dominant native species, *S. airoides*, remains uncommon elsewhere in this area. As a moderately productive bunch grass, this species is highly desirable for a variety of eco-system services and has maintained its abundance against the increased densities of the introduced brome grasses.

The success of *B. tectorum* is attributed to this plant's ability to exploit early growing season moisture, but its ability to invade and grow in a relatively low nitrogen soil remains an enigma. The annual grasses *B. tectorum* and *B. arvensis* have colonized areas between the initial seeded sites of the 1998 planting and may have replaced species no longer common on the area.

The use of a seed mix in low nutrient soils initially generated a novel, native plant community, but 12 years later the site appears vulnerable to invasive species and total native species cover has dropped below 50%. The presence of *S. airoides*, an uncommon local plant, appears to have mitigated the native decline. Hence, the novel low carbon, low nitrogen soil used in the restoration is not a guaranteed, long-term solution for preventing invasions in restored grasslands.

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Predicting Post-Fire Tree Survival for Restoring Oak Ecosystems ☉

Scott R. Abella (corresponding author: University of Nevada Las Vegas, School of Life Sciences, Las Vegas and Natural Resource Conservation LLC, 1400 Colorado Street, Boulder City, NV 89005, USA, scott.abella@unlv.edu), LaRae A. Sprow (Metroparks of the Toledo Area, Toledo, OH), and Timothy A. Schetter (Metroparks of the Toledo Area, Toledo, OH).

Reducing tree encroachment is challenging for restoring light-requiring habitats including prairies, savannas, and woodlands. Such ecosystems frequently support high biodiversity and are of keen interest for restoration (Haney et al. 2008). Periodic fires often limited tree recruitment during the evolutionary history of these ecosystems, maintaining open conditions (Hutchinson et al. 2012). Prescribed fire is a restoration strategy for reducing tree encroachment that can be cost-effective (compared to mechanical cutting) and have other advantages, such as avoiding soil disturbance from mechanized equipment. However, the effectiveness of prescribed fire hinges on its ability to selectively remove undesired trees. Knowledge of the largest trees that fires can top-kill could aid restoration planning for identifying sites amenable to fire management, versus sites where trees are likely too large for fire to be effective.

In eastern North America, one of the most extensive restoration goals is reestablishing open-structured oak ecosystems, including a continuum of habitat from oak savanna to open forests maintained through fire (Dey and Hartman 2005). During the last century, non-oak tree species such as *Acer rubrum* (red maple) have formed dense understories below oak canopies due to the cessation of fires ignited by Native Americans and early Euro-American settlers, the fragmentation of landscape fuel continuity, fire suppression, and the alteration of fuel types. Small stems of encroaching non-oak species are generally intolerant to fire, but their resistance increases with size (Hruska and Ebinger 1995). Moreover, in open sites during fire-free periods, high densities of oaks can

Figure 1. Examples of burn sites in forest (left) and oak savanna (right) in Oak Openings Preserve, northwestern Ohio, USA. The center foreground around the measuring tape in the left photo shows top killed and resprouting *Acer rubrum* **trees that were < 13 cm in diameter at 1.4 m (DBH). The larger tree in the left foreground is a 32 cm DBH** *Quercus velutina.* **The photo on the right shows top killed and resprouting small** *Q. velutina* **(< 3 cm DBH), while** *Q. velutina* **ranging from 4–9 cm DBH (center and left-center of the photo) had live canopies.** *Photos by S.R. Abella, August 2018, five months after April 2018 prescribed fires.*

attain sizes resistant to most fires, potentially undermining restoration goals of maintaining open structure (Cole et al. 1992). While there is a small, slowly growing body of research modeling post-fire survival based on tree size in eastern hardwoods (e.g., Loomis 1973, Regelbrugge and Smith 1994, Dey and Hartman 2005, Keyser et al. 2018), predicting the sizes of trees killable by restoration burns across the diversity of species, sites, and fire severities in this biome remains challenging.

Our objective was to develop models using stem diameter and trunk scorch to predict tree survival following restoration burns. We conducted the study in the 1497-ha Oak Openings Preserve, managed by the Metroparks of the Toledo Area, within the 40,000-ha Oak Openings region in northwestern Ohio, USA. Climate is temperate with warm, humid summers and cold winters. Summer precipitation (May through August), measured 10 km from the preserve, averaged 34 cm/year from 1955 through 2018 (Toledo Express Airport weather station; National Oceanic and Atmospheric Administration, Asheville, North Carolina). During 1817–1832 land surveys, the region including the preserve supported a fire-maintained mixture of prairie, oak savanna, and oak woodland (Brewer and Vankat 2004). Much of the region, now long without fire, supports closed-canopy forest with overstory *Quercus velutina* (black oak) and *Quercus alba* (white oak) and dense understories of non-oak trees (e.g., *A. rubrum, Sassafras albidum* [sassafras]). Non-oak trees were present but rare during the pre-Euro-American settlement land surveys. Based on the 1817–1832 reference conditions and a goal of stimulating groundlayer plant diversity, the ecological restoration objective in this study was to reestablish open-structured oak ecosystems with ≤ 50% canopy cover,

reduce the density of non-oak trees, and reinstate fire as a process maintaining oak ecosystems.

In August 2018, we sampled four sites that the Metroparks of the Toledo Area burned once in either April 2017 (two sites) or April 2018 (two sites). Our monitoring at 1–2 growing seasons post-fire corresponds with what Loomis (1973) recommended as the ideal period for assessing post-fire sapling survival in eastern hardwoods by including potential delayed mortality and time for resprouting. The sites were 7–18 ha in size and over 0.5 km apart, separated primarily by forest vegetation within the preserve. Two of the sites were closed-canopy forest with *Q. velutina-Q. alba* overstories and non-oak (mostly *A. rubrum* and *S. albidum*) understories (Figure 1). The other two sites were savanna and included areas of small *Q. velutina* and *Q. alba* that were 1–10 cm in diameter at 1.4 m (DBH). Small stems of these species were generally absent from the forested sites. The prescribed fires at all sites were by ring-pattern ignition, including backing, flanking, and head fires. Flame lengths were typically < 1 m. At the time of ignition, relative humidity ranged from 32–46% among fires and wind speeds from 1–18 km/hour.

To quantify post-fire tree survival, we followed the National Park Service (2003) fire effects monitoring protocol using 20 × 50 m (0.1-ha) plots. We randomly located three plots in each of the two forested sites and one plot (owing to the smaller area containing trees) in each savanna site within patches containing small *Q. velutina* or *Q. alba*. For each tree ≥ 1 cm DBH on plots, we recorded the species, DBH, maximum scorch height on the trunk (height of visible scorch measured to the nearest 0.1 m), and the percent surface area of the trunk scorched from the ground up to 1 m. For multi-stem trees splitting below 1 m,
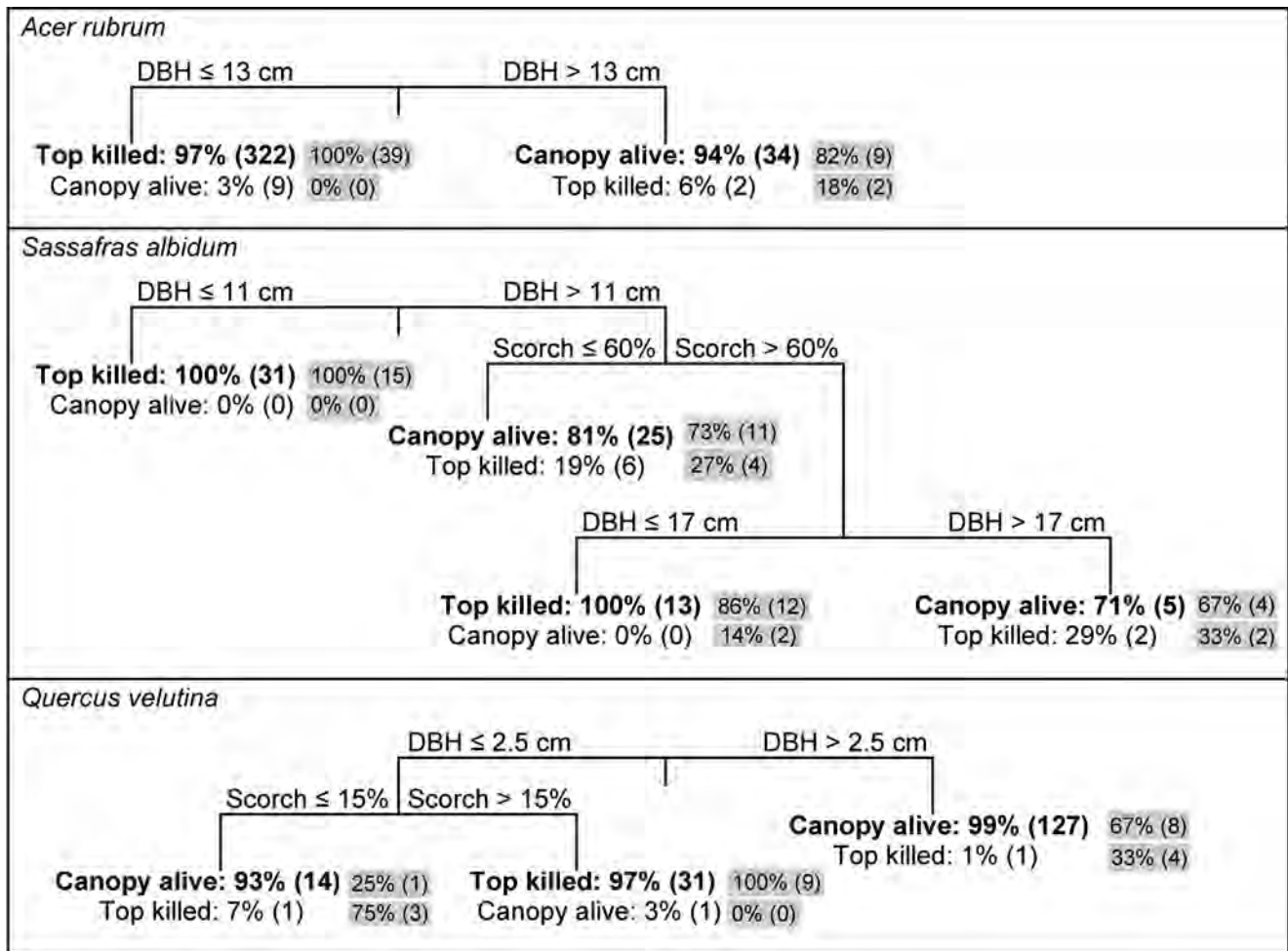
Figure 2. Classification tree models predicting the post-fire status (either top killed canopy plus basal resprouting or live canopy) of three tree species as a function of diameter at 1.4 m (DBH) and percent of trunk scorched from the ground to 1 m in oak ecosystems of Oak Openings Preserve, northwestern Ohio, USA. These models can be read as dichotomous keys. The terminal nodes provide the predicted status in bold with percentages of trees and the number of trees in parentheses. Validation data are shown in gray boxes. For example, 97% of *Acer rubrum* ≤ 13 cm DBH in the model-construction data were top killed after fire. All 39 validation stems of this size were also top killed, supporting the reproducibility of the model. Kappa statistics for the models were as follows: *A. rubrum*, 0.84; *Sassafras albidum*, 0.68; and *Quercus velutina*, 0.88. A model improving upon using simply the observed values could not be developed for *Quercus alba* (Kappa statistic = –0.02). The Kappa statistic is a measure of agreement between predicted and observed values after accounting for agreement expected by chance. The statistic ranges from –1 to 1, with negative values indicating model agreement worse than expected by chance, 0 indicating agreement no better than expected by chance, and 1 indicating perfect agreement.

we measured each stem as a separate tree. We categorized the status of trees as either dead (top killed with no live canopy and no basal resprouting), top killed with basal resprouting, or live canopy.

To model the status of trees separately by species as a function of DBH and scorch variables, we used classification trees implemented in the software Weka 3.8 (University of Waikato, Hamilton, New Zealand). Classification trees partition data into increasingly homogenous subsets and predict categorical outcomes (in our study, one of the three post-fire categories of tree status) using explanatory variables. For these models for each species, we combined data from all fires and plots because the percentage of

trees among categories varied little among plots and fires. For example, the percentage of *A. rubrum* trees 1–13 cm DBH that were top killed minimally varied from 91–97% among fires. Because nearly all (98–100%) top killed trees among species resprouted (i.e. trees completely killed were virtually absent), we excluded the 11 trees (1.6% of 706 trees) that were completely dead and simplified models to predict top killed plus resprouting versus not top killed. This resulted in a total of 356 *A. rubrum*, 74 *S. albidum*, 172 *Q. velutina*, and 93 *Q. alba* live trees on plots and all were used for modeling. To limit overfitting, we set five as the minimum number of observations for a terminal node.

To assess model reproducibility, we collected a 125-tree validation data set including the same variables as were recorded for trees on plots. We obtained the validation data by randomly selecting a south-north transect line (which did not overlap with plots) through each burn that we walked and measured trees within 2 m of the line. We continued until 25 trees were measured per fire for *A. rubrum* and *S. albidum*. A total of 25 *Q. velutina* validation trees were measured in the two savanna sites.

We developed models that predicted post-fire status better than naïve models (the observed percentages of trees by status category) for three of the four species (Figure 2). DBH drove post-fire status for *A. rubrum*, with 13 cm being a threshold. Over 97% of *A. rubrum* trees with DBH ≤ 13 cm were top killed and resprouting. In contrast, less than 6% of *A. rubrum* larger than 13 cm DBH were top killed. The model was robust under validation, with 96% prediction accuracy for the 50 *A. rubrum* validation trees.

For *S. albidum*, both DBH and the percentage of trunk scorch were important to post-fire status. All 46 *S. albidum* trees ≤ 11 cm DBH in the model development and validation data sets were top killed and resprouting. For trees larger than 11 cm DBH, most survived if trunk scorch did not exceed 60% from the ground to 1 m up the trunk. If scorch exceeded 60%, a 17-cm DBH cutoff apparently regulated canopy survival.

Small *Q. velutina* trees avoided top kill better than the other species. Over 99% (127 of 128) of *Q. velutina* larger than 2.5 cm DBH had live canopies in the modeled data. The model was likely overfit, however, as only 8 of 12 trees (67%) of this size were correctly classified in the validation data. If the model threshold was increased to 4 cm DBH for canopy survival, validation accuracy increased to 92%. For small stems, a threshold of 15% trunk scorch was important to survival. Canopies could survive on stems as small as 1–2 cm DBH if trunk scorch did not exceed 15%.

With 84 of 93 (90%) *Q. alba* trees exhibiting canopy survival and the remainder top killed and resprouting, no model using DBH or scorch improved upon a naïve model.

Several functional traits related to minimizing exposure of the cambium to heat may account for differential fire resistance among tree species (Harmon 1984). These traits include bark thickness, bark and wood density affecting heat transfer, thermal conductance, and concentrations of flammable chemicals (Hengst and Dawson 1994). Small *A. rubrum* have among the thinnest bark of eastern hardwood species. Using Harmon's (1984) equations in the Great Smoky Mountains, for example, a 13 cm DBH *A. rubrum* has bark 0.27 cm thick. A *Q. velutina* of the same size has bark 3× thicker. Although bark thickness is similar for *S. albidum* and *Q. velutina*, *S. albidum* bark is more prominently ridged and may contain more volatile chemicals (Rowe and Conner 1979). These traits could account for why *S. albidum* exhibited greater trunk scorch than comparably sized trees of other species and why its

canopy survival, even for large-DBH trees, was variable and linked with percentage scorch.

Our results might have varied given different sets of contingencies. Precipitation from May through August was close to the 34-cm long-term average for this period in 2017 (104%) and 2018 (115%). Resprout percentages could have been lower and the number of trees killed outright higher under drier conditions, but the high resprout percentage (98.4%) we found seems typical. For example, Perala (1974) similarly found a 99% resprout percentage for *A. rubrum* after prescribed fire in Minnesota. It is possible that relaxing burn prescriptions to achieve greater fire severity could expand the size range of trees killed. This strategy, though, is not always desirable under constraints on burning in today's landscape. Its potential effectiveness is also unclear, given the available fuels and that thick-barked, large trees may resist all but the most severe fires. Multiple, low-severity fires over a period of years, if sufficiently frequent, have limited formation of sapling layers in upland oak ecosystems, but often cannot top-kill larger stems still alive after the initial burn (Haney et al. 2008, Hutchinson et al. 2012). Our data suggest that low-severity restoration burns can top-kill stems up to 13 cm DBH for *A. rubrum*, 11 cm DBH for *S. albidum* unless appreciable trunk scorch occurs, and about 4 cm DBH for *Q. velutina*.

Acknowledgments

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Spekboom (*Portulacaria afra)* Planting in Degraded Thickets Improves Soil Properties and Vegetation Diversity ◕

Bryce Panter (Department of Environmental Science, Rhodes University, Grahamstown 6140, South Africa) and Sheunesu Ruwanza (corresponding author: Department of Environmental Science and Centre for Invasion Biology, Rhodes University, Grahamstown 6140, South Africa, ruwanza@yahoo.com)

The South African thicket biome is dominated by fragmented dense clumps of spiny shrublands (Cowling 1984, Vlok et al. 2003), which can support game farming, ecotourism, and firewood for local communities. However, substantial browsing by domestic animals, mostly goats and sheep, has transformed the thicket biome, leading to soil and vegetation degradation (Mills and Fey 2004). The problem is so severe that an estimated 46% of the naturally occurring Spekboom Thicket vegetation alone has been heavily

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degraded by domestic herbivores (Lloyd et al. 2002). In recognition of the problem, the South African government initiated the Subtropical Thicket Restoration Project (van der Vyver et al. 2013), whose dual mandate is to ecologically restore degraded thickets and use the initiative to create employment. The project identified *Portulacaria afra* (spekboom) as the plant that has the potential to restore these degraded thickets (Mills et al. 2007, Sigwela et al. 2009).

Spekboom is a succulent tree that reproduces vegetatively and establishes easily after transplant from cuttings. It has the potential to shade soils, return organic matter, and attract seed dispersers (Mills and Cowling 2010), facilitating soil and vegetation recovery after its introduction. Previous studies that have examined the efficacy of spekboom planting for restoration purposes have shown that spekboom introduction improves soil properties, especially carbon (Mills and Cowling 2010, van der Vyver et al. 2013), a result of spekboom's ability to alter litter composition and decomposition rate. Changes in soil properties can facilitate gemination and establishment of native plants underneath spekboom, suggesting that spekboom may function as a nurse plant in ecological restoration (Rens et al. 2008). To our knowledge no study has monitored both soil (physical and chemical properties) and vegetation (plant diversity) recovery following spekboom planting. We examined whether spekboom planting facilitates both soil and vegetation recovery by comparing soil physicochemical properties and vegetation diversity in natural, spekboom-planted, and degraded sites in Copper Moon Game Reserve, located in Eastern Cape, South Africa.

Three adjacent natural, spekboom planted, and degraded sites (approximately 50 m apart) were identified at Copper Moon Game Reserve (33°12′59.65″ S, 25°31′06.31″ E). Vegetation in the area is an ecotone between Albany Spekboom Thicket and Saltaire Karroid Thicket. Soils are sandy and derived from the underlying Cape and Karoo shale. Mean annual rainfall is approximately 409 mm and mainly falls in summer. Temperature ranges from an average 8°C in winter to an average 30°C in summer (Vlok et al. 2003).

The spekboom-planted site, which used to be a grazing area, was planted in 2005 with truncheons (woody cuttings) collected from the fenced natural site. Information regarding the impact of grazing in the spekboom-planted site is limited, however Google Earth images suggest that the site looked similar to the degraded site prior to planting. The spekboom-planted site was a trial site measuring approximately 50 × 50 m and is fenced to prevent animal browsing. The truncheons were planted at a depth of approximately 15 cm, at 1.5-m row spacing and 1-m plant spacing. The natural site is dominated by native thicket vegetation, *Acacia karroo*, *Portulacaria afra*, *Boscia oleoides,* and *Crassula capitella* (Mucina and Rutherford 2006). The degraded site, which is open to animal grazing, is dominated by grasses and a few scattered trees and shrubs. The sites are on a gentle north-east facing slope of