sequoia sempervirens* (D. Don) Endl.], hemlock [*Tsuga canadensis* (L.) Carr.] or mangrove [*Rhizophora* spp.] forests; coral or oyster reefs). They are featured prominently in poetry, prose and other expressions of popular imagination (Ellison & Baiser 2014) that motivate broad attention and concern for the systems they define and support.

Nonetheless, it is surprisingly difficult to identify conclusively foundation species without long-term experimental data such as those described by Elumeeva et al. (2017) in this issue of the *Journal of Vegetation Science*. A nearly quarter-century-long removal experiment (1987–2011) revealed that two narrow-leaved tussock-forming grasses, *Festuca varia* Haenke and *Nardus stricta* L. "determine the functional structure and composition of the community (i.e. plot-level species richness, above-ground biomass, community biomass-weighted specific leaf area and dry matter content, and inter-annual dynamics of other species in the assemblage), and *remarkably* (emphasis added), species from the same (functional) group are not able to completely replace them" (Elumeeva et al. 2017). Perhaps what is more remarkable than their decisive identification of a foundation species is that a steady accretion of case studies (Fig. 1b) has not yet been synthesized into a general framework to help identify them before they change in abundance, shift their geographic ranges or decline to the point that they can no longer serve their foundational roles.

Unsurprisingly, the alpine systems that Elumeeva et al. (2017) studied are changing rapidly because of anthropogenically-driven climatic change and shifts in land use (Elumeeva et al. 2013). In all *F. varia* and *N. stricta* plots, changes in overall species composition are consistent with declining snow cover and upslope movement of species from lower elevations (Elumeeva et al. 2013). We would go further, and hypothesize that the structure and dynamics of these communities are being affected as much by the changes in abundance of these foundation species as by climatic and land-use changes.

It has been nearly a half-century since the concept of a foundation species entered the literature (Dayton 1972).

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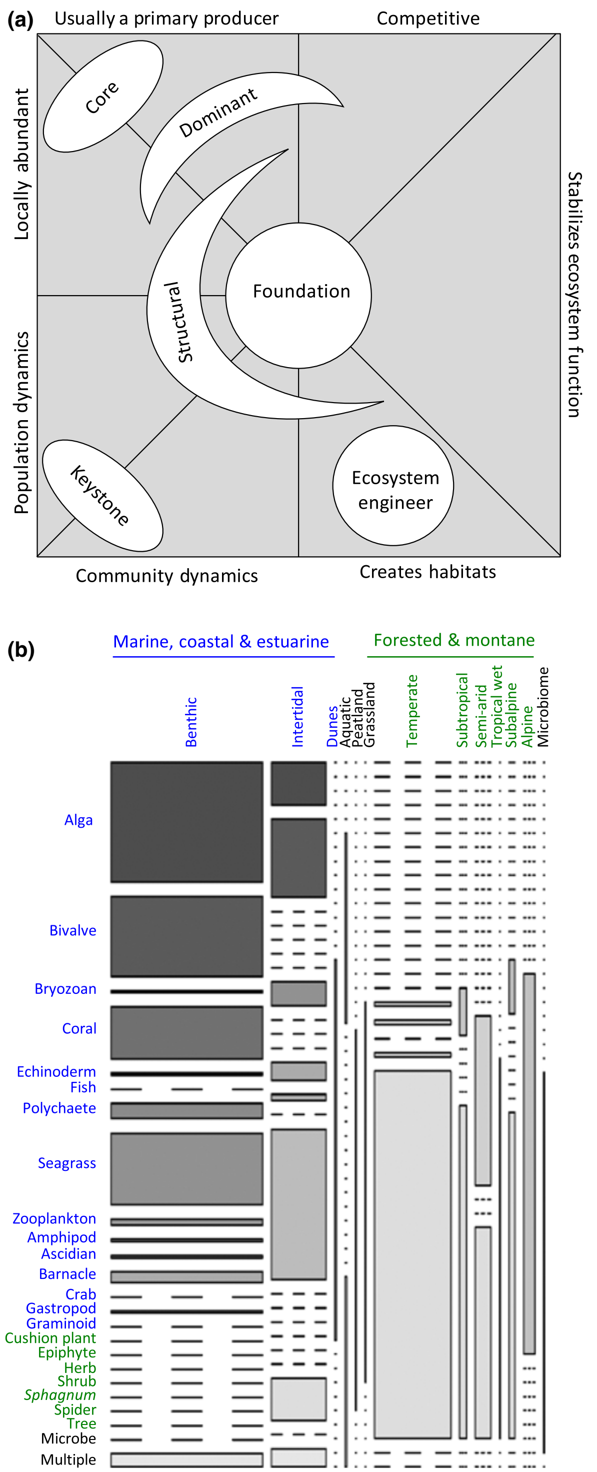

Fig. 1. (**a**) Foundation species are distinct from other types of "important" species. Each important species identified by ecologists has at least one of seven definable traits, but foundation species have all seven. (**b**) Mosaic plot illustrating relative frequency of different functional groups of foundation species and habitats studied in all publications on foundation species indexed in the Web of Science (n = 380: 2004–2016; 7 reviews excluded). [Colour figure can be viewed at wileyonlinelibrary.com]

More than a decade ago, Ellison et al. (2005) called on scientists to fill knowledge gaps on how foundation species respond to environmental changes and biotic threats. Worldwide, foundation species continue to decline rapidly, with predictable consequences. For example, as *T. canadensis* disappears from eastern North American forests, observations and experiments have revealed changes in biodiversity and ecosystem processes (reviewed in Ellison 2014). Just as Elumeeva et al. needed 20 yr of experimental data to strongly support the hypothesis that *F. varia* and *N. stricta* are foundation species of alpine grasslands, so too did it take >10 yr of experimental data to support the foundational role of *T. canadensis* (Ellison 2014). Collecting such long-term data and testing associated ecological hypothesis may be intellectually gratifying, but we cannot depend solely on a piecemeal library of case studies (Fig. 1b) from which to infer the identity of foundation species and the means to conserve and manage them while they are still abundant. We must do better, and we can.

First, consider studying common species rather than rare ones (Gaston & Fuller 2007). Yes, rare ones often are of immediate conservation and management concern, but, except for some keystone species, their role in controlling biodiversity and ecosystem processes is not especially large. Second, spend more time reading – and applying – the scientific literature. Which is more remarkable: that Elumeeva et al. (2017) appear to be unaware of a nearly 50-yr-old ecological concept, or that *F. varia* and *N. stricta* have irreplaceable traits in an alpine grassland? Synthesis needs case studies, but case studies also need context. Third, read place-based poetry and literature. If a species shows up in these sources that scientists infrequently explore, it might be a good candidate for a foundation species and worthy of additional scrutiny.

By using these three practices in our search to understand the world, we might identify foundation species more rapidly. But if we continue to ignore foundation species while they are still common and abundant, and do not recognize their contributions to ecosystem sustainability and cultural identity before they are lost, we not only are missing critical information about the system, but also poorly serve the environment and the people who trust us to conserve it.

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