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Puzzling the Grassy Archipelago: Insights from Alfred Russel Wallace into the origin and maintenance of high-elevation grassy balds

— Jim Costa

Roan Mountain looms large literally and figuratively — literally as home to the largest and most spectacular of the southern Appalachian high-elevation grassy balds, and figuratively in posing perhaps the greatest ecological mystery of our region. In his renowned 1932 book *The Natural Gardens of North Carolina*, B. W. Wells commented that "No plant communities in the state have been more puzzling to the ecologist than those that come under the designation of mountain balds." Moreover, not until "intensive studies...are made and continued over many years," Wells further reflected, "will ecological science begin to solve the riddle of the balds." Ninety-four plus years and many "intensive studies" later, however, the origin and evolution of Roan's grassy mantle is an ecological riddle still.

Some southern Appalachian grassy balds are known to be relatively recent and anthropogenic in origin. Roan and several others, however, are clearly ancient — home to a plethora of sun-loving grasses and forbs that include, tellingly, native grasses and a number of rare endemic and disjunct glacial relicts — plant species more typical of the far north. These largely treeless grasslands lie below climatic treeline — collectively you might think of them as an archipelago of grassy islands in the great forest sea. But was Roan and similar balds once forested to their summits like their neighboring mountain peaks? If so, how and when did the trees disappear? And, just as importantly, not re-appear? Why, as Wells put it, "this hesitancy to go back to forest when forests are all around them?" Over the years a range of natural and anthropogenic causes have been hypothesized to account for the origin and maintenance of the balds. Perhaps they are communities shaped by certain qualities of the soil, frequent fire, or relentless high-elevation winds, snow, and ice? Or are they relics of Native American and then settler activity: regular burning, tree girdling, and later, livestock grazing?

Brown plot, Round Bald

The first idea that might come to mind is a logical one: maybe woody trees and shrubs just can't grow there. This is precisely what ecologist Dalton Brown set out to investigate at Roan in the 1930s. As part of his doctoral research, Brown created several plots consisting of transplanted red spruce and Fraser fir tree seedlings atop Round Bald and tracked their growth and survivorship over several years. As the plot remnants visible today some 9 decades later attest, these trees can indeed survive and even (very slowly) grow. But they do not thrive, nor reproduce, apparently: the Brown plots today seem frozen in time, huddled trees like lonely islands in a sea of grass. Yet there is evidence of slow but steady encroachment of woody vegetation from the

periphery, with blueberry and blackberry in the vanguard and rhododendron, spruce and fir close behind. It is estimated that Roan's grassy balds have shrunk to less than 25% of their historical extent owing to the slow march of woody vegetation. Do these changes offer any insights into the nature of the balds? They may suggest that something has acted to maintain the open grasslands over the centuries, removing woody vegetation or preventing it from getting established to begin with — some kind of regular disturbance perhaps.

One compelling model incorporating both environment and disturbance, the "Climate-Herbivore Hypothesis" of ecologists Peter Weigl and Travis Knowles, posits that the grassy balds initially formed in the transition from tundra as the last glacial period waned, and were afterward maintained as grassland by grazers — first megaherbivores (such as mastodons, mammoths, musk oxen, giant ground sloths, and others, evidence for which has been found at nearby sites in Tennessee and Virginia), and later "meso" herbivores such as bison, elk, and deer. With the subsequent decline of those second-tier grazers (the last recorded elk taken by hunters in North Carolina was in the late 1700s), did settlers' goats, sheep, and cattle take their place as the herbivores keeping the grassy balds...well, bald? Plenty of early records show that settlers around Roan and some other high-elevation balds of the region did indeed use the balds as summer pasture, and more recent management efforts to mimic their ecological role — namely knocking back woody vegetation by various means, from goats to weed-whackers — have been shown to have a positive effect on the sun-loving grass and forb species of the balds.

Roan Mountain looking toward Round Bald

An important but often overlooked ecological dynamic central to the Climate-Herbivore Hypothesis was first suggested in the late 1850s by a naturalist who never studied, or indeed even laid eyes on, a grassy bald: the renowned 19th century traveler-naturalist Alfred Russel Wallace, famed as the author of the travel memoir *The Malay Archipelago*, co-discoverer with Darwin of the principle of natural selection, and discoverer of the eponymous Wallace Line that delimits the Indo-Malayan and Austral-Asian biogeographic realms. While traveling in tropical southeast Asia Wallace was struck by another kind of anomalous grassland: grassy tropical plains such as those of lowland Halmahera Island in Indonesia, or the *llanos* of the Orinoco River in South America. Much like the grassy balds, these too are island-like treeless grassland communities, surrounded by forest yet somehow remaining treeless. "Climate or soil will not account for it," Wallace observed in his field notebook. He proposed an explanation: if low-lying areas were uplifted relatively rapidly by geological processes, the newly exposed

plains might be colonized far more quickly by grasses than other species, given how abundant grass seeds are relative to those of woody plants, and how much faster and further they are dispersed. Once established, the grasses have an edge: "seeds of grasses carried by the wind or by birds will vegetate immediately & cover it, then forbidding the advance of forest," Wallace wrote, continuing: "Ground once taken possession of by grasses cannot be reconquered by forest even if surrounded by it."

Wallace was essentially describing what modern ecologists call competitive exclusion, where one species has an edge over others and excludes them from an area, or bars them from getting a foothold to begin with. Intriguingly, Wallace dated this notebook entry January 20, 1858, just a few weeks before his "eureka moment" discovering the principle of natural selection. It seems likely that ruminating on the competition dynamic inherent in anomalous grassy "islands" surrounded by forest, much like grassy balds, may have helped inspire his great insight into the evolutionary process itself. It is interesting to note that the idea of dense, grass-dominated vegetation inhibiting the establishment of woody plant seedlings in balds was later suggested by several 20th-century botanists and ecologists, though these naturalists had no way of knowing that Wallace had proposed such a process in the previous century.

The dispersal/competition dynamic Wallace proposed to explain the puzzle of low-elevation tropical grasslands surely applies to high-elevation grassy balds as well. Grasslands of the southern Appalachians are thought to have increased in abundance through the Pliocene, and would have naturally succeeded tundra at higher elevations in the southern mountains as climate warmed in post-glacial times — much like today's pajonal or grass páramo, high-altitude grasslands, are found just below the treeless zone in the high Andes. In certain places, facilitated by climate, the grasses may have become well enough established to form a near-impenetrable barrier to tree and shrub seeds. Natural grazing may have later helped maintain such grasslands, followed later still by the grazing of domesticated livestock. A dynamic of this sort could explain why grasslands like those of Roan are highly resistant to woody invasion from within the bald but less so on its periphery, and why disturbance past and present, from grazing herbivores to today's weed-whacking and bush hogging, appears necessary to maintain their open character. This might be dubbed the "climate-competitive exclusion-herbivore" hypothesis.

Needless to say, puzzles remain. A major one is why we don't see extensive balds in high-elevation areas seemingly more accessible than Roan and other grassy balds to both natural grazers and humans with their livestock. We may never fully understand the factors behind the formation and maintenance of high-elevation grassy balds, but it is clear that the woody encroachment noted at Roan by D. M. Brown nearly 75 years ago has continued. As seedlings at the interface of the balds and surrounding forest become established, Brown observed, "ultimate natural forestation of the entire bald is not improbable." Which means that regardless of how they formed, the long-term persistence of the balds and their botanical rarities lies in our hands. The conservation imperative that the balds present us with would have surely resonated with Wallace, an early voice for conservation. Lamenting the pace of environmental degradation and species extinction in his time, Wallace likened species to letters that make up the volumes of Earth history, their extinction an irresponsible and irrevocable loss of that record, disrupting the continuity and mutual interactions of species in the web of life. In failing to take action now, Wallace wrote in 1863, "future ages will certainly look back upon us as a people so immersed in the pursuit of wealth as to be blind to higher considerations."

Fortunately, thanks to the cooperative efforts of governmental agencies such as National Park Service and the U.S. Forest Service and volunteer conservation organizations like the Southern Appalachian Highlands Conservancy and Friends of Roan Mountain, action has been and is being taken: the management of the balds continues, ensuring the continuity of a unique southern Appalachian biological community — especially majestic Roan Mountain, the largest "island" in the grassy bald archipelago, as beautiful as it is puzzling.

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Jim Costa, professor of biology and executive director of the Highlands Biological Station of Western Carolina University, is an evolutionary biologist and Darwin and Wallace scholar, an author, and a recipient of the Alfred Russel Wallace Medal and the Stephen Jay Gould Prize of the Society for the Study of Evolution. Jim will be our speaker on Friday, Sept.18 at 7:30 p.m. at the Roan Mountain State Park Conference Center.

GIFTS AND MEMORIALS

Friends of Roan Mountain gratefully acknowledges these charitable gifts

Linda Good **Doug Judin**

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Join us for our Annual Membership Meeting

Saturday, September 19, at 5:45 PM in the conference center, where you will receive information regarding the activities, projects and finances of the organization. The election of board members will be held. The following have been nominated for this year's election:

Aubrie Abernethy, Nancy Barrigar, Jennifer Bauer, Tracy Campbell,

Larry McDaniel, Ken Turner, Tyler Wicks

Nominations from the floor may be made at the meeting. The annual meeting provides an opportunity for the membership to give input concerning the policies and activities of FORM. Any member wishing to submit an item for the agenda of the annual meeting may do so by contacting Gary Barrigar, friendsofroan@gmail.com.