

Rethinking foundation species in a changing world: The case for *Rhododendron maximum* as an emerging foundation species in shifting ecosystems of the southern Appalachians



Maura P. Dudley^{a,*,1}, Mary Freeman^b, Seth Wenger^a, C. Rhett Jackson^c, Catherine M. Pringle^a

^a Odum School of Ecology, University of Georgia, University of Georgia, 140 E. Green St, Athens, GA30602, United States

^b US Geological Survey, Patuxent Wildlife Research Center, 180 E. Green St, Athens, GA 30602, United States

^c Warnell School of Forestry and Natural Resources, University of Georgia, 180 E. Green St, Athens, GA30602, United States

ABSTRACT

“Foundation species” are widespread, abundant species that play critical roles in structuring ecosystem characteristics and processes. Ecosystem change in response to human activities, climate change, disease introduction, or other environmental conditions may promote the emergence of new foundation species or the decline of previously important foundation species. We present rhododendron (*Rhododendron maximum*) as an example of an emerging foundation species in riparian forest and headwater stream ecosystems of the southern Appalachian Mountains and use its example to propose a dynamic approach to recognizing foundation species. As other species have declined, rhododendron has increased in abundance, biomass, and ecosystem importance, and now dominates the riparian zones and mesic uplands of much of the region. Rhododendron structures, stabilizes, and modulates functions within both terrestrial and aquatic ecosystems. Studies of forest ecosystem response to environmental conditions indicate that rhododendron may increase the resistance and resilience of its associated ecosystems to predicted anthropogenic stress, including climate change, nitrogen enrichment, and invasive species. A more dynamic conception of foundation species as dependent on ecosystem states will help ecologists to focus on ecosystem processes and services, rather than on historically dominant species, for restoration strategies.

1. Introduction

As human activities alter species composition globally, the conservation of ecosystem structure and function will depend on identifying those species which play important roles in structuring and stabilizing current ecosystems. The term “foundation species” was originally introduced to identify the *most important* species within ecosystems (Dayton, 1972), but currently accepted characteristics of foundation species also indicate that they: (1) are widespread and abundant; (2) act as structuring elements; (3) create stable conditions; (4) support associated flora and fauna; and (5) modulate ecosystem processes (Angelini et al., 2011; Ellison, 2014). Foundation species often have no functional substitutes, and their loss can result in large and irreversible changes to ecosystems (Ellison et al., 2005). Local and regional declines or extirpation of foundation species are pervasive in every major ecosystem across the globe, including freshwater, marine, and terrestrial systems (Ball et al., 2009; Palik et al., 2012; Ramus et al., 2017).

Despite their importance to current ecosystems, many foundation species are only identified after pathogens, deforestation, urban development, climate change, or eutrophication have functionally

eliminated them, either globally or regionally (Angelini et al., 2011). Examples include the American chestnut (*Castanea dentata*, Ellison et al., 2005), eastern hemlock (*Tsuga canadensis*, Ellison et al., 2005), American elm (*Ulmus americana*, Orwig et al., 2013), tanoak (*Notholithocarpus densiflorus*, Dillon et al., 2013), the seagrass *Amphibolis antarctica* (Thomson et al., 2015), the blue mussel (*Mytilus edulis*, Sorte et al., 2017), and populations of various coral species (Graham, 2014). Retrospective application of the term “foundation species” often has little relevance for ongoing and future ecosystem management. As foundation species disappear, and environmental conditions change, remaining species shift in abundance and dominance, leading to different interactions and dynamics (Ellison et al., 2014). By the time the importance of former foundation species is recognized, a novel ecosystem may have already developed (Fig. 1).

Here we argue for the importance of identifying *emerging* foundation species—those that play defining roles under altered current conditions and will likely continue to dominate under predicted future conditions. Our concept of emerging foundation species is closely related to the idea of “novel ecosystems,” also called “no-analog ecosystems” and “emerging ecosystems” (Milton, 2003; Williams and Jackson, 2007; Hobbs et al., 2009), which has received a great deal of attention in the

* Corresponding author at: 4239 Browning Chase Dr., Tucker, GA 30084, United States.
E-mail address: maurapdudley@gmail.com (M.P. Dudley).

¹ Permanent home address: 4239 Browning Chase Dr, Tucker, GA 30084, United States.

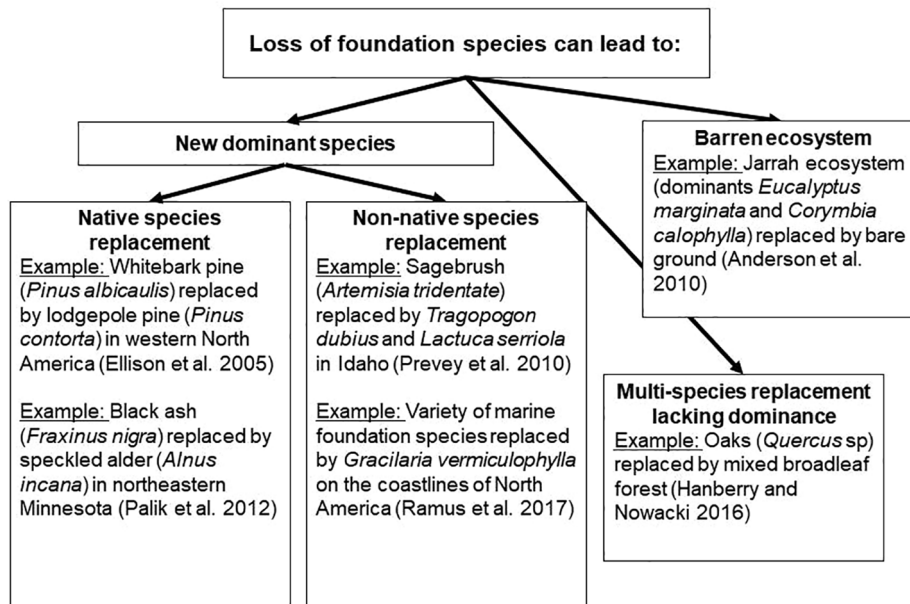


Fig. 1. Examples of ecosystem trajectories after the loss of a foundation species. (See above-mentioned references for further information.)

literature. These new ecosystem combinations often revolve around a newly dominant species (or species group, such as lianas in Neotropical forests; Schnitzer and Bongers, 2011), sometimes even invasive species. For example, in their paper on novel ecosystems, Hobbs et al. (2009) explain how reintroduced Turkey oak (*Quercus cerris*) in the UK anchors an ecologically important multi-trophic interaction involving gall wasps, birds, caterpillars, and native oaks. Turkey oak could be considered an emerging foundation species in areas where it has become abundant, despite the fact that some consider it to be non-native. In fact, there is nothing in the foundation species definition that limits it to native species, and even widespread invasive species such as cheatgrass (*Bromus tectorum*) or the red alga *Gracilaria vermiculophylla* (Ramus et al., 2017) could be considered foundation species. We argue that the question of whether a species is desirable to humans is separate from the question of whether it plays a foundational role, and proactive identification of species integral to current ecosystem structure and function, regardless of their historical dominance or origin, would be helpful in guiding management decisions.

Here we have three objectives: (1) to propose an expansion of the term foundation species to include emerging foundation species: species that currently dominate shifting ecosystems as a result of past disturbance and will likely continue to dominate under changing future conditions (Table 1); (2) to present rhododendron (*Rhododendron maximum*) as an example of an emerging foundation species in riparian forest and potentially headwater stream ecosystems of the southern Appalachian Mountains; and (3) to use lessons learned from our study of rhododendron to offer suggestions for the management of emerging foundation species.

2. Shifting foundation species in southern Appalachian forests

Over the last century, the structure and function of southern Appalachian forests has changed substantially with the loss of two foundation species, American chestnut and eastern hemlock (Fig. 2). For 4,000 years, the burning regimes employed by Native Americans supported the co-dominance of American chestnut and oaks (Ellison et al., 2005). American chestnut was considered a foundation species, comprising up to 40% of the forest basal area, influencing forest composition via allelopathic compounds, contributing recalcitrant large woody debris to streams, and serving as an important mast species for forest consumers (Van Lear et al., 2002; Vandermast and Van Lear,

Table 1

Definitions of foundation species and emerging foundation species.

In this paper, we define the term “foundation species” based on Dayton’s (1972) original definition and commonly accepted characteristics of foundation species as they have been described in the literature over the last 40 years:

- Widespread and abundant
- Act as structuring elements
- Create stable conditions
- Support associated flora and fauna
- Modulate ecosystem processes

We propose the term “emerging foundation species” as a sub-category of foundation species defined by the following criteria:

- Unlike most currently accepted foundation species, emerging foundation species will have **reached dominance relatively recently** in human experience of an ecosystem. In many cases, emerging foundation species will become prominent only after human activities have led to a restructuring of the ecosystem through changes to species composition
- We also propose that emerging foundation species should also be characterized by their **ability to persist in anticipated future conditions** (e.g., as predicted by climate change models) created by continued human activities at regional and global scales. These can include climate change, nutrient enrichment, and global reorganization and elimination of species.

2002; Ellison et al., 2005). Heavy logging, fire exclusion, and introduction of chestnut blight at the turn of the twentieth century led to the functional extirpation of American chestnut (Vandermast et al., 2002).

As American chestnut disappeared, eastern hemlock became an increasingly important overstory species, particularly in mesic areas (Van Lear et al., 2002). Comprising up to 35% of riparian forest basal area, eastern hemlock exerted a dominant influence on both terrestrial and aquatic ecosystems in the southern Appalachians (Ford and Vose, 2007; Ford et al., 2012; Webster et al., 2012). Eastern hemlock’s status as a foundation species within this region was short-lived: the introduction of the hemlock woolly adelgid (*Adelges tsugae*) in the mid-1980’s led to its current functional extirpation from most southern Appalachian forests (Ellison et al., 2005).

The loss of these foundation species, cessation of fire and grazing, and increased soil acidity from atmospheric deposition in the early twentieth century facilitated the regional expansion and dominance of an unexpected species: the native understory shrub rhododendron (*Rhododendron maximum*; Vandermast et al., 2002; Stehn et al., 2011; Ford et al., 2012). Studies conducted within the Appalachian Mountain

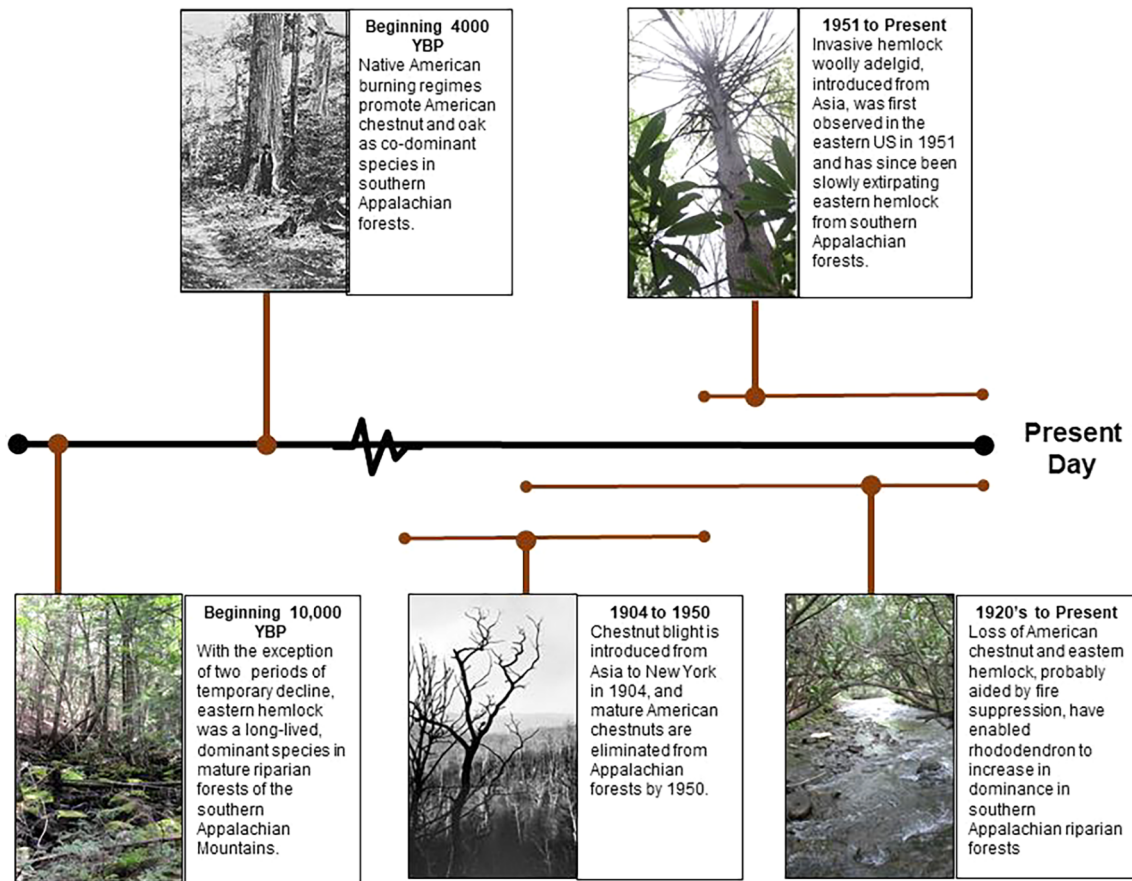


Fig. 2. Timeline of foundation species compositional changes in southern Appalachian forests. Photo Credits: Eastern hemlock (*Tsuga canadensis*) along Rugland Brook, Petersham, Massachusetts. Photograph copyright Aaron M. Ellison and used with permission, https://www.fs.usda.gov/Internet/FSE_MEDIA/fseprd590425.jpg American chestnut from Pisgah Forest, North Carolina, 1914, United States Forest Service. American chestnut blight in the Chattahoochee National Forest in north Georgia, 1930, United States Forest Service.

regions indicate that the expansion of rhododendron since the extirpation of chestnut has been substantial. A study from the Coweeta watershed in North Carolina found peak rhododendron establishment occurred just after the decline of American chestnut, with a 50% increase in rhododendron coverage between 1934 and the 1970s (Elliott and Vose, 2012). A more recent analysis using satellite imagery indicates that rhododendron has continued to expand by more than 38% over the last 25 years in the Weimer Run watershed in West Virginia (Atkins et al., 2018). Evidence from the literature suggests that rhododendron meets all five of the characteristics for emerging foundation species in riparian forest ecosystems and may also be playing a significant and influential role in headwater stream ecosystems (Fig. 3).

3. Rhododendron is an emerging foundation species in southern Appalachian riparian forests

3.1. Widespread and abundant

Found throughout the Appalachian Mountains, rhododendron reaches its greatest dominance and density in the southern Appalachians, covering an estimated 30 million ha (Rivers et al., 1999). Individual rhododendron thickets can be greater than 20 ha in extent, reach 4–6 m height, and achieve densities of 23,747 stems per ha (Plocher and Carvell, 1987; Hedman and Van Lear, 1995). One study in North Carolina estimated that rhododendron comprises up to 6.3% of total aboveground biomass and 82% of the understory biomass, 41.6% of leaf biomass, and 16.1% of leaf area (Elliott and Vose, 2011). Site descriptions in studies of forest ecosystems throughout the southern

Appalachian region indicate that rhododendron is ubiquitous.

3.2. Structuring element in forests

Rhododendron is a dominant structuring element in southern Appalachian riparian forests due to its physical form (evergreen shrub) and its significant influence on understory, forest floor, and soil attributes. Rhododendron significantly reduces total understory photosynthetically active radiation (12–33% of non-rhododendron areas, Clinton, 1995) and the abundance and intensity of sunflecks (Lei et al., 2006). Because rhododendron's recalcitrant leaf litter and root matter decompose slowly, litter and soil beneath rhododendron thickets have higher organic matter and lower nutritional quality (higher C:N ratios) than sites without rhododendron (Beckage et al. 2000, Wurzbarger and Hendrick, 2007; Horton et al., 2009). Soil conditions beneath rhododendron thickets also have lower moisture, cooler temperatures, lower pH, elevated aluminum concentrations, and decreased cation concentrations relative to non-rhododendron areas (Clinton and Vose, 1996; Nilsen et al., 2001; Horton et al., 2009). With lower water requirements than many deciduous species, rhododendron can reduce mean riparian forest transpiration rate and stabilize annual transpiration compared to sites with only hardwoods (Ford and Vose, 2007).

3.3. Creates stable conditions for some species

Rhododendron stabilizes forests through its persistence in the landscape and the ecosystem resistance it imparts during disturbance. Once established, rhododendron is difficult to remove by natural

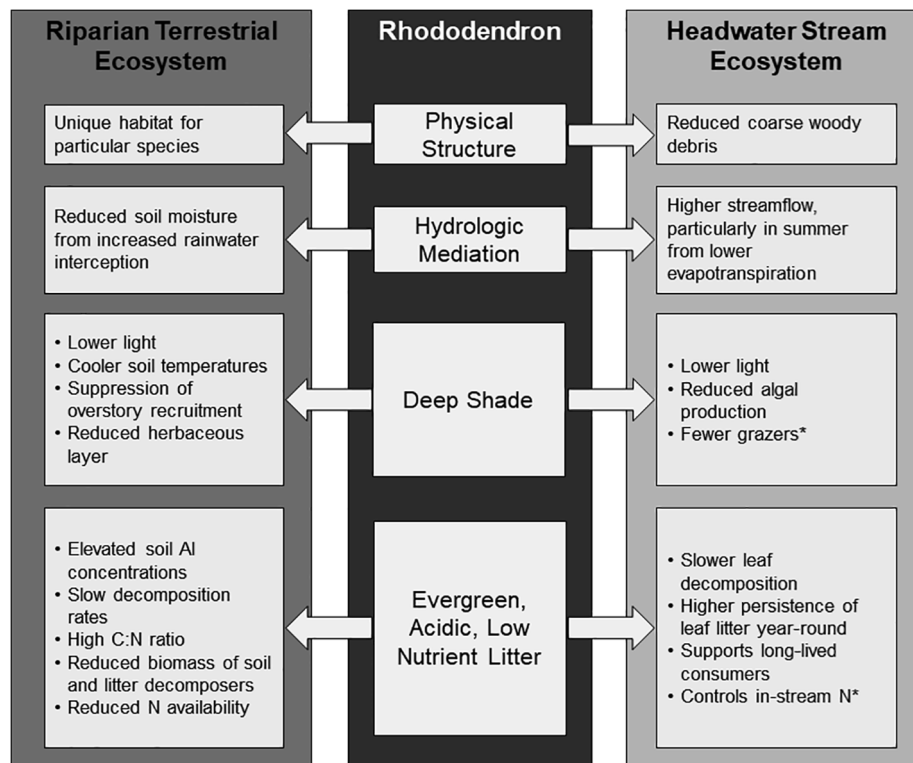


Fig. 3. Key attributes of rhododendron that enable it to uniquely affect riparian terrestrial and headwater stream ecosystems in southern Appalachian forests relative to deciduous-only forests.

disturbance (e.g. forest fires, [Wahlenberg and Doolittle, 1950](#)) and anthropogenic means (e.g. cutting, burning, pesticide, combinations, [Harrell and Zedaker, 2010](#)). Individual rhododendron leaves can persist on the plant for 5 + years ([Lipscomb and Nilsen, 1990](#)). Numerous studies suggest that when rhododendron is present in the understory, many abiotic (e.g. light, soil moisture, temperature) and biotic (e.g. tree recruitment) attributes of the forest remain unchanged after several types of disturbance, including overstory gap creation ([Beckage et al., 2000](#)), pest defoliation ([Chastain et al., 2006](#)), and loss of another foundation species (i.e. eastern hemlock, [Ford et al., 2012](#)). However, the presence of rhododendron can potentially alter ecosystem attributes and species by promoting disturbance under certain environmental conditions: in extremely wet conditions, rhododendron can increase landslide susceptibility ([Hwang et al., 2015](#)), and in severe drought conditions, its higher fuel load can increase its flammability ([Stottlemeyer et al., 2009](#)).

3.4. Influences floral and faunal composition

Rhododendron controls canopy species composition through suppression of seed germination ([Clinton and Vose, 1996](#)), growth ([Lei et al., 2002](#)), and tree recruitment to higher size classes ([Van Lear et al., 2002](#)); recent experimental removals of rhododendron found that tree seedling density increased 10-fold in response to treatment ([Elliott et al., 2018](#)). Reduced survival of seedlings has been attributed to rhododendron's influence on abiotic characteristics of the understory, including reduced light, soil moisture, and nutrient availability ([Kincaid, 2012](#)). Several studies demonstrate that rhododendron's influence on tree recruitment can alter the trajectory of forest ecosystem succession ([Elliott and Vose, 2011](#), [Krapfl et al., 2011](#)), with greater effects on future forest composition than the legacy of large-scale logging ([Vandermast and Van Lear, 2002](#)).

Rhododendron also affects the composition of other above- and below-ground forest ecosystem communities. Presence of rhododendron was negatively correlated with the diversity of ground layer plant

communities ([Stehn et al., 2011](#)) and the seed bank richness for herbaceous species ([Cofer et al., 2018](#)). Some soil communities (e.g. fungi, [Wurzburger et al., 2011](#)) are more diverse beneath rhododendron thickets, while other decomposer groups are less diverse (e.g. microarthropods, [Ball et al., 2009](#)) or less abundant (e.g. truffles, [Loeb et al., 2000](#)). Rhododendron leaves can support complex communities of algae, lichens, bacteria, heterotrophic protists, fungi, slime molds, and microinvertebrates, and the plant is the only documented host of ten liverwort taxa and one epiphyllous bryophyte ([Risk et al., 2011](#)). One rare orchid, Appalachian twayblade (*Listera smallii* Weigand), only grows beneath rhododendron thickets ([Vandermast and Van Lear, 2002](#)). Other studies have documented that rhododendron provides food and refuge to forest mammals, including white-tailed deer (*Odocoileus virginianus*; ~31% of winter diet, [Johnson et al., 1995](#)), the relatively rare eastern spotted skunk (*Spilogale putorius*; [Reed and Kennedy, 2000](#)), and forest rodents ([Lei et al., 2002](#)).

3.5. Modulates ecosystem processes

Rhododendron affects numerous riparian forest ecosystem processes, including decomposition and nutrient cycling. Rhododendron's recalcitrant leaves are less palatable to consumers, leading to reduced biomass of soil decomposer communities (bacteria, fungi, copepods, arthropods), slower decomposition, and increased carbon sequestration ([Ball et al., 2009](#); [Chastain et al., 2006](#); [Horton et al., 2009](#)). Higher organic matter accumulation can also lead to retention of associated nutrients within leaf litter (e.g. up to 24% of cycling forest nitrogen, [Monk et al., 1985](#)). Rhododendron further alters nitrogen availability by creating compounds that inhibit nitrification ([Wurzburger and Hendrick, 2007](#)). A recent study found that removal of both rhododendron plant and its associated leaf litter increased the availability of nitrogen to soil organisms ([Osburn et al., 2018](#)). Rhododendron can also limit the availability of cations through tissue storage ([Nilsen et al., 2001](#)) and reduction of soil pH which affects leaching from the system ([Yeakley et al., 2003](#)).

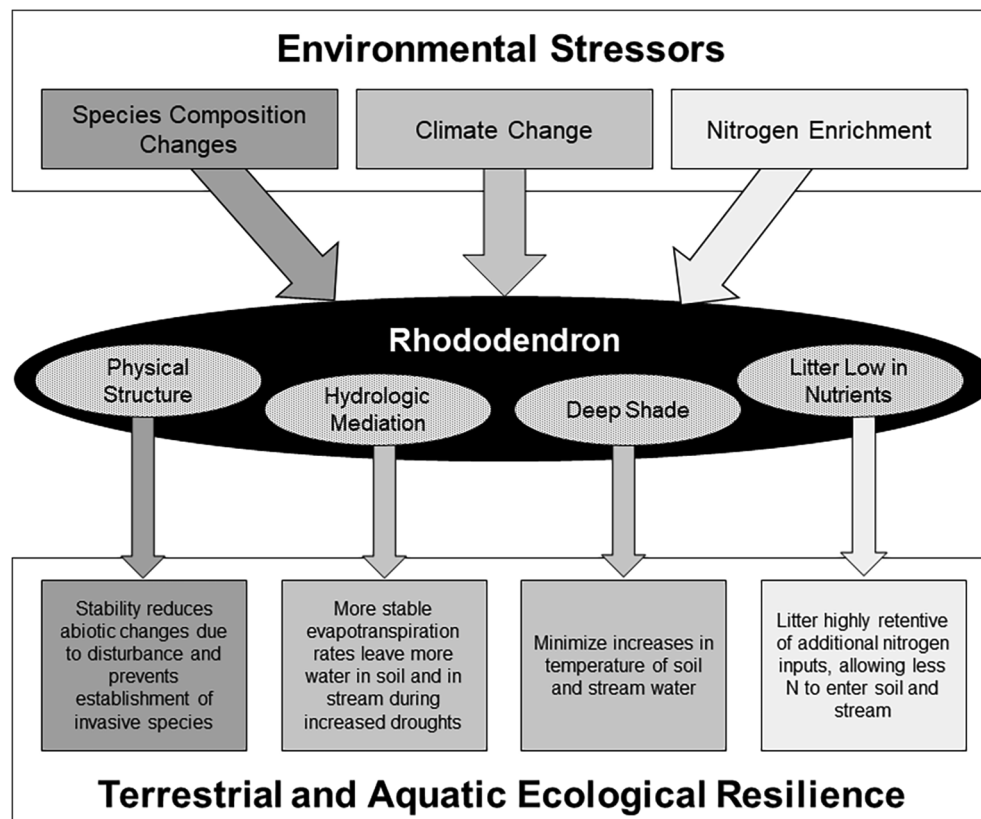


Fig. 4. Conceptual diagram of how the effects of global environmental stressors are mediated through key attributes of rhododendron in terrestrial riparian and headwater stream ecosystems.

4. Is rhododendron an emerging foundation species in headwater streams?

Previous studies have demonstrated tight linkages between riparian vegetation communities and the ecosystem structure and function of adjacent headwater streams (Kominoski et al., 2013). But can an *individual* riparian species exert sufficiently strong effects on stream ecosystems relative to abiotic (e.g. flow, sediment, Tant et al., 2015) and in-stream biotic (e.g. consumers) forces to act as a foundation species for stream ecosystems? Studies suggest that rhododendron may also be an emerging foundation species in headwater streams through its influence on three aspects of stream ecosystems: algal production, litter inputs, and nitrogen dynamics.

Reduction of light by rhododendron may inhibit algal primary production, particularly during deciduous leaf-off. In deciduous forest streams, algal growth often peaks during the winter and spring without rhododendron, but streams shaded by rhododendron's evergreen understory remain light-limited throughout the year (Dudley, 2018). Only one preliminary study has directly quantified rhododendron's negative effect on algal primary production in the southern Appalachians (Dudley, 2018). However, a study in western Ireland found that a different species of invasive rhododendron (*Rhododendron ponticum*) significantly suppressed algal primary production and grazer abundance (Hladyz et al., 2011). Because algae are a small biomass, but high quality, food resource in southern Appalachians headwater streams, even a small reduction in algae by rhododendron could have cascading effects on the rest of the stream food web (Bumpers et al., 2017).

Detrital inputs from associated riparian vegetation provide most of the energy in southern Appalachian headwater streams (Wallace et al., 2015), and riparian areas dominated by rhododendron could alter the timing, quantity, and quality of detrital inputs in biologically significant ways (Dudley, 2018). Rhododendron leaf litter inputs primarily occur in autumn, but unlike deciduous species, its leaves can drop year-round

(Monk et al., 1985). Like terrestrial detritivores, aquatic consumers also find rhododendron's recalcitrant leaf litter to be less palatable, thus reducing abundance and altering composition of aquatic microbes (Kominoski et al., 2009). Consequently, rhododendron leaves have lower decomposition rates in streams, and their presence in mixed-species leaf packs can even alter decomposition of other species (Kominoski et al., 2009). However, rhododendron leaf litter can also persist longer in streams, providing a critical summer food source for long-lived consumers when more labile leaf species have been consumed (Schofield et al., 2001). Furthermore, rhododendron's reduction of overstory canopy species could reduce inputs of coarse woody debris to streams (Webster et al., 2012).

By storing and reducing nitrogen availability in riparian forest soils, rhododendron likely limits leaching of nitrogen from terrestrial to headwater stream ecosystems (but see Yeakley et al., 2003). Rhododendron leaf litter inputs to streams can also potentially change in-stream nitrogen uptake dynamics. Under low nitrogen concentrations, lower microbial growth on in-stream rhododendron leaf litter could decrease N demand from streamwater, as has been found in other species with recalcitrant litter (Pastor et al., 2014). But under nutrient enrichment conditions, in-stream rhododendron litter responds more strongly to higher streamwater N + P concentrations, including 4.4x greater breakdown rates and higher percent change in fungal and bacterial biomass (Tant et al., 2015).

Preliminary research conducted in headwater streams suggests that rhododendron may play an important role in structuring and modulating ecosystem processes within these ecosystems. However, much of our knowledge of the role rhododendron plays in streams is based on our understanding of its effect on abiotic conditions in the terrestrial ecosystem (e.g. its effect on light) or through patch-scale leaf pack studies (e.g. Kominoski et al., 2009). Reach- or watershed-scale research, which utilizes naturally existing differences in rhododendron abundance or directly manipulates the presence of rhododendron (e.g.

Table 2
Rhododendron management options and potential outcomes.

Management Options	Potential Outcomes
No control of rhododendron spread and dominance	Rhododendron continues to persist and spread uncontrolled <ul style="list-style-type: none"> ■ Elimination of hardwood species from some areas and creation of rhododendron heath balds, increased homogeneity of ecosystem functions on the landscape (Krapfl et al. 2011, Brantley et al. 2013) ■ Potentially decreased soil moisture and increased nutrient retention under changing conditions, including warmer and/or drier climate, nutrient enrichment, and spread of invasive species Rhododendron eventually becomes self-limiting because of <ul style="list-style-type: none"> ■ Increased light conditions that damage leaves and stems (Lipp and Nilsen 1997) increased winter injury (Spencer 1932) ■ Rhododendron on drier or otherwise less ideal sites susceptible to dieback (Baird et al. 2013)
Widespread extirpation of rhododendron	Rhododendron removal is unsuccessful and/or prohibitively expensive (Harrell and Zedaker, 2010) Restoration of hardwood forests in riparian areas without evergreen understory component through frequent burning regimes (Dobbs and Parker 2004) <ul style="list-style-type: none"> ■ Higher landscape-level diversity ■ Loss of specific species dependent on rhododendron (e.g. Risk et al. 2011) ■ Loss of rhododendron effects on soil moisture and nutrients under future conditions Creation of new novel ecosystem, possibly dominated by an exotic invasive species Rhododendron dominates most riparian forests and hardwoods dominate mid-slope and upland areas <ul style="list-style-type: none"> ■ Potentially the most cost-effective ■ Preserves rhododendron effects on streams ■ Promotes hardwood growth in some former rhododendron areas ■ Supports heterogeneity of ecosystem functions
Selective removal of rhododendron in mid-slope and upland areas	

Table 3
Experimental and analytical methods that were used to establish eastern hemlock as a foundation species, and could be used to identify emerging foundation species, such as rhododendron.

Method	Example
Historical mapping of previous species distribution	Used historical documents, stand mapping, and dendrochronological analyses to reconstruct 250 years of landuse history to identify the contingent nature of <i>T. canadensis</i> establishment as a foundation species in New England (Ellison et al. 2014)
Current mapping of species using GIS (if feasible), potentially to assess changes in species composition over time	Integrated spatial modeling with field measurements to model eastern hemlock distribution in the southern Appalachian Mountains (Narayanan et al. 2010)
Observational studies, including comparisons of locations where species are naturally present or absent	Compared hardwood and hemlock-dominated streams to study differences in stream temperature, nitrate, pH, discharge, and light to predict how loss of eastern hemlock would likely affect stream ecosystems (Roberts et al. 2009)
Utilization of natural experiments in which a species is naturally removed with minimal other disturbances, such as species-specific pest removal	Conducted observations of stream ecosystem for 6 years starting from the initial infestation of hemlock woolly adelgid; Examined changes to temperature, light, canopy openness, litterfall, large wood, and benthic organic matter (Webster et al. 2012)
Plot-scale experimental manipulation of species presence/absence	Established 20 × 20 m treatment plots for two treatments (hemlock woolly adelgid-infested hemlock trees and girdled hemlock plots) and one reference type (hardwood dominated plots); Compared light, soil moisture, and ground layer vegetation among plot types (Ford et al. 2012)
Long-term, large-scale experimental manipulation of species presence/absence using a before-after-control-impact-design	Harvard Forest Hemlock Removal Experiment was a multi-hectare, decades-long before-after-control-impact experiment that was used to test the hypothesis that eastern hemlock was a foundation species (Ellison 2014)

Dudley, 2018), is needed to better determine rhododendron's importance to multiple abiotic and biotic components of southern Appalachian streams and determine if rhododendron's influence meets all characteristics of emerging foundation species within aquatic ecosystems.

5. Rhododendron in a changing world

Barring elimination by an introduced pathogen or wide-scale changes in land management, rhododendron appears likely to strongly influence terrestrial and aquatic ecosystems in the southern Appalachians into the future. Furthermore, rhododendron will likely continue to mediate ecosystem response to disturbance and increase ecosystem resistance under three types of chronic anthropogenic stressors: introduction of invasive species, climate change, and alterations to the nitrogen cycle (Fig. 4).

Previous studies indicate that rhododendron stabilizes ecosystems in the wake of disturbance by introduced pathogens (e.g. gypsy moths, Chastain et al., 2006; hemlock woolly adelgid, Ford et al., 2012), and it could remain important as future pathogen introductions further change overstory canopy conditions. Because rhododendron slows mineral cycling during disturbance events, its presence may be

particularly influential in protecting water quality of associated stream ecosystems (Chastain et al., 2006). Additionally, rhododendron's longevity on the landscape and suppression of other plants may prevent the establishment or spread of non-native invasive plant species in southern Appalachian riparian forests (Anderson et al., 2010), as other foundation species have been shown to do in their respective ecosystems (e.g. *Juniperus monosperma*, Kane et al., 2011).

Rhododendron may buffer the effect of climatic variability on stream and terrestrial ecosystems. Rhododendron's dense shade keeps soil cooler (Nilsen et al., 2001), and may reduce effects associated with increasing temperature. In addition, rhododendron's lower, more stable rate of evapotranspiration relative to deciduous trees could lead to smaller reductions in stream flow during increased frequency and intensity of dry conditions predicted for the southern Appalachians (Brantley et al., 2013). Rhododendron's higher rates of organic matter accretion could potentially mitigate climate change at regional scales (Chastain et al., 2006). Alternatively, increases in hydrologic variability could destabilize rhododendron-dominated areas due to increased fire intensity during dry conditions and landslides in wet conditions (Hales et al., 2009).

Finally, rhododendron may moderate ecosystem response to global changes in nitrogen cycling. Nitrogen enrichment to southern

Appalachian ecosystems could occur due to leakage during disturbance events (Chastain et al., 2006) and temperature-induced mineralization (Brookshire et al., 2011). Rhododendron's ability to retain and store nitrogen in terrestrial ecosystems and (as in-stream litter) convert water-column nitrogen into consumer biomass (Manning et al., 2016) could reduce the effects of nutrient enrichment locally and downstream.

However, it is possible that rhododendron's dominance may be diminished under specific future conditions. While evergreen species with sclerophyllous leaves will likely benefit from increased carbon dioxide and reduced leaf damage under warming temperatures in winter, a changing climate that results in drier conditions could disproportionately affect rhododendron due to its shallow roots (Brantley et al. 2013). A study examining changes to rhododendron coverage in the landscape shows that rhododendron loss may occur more frequently on drier topographies (Dobbs and Parker, 2004). Dry conditions (as well as other changing abiotic conditions, such as increased aluminum and lower calcium levels in soils) are thought to increase its susceptibility to dieback from nematode parasites (Baird et al., 2013). Additionally, novel invasive pathogens could extirpate rhododendron from southern Appalachian landscapes, as they did to American chestnut and eastern hemlock.

6. Management implications and lessons learned

Our study of rhododendron as an emerging foundation species offers several important insights for the management of shifting ecosystems under current and potential future conditions:

- **Lesson 1:** Rapid and significant anthropogenic change has enabled emerging foundation species to occupy their present dominant roles in today's ecosystems, often via irreversible changes to species composition and ecosystem function. We argue that acceptance of emerging species as the current and future drivers of evolving ecosystems would facilitate recognition of the irreversible state of many ecosystems and would enable managers to proactively pursue a wider range of appropriate and feasible management strategies.
- **Lesson 2:** The case of rhododendron highlights the importance of first identifying a dominant species based on the strength of its ecological connections, and then explicitly considering management options that maximize services and minimize disservices. Ecologists and managers may fail to identify emerging foundation species because of lack of prior dominance, negative effects on immediate management objectives, or biases associated with the current definition of foundation species (e.g. determining whether a species creates "stable conditions" depends on how stability is defined). Yet acknowledgement of the foundational role of a particular species allows for more informed management with explicit consideration of likely outcomes and feasibility of different strategies (Table 2). For instance, if hardwood recruitment is an objective, managers may wish to remove rhododendron since it can inhibit seedling survival. Conversely, rhododendron removal may also have important, unintended, disruptive, and potentially destabilizing consequences. While managers may ultimately choose to eradicate rhododendron or other emerging foundation species to achieve specific objectives, we argue that recognition of dominance and roles within an ecosystem is important to making such a decision, particularly at regional scales.
- **Lesson 3:** Few studies have proposed or documented that a foundation species in one ecosystem can also have the potential to play a dominant role in another ecosystem (but see Jules et al., 2014; Youngquist et al., 2017). Identification of foundation species located at ecosystem boundaries, such as rhododendron at the terrestrial-stream interface in the southern Appalachians, is important due to potential effects on multiple ecosystems.
- **Lesson 4:** Our analysis of rhododendron highlights the need to

consider how emerging foundation species will respond under predicted future environmental conditions, a question already being addressed for historically dominant foundation species (e.g. Gellie et al., 2016). While dominance by rhododendron may create certain disservices for humans (e.g. suppression of desirable hardwoods), its potential to mediate the disturbance effects of climate change, species invasions, and nitrogen enrichment may also be important management considerations. Furthermore, many emerging foundation species are the product of global change and may already be well-adapted to future changes, thus creating more stable conditions and potentially reducing the feasibility of removal.

- **Lesson 5:** The challenges in early identification of potential emerging foundation species highlights knowledge gaps and areas for increased study on species interactions under current and potential future conditions (Table 3). In particular, there is a critical need for a direct, experimental approach that manipulates species presence and absence in a controlled way (Ellison et al., 2005). These experiments will be most informative if conducted at sufficiently large scales to assess the full range of ecosystem properties that might change were a potential emerging foundation species to be lost (Angelini et al., 2011).

Acceptance of the emerging foundation species concept may require a shift in our approach to management, conservation, and restoration of ecosystems in a changing world. Species composition and environmental conditions have been altered substantially at a global scale and return to former conditions and historic species dominance are often not realistic nor feasible. Management actions that fail to account for current dynamics of dominant species could unintentionally lead to ecosystem destabilization or loss of resilience to future change. Greater understanding of the potential transience of dominant species will enable management approaches to be pragmatic in meeting future conservation and restoration challenges.

CRedit authorship contribution statement

Maura P. Dudley: Conceptualization, Writing - original draft. **Mary Freeman:** Writing - review & editing. **Seth Wenger:** Writing - review & editing. **Rhett Jackson:** Writing - review & editing. **Catherine M. Pringle:** Supervision, Funding acquisition, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Aaron Ellison for his comments on earlier drafts of this manuscript. We also appreciate insightful comments provided by Mac Callahan and two anonymous reviewers. This study was funded by the Coweeta LTER Project, which was funded by National Science Foundation grants DEB-1637522, DEB-1440485. Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

References

- Anderson, P., Brundrett, M., Grierson, P., et al., 2010. Impact of severe forest dieback caused by *Phytophthora cinnamomi* on macrofungal diversity in the northern jarrah forest of Western Australia. *Forest Ecol Manage* 259, 1033–1040.
- Angelini, C., Altieri, A.H., Silliman, B.R., et al., 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience* 61, 782–789.
- Atkins, J.W., Epstein, H.E., Welsch, D.L., 2018. Using Landsat imagery to map understory shrub expansion relative to landscape position in a mid-Appalachian watershed.

- Ecosphere 9, e02404. <https://doi.org/10.1002/ecs2.2404>.
- Baird, R., Wood-Jones, A., Varco, J., et al., 2013. All taxa biodiversity inventory survey of select soil and plant ecological parameters associated with rhododendron decline in the Great Smoky Mountains and surrounding area. *Southeast. Nat.* 12, 703–722.
- Ball, B.A., Bradford, M.A., Coleman, D.C., et al., 2009. Linkages between below and aboveground communities: decomposer responses to simulated tree species loss are largely additive. *Soil Biol. Biochem.* 41, 1155–1163.
- Beckage, B., Clark, J.S., Clinton, B.D., et al., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. *Can. J. For. Res.* 30, 1617–1631.
- Brantley, S., Ford, C.R., Vose, J.M., 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. *Ecol. App.* 23, 777–790.
- Brookshire, E.N.J., Gerber, S., Webster, J.R., et al., 2011. Direct effects of temperature on forest nitrogen cycling revealed through analysis of long-term watershed records. *Glob. Change Biol.* 17, 297–308.
- Bumpers, P.M., Rosemond, A.D., Maerz, J.C., et al., 2017. Experimental nutrient enrichment of forest streams increases energy flow to predators along greener food-web pathways. *Freshwater Biol.* 62, 1794–1805.
- Chastain, R.A., Townsend, P.A., 2007. Use of Landsat ETM and topographic data to characterize evergreen understory communities in Appalachian deciduous forests. *Photogramm. Eng. Rem. S.* 73, 563–575.
- Chastain, R.A., Currie, W.S., Townsend, P.A., 2006. Carbon sequestration and nutrient cycling implications of the evergreen understory layer in Appalachian forests. *Forest Ecol. Manag.* 231, 63–77.
- Clinton BD. 1995. Temporal variation in photosynthetically active radiation (PAR) in mesic southern Appalachian hardwood forests with and without *Rhododendron* understories. Proceedings of the 10th Central Hardwood Forest Conference; 5-8 March 1995; Morgantown, WV. Gen. Tech. Rep. NE-197. Randor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 534-540.
- Clinton, B.D., Vose, J.M., 1996. Effects of *Rhododendron maximum* L. on *Acer rubrum* L. seedling establishment. *Southern Appalachian Botanical Soc.* 61, 38–45.
- Cofer, T.M., Elliott, K.J., Bush, J.K., et al., 2018. *Rhododendron maximum* impacts seed bank composition and richness following *Tsuga canadensis* loss in riparian forests. *Ecosphere* 9, e02204. <https://doi.org/10.1002/ecs2.2204>.
- Dayton PK. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: Parker BC (Ed). Proceedings of the Colloquium on Conservation Problems in Antarctica. Lawrence, KS: Allen Press.
- Dillon, W.W., Meentemeyer, R.K., Vobler, J.B., Cobb, R.C., Metz, M.R., Rizzo, D.M., 2013. Range-wide threats to a foundation tree species from disturbance interactions. *Madroño* 60, 139–150.
- Dobbs, M.M., Parker, A.J., 2004. Evergreen understory dynamics in Coweeta Forest, North Carolina. *Phys. Geogr.* 25, 481–498.
- Dudley MP. 2018. Assessing the importance of a dominant understory shrub, *Rhododendron maximum*, to riparian forest and headwater stream ecosystems of the southern Appalachian Mountains. Athens, GA: University of Georgia.
- Elliott, K.J., Vose, J.M., 2011. The contribution of the Coweeta Hydrologic Laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests. *Forest Ecol. Manag.* 261, 900–910.
- Elliott, K.J., Vose, J.M., 2012. Age and distribution of an evergreen clonal shrub in the Coweeta Basin: *Rhododendron maximum* L. 1. *B Torrey Bot. Club* 139, 149–166.
- Ellison, A.M., Bank, M.S., Clinton, B.D., et al., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3, 479–486.
- Ellison, A.M., 2014. Experiments are revealing a foundation species: a case study of eastern hemlock (*Tsuga canadensis*). *Adv. Ecol.* 2014. <https://doi.org/10.1155/2014/456904>.
- Ellison, A.M., Lavine, M., Kerson, P.B., et al., 2014. Building a foundation: land-use history and dendrochronology reveal temporal dynamics of a *Tsuga canadensis* (Pinaceae) forest. *Rhodora* 116, 377–427.
- Ford, C.R., Vose, J.M., 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecol. Appl.* 17, 1156–1167.
- Ford, C.R., Elliott, K.J., Clinton, B.D., et al., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos* 121, 523–536.
- Gellie, N.J., Breed, M.F., Thurgate, N., Kennedy, S.A., Lowe, A.J., 2016. Local maladaptation in a foundation tree species: implications for restoration. *Biol. Conserv.* 203, 226–232.
- Graham, N.A., 2014. Habitat complexity: coral structural loss leads to fisheries declines. *Curr. Biol.* 24 (9), R359–R361.
- Hales, T.C., Ford, C.R., Hwang, T., et al., 2009. Topographic and ecological controls on root reinforcement. *J. Geophys. Res.* 114, F03013. <https://doi.org/10.1029/2008JF001168>.
- Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Sci Rev* 145, 94–103.
- Harrell C and Zedaker S. 2010. Effects of prescribed burning, mechanical, and chemical treatments to curtail rhododendron dominance and reduce wildfire fuel loads. Proceedings of the 14th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-121, Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.
- Hedman, C.W., van Lear, D.H., 1995. Vegetative structure and composition of southern Appalachian riparian forests. *B Torrey Bot. Club* 122, 134–144.
- Hladyz, S., Abjornsson, K., Giller, P.S., et al., 2011. Impacts of an aggressive riparian invader on community structure and ecosystem function in in stream food webs. *J. Appl. Ecol.* 48, 443–452.
- Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24 (11), 99–605.
- Horton, J.L., Clinton, B.D., Walker, J.F., et al., 2009. Variation in soil and forest floor characteristics along gradients of ericaceous, evergreen shrub cover in the southern Appalachians. *Castanea* 74, 340–352.
- Hwang, T., Band, L.E., Hales, T.C., et al., 2015. Simulating vegetation controls on hurricane-induced shallow landslides with a distributed ecohydrological model. *J. Geophys. Res.-Biogeo.* 120, 361–378. <https://doi.org/10.1002/2014JG002824>.
- Johnson, A.S., Hale, P.E., Ford, W.M., et al., 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. *Am. Midl. Nat.* 1 (33), 18–35.
- Jules ES, Carroll AL, Garcia AM, Steenbock CM, Kauffman MJ. 2014. Host heterogeneity influences the impact of non-native disease invasion on populations of a foundation tree species. *Ecosphere* 5: 105. <http://dx.doi.org/10.1890/ES14-00043.1>.
- Kane, J.M., Meinhardt, K.A., Chang, T., Cardall, B.L., Michalet, R., Whitham, T.G., 2011. Drought-induced mortality of a foundation species (*Juniperus monosperma*) promotes positive afterlife effects in understory vegetation. *Plant Ecol.* 212 (5), 733–741. <https://doi.org/10.1007/s11258-010-9859-x>.
- Kincaid, J.A., 2012. Regeneration dynamics of *Tsuga canadensis* in the southern Appalachian Mountains, USA. *Trees* 26, 1045–1056.
- Kominoski, J.S., Hoellein, T.J., Kelly, J.J., et al., 2009. Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? *Oikos* 118, 457–463.
- Kominoski, J.S., Follstad Shah, J.J., Canhoto, C., et al., 2013. Forecasting functional implications of global changes in riparian plant communities. *Front. Ecol. Environ.* 11, 423–432.
- Krapfl, K.J., Holzmueller, E.J., Jenkins, M.A., 2011. Early impacts of hemlock woolly adelgid in *Tsuga canadensis* forest communities of the southern Appalachian Mountains. *J. Torrey Bot. Soc.* 138, 93–106.
- Lei, T.T., Semones, S.W., Walker, J.F., et al., 2002. Effects of *Rhododendron maximum* thickets on tree seed dispersal, seedling morphology and survivorship. *Int. J. Plant Sci.* 163, 991–1000.
- Lei, T.T., Nilsen, E.T., Semones, S.W., 2006. Light environment under *Rhododendron maximum* thickets and estimated carbon gain of regenerating forest tree seedlings. *Plant Ecol.* 184, 143–156.
- Lipp, C.C., Nilsen, E.T., 1997. The impact of subcanopy light environment on the hydraulic vulnerability of *Rhododendron maximum* to freeze-thaw cycles and drought. *Plant Cell Environ.* 20, 1264–1272.
- Lipscomb, M.V., Nilsen, E.T., 1990. Environmental and physiological factors influencing the natural distribution of evergreen and deciduous ericaceous shrubs on northeast and southwest-facing slopes of the southern Appalachian Mountains II. Irradiance tolerance. *Am. J. Bot.* 77, 108–115.
- Loeb, S.C., Tainter, F.H., Cázarez, E., 2000. Habitat associations of hypogeous fungi in the southern Appalachians: implications for the endangered northern flying squirrel (*Glaucomys sabrinus coloratus*). *Am. Midl. Nat.* 144, 286–296.
- Manning, D.W.P., Rosemond, A.D., Benstead, J.P., et al., 2016. Convergence of detrital stoichiometry predicts thresholds of nutrient-stimulated breakdown in streams. *Ecol. Appl.* 26, 1745–1757.
- Milton, S.J., 2003. Emerging ecosystems—a washing-stone for ecologists, economists and sociologists? *News and views. South African Journal of Science* 99 (9 & 10), 404–406.
- Monk, C.D., McGinty, D.T., Day, F.P., 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. *B Torrey Bot. Club* 112, 187–193.
- Narayananaraj, G., Bolstad, P.V., Elliott, K.J., et al., 2010. Terrain and landform influence on *Tsuga canadensis* (L.) Carrière (Eastern Hemlock) distribution in the southern Appalachian Mountains. *Castanea* 75, 1–18.
- Nilsen, E.T., Clinton, B.D., Lei, T.T., et al., 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? *Am. Midl. Nat.* 145, 325–343.
- Orwig, D.A., Plotkin, A.A.B., Davidson, E.A., Lux, H., Savage, K.E., Ellison, A.M., 2013. Foundation species loss affects vegetation structure more than ecosystem function in a northeastern USA forest. *PeerJ* 1, e41.
- Osburn, E.D., Elliott, K.J., Knoepf, J.D., et al., 2018. Soil microbial response to *Rhododendron* understory removal in southern Appalachian forests: effects on extracellular enzymes. *Soil Biol. Biochem.* 127, 50–59.
- Palik, B.J., Ostry, M.E., Venette, R.C., et al., 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. *Forest Ecol. Manag.* 269, 26–30.
- Pastor, A., Compson, Z.G., Dijkstra, P., et al., 2014. Stream carbon and nitrogen supplements during leaf litter decomposition: contrasting patterns for two foundation species. *Oecologia* 176, 1111–1121.
- Plocher, A.E., Carvell, K.L., 1987. Population dynamics of Rosebay rhododendron thickets in the southern Appalachians. *B Torrey Bot. Club* 114, 121–126.
- Prevey, J.S., Germino, M.J., Huntly, N., 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecol. Appl.* 20, 1890–1902.
- Ramus, A.P., Silliman, B.R., Thomsen, M.S., et al., 2017. An invasive foundation species enhances multifunctionality in a coastal ecosystem. *P Natl. A Sci. USA* doi/10.107353114.
- Reed, A.W., Kennedy, M.L., 2000. Conservation status of the eastern spotted skunk *Spilogale putorius* in the Appalachian Mountains of Tennessee. *Am. Midl. Nat.* 144, 133–138.
- Risk, A.C., Richardson, C., Davison, P., 2011. Epiphyllous bryophytes in the Appalachian Plateau of Kentucky and Tennessee, U.S.A. *Bryologist* 114, 289–297.
- Rivers CT, van Lear DH, Clinton BD, et al. 1999. Community composition in canopy gaps as influenced by presence or absence of *Rhododendron maximum*. 10th Biennial Southern Silvicultural Research Conference, Shreveport, LA, 16-18 February 1999.
- Roberts, S.W., Tankersley, R., Orvis, K.H., 2009. Assessing the potential impacts to

- riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. *Environ. Manage.* 44, 335–345.
- Schnitzer, S.A., Bongers, F., 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecol. Lett.* 14, 397–406.
- Schofield, K.A., Pringle, C.M., Meyer, J.L., et al., 2001. The importance of crayfish in the breakdown of rhododendron leaf litter. *Freshwater Biol.* 46, 1191–1204.
- Sorte, C.J., Davidson, V.E., Franklin, M.C., Benes, K.M., Doellman, M.M., Etter, R.J., Hannigan, R.E., Lubchenco, J., Menge, B.A., 2017. Long-term declines in an intertidal foundation species parallel shifts in community composition. *Glob. Change Biol.* 23 (1), 341–352.
- Spencer, E.L., 1932. Natural distribution of *Rhododendron maximum* in New Jersey. *B. Torrey Bot. Club* 59, 401–414.
- Stehn, S.E., Webster, C.R., Jenkins, M.A., et al., 2011. High-elevation ground-layer plant community composition across environmental gradients in spruce-fir forests. *Ecol. Res.* 26, 1089–1101.
- Stottlemeyer, A.D., Shelburne, V.B., Waldrop, T.A., et al., 2009. Fuel characterization in the southern Appalachian Mountains: an application of landscape ecosystem classification. *Int. J. Wildland Fire* 18, 423–429.
- Tant, C.J., Rosemond, A.D., Helton, A.M., et al., 2015. Nutrient enrichment alters the magnitude and timing of fungal, bacterial, and detritivore contributions to litter breakdown. *Freshw. Sci.* 34, 1259–1271.
- Thomson, J.A., Burkholder, D.A., Heithaus, M.R., Fourqurean, J.W., Fraser, M.W., Statton, J., Kendrick, G.A., 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. *Glob. Change Biol.* 21 (4), 1463–1474.
- van Lear DH, Vandermast DB, Rivers CT, et al. 2002. American chestnut, rhododendron and the future of Appalachian cove forests. Published in *Outcalt, K.W. ed. 2002. Proceedings of the eleventh biennial southern silvicultural research conference. Gen. Tech. Rep SRS-46. Asheville, NC:U.S. Department of Agriculture, Forest Service, Southern Research Station. 622.*
- Vandermast, D.B., Van Lear, D.H., 2002. Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecol. Manag.* 155, 97–106.
- Vandermast, D.B., van Lear, D.H., Clinton, B.D., 2002. American chestnut as an allelopath in the southern Appalachians. *Forest Ecol Manag* 165, 173–181.
- Wahlenberg, W.G., Doolittle, W.T., 1950. Reclaiming Appalachian brush lands for economic forest production. *J. Forest.* 48, 170–174.
- Wallace, J.B., Eggert, S.L., Meyer, J.L., et al., 2015. Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. *Ecology* 96, 1213–1228.
- Webster, J.R., Morkeski, K., Wojculewski, C.A., et al., 2012. Effects of hemlock mortality on streams in the southern Appalachian Mountains. *Am. Midl. Nat.* 168, 112–131.
- Williams, J.W., Jackson, S.T., 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5 (9), 475–482.
- Wurzburger, N., Hendrick, R.L., 2007. Rhododendron thickets alter N cycling and soil extracellular enzyme activities in southern Appalachian hardwood forests. *Pedobiologia* 50, 563–576.
- Wurzburger, N., Higgins, B.P., Hendrick, R.L., 2011. Ericoid mycorrhizal root fungi and their multicopper oxidases from a temperate forest shrub. *Ecol. Evol.* 2, 65–79.
- Yeakley, J.A., Coleman, D.C., Haines, B.L., et al., 2003. Hillslope nutrient dynamics following upland riparian vegetation disturbance. *Ecosystems* 6, 154–167.
- Youngquist, M.B., Eggert, S.L., D'Amato, A.W., et al., 2017. Potential effects of foundation species loss on wetland communities: a case study of black ash wetlands threatened by emerald ash borer. *Wetlands* 37, 787–799.