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Conserving Pollinators in North American Forests: A Review

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ABSTRACT: Bees and butterflies generally favor open forest habitats regardless of forest type, geographic region, or methods used to create these habitats. Dense shrub layers of native or nonnative species beneath forest canopies negatively impact herbaceous plant cover and diversity, and pollinators. The presence of nonnative flowers as a source of nectar, pollen, or larval food can have positive or negative effects on pollinators depending on the situation, but in cases where the nonnatives exclude native plants, the results are almost always negative. Roads and roadside corridors offer an opportunity to increase open, pollinator-friendly habitat even in dense forests by thinning the adjacent forest, mowing at appropriate times, and converting to native herbaceous plant communities where nonnative species have been planted or have invaded. Efforts to improve forest conditions for pollinators should consider the needs of specialist species and vulnerable species with small scattered populations. Conservation of bees and butterflies, as well as other pollinating species, in forested areas is important for most forest plant species, and forests may serve as reservoirs of pollinators for recolonization of surrounding habitats.

Index terms: fire, forest management, invasive species, prescribed burning, verges

INTRODUCTION

Nearly 90% of the world's flowering plants rely on pollination by animals (Ollerton et al. 2011), and of those, bees are considered to be the primary group responsible (Winfree et al. 2011). Native pollinators provide most of the pollination in forests and grasslands of the United States (Mader et al. 2011), where many wild forb and tree species require their services. Additionally, native pollinators from these natural areas contribute substantially to the pollination of adjacent crops, often without the need for managed honey bees (Garibaldi et al. 2013; Morandin and Kremen 2013). The consensus among experts is that pollinators are in decline, and publication of "The Forgotten Pollinators" (Buchmann and Nabhan 1996) raised awareness of the problem. Bees, flies, and butterflies are considered the best native pollinators, and the United States alone has approximately 4000 species of bees (Moisset and Buchmann 2011) and 575 species of butterflies (NABA 2016). Although evidence is growing that many pollinators and their functions are declining (Potts et al. 2010; Burkle et al. 2013), not enough information is available to assess the conservation status of most species (National Research Council 2007). Nevertheless, the Xerces Society lists 31 species of bees (Xerces Society 2016a) and 58 species of butterflies (Xerces Society 2016b) in North America that are vulnerable, imperiled, critically imperiled, or even possibly extinct. Of the butterflies, 24 are listed as federally endangered. Some evidence indicates that while at least one of the 46 bumble bee species known to occur in North America has gone extinct, half may

now be at risk (Grixti et al. 2009; Williams et al. 2014). Other bee genera have received less attention, despite accounting for >95% of known species (Bartomeus et al. 2013) and playing essential roles as pollinators of most native tree and forb species in our forests. A study using historical data sets found a 50% reduction in bee species over a 120-year period, resulting in major changes to the plant-pollinator network (Burkle et al. 2013). This underscores the paucity of information on the status of most native bees in North America (Cane and Tepedino 2001). The many factors implicated in the declines of bee and butterfly populations include habitat fragmentation, nonnative plants, pathogens, nonnative insects, bio-control agents, overgrazing by white-tailed deer, herbicides and insecticides, fire (too frequent), shrub encroachment due to fire suppression, right-of-way management, harvesting of wild plants, logging of mature forests, and losses of open forests and forest clearings (van Swaay et al. 2006; Miller and Hammond 2007; Cameron et al. 2011; Schweitzer et al. 2011; Szabo et al. 2012; Fartmann et al., 2013).

Forests currently cover more than one third of the land area in North America (World Bank 2016) and provide important resources for many pollinators. In addition to supporting forest specialists (Winfree et al. 2007), a large number of generalists are known to move readily between forests, agricultural fields, and other land-use types (Blitzer et al. 2012; Monasterolo et al. 2015). Some forest conditions favor pollinators more than others and there is a growing interest in optimizing management practices for pollinator conservation.

Over the past century, forests of the United States have undergone dramatic changes. Forests were altered by extensive logging and repeated wildfires in the late 19th and early 20th century (Ahren 1929, 1933). Bohart (1971) suggested that this forest clearing, at least in eastern North America, resulted in higher bee populations than existed prior to European arrival. Support for this idea comes from more recent work by Winfree et al. (2007), who found a negative correlation between bee numbers and forest cover in the northeastern United States. Reforestation and fire exclusion to prevent wildfires were implemented over large areas to restore ecosystems degraded by earlier logging and agricultural practices (Lilliard 1947; Clark 1984; Williams 1989; Stanturf et al. 2002; Barnett 2014). These practices, which promote high planting densities, increased tree growth, and continued fire exclusion, have resulted in unnaturally dense stands with closed canopies and dense shrub layers beneath (Carroll et al. 2002; Schwilk et al. 2009).

As part of the “National Strategy to Promote the Health of Honey Bees and Other Pollinators,” the federal government released “Pollinator-Friendly Best Management Practices for Federal Lands” (USDA 2016). These management practices were developed from the most current scientific research; however, they emphasize the need for updates as new evidence becomes available. Thus, as the practices are implemented and evaluated, it is expected that they will be revised to reflect new findings. The primary goal of this article is to review what is currently known about conserving pollinators in forested regions of North America, with a focus on how pollinators are impacted by common forest management practices, roadside and powerline corridors, and nonnative plant species. The objectives of pollinator conservation can range from maintaining the greatest number of species possible, maximizing an ecosystem service, or sustaining viable populations of endangered species. It is important to recognize that no single approach can be expected to benefit every species of pollinator, given differences in host and habitat requirements, nesting behavior, and other life history characteristics. While

we seek to identify general patterns based on existing evidence, we necessarily stop short of making specific management recommendations. The optimal management plan for a particular location will depend on a variety of local factors, including conservation priorities, forest type, land-use history, etc. Using this article as a starting point, managers are encouraged to consult local experts or delve deeper into the literature most relevant to their focal organism(s) and system of interest. This review is limited to pollinating insects, with bees and butterflies dominating the current literature.

Aside from sharing a need for floral resources, the ecology of butterflies differs from that of bees in some important ways. For example, bees require nectar and pollen throughout their life cycle, while butterflies only utilize nectar as adults. Most larval lepidopterans (butterflies and moths) are leaf-feeders that do not require any parental provisioning of floral resources. Bees, by contrast, must collect sufficient pollen and nectar to support their developing brood as well as their own energy needs. While most bee species develop in underground nests or in other relatively protected places, butterfly caterpillars are exposed on their host plants where they may be more sensitive than most bees to management tools like prescribed fire or mowing. Conservation efforts aimed at both butterflies and bees should keep these differences in mind (Alanen et al. 2011).

In this article, we consider a forest condition or management practice to generally benefit pollinators when it results in a measureable increase in the number of species and/or abundance of bees and/or butterflies. Despite our focus on community responses, we recognize that conservation goals will vary among study systems and may sometimes be limited to particular species of concern. Moreover, it should be noted that abundance alone may not always be the best metric with which to gauge an impact. Reproductive performance, for instance, can sometimes be more meaningful (Palladini and Maron 2014). Finally, although our focus is centered on conserving pollinators in North American forests (excluding Mexico), key references

from other Northern-hemisphere temperate forests are also considered. This review is organized into three main sections. First we discuss the effects of forest management on pollinators, with a focus on thinning/gap creation and prescribed fire. Next, we consider the value of roadside and powerline corridors and how best to manage these avenues of open habitat. Finally, we review the variable effects of nonnative species on bee and butterfly communities before ending with some concluding thoughts.

FOREST MANAGEMENT

As a group, pollinators are generally more abundant in open forests relative to closed forests (Fye 1972), although information on forest-obligate species remains limited (Winfree 2010). Temperature and the amount of light within a habitat are the most important abiotic factors affecting foraging by bees (Herrera 1997; Polatto et al. 2014), and soil-nesting bees seem to benefit from patchy ground with ample sun exposure (Vaughan et al. 2015). With some important exceptions, butterflies are generally more numerous in nonforested habitats than in forests (Schmitt 2003; Miller and Hammond 2007; Schweitzer et al. 2011), and, like bees, benefit from more open forest conditions. In a study of successional stages following coppicing (i.e., harvesting young stems sprouting from the roots of previously-cut trees) in France, for instance, higher butterfly species richness and density occurred in relatively open early to mid-successional stages compared to more closed canopy late-successional stages (Fartmann et al. 2013). This pattern held true for resident and migratory species, as well as threatened species, and was attributed to warmer conditions and greater availability of nectar and larval host plants in the more open forests. Likewise, Benes et al. (2006) showed that the transition from relatively open forests to closed-canopy forests brought about by abandonment of coppicing in the Czech Republic negatively impacted butterflies. More recently, Hanula et al. (2015) examined seven forest types typical of the Piedmont region of the southern United States and found that lower leaf area index (i.e., more light) resulting from lower

stand densities (basal area) was associated with greater numbers and species richness of bees. The highest species richness and bee abundance occurred in mature pine forests with open canopies and little shrub cover, which are created and maintained by regular thinning and frequent prescribed burning (Figure 1). High species richness and bee abundance also occurred in recently cleared forests. In contrast, mature pine forests with similar canopy cover, but a dense shrub layer, had fewer bees and fewer species because of the shading provided by the shrubs (Figure 1). Forests that provided the best long-term pollinator habitat had high herbaceous ground cover and were being managed as foraging habitat for red-cockaded woodpeckers (*Leuconotopicus borealis* del Hoyo and Collar), an endangered species.

Although traditionally used to achieve different objectives, several widely used forest management techniques, such as thinning, or prescribed fire (see below), result in more open forests and have the potential to benefit pollinator communities. Encouragingly, this suggests improving forest conditions for pollinators may be consistent with other management goals.

Thinning and Gap Creation

Forests have traditionally been thinned (i.e., the selective removal of trees to reduce tree density) to improve tree vigor, which results in increased growth rates and a lower incidence of pest outbreaks. By making forests more open, however, thinning may also result in benefits to pollinators. Similarly, certain management approaches (e.g.,

group-selection harvests) create gaps in the forest canopy, resulting in open areas that may also benefit pollinators. Indeed, both thinning and gap creation have consistently been shown to benefit pollinators in a variety of forest types across North America. For example, Romey et al. (2007) examined the effects of small scale (approximately 2 ha) tree removals from a northern hardwood forest in New York resulting in 30, 60, and 100% overstory tree removal and found the greater the forest cover removed, the higher the bee abundance and diversity in the openings. All three treatments increased bee community attributes over untreated controls. In the pinyon-juniper woodlands of the southwestern United States, Kleintjes et al. (2004) studied the effect of thinning the overstory canopy by 70% followed by mulching of the



Figure 1. Upper left is upland hardwood forest with a dense shrub layer consisting of native species; to its right, the same forest after the shrub layer was cut and subsequently burned (Photos by T. Waldrop) creating improved pollinator habitat for both bees and butterflies (Campbell et al. 2007). Lower left is a mature loblolly pine stand with a dense midstory of shrubs and small trees that was poor habitat for bees; lower right is a similar stand that has been frequently burned and provides good habitat for bees (Hanula et al. 2015).

logging residue and found the treatment increased both forb and grass cover, and butterfly species richness and abundance. Also working in the southwestern United States and finding a similar result, Waltz and Covington (2004) reported increased butterfly richness and abundance in thinned and burned ponderosa pine forests compared to untreated control stands. In that study, the researchers saw few differences in plant community composition between the two treatments, suggesting that butterflies may be responding to the sunnier conditions in the thinned forest treatment. In Japan, Taki et al. (2010) found thinning to result in higher numbers of both bees and butterflies in *Cryptomeria* plantations. Proctor et al. (2012) studied group selection harvesting in northern hardwood forests of Ontario, Canada, and found gaps had more bees than intact forest and the two habitats had different bee community composition but similar numbers of bee species. In the Czech Republic, Slamova et al. (2013) found that a butterfly species of conservation concern, *Erebia aethiops* Esper, is threatened by canopy closure. Interestingly, males were more numerous in sparsely wooded areas, whereas female densities were highest in grassland patches, indicating the need for both habitat types. In Germany, Hermann and Steiner (2000) argued that the light-demanding forest butterfly species *Satyrium ilicium* Esper is facing extinction due to the abandonment of practices such as coppicing that helped maintain open forest conditions.

The interface between fields and forests is often abrupt and there is great interest in improving this transition zone to benefit pollinators. Korpela et al. (2015) compared pollinator communities in forest edges that had been partially cleared of trees to unmanipulated reference edges in an effort to understand the effects of this field-forest ecotone on pollinators in Finland. The treatments involved clear-cutting 5 m into the forest and thinning for an additional 20 m. Both treatments resulted in greater bumblebee abundance, total pollinator species richness, and abundance of butterfly habitat specialists relative to the reference. These effects were most apparent at the clear-cut edge than in the thinned areas, especially for bumblebee abundance, presumably

due to improved microclimate and greater floral resources in cleared areas. Floral resource availability appeared to be less crucial to butterflies than to bumblebees in the study, suggesting these insects respond more to open and warmer conditions. This may reflect the fact that bumblebees must collect enough nectar and pollen to support their brood, whereas butterflies only need enough nectar to fuel their own activities (Korpela et al. 2015).

Prescribed Fire

Prescribed (i.e., controlled) fires are widely used in forests to suppress the shrub-layer and reduce fuel loads, thus stimulating herbaceous vegetation and minimizing the risk of wildfires. Studies from a wide range of temperate forest types indicate that prescribed fire can be a highly effective tool in improving forest habitat for both bee and butterfly communities. In the southwestern United States, Nyoka (2010) compared treatments designed to reduce wildfire risk, which included thinning from below, prescribed burning, and thinning followed by prescribed burning. Only thinning plus burning resulted in higher numbers of bees as well as greater cover and species richness of flowering plants compared to untreated areas. Similar results were found for butterflies in ponderosa pine forests, where Waltz and Covington (2004) reported significantly greater numbers of species and individuals from thinned and burned stands compared to untreated controls. Huntzinger (2003) reported many times more butterfly species in burned forests compared to unburned forests at sites in Oregon and California. These results were attributed to higher total areas of sunlit patches in burned forests. Working in southern Appalachian hardwood forests, Campbell et al. (2007a) found similar results when they compared removal of a native understory shrub, which was the dominant component of the understory as a result of long-term fire exclusion, to prescribed burning and shrub removal followed by burning. Both butterfly and bee communities responded positively to the combined treatments, but not to the treatments individually. Examining the underlying reasons showed that the combined treatment resulted in hotter

prescribed fires that killed some of the overstory trees, essentially thinning the forest and reducing canopy cover. Wagner et al. (2003) stressed the need for prescribed fire, mechanical cutting, or a combination of both for maintaining the open-canopy shrubland barrens required by rare butterfly and moth species in northeastern US forests. Strahan et al. (2015) examined the plant community composition in ponderosa pine forests following thinning, prescribed burning, or both, and found that thinning plus burning provided the greatest benefit in restoring understory herbaceous plant communities.

Campbell (2005) found that flower-visiting Hymenoptera in general were more abundant in recently burned longleaf pine compared to undisturbed controls, while bees in the family Halictidae were more abundant in all disturbed plots, which included thin and burn, burn only, thin only, and herbicide treatment of an abundant native shrub layer followed by burning. Breland (2015) found an increase in bee richness the year immediately after prescribed fire in longleaf pine savannas compared to two years post burn. Conversely, Fultz (2005) examined the effects of even and group shelterwood treatments in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in Montana on flower-visiting insects and compared those to unlogged controls and open meadows. In her study, half of the group including even shelterwood treatment plots and all of the control plots, were burned in 2002 and 2003 during her second and third year of sampling. Burning had no effect on bee abundance or species richness, but open meadows and the two shelterwood treatments had higher numbers of individuals and species, and the unlogged old growth controls had the lowest, even though the controls had prescribed burns during the study.

Despite the many reports of positive effects of prescribed fire on pollinator communities, it should be mentioned that burning can also have negative effects, depending on the intensity and frequency of fire and the pollinator species involved. This is even true for species that depend on historically fire-maintained habitats, especially for species with severely restrict-

ed distributions. The endangered Karner blue butterfly (*Lycaeides melissa samuelis* Nabokov), for example, depends on oak barren/savanna habitats in the great lakes region of North America. Because fire plays a key role in maintaining the open forest conditions required by the Karner blue, fire suppression is one factor contributing to the species' decline (Shuey 1997). Efforts to maintain habitat for the butterfly through prescribed fire, however, must be planned carefully to prevent complete mortality of the remaining small, isolated populations of the species (Kwilosz and Knutson 1999). For conservation of butterfly species associated with pine barrens and other open habitats in the northern United States, some researchers have warned against burning too frequently and suggest that alternative management approaches (e.g., mowing) may be equally or more effective for certain species (Swengel 1998). Schweitzer et al. (2011) recognized the important role fire plays in maintaining habitat conditions in US forests, but they suggest caution in timing, spacing, and size of burns to ensure fire-free refugia nearby from which populations can rapidly recolonize recently burned areas. This is especially important in butterfly conservation, considering that the eggs, larvae, and pupae of many butterfly species are completely exposed on their host plants and are likely to suffer high mortality.

FOREST ROADS AND POWERLINE CORRIDORS

Open habitats are known to support diverse and abundant communities of pollinators like bees and butterflies (Hopwood 2008; Wojcik and Buchmann 2012). This means that forest roads and powerline corridors present opportunities to provide pollinator friendly habitat even in areas with dense forests (Figure 2), especially given that roadsides cover more than 4 million hectares in the United States (Forman et al. 2003). These two habitats tend to be managed differently from one another in that roadsides are often cleared much more frequently (typically at least once per year) than powerlines (approximately every 4+ y) (Russell et al. 2005). Russell et al. (2005) compared bee communities between powerlines characterized by dense scrub and neighboring grassy fields that were mowed annually in Maryland. Powerlines yielded more spatially rare species, more cavity nesting bees, and more parasitic bees than the mowed fields, suggesting that bees may benefit from less-frequent efforts to control vegetation in open habitats. More recently, Berg et al. (2011) compared butterfly communities among roadsides, powerline corridors, clear-cuts, and semi-natural pastures in Sweden. Significantly more butterfly individuals and species were collected in powerline habitat compared to the other habitats. The

researchers attributed this to the powerlines being less intensively managed than the other habitats (e.g., most seminatural pastures are continuously grazed by livestock throughout the season). Schweitzer et al. (2011) mentioned that many butterflies utilize powerline right-of-ways in the United States, including some very rare species. Research aimed at optimizing the timing and frequency of vegetation control, as well as understanding the effects of planting and maintaining native plant species in favor of exotics, is needed. Mowing such areas less frequently, and only during the dormant season, may help minimize negative impacts on butterflies (Valtonen et al. 2006; Schweitzer et al. 2011).

In addition to providing floral and larval host plant resources, roadside and powerline habitats also have the potential to benefit pollinators by providing corridors for movement (Fye 1972; Munguira and Thomas 1992; Hopwood 2008; Haddad et al. 2011; Skórka et al. 2013; Jackson et al. 2014). Most solitary bees have limited foraging distances (Gathman and Tscharrntke 2002; Zurbuchen et al. 2010), therefore roads and powerlines with adequate nesting habitat and forage could provide their complete habitat needs. The benefits of roads and powerlines as habitat corridors depend on the pollinator species. Corridors were beneficial for movement of most butterfly species between habitat patches but had no



Figure 2. A forest road with dense stands on both sides shading the road (left), making it less suitable for pollinators. Right photo is a similar road with wider edges and thinned stands, allowing in more light for plants and pollinators.

effect on movement of large-bodied carpenter bees (Haddad et al. 2003). Other bee species have not been studied. Berg et al. (2011) found butterfly species with limited dispersal abilities to be more abundant in powerlines than in roadsides, suggesting powerlines may provide more important dispersal corridors for these species. One advantage of powerlines relative to roads is the absence of vehicles, which might be a direct source of mortality (Wojcik and Buchmann 2012). Additionally, roads may be deterrents to movement of some pollinators (Bhattacharya et al. 2003; Franzén et al. 2009).

For butterflies, road mortality is directly related to the amount and speed of traffic (Munguira and Thomas 1992; McKenna et al. 2001; Ries et al. 2001; Rao et al. 2007; Skórka et al. 2013), so mortality on forest roads should be less than on busy highways. Forest roads are not without risks since butterflies are often seen “puddling” on them (authors’ pers. obs.) to obtain sodium or other nutrients (Boggs and Jackson 1991), which may increase their risk of mortality from cars. Puddling is predominately a male behavior (e.g., Collenette 1934; Molleman et al. 2005); therefore, the overall impact of road mortality on population levels may be less than expected. Despite some negative effects of roads on pollinators, the value of roadsides as habitat appears to greatly outweigh negative effects of movement across them (Munguira and Thomas 1992; Ries et al. 2001; Skórka et al. 2013).

Finally, like fire or mowing, grazing by livestock or wild ungulates can potentially benefit pollinators by helping to maintain open conditions, but overgrazing can be detrimental, and some grazers can be more harmful than others (Benes et al. 2006; Hatfield and LeBuhn 2007). Negative effects of grazing can include the elimination of food plants for caterpillars, reduction or elimination of nectar and pollen sources, destruction of ground nests of bees, and direct trampling of pollinators (Kearns et al. 1998). Sheep grazing affected pollinators of a rare plant in California in all these ways (Sudgen 1985). Likewise, overgrazing by cattle or elk along riparian areas can diminish or eliminate willow shrubs or trees

(Kolvalchik and Elmore 1991; Kay 1997), an important bee-pollinated plant in many areas (Ostaff et al. 2015). Overgrazing by whitetail deer is considered one of the most serious threats to forest butterflies in the eastern United States (Schweitzer et al. 2011). Heavy grazing can shift plant communities to less palatable and often exotic species (Vavra et al. 2007; Knight et al. 2009), with the potential to negatively impact pollinator communities.

Carter and Anderson (1987) proposed a design for improving forest roads for butterflies that would likely benefit bees and other pollinators as well. They suggested a series of 20 by 25-m forest cutouts along roads that would be maintained as open habitat by mowing. In addition, they suggested creating “corner glades” at road intersections by cutting the trees on each corner and maintaining the habitat as openings. Although the design of openings, their spacing, and the frequency and timing of mowing would need to be tailored by region and forest type, it is clear that roadsides managed to increase flowering plant abundance and diversity would benefit pollinators.

NONNATIVE PLANTS

As reviewed separately below, nonnative plant species may affect pollinator communities in two important ways: by introducing novel food resources and by altering native plant communities. The first of these can be further partitioned into floral and foliar resources.

Novel Food Resources

The findings from studies examining the impacts of native vs. nonnative floral resources on pollinator communities are mixed. While most suggest pollinators are favored by plant communities dominated by native species, some nonnative plant species appear to have positive or neutral effects. Williams et al. (2011) and Chrobok et al. (2013) found that, although pollinators use nonnative flowers, pollinator visitation is greater on native species. Bartomeus et al. (2008) studied two nonnative species with showy flow-

ers and found that one facilitated flower visitation to native plant species, while the other competed for pollinators. Tepedino et al. (2008) found that bee visitation to three species of invasive plants did not negatively affect visitation to co-flowering native species and suggested that the nonnative plants would increase the carrying capacity of the ecosystems for native, generalist bees. More recently, Salisbury et al. (2015) reported a greater abundance of total pollinators in garden plots planted with native and near-native plants compared to those planted with nonnative species. While these findings suggest gardens containing native plant species may provide optimal resources for pollinators, the researchers suggest certain late-flowering exotic plant species may benefit some bees by extending the flowering season.

Most studies addressing such questions have focused on the abundance of pollinators, but few have examined the effects of nonnative plants on their reproductive performance. This is an important distinction, as a higher abundance of bees may reflect a concentration of bees in resource-rich sites as opposed to actual population growth. To address this question, Palladini and Maron (2014) studied the survival and fecundity of the cavity nesting bee, *Osmia lignaria* Say, along a gradient in floral resource availability. They found the number of nests increased with native forb abundance and decreased with the number of nonnative forb species. Although fecundity increased with native forb species richness, offspring mortality caused by a parasite was higher in sites dominated by native forbs. Such findings support the view that animal-pollinated nonnative plants generally have a negative effect on pollinator communities (e.g., Traveset and Richardson 2006; Morales and Traveset 2009; Pyšek et al. 2011), but also underscore the variable responses of bee communities to the availability of nonnative plant pollen and nectar.

In addition to introducing novel floral resources, nonnative plants also represent a large potential resource for herbivorous insects, including lepidopteran caterpillars. Thirty-four and 21% of butterfly species in California and New Jersey, respectively, have been reported to oviposit, or feed

upon nonnative plant taxa (Graves and Shapiro 2003; Schweitzer et al. 2011). In some cases, nonnative plants appear to benefit certain butterfly species, resulting in expanded ranges and extended flight periods. Other butterfly species have been negatively impacted (Schweitzer et al. 2011). Some, for instance, are known to lay eggs on nonnative plants toxic to their larvae (Graves and Shapiro 2003; Morton et al. 2015), although most generalist caterpillar species avoid foliage from nonnative shrub species (Fickenscher et al. 2014).

Despite some beneficial effects, the net collective impact of having nonnative plants available as larval food resources appears to be strongly negative for butterfly communities. In a common garden experiment, for example, Burghardt et al. (2010) compared the abundance and species richness of caterpillars in plots planted with native species, nonnative congeners (species belonging to the same genus as the natives), or nonnative species with no close relatives in the study area. Fewer caterpillars were collected in plots planted with nonnative species. This was especially true when nonnative species were more distantly related to the native species in the study area. Specialist butterfly species were less common in plots planted with nonnative plant species. This observation is likely due to host plant fidelity and diet specialization in some Lepidoptera and the associated reliance of those species on defensive secondary compounds of their host plants. The limited value of nonnative plants to specialist species is important to recognize as these species are inherently of greater conservation concern than generalists (Hardy et al. 2007). Butterfly communities with a collectively greater degree of specialization, such as those of woodland habitats (Tudor et al. 2004; Ohwaki et al. 2007), may be particularly sensitive to invasion by nonnative plants.

Altering Native Plant Communities

Although the role of invasive plants as competitors for pollination services is not always clear, their role in displacing native plants and altering habitats is well established (Vilà et al. 2011). One of the most

widely studied invasive plants in North America is bush honeysuckles, *Lonicera* spp., and several studies provide clear evidence that these large shrubs reduce species richness, abundance, and growth of herbaceous and understory woody plants, alter soils, and affect tree growth (Hutchinson and Vankat 1997; Luken et al. 1997; Medley 1997; Gould and Gorchov 2000; Collier et al. 2002; Hartman and McCarthy 2004, 2007; Runkle et al. 2007; McKinney and Goodell 2010; Boyce 2015). Chinese privet (*Ligustrum sinense* Lour.), another invasive shrub, has similar impacts in southern riparian forests (Merriam and Feil 2002; Hanula et al. 2009; Greene and Blossey 2012; Hudson et al. 2013; Lobe et al. 2014). Invasive species impacts on native plant communities are not limited to shrubs. Communities invaded by Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), an annual grass common to eastern North America, impact plant communities in similar ways (Oswalt and Oswalt 2007; Judge et al. 2008; Adams and Engelhardt 2009; Beasley and McCarthy 2011), as does cheatgrass (*Bromus tectorum* L.) in the West (Mack 1981; Knapp 1996; Parkinson et al. 2013). These are just a few examples supporting the common observation that native plant diversity and abundance is reduced where invasive plants dominate.

The removal of invasive plants can be expected to benefit native plant communities, but few studies have investigated the effects of such restoration efforts on pollinator communities. McKinney and Goodell (2010) examined the effect of bush honeysuckle and its removal on pollination of a native plant beneath its canopy. Through a series of experiments, they demonstrated that shading by the shrub inhibited flower visitation, resulting in poor seed set beneath the shrub canopy. In a study started in 2005, removing Chinese privet from riparian forests increased bee abundance 10-fold and species richness 4-fold two years after removal when compared to heavily invaded forest (Hanula and Horn 2011b; Figure 3). Surprisingly, bee communities in privet removal plots were comparable to riparian forests with no history of privet invasion. Increased herbaceous plant cover, diversity, and

evenness were associated with bee communities in forest with privet removed and in previously uninvaded forest. Butterflies exhibited similar trends, although butterfly communities in forests where privet was removed were not similar to uninvaded forests after only two years (Hanula and Horn 2011a). However, the improvement in pollinator habitat was still evident five years after removal, despite establishment of Japanese stiltgrass in some plots, and both butterfly and bee communities were similar to the uninvaded forests (Hudson et al. 2013). A similar rapid recovery of pollinator communities occurred following removal of glossy buckthorn shrubs (*Rhamnus frangula* L.) from prairie fen wetlands in Michigan (Fielder et al. 2012). Like privet, removal of glossy buckthorn resulted in increased native plant cover and diversity within two years and an immediate increase in both bee and butterfly abundance and diversity. Clearly, the majority of studies have focused on examining the response of pollinator communities to plant invasions. By contrast, other studies have documented the impact of invasive plant removals on flower visitation to rare native plants. Baskett et al. (2011) removed invasive baby's breath (*Gypsophila paniculata* L.) and spotted knapweed (*Centaurea maculosa* L.) from a dunes habitat and reported increased flower visits to a rare plant in removal plots despite recovering more pollinators during sweep net surveys in invaded sites. In England, Carvalheiro et al. (2008) suggested that the removal of the alien invader *Cotoneaster horizontalis* Decne., could potentially result in a significant decline in ant populations, the primary pollinators of a rare plant, by reducing floral resource availability. They suggest assessing small scale removals to determine the effects on pollinators of rare plants, and where negative effects are observed, implementing staged removals to minimize them while still improving the overall conservation of the habitat.

Balancing Pollinator Conservation with Invasive Plant Control

Although beyond the scope of the current review, it should be mentioned that efforts to improve conditions for pollinators in for-



Figure 3. A riparian forest with a dense understory of Chinese privet (left), and the same forest five years after privet was removed (right). The forest following privet removal had much higher numbers of individuals and species of bees and butterflies than uncleared forest (Hanula and Horn 2011a, 2011b; Hudson et al. 2013).

ests and along roadsides have the potential to facilitate nonnative plant invasion. As many nonnative plants are favored by open and disturbed conditions, the establishment and spread of these species may be facilitated by reductions in tree and shrub cover (Jenkins and Parker 2000; Dodson and Fiedler 2006; Aubin et al. 2007; Shields and Webster 2007; Burke et al. 2008; Hausman et al. 2010) as a result of increased resource availability (e.g., light) and decreased plant competition (McEvoy et al. 1993; D’Antonio and Meyerson 2002). Since nonnative plants frequently occur along roadways, roads can act as conduits for their spread (Greenberg et al. 1997; Gucinski et al. 2001) and invasion into neighboring habitats (Gelbard and Belnap 2003; Christen and Matlack 2009; Birdsall et al. 2012). More research is needed, but the potential for increased threats from invasive plant species following management aimed at improving conditions for pollinators should be anticipated and, ideally, included in management plans.

CONCLUSION

The data thus far clearly show that bee and butterfly communities benefit (e.g., generally becoming more abundant and/or species rich) from open forest conditions

regardless of forest type or geographic region. Methods used to create these open forest habitats include fire (Grundel et al. 2010; Taylor and Catling 2011), harvesting or thinning (Fye 1972; Fultz 2005; Romey et al. 2007; Taki et al. 2010; Proctor 2012; Neill and Puettmann 2013), shrub removal (Hanula and Horn 2011a, 2011b; Hudson 2013) or a combination of these (Rudolph and Ely 2000; Campbell 2005; Rudolph et al. 2006a, 2006b; Campbell et al. 2007a b). Dense shrub layers negatively impact herbaceous plant cover and diversity (e.g., Woods 1993; Baker and Van Lear 1998; Collier et al. 2002; Gerber et al. 2008; Hudson et al. 2014) and, in turn, pollinators (McKinney and Goodell 2010; Hanula et al. 2011a, 2011b; Fielder et al. 2012; Hudson et al. 2013; Hanula et al. 2015). Despite the benefits of more open forests to most pollinator species, interventions aimed at creating these conditions have the potential to negatively impact rare species with small, scattered populations. Where such species occur, their habitat needs should be considered. This may require smaller or less-frequent interventions, creation of habitat refugia (areas protected from prescribed fire, for instance) from which they can recolonize treated areas, or both.

Because more open forests are less sus-

ceptible to pests and diseases (Fettig et al. 2007), efforts to improve pollinator habitat by opening up forests are consistent with those aimed at improving forest health. For example, Element 3 “Control and Management” of invasive plants species within *The USDA Forest Service National Strategic Framework for Invasive Species Management* (USDA Forest Service 2013) would simultaneously improve forest health and pollinator habitat by clearing nonnative plants from the forest understory and roadsides. Likewise, the recent arrival of the invasive European woodwasp (*Sirex noctilio* F.) to North America may affect pine forest management, particularly in the southern United States where large areas of loblolly pine forest are rated as high risk for damage by this insect (Chase 2013). Thinning to increase the vigor of the remaining trees is considered the best preventative treatment for *S. noctilio* (Haugen et al. 1990; Dodds et al. 2010), which would also likely benefit pollinators. Likewise, conifer stands that are too dense and have significant midstory tree and shrub layers are more susceptible to bark beetle attacks (Fettig et al. 2007; Nowak et al. 2015). Thinning is one of the most widely used and effective forest management tools to reduce stand risk of bark beetle damage. Nowak et al. (2015)

also demonstrated that prescribed burning can reduce the probability of southern pine beetle (*Dendroctonus frontalis* Zimmerman) infestation in unthinned pine stands. Fuel reduction treatments to minimize risks of wildfires, as part of the Healthy Forest Restoration Act (USFS 2014), including thinning, removal of ladder fuels, and prescribed burning have the added benefit of creating habitat favorable to pollinators (Waltz and Covington 2004; Miller and Hammond 2007; Nyoka 2010).

There are more than 560,000 km of forest roads in the United States (Coghlan and Sowa 1998), which have the potential to increase pollinator habitat within forests. Small solitary bees have limited foraging ranges (Gathmann and Tscharrntke 2002; Zurbuchen et al. 2010), so improving management of forest roadsides offers an opportunity to create linear openings that will increase available habitat and could facilitate gene flow throughout the forest. Conservation of bees and butterflies, as well as other pollinators, in forested areas is important for many forest plant species, and forests may serve as reservoirs of pollinators for recolonization of surrounding habitats.

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