Bunchgrass is the Piney Woods Trinity By Dr. Kyle E. Harms, Department of Biological Sciences,

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Well-managed, high-diversity groundcover - dominated by wiregrass (Aristida stricta) - at Eglin Air Force Base, Florida. Photo by Kyle E. Harms.

You would not want to hear rivets popping out of your airplane's skin at 30,000 feet over the Southeastern Coastal Plain as you flew between, say, Baton Rouge and Atlanta. That is precisely why Paul and Anne Ehrlich used the rivet metaphor when they described the alarming, bit-by-bit loss of biodiversity (Ehrlich & Ehrlich 1981). A point they wished to make was that even if the loss of one redundant rivet does not necessarily portend dire consequences, losing too many - or the wrong ones - indeed would be catastrophic.

In any case, the metaphor is a good one, in spite of some clear limitations. Rivets are replaceable (if one pops out in flight, it could be replaced once the airplane touches down), whereas species are not (extinction is forever). The metaphor is also limited if it is interpreted (albeit incorrectly) to mean that species are equivalent. In this sense, different species are more like the different components of the airplane. The consequences differ for losing a rivet, the nose cone, or an engine. The airplane does not fly in the absence of a critical component.

With increasing emphasis on restoration of longleaf "piney woods" and their high-diversity groundcover (Kirkman & Jack 2018), it is important to identify the critical components that together constitute functional and sustainable communities and ecosystems. Many would agree that native bunchgrasses are critical components of longleaf plant communities. In fact, the scientific literature contains claims that each of the few select species of native bunchgrasses that physically dominate the highdiversity groundcover is such a critical component of its community that I am compelled to call each one a longleaf piney woods "trinity species," i.e., a combination foundation species, keystone species, and ecosystem engineer.

Paul Dayton (1972) gave us the term "foundation species" (based on his research on the structural significance of benthic sponges for nearshore Antarctic marine communities): "those

which have a disproportionately important influence on the structure of the community." Hovanes et al. (2018) applied this term to the native bunchgrasses that constitute the physically dominant element of well-managed, high-diversity longleaf piney woods groundcover.

Based on his observations of the outsized influence *Pisaster* sea stars have on rocky intertidal communities along the Pacific Northwest coast, Bob Paine (1969) coined the term "keystone species." Paine and colleagues defined a keystone species as "one whose effect is large, and disproportionately large relative to its abundance" (Power et al. 1996). Among several others who have referred to piney woods bunchgrasses as keystone species, Clewell (1989) stated that "wiregrass [Aristida stricta] is the keystone species for determining the fire regime."

Clive Jones et al. (1994) identified "ecosystem engineers" as species that "directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials... they modify, maintain and create habitats." In addition to "allogenic engineers" such as beavers, which change the environment due to their activities, they distinguished "autogenic engineers," which change the environment via their own physical structures (i.e., their living and dead tissues). In her master's thesis, Kaplan (2005) pointed out that ecosystem engineer is an especially apt term for our dominant native bunchgrasses, owing to their combined prominence in the groundcover and their hefty influence on fire behavior.

Although it has been argued in the literature that wiregrass, little bluestem (*Schizachyrium scoparium*), slender bluestem (*S. tenerum*), and certain other bunchgrasses that physically dominate the piney woods groundcover each meets the requirements to be considered a critical trinity species, relatively little research has been done on the specific roles that these bunchgrasses play. It has long been known and understood by land managers and restoration professionals that these bunchgrasses are especially influential through carrying fire (see discussion and many references in Noss 2018). In ongoing research, we are also learning how these species in the trinity bunchgrass guild or functional group interact with and influence other members of their associated groundcover assemblages.

For example, trinity bunchgrasses appear to organize into characteristically over-dispersed patterns (Hovanes et al. 2018). This means that individual bunchgrass tussocks tend to be a bit farther from one another than we would expect by chance. Three potential causes seem especially likely. First, inter-tussock competition for light or belowground resources (nutrients or water) could cause tussocks to space themselves on the landscape. Second, plant-soil feedbacks mediated by microbes could result

in reduced conspecific recruitment near established tussocks. Third, overlapping biomass between tussocks' root crowns could create fuel cells (sensu Hiers et al. 2009) with ramped-up local fire intensity and severity relative to the adjacent fuel cells directly over the rooted portions of the tussocks. (As an aside, Gagnon et al. [2010] suggested that especially flammable species, such as our native bunchgrasses, might possess adaptations for flammability to better survive frequent fires. If a plant burns hot, but fast, relatively little heat might penetrate to the belowground organs from which a surviving plant could resprout. Less

flammable fuel directly above the roots, but more fuel between tussocks could be the spatially periodic fuel-cell pattern that drives tussock over-dispersion.)

Irrespective of the causes of over-dispersed bunchgrass patterning, the spatial arrangement has consequences for the overall community and ecosystem. At the community level, the interstitial spaces among tussocks provide opportunities for colonization and persistence by smaller-stature groundcover species. At the ecosystem level, over-dispersed bunchgrasses (as long as they are not too far apart from one another) could carry fire across the landscape more readily than randomly spaced or clumped tussocks would.

Any ol' species of dominant grass simply won't do. Dominant native bunchgrasses form discrete tussocks whereas exotic grasses that form lawns, sods, turfs, or otherwise densely packed swards or stands, such as bahiagrass (*Paspalum notatum*) and cogongrass (*Imperata cylindrica*), render the groundcover depauperate in species. Brewer (2008) provides a clear example of the dire consequences for diversity of substituting non-native cogongrass for native bunchgrass in piney woods groundcover.

My principal objective in this article is not to oversell the "trinity" idea (which I am mostly suggesting just for fun), but to highlight the importance of identifying, understanding, and restoring the critical components of piney woods ecosystems (a subject that warrants continued serious attention). Accumulating research suggests that whether or not native wiregrass, little bluestem, and their ilk meet all the criteria to be considered "trinity bunchgrasses," they appear to be critical components of natural and well-restored longleaf piney woods ecosystems.

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Over-dispersed individuals of slender little bluestem (Schizachyrium tenerum) and one lone longleaf pine (Pinus palustris) sapling in June 2009, 24 days after a prescribed fire, at Camp Whispering Pines, Louisiana. Photo by Kyle E. Harms.



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