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The effects of post-wildfire salvage logging on plant reproductive success and pollination in *Symphoricarpos albus*, a fire-tolerant shrub

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ABSTRACT

Post-wildfire salvage logging is an increasingly used land management tool with poorly understood ecological consequences for understory flowering plants and their interactions with pollinators. Understanding these consequences of salvage logging is important because an essential aspect of post-wildfire forest succession involves pollination and plant reproduction. For snowberry (*Symphoricarpos albus*), an ecologically-important and fire-tolerant shrub, we tested the long-term effects of post-wildfire logging on plant reproduction and pollen limitation using a supplemental-pollen experiment coupled with pollinator observations of *S. albus* and of potential co-flowering competitors of *S. albus*. Nearly a quarter century after these disturbances, we found no effects of post-wildfire logging on the reproduction of naturally-pollinated plants. The reproduction of some *S. albus* individuals were pollen limited, but only in unlogged areas, suggesting that plants in unlogged areas have higher potential reproduction compared to those logged areas but are unable to achieve this higher level of reproduction due to lack of pollination. This pollen limitation of *S. albus* reproduction is consistent with the relatively high floral densities of potential competitors of *S. albus* and generally low pollinator visitation rates in unlogged areas. Together, these results suggest that legacies of post-wildfire logging may restrict the reproductive potential of this shrub for at least several decades after the logging is complete, but this restriction is likely due to altered abiotic conditions and not via lack of pollination.

1. Introduction

Forest disturbances, including wildfires, are increasing in frequency and severity (e.g., Westerling et al., 2006). As a result, management options like post-wildfire salvage logging are likely to become more common (e.g., Lindenmayer et al., 2008). Wildfire and post-wildfire logging influence biotic and abiotic conditions that can affect understory plant reproductive success through a variety of pathways, both positively and negatively, in previously forested landscapes. For instance, given that the majority of flowering plant species require insect pollinators for reproduction (e.g., Potts et al., 2010) and pollen limitation of plant reproduction is widespread (e.g., Knight et al., 2005), wildfire and post-wildfire logging could indirectly influence levels of pollen limitation through changes in pollinator communities. Wildfires create early successional habitat (Lindenmayer & Noss, 2006; Swanson et al., 2011) that generally benefits forb and pollinator abundance and diversity (Potts et al., 2003; Romey et al., 2007; Grundel et al., 2010; Pengelly & Cartar, 2010; Jackson et al., 2014), and post-wildfire logging can enhance community-wide pollinator abundance and diversity even further (Heil and Burkle, 2018). Thus, forbs in burned landscapes, and especially in post-wildfire logged areas, may have low levels of pollen limitation of reproduction.

The effects of wildfire and post-wildfire logging on pollination services to a focal plant species may also be strongly influenced by the identity and abundance of co-flowering species in the surrounding community. If plant species with overlapping flowering phenologies also share pollinators (hereafter, “potential competitors”), the possibility arises for these plants to compete with each other for pollinators or to facilitate their pollination by attracting more pollinators to the area than would have been possible by each species alone (e.g., Rathcke, 1983). Therefore, because wildfire and post-wildfire logging alter both floral and pollinator communities, including potential floral competitors and pollinator visitation rates (Heil and Burkle, 2018), investigating these effects with respect to focal plants of interest will aid in the understanding of pathways by which pollination services and reproduction are affected.

Wildfire and post-wildfire logging may also influence the availability of abiotic resources important for understory plant reproduction (Potts et al., 2003; Lindenmayer et al., 2008). For example, wildfires augment the availability of sunlight and soil nutrients (i.e., nitrogen,

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phosphorus, and potassium) that are important for plant growth and seed development (Rundel, 1981; Kutiel & Naveh, 1987; le Maitre & Midgley, 1992; Potts et al., 2001). Additionally, post-wildfire logging can compact and erode soil, which restricts plant growth (Lindenmayer & Noss, 2006), and can reduce coarse woody debris (CWD) (Hopkins et al., 2014), which suppresses forb habitat (Tinker & Knight, 2000; Vázquez et al., 2011), is an important nesting resource for cavity-nesting bees (Harmon & Sexton, 1996; Moretti et al., 2009; Williams et al., 2010; Mateos et al., 2011; Vázquez et al., 2011), and has a key role in long-term ecosystem nutrient cycling (Tinker & Knight, 2000). Post-wildfire logging can also further reduce forest canopy cover (e.g., Hernández-Hernández et al., 2017; Peterson and Leach, 2008), which can increase sunlight for understory plant growth (Perkins et al., 1988; McIver & Starr, 2000; Morissette et al., 2002; Lindenmayer et al., 2008) and, in turn, influence other abiotic conditions, like reduce soil moisture (Balisky and Burton, 1995). Thus, there are complex—and possibly interacting—factors at play in post-wildfire landscapes that have the potential to strongly affect plant reproductive success.

Despite the potential of these disturbances to influence pollination services and plant reproductive success, the majority of post-wildfire land management options like salvage logging are focused on tree regrowth and regeneration without considering ecological consequences for biodiversity more broadly (Belote and Aplet, 2014). In particular, the implications of post-wildfire logging for plant-pollinator interactions, pollination services, and the reproductive success of flowering plants have largely been ignored. Investigating the magnitude of pollen limitation of plant reproductive success can provide insight into the mechanisms by which these disturbances influence plant populations.

To our knowledge, only one previous study has examined the effect of the combination of fire and logging on plant reproductive success. In this case, prescribed fire and tree retention logging (i.e., retaining single trees or forest patches at the time of harvest) enhanced *Vaccinium vitis-idaea* (lingonberry) flowering, whereas V*accinium myrtillus* (bilberry) reproduction was higher in areas that were unlogged, regardless of fire (Rodriguez and Kouki, 2015). Although both bilberry and lingonberry species require insects for pollination, their reproductive success was not related to bee abundance and diversity, indicating that reproduction was likely not pollen limited, regardless of disturbance levels (Rodriguez & Kouki, 2015). To begin to build our understanding of the effects of post-wildfire management on pollination and understory plant reproduction, we focused on *Symphoricarpos albus* (snowberry), a widespread, self-incompatible, bee-pollinated, fire-tolerant, and ecologically important shrub species (e.g., important browse for wildlife and habitat and food for birds and mammals) (reviewed in McWilliams, 2000).

In a mixed-conifer system in Montana USA, we investigated (1) how post-wildfire logging influenced reproductive success and pollen limitation in *Symphoricarpos albus* using a pollen supplementation experiment in both logged and unlogged areas of a wildfire. To better understand patterns in *S. albus* reproduction and pollen limitation, we also studied (2) the floral densities of *S. albus* and the visitation rates, species richness, and composition of floral visitors to *S. albus,* (3) the floral densities of and visitation rates to the other plant species that co-flowered and shared floral visitors with *S. albus* (i.e., potential competitors for pollinators), and (4) several environmental conditions (i.e., coarse woody debris and canopy cover) that may be influenced by post-wildfire logging and important for plant reproductive success in logged and unlogged areas. We chose to perform this study in an area that experienced wildfire and post-wildfire logging nearly a quarter century ago in order to assess any long-term consequences of these disturbances for plant reproduction. In particular, we previously found no effects of post-wildfire logging on local abundances or on species richness of bees from local to landscape scales compared to those of unlogged areas within the wildfire perimeter (Heil and Burkle, 2018), though floral visitors specific to *S. albus* and its potential competitors have not been investigated. Thus, we expected any amount of pollen limitation of *S. albus* reproduction to be similar between logged and unlogged areas and that any differences in reproductive success between logged and unlogged areas were likely due to long-term effects of these disturbances on abiotic factors important for snowberry reproduction. Alternatively, given that we previously found differences in bee community composition between post-wildfire logged and unlogged areas (Heil and Burkle, 2018), if the presence of pollinators specific to *S. albus* were affected by logging, there could be subsequent effects on reproductive success and pollen limitation. This field experiment is one of few studies that extends the investigation of effects of forest management practices on flowering plant and pollinator communities to include understory plant reproductive success and potential mechanisms driving those effects.

2. Methods

2.1. Study system

This study was conducted in post-wildfire logged and unlogged areas within the Thompson Creek wildfire perimeter (burned in 1991, 2824 ha) in the Gallatin National Forest near Pray, Montana, USA (45°14′N, 110°33′W). This region is characterized by montane mixed-conifer forest composed of *Pseudotsuga menziesii*, *Pinus contorta*, *Picea engelmanii*, and *Abies lasiocarpa*. Post-wildfire salvage logging (in these cases, patch cutting of dead trees) occurred in 1993 in six stands of this wildfire that burned with mixed-severity (data and locations acquired from U.S. Forest Service, though the exact forest structure of these areas pre-fire or immediately post-fire is unknown). This logging removed on average 0.035 trees per m^2 (range: 0.0020 to 0.084 trees per m^2; median: 0.016 trees per m^2), based on our observations of stumps (diameter range: 10 cm to over 30 cm) at logged sites. Heil and Burkle (2018) and Burkle et al. (2015) contain detailed information on site selection and characteristics. In short, wildfire severity data from the Monitoring Trends in Burn Severity program (Eidenshink et al., 2007; MTBS.gov) were used to select four similar 15 ha. areas (i.e., 2 logged and 2 unlogged areas with similar elevation, slope, and aspect; Table S1) that each burned with mixed-severity wildfire, and nine sites within each of these areas were randomly selected using a stratified design with the GRTS package in R to prevent spatial clustering and to maintain equivalent fire severities of sites between logged and unlogged areas (Burkle et al., 2015; Heil and Burkle, 2018). Thus, although the selection of stands to log was likely not originally random, we selected unlogged areas as similar as possible for comparison. Thirty-three of these sites (17 logged and 16 unlogged) contained *Symphoricarpos albus*, and a subset (4 logged and 4 unlogged) of the 33 sites were randomly selected for the pollen supplementation experiment (see below). While the closest sites were ca. 100 m apart (i.e., close enough for large-bodied pollinators to fly between them), we observed no spatial autocorrelation of flowers or bees across sites within any of our selected areas (Heil and Burkle, 2018).

Symphoricarpos albus is a small-statured shrub with few, large flowers, and it has two ovules with the capacity to produce a maximum of two seeds. Individuals of *S. albus* are abundant and widespread species throughout this study system. We chose *S. albus* plants of similar size (i.e., 1–2 feet tall and 15–60 flowers) in order to reduce the contribution of size variability in our measurements of reproductive success. Further, to limit potential variability in local conditions that can influence plant reproduction (e.g., sunlight, soil nutrients, potential mates), we selected plants that were located within 25 m of each other at each site. These are standard methods for plant selection in supplemental pollination experiments (e.g., Fazzino et al., 2011; Walsh et al., 2014).

2.2. Pollination methods and plant reproduction

To determine the degree to which *Symphoricarpos albus* reproduction was pollen limited in post-wildfire logged versus unlogged areas,