The Importance of Forests in Bumble Bee Biology and Conservation

JOHN M. MOLA⊙, JEREMY HEMBERGER, JADE KOCHANSKI, LEIF L. RICHARDSON, AND IAN S. PEARSE

Declines of many bumble bee species have raised concerns because of their importance as pollinators and potential harbingers of declines among other insect taxa. At present, bumble bee conservation is predominantly focused on midsummer flower restoration in open habitats. However, a growing body of evidence suggests that forests may play an important role in bumble bee life history. Compared with open habitats, forests and woody edges provide food resources during phenologically distinct periods, are often preferred nesting and overwintering habitats, and can offer favorable abiotic conditions in a changing climate. Future research efforts are needed in order to anticipate how ongoing changes in forests, such as overbrowsing by deer, plant invasions, and shifting canopy demographics, affect the suitability of these habitats for bumble bees. Forested habitats are increasingly appreciated in the life cycles of many bumble bees, and they deserve greater attention from those who wish to understand bumble bee populations and aid in their conservation.

Keywords: bumble bees, woodlands, forest conservation, insect decline, habitat complementarity

Bumble bee conservation and management has garnered considerable attention because of bees' role as pollinators of economically and ecologically important crops and wild plants. The precipitous decline of several bumble bee species has been documented in the twenty-first century, raising alarm about the viability of these charismatic species (Cameron and Sadd 2020). Because of this, bumble bees have become a focal taxon for understanding and preventing the loss of insect biodiversity more broadly (Goulson and Nicholls 2016, Wagner et al. 2021). Threats to bumble bee populations include habitat loss, novel pathogen exposure, climate change, and pressures from intensive agriculture, such as pesticide applications (Cameron and Sadd 2020). One of the primary tasks for bumble bee conservation is developing a greater understanding of the habitat requirements of species throughout their life cycle and incorporating that knowledge into restoration and management plans.

Successful bumble bee conservation relies on an understanding of the parts of landscapes used throughout bees' life cycles (figure 1). Most bumble bees have an annual social life cycle, with queens emerging in early spring as solitary individuals. These lone queens seek nesting sites and then begin foraging for the initial pollen and nectar resources needed to establish their nests. As colonies grow by producing successive cohorts of workers across the growing season, they demand more resources. Successful colonies begin producing males and gynes late in the growing season. Finally, colonies senesce, with only gynes seeking sites to establish hibernacula and overwinter. Because bumble bees have relatively long flight seasons, they may make use of different land cover types that contrast or complement in their value over time by providing resources at different points in the season (Mandelik et al. 2012) or vary in their abiotic conditions. Forests can provide seasonally distinct floral resources from other habitats (e.g., Mola et al. 2021) and may be primary sites of nesting and overwintering (reviewed in Liczner and Colla 2019). As such, forests may serve as complementary habitats, supporting bumble bees in ways that are less readily apparent than midsummer foraging in open habitats but nonetheless critical.

Research on bumble bees has been primarily focused on their midsummer stage, when workers reach peak abundance and are readily found on flowers (Goulson 2009). Understandably, this focus arises because that is when the most individuals can be observed as colony sizes are at their peak and numerous workers can be found foraging. These types of studies have revealed important insights into the habitat needs and stressors of bumble bees, such as the relationship between landscape context and bumble bee diversity (e.g., Hines and Hendrix 2005) or patterns of disease prevalence (e.g., McNeil et al. 2020). However, this focus commonly overlooks other key points in the bumble bee
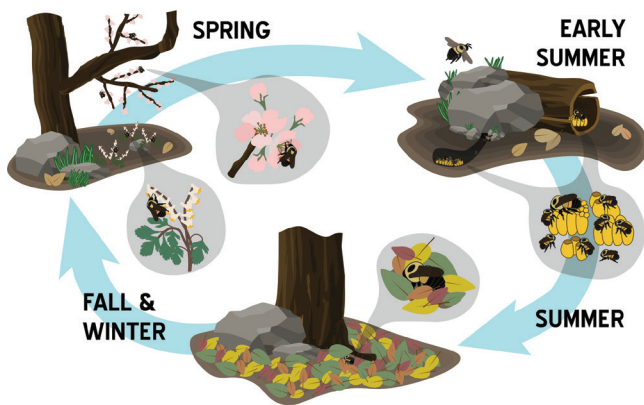

Figure 1. Bumble bee life cycle with emphasis on the role of forests as sites of foraging, nesting, and overwintering. This example is based on a temperate deciduous forest; forests can provide critical sources of early season forage within tree canopies or via forest floor ephemerals. Early summer colonies begin developing in a variety of substrates such as underground cavities or hollow logs. Although many types of forests decline in their importance as foraging sites in the summer, forests again become common sites of overwintering queens in the fall through winter.

life cycle—namely, the solitary phase of life for wild queens and males, early season foraging, nesting, mating, and overwintering. Despite their lower numerical abundance, recent studies have shown that these phases of bumble bee life history are especially important in determining the trajectory of their populations (Crone and Williams 2016, Carvell et al. 2017). Because forests in many regions contrast with open habitats in terms of their flowering phenology, structural features, and abiotic conditions, these habitats may be particularly relevant to the understudied portions of the bumble bee life cycle. When considering the bumble bee year more broadly to include early floral resources or nesting and overwintering habitat, the role of forests, forest edges, and other woody habitats becomes more central in our understanding of bumble bee biology.

Forests can vary greatly along axes of canopy openness, mesic versus xeric conditions, successional stage, and more. In some instances, forests are unsuitable habitats for bumble bees (e.g., unbroken swathes of closed canopy evergreen forest), but in many landscapes, a variety of forest types such as open canopy mixed conifer forests (Mola et al. 2020a), oak woodlands (Wray et al. 2014), aspen groves (Gonzalez et al. 2013), early successional (Taki et al. 2013), or old growth forests (Proesmans et al. 2019) may all play a role in bumble bee ecology for all or part of their life cycle. Readers should interpret the term *forest* broadly to include a range of variability and not all types are going to function in the same way as bee habitat (e.g., some forest types may be quality nesting, overwintering, and foraging habitat, whereas others may only be suitable for overwintering and offer few floral resources). For the purposes of this review, we define *forests*

relatively broadly to include a variety of landcovers containing woody plant species. We consider work focusing on forest interiors and edges, riparian corridors, open and closed canopy alike. We hope our discussion will allow readers to combine knowledge from their forest type or woody habitat of interest to bumble bee life history to make informed ecological inferences.

In this article, we consider the role of forests in bumble bee life cycles and its importance for conservation planning. First, we review evidence from landscape-level studies about the connection between forests and the abundance of bumble bee species. We relate these trends to the life history of bumble bees to develop general expectations for the relationship between forests and bumble bees. Next, we consider threats to forests that may limit their suitability as bumble bee habitat and explore how forests can be managed to support bumble bees. We contextualize our discussion by highlighting an endangered bumble bee species, the rusty-patched bumble bee (*Bombus affinis*; box 1). Because there are still many uncertainties as to the role of forests in bumble bee conservation, we conclude with a discussion of major research themes relating to bumble bees and forests that are likely to inform conservation efforts and improve our understanding of the basic biology of bumble bees.

How bumble bees use forests

The overwhelming majority of bumble bee observations occur in open areas, so why argue for the importance of forests for these species? Bumble bees use forested habitat in different ways throughout their life cycle (figure 1). Casual observations of bumble bees and many bumble bee monitoring programs do not observe these bumble bees in forests because they concentrate primarily on summer bumble bee communities, largely composed of foraging workers. However, the bumble bee life cycle is complex (figure 1), and evidence points to an outsized importance of some of the more cryptic life stages as drivers of bumble bee demography (Carvell et al. 2017). These life stages often occur in forests.

Forage. Bumble bees have a long foraging season, often spanning the flower production of many species or habitats over several months (Williams and Osborne 2009, Timberlake et al. 2019). Therefore, populations are sensitive not only to the total amount of resources but also their availability through time (Carvell et al. 2017, Malfi et al. 2019, Hemberger et al. 2020). In most species, hibernating queens emerge in early spring, when the earliest flowers emerge (e.g., willows and forest understory herbs), and complete colony reproduction in late summer or early fall (figure 1). Colonies require a continuous supply of floral resources because they do not store large amounts of pollen or nectar (Timberlake et al. 2019). The availability of floral resources in the early season, when queens are establishing colonies or the first workers begin foraging, is especially important for colony success (Carvell et al. 2017, Watrous et al. 2019,

Woodard et al. 2019). When a resource gap occurs at the establishment phase colonies rarely recover from it (Malfi et al. 2019).

Because forest herbs and trees often flower before plants in other habitats, they may be especially important to queens, colony establishment, and forest specialist species. In many areas, the first flowering resources are found within forest canopies or understories (Inari et al. 2012, Bertrand et al. 2019, Proesmans et al. 2019), and some of the last are in forest shrubs, edges, or in canopy gaps (Walters and Stiles 1996, Sakata and Yamasaki 2015). In Illinois, in the United States, the peak estimated flowering date of plants used by bumble bees is 81 days earlier in forests than in grasslands or wetlands (Mola et al. 2021). In these regions, records of spring bumble bee queens overlap most strongly with flowering in forests (Mola et al. 2021). In Japan, bumble bee population cycles are driven in large part by the availability of springtime resources in forest canopies the previous season (Inari et al. 2012). In Europe, tree pollens represent roughly 80% of early season pollen loads in *Bombus terrestris* (Kämper et al. 2016, Bertrand et al. 2019), suggesting a critical role of forests in the early foraging of this generalist species. In eastern North America, where pathogens are thought to be responsible for the decline of some bumble bee species, *Bombus impatiens* in habitats with higher spring floral abundance (predominantly forests), had lower pathogen loads (McNeil et al. 2020). As well, some species such as *Bombus vagans*, *Bombus. ardens*, or *Bombus terricola* complete almost their entire colony life cycles within forests, specializing on plants within the canopy and understory.

Within the world's deciduous forests, resource abundance can be high early in the spring, when canopy trees and shrubs flower and leaf-out has not yet shaded spring ephemerals. However, within open canopy forests, flowering phenology may have a different distribution. For example, in the open canopy conifer forests of the western United States, species such as mountain pennyroyal (*Monardella odoratissima*) and waterleaf phacelia (*Phacelia hydrophylloides*) can flower well into the bumble bee foraging season (Mola et al. 2020a). Some temperate deciduous forests also have late-season herbaceous flowers used by bumble bees (e.g., Kato et al. 1990), but these flowers may be less common than in decades past because of degradation by deer browse and other factors (Sakata and Yamasaki 2015). Considering both ends of the flowering season is important for bumble bees as the abundance of late-flowering resources is associated with elevated gyne and male production by colonies (Rundlöf et al. 2014) and may be important in explaining interannual variability in colony abundance (Timberlake et al. 2020). Given these examples, it seems likely that overall woody habitats provide resources that are complementary or at least supplemental to those of adjacent open habitats.

In addition to the total availability of resources, a preference for different plant species because of nutritional composition, resource return rate, or other factors is worth considering. For example, bumble bees selectively forage to balance dietary protein:lipid ratios (Vaudo et al. 2016, Woodard and Jha 2017). Rivers-Moore and colleagues (2020) documented a preference among bees, including bumble bees, for certain plants within woody habitats over those available in open habitats although exactly why these pollens were preferred was not identified, but it is possible these patterns are driven by phylogenetically conserved foraging preferences (Wood et al. 2021). At present, it is not clear if colonies perform better when accessing resources in woody environments over those in open habitats. One study showed that *B. impatiens* colonies experimentally placed in forest, open, and forest-edge habitats achieved similar nutrient ratios, but the colonies located within forests did not grow as rapidly (Vaudo et al. 2018). By contrast, Pugesek and Crone (2021) found that wild *B. impatiens* colonies monitored in forest patches had higher gyne production than those found in meadows, but these forest fragments were relatively small. Long travel distances limit productivity and reproductive output (Cresswell et al. 2000), but given the permeability of forests by foragers (Kreyer et al. 2004, Mola et al. 2020a), these limitations are likely due to total travel distance and resource availability rather than connectivity (Herrmann et al. 2017). Understanding how forested and open habitats complement bumble bee diets beyond raw abundance or phenological complementarity is likely of great importance for informing habitat management plans targeting pollinators. However, more work is needed to understand habitat differences in resource quality and their consequences for bumble bees.

Nesting and overwintering. Most bumble bee conservation efforts are focused on increasing available forage in the form of floral resources (Dicks et al. 2015, Requier and Leonhardt 2020); however, this is only one component of bumble bee habitat. The degree to which overwintering and nesting resources limit bumble bee populations is an ongoing area of debate (Roulston and Goodell 2011, Liczner and Colla 2020), but the provision of at least some habitat within the landscape is a necessity. Unlike foraging habitat, forests are commonly recognized as sites of nesting and overwintering within management documents and restoration initiatives (e.g., the draft recovery plan for *Bombus affinis*; USFWS 2019).

Bumble bees nest both below and above ground. Bumble bee nests, although they are cryptic, may be found through observations of spring nest-searching queens, careful observation of workers returning from foraging bouts, scent-detecting dogs, and radiotelemetry (Svensson et al. 2000, Mola and Williams 2019, Liczner et al. 2021). Preferred and actual nesting locations can be inferred indirectly on the basis of the nest searching behaviors of bumble bee queens and genetic mark–recapture method. On the basis of the available evidence, forests seem to be favorable and common nesting habitats for many species (Lanterman et al. 2019, Liczner and Colla 2019). In the US, nest searching bumble bee queen abundance was positively associated

with the amount of forest within 1 kilometer of study sites (Lanterman et al. 2019). Likewise, at multiple locations, bumble bee colony density was associated with a greater amount of forest or woodland in the landscape (Jha and Kremen 2013, Pfeiffer et al. 2019), with the authors suggesting these trends are due to the availability of nesting habitat. In Europe, nest searching bumble bee queens are often found within wooded areas or alongside edge habitats (Svensson et al. 2000, Kells and Goulson 2003). A community science project in the United Kingdom documented high nest densities along linear features such as hedgerows and forest edges but lower density in grassland and forest interiors (Osborne et al. 2008). However, this study did not correct for differences in detection rates between habitats that may be lower in forests (Pugesek and Crone 2021). It is worth noting that the taxonomic and geographic coverage of studies on nesting and nest seeking behaviors is currently somewhat limited. Studies conducted in Europe postagricultural intensification (Svensson et al. 2000, Kells and Goulson 2003) may overrepresent subgenera that are more associated with woodlands (e.g., *Pyrobombus*, *Bombus sensu stricto*), and surface nesting in open habitat is common for many species as well (Liczner and Colla 2019). Regardless, it appears that forests, forest edges, and the many microhabitats that they provide (Ouin et al. 2015) are common sites of nesting for many species.

These observations, both direct and indirect, suggest that bumble bee nesting sites are often located within forests. Do forests also increase the success of those nests? To date, the evidence for this is sparse and contrasting. Pugesek and Crone (2021) found that *B. impatiens* nests in similar densities in open habitat and forests but that the reproductive success of colonies within forests was nearly three times higher. In contrast, in an experimental study of the rates of predation on artificially placed bumble bee nests, nests placed in forests experienced greater predation than those placed in open habitats (Roberts et al. 2020). More work is needed to understand the fitness consequences of bumble bee nests placed in forested and open habitats.

Direct quantification of overwintering is rare, although scattered records suggest that forests are the most common overwintering habitats for many bumble bees (Liczner and Colla 2019). Overwintering queens are commonly documented in shaded areas near trees (Sladen 1912, Plath 1934, Alford 1969). On the coast of California, *Bombus vosnesenskii* queens were found overwintering in well-composted duff layers beneath cypress trees but not in adjacent open habitats (Williams et al. 2019). It is possible that the sheltered environments under trees provide coverage from rain or buffer against poor environmental conditions. Alternatively, undisturbed litter layers may be less common in open habitats, resulting in less frequent overwintering (Liczner and Colla 2019). Rotting logs and other woody debris may be important overwintering substrate (Frison 1926, Alford 1969), but these microhabitats may be absent from early succession forests. Generally, much is still to be learned about the importance of different habitats to overwintering and the

success of individuals overwintering in different substrates, but it is recognized that forests are important habitats for the overwintering of many species.

Abiotic effects

Forested environments have distinct abiotic conditions compared with open habitats such as grasslands and meadows. Bumble bee abundance can vary considerably from year to year, based in part on the direct and indirect impacts of annual climate conditions (Ogilvie et al. 2017), and forest microsites may buffer against this variation. At the same time, human use of forest differs considerably from that of open spaces that are more likely to experience impacts from agrochemicals (Bentrup et al. 2019). As such, it is useful to consider beyond the biotic effects of wooded habitats and consider the role that microclimates and physical attributes of forests may play in bumble bee biology and conservation.

Microclimates. The foraging of bees and other insects can be strongly influenced by weather conditions, predominantly air temperature, precipitation, and wind speed. Pollinator energetic costs are increased in high winds, resulting in reduced foraging efficiency and pollination success (Vicens and Bosch 2000, Brittain et al. 2013). Forested areas can reduce wind speed in adjacent environments and moderate air temperatures in both natural and urban environments. Both factors may reduce the energetic costs of foraging for bees within or adjacent to forests (Papanikolaou et al. 2017). For example, air temperatures are warmer downwind of windbreaks (McNaughton 1988), potentially resulting in longer available windows of foraging. Although they do not test abiotic conditions directly, Gonzalez and colleagues (2013) suggested one possible explanation for their finding that bumble bees were more common in aspen groves than adjacent grasslands was improved microclimatic conditions under the tree canopy—namely, reduced temperatures in summer. Temperature differences between forested and open habitats should be considered not only for foraging, but also nesting and overwintering. Heat waves have been suggested as a stressor for bumble bee colonies (Rasmont and Iserbyt 2012). Nests within shaded forested areas may be better protected from these extreme temperature swings compared with open field habitats. Maintenance of existing forested areas or the planting of windbreaks within agricultural landscapes can assist in the delivery of pollination services by bumble bees and potentially buffer against warming temperatures and associated unfavorable foraging conditions.

Correlations between bumble bees and forest cover

Many landscape-scale studies have looked at the relationship between forest cover and bumble bee abundance or diversity. Generally, increased landscape complexity or heterogeneity is positively correlated with pollinator diversity and abundance suggesting these landscapes offer more patches for
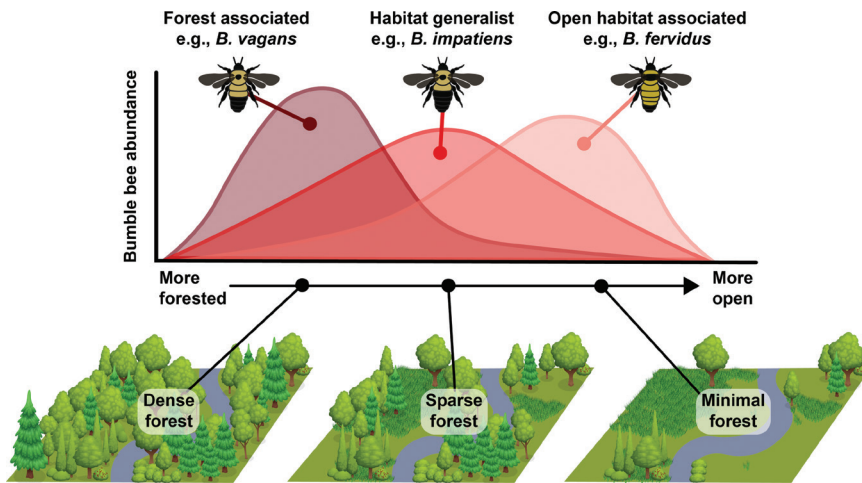
Figure 2. A hypothesized relationship between forest cover and the abundance of bumble bees varying in their association with forests. Some species, such as **Bombus vagans,** *are strongly associated with forest throughout their range and are expected to be present in high abundance at more densely forest sites and then absent from open areas far from forests. Others show opposite patterns, being associated with open habitats, such as* **Bombus fervidus.** *Generalist species may be present across the continuum of forest types, but may reach peak abundance at intermediate levels of forest cover or have a more uniform distribution. Example species follow from the results of Richardson and colleagues (2019).*

habitat specialists (Tscharntke et al. 2012, Mallinger et al. 2016). Several studies demonstrate clear positive relationships between forest cover and bumble bee abundance or diversity (Wray et al. 2014, Rivers-Moore et al. 2020, Sõber et al. 2020), spring queen abundance (Lanterman et al. 2019), or estimated colony density from molecular analysis (Jha and Kremen 2013, Pfeiffer et al. 2019). Negative relationships between bumble bee abundance and forest cover have also been reported (Winfree et al. 2007, Mandelik et al. 2012), as well as contrasting results among species (Richardson et al. 2019).

The variation in observed associations between bumble bee abundance and forest cover is likely driven by variation in the amount of forest cover considered in a study and the bumble bee species involved (figure 2), as well as methods differences in bumble bee surveys. A general model of bumble bee–forest associations might consider a continuum of forest density or fragmentation as a primary niche axis for bumble bees and acknowledge that different species might associate with species-specific optimal levels of forest density or fragmentation (figure 2).

Different bumble bee species have differing habitat optima along a forest gradient, resulting in landscapes with higher heterogeneity (i.e., intermediate levels of forest and open habitat) being most favorable for total species richness (figure 2). Quantitative surveys support this notion, with some bumble bees more associated with forest habitats than others (Richardson et al. 2019). In cases in which forests are very dense and few flowers are present

within the habitat, negative relationships begin to arise (e.g., Loffland et al. 2017) with bumble bees only found in natural or artificial forest gaps (Kolosova et al. 2016, Moquet et al. 2017). In contrast, the amount of forest and forest edge in the surrounding landscape can positively predict abundance (Wray et al. 2014, Banaszak and Twerd 2018, Rivers-Moore et al. 2020). Fragmentation of forests can favor generalist bumble bees associated more with open habitats, resulting in an overall reduction in species diversity and the loss of forest specialists (Gómez-Martínez et al. 2020). Some species may have an affinity for forests and use woody habitats for the majority of their colony development, such as the aptly named tree bumble bee (*Bombus hypnorum*; Crowther et al. 2014). Other species may only use forested habitats seasonally. For example, in Japan, *B. ardens* is found in forests for most of its colony cycle but *Bombus diversus* visits forests only early in the season before switching to open habitat (Ushimaru et al. 2008, Inari et al. 2012).

In addition to variation among species, differences in survey methods can bias observed associations between bumble bees and forest habitats. First, because bumble bees may rely on forests the most early in their life cycle, surveys later in the season may affect the observed relationship between a bumble bee species and forest habitat (Proesmans et al. 2019). Notably, even in examples in which a positive bumble bee–forest correlation is found, surveys were conducted in summer when workers are present, well after the point in time when forests may be of most importance to bumble bees (Mola et al. 2021). Second, the scale of surveys may influence observed relationships. For example, Moquet and colleagues (2017) found positive relationships between bumble bee abundance and surrounding spruce forest cover, but argued the increased abundance was due to concentration effects of bumble bees on limited forage resources found only in gaps and not due to forest cover per se.

Of note is that a substantial portion of the studies documenting foraging by bumble bees in forests demonstrate the use of plants within natural or artificial forest edges or ecotones, rather than deep within forests themselves (McKechnie et al. 2017, Sõber et al. 2020, Lee et al. 2021). It is unclear whether bumble bees prefer forest edges or whether this connection is caused by modern-day changes to forest structure. In high-quality old growth forests, there may be rich understory resources, but in many modern or degraded forests, there may not be sufficient solar radiation to sustain favorable foraging temperatures or herbaceous cover beyond the forest edge (Proesmans et al. 2019).

Table 1. Threats to forests and their potential impact on bumble bee populations.

Threat	Hypothesized impact on bumble bees	Key references
Fragmentation	• Loss of forest habitat specialists, increase in generalist species	*Ouin* et al. 2015, Proesmans et al. 2019, Gómez-Martínez et al. 2020
	• Changes in edge microclimates affecting foraging, nesting, and overwintering conditions	
Loss of old growth forests	• Change in forest floor structure suitable for overwintering	*Varhola* et al. 2010, *Lindenmayer* et al. 2012, Jackson et al. 2014, Proesmans et al. 2019
	• Loss of understory herbs	
	• Loss of old trees, stumps, and nesting cavities	
Overbrowsing by deer	• Loss of bumble bee forage plants	*Shelton* et al. 2014, Sakata and Yamasaki 2015, Nakahama et al. 2020
	• Change in forest structure may affect suitability of nesting and overwintering, directionality unknown	
Introduced earthworms	• Changes to forest floor structure, moisture, and soil compaction may affect overwintering and nesting	*Bohlen* et al. 2004, *Laushman* et al. 2018
	• Loss of bumble bee forage plants	
Wild and prescribed fire	• Varied impacts depending on forest type, presumed increases in floral abundance due to increased light levels and postfire bloom	Burkle et al. 2019, Carbone et al. 2019, Galbraith et al. 2019
	• Potential mortality of queens and colonies during overwintering or nesting	
	• Loss of microclimate buffering if canopy severely reduced	
Logging	• Varied impacts depending on logging intensity, type of machinery used, seasonality, soil disturbance, etc., likely increases in forage and bee abundance, especially along edges	Pengelly and Cartar 2010, Jackson et al. 2014
	• Potential long-term negative impact due to loss of microhabitat structure	
Invasive plants	• Loss of floral abundance although some invaders are suitable forage	McKinney and Goodell 2010, Hanula et al. 2016, Gibson et al. 2019
	• Increased shade reduces foraging	
Changing flowering phenology	• Phenological mismatch	Burkle et al. 2013, Kudo and Cooper 2019
Pesticide concentration	• Potential transfer to overwintering queens in soil	Hladik et al. 2016, Bentrup et al. 2019
	• Uptake into nectar and pollen	

Note: The key references are not intended to be an exhaustive list. The italicized references are about the threat but do not directly study bees. See the main text for further details.

In managing forests to support bumble bees, it may be important to consider how particular bumble bees use forests. For example, *B. terrestris* is invasive throughout Hokkaido, Japan, where it displaces native species in open or agricultural habitats but not in forested areas (Ishii et al. 2008, Nukatsuka and Yokoyama 2010). In general, phenology varies substantially among bumble bee species, and, at least in temperate habitats, bumble bee species that emerge earlier in spring are more likely to rely on floral resources in forests (Colla and Dumesh 2010, Mola et al. 2021), suggesting that there may be predictable differences in how forest management may affect different bumble bee species. However, more work is needed to show the generality of a positive correlation between forest-affiliation and early phenology. Of final note in interpreting the correlations between bumble bees and forest cover is the need for careful consideration of the problem of shifting baselines (Pauly 1995, Collins et al. 2020). In contemporary landscapes, the large-scale elimination of grasslands (Samson and Knopf 1994, Wesche et al. 2012), and therefore, open habitat associated species may have already occurred, potentially biasing modern surveys toward more forest associated species. As such, some caution is warranted in interpreting a general pattern of increased landscape-scale forest cover leading to increased bumble bee abundance and diversity. However, it seems fair to conclude that heterogenous landscapes composed of a mix of forested and open landscapes are likely to support abundant and diverse bumble bee communities in most regions.

Threats to forests as bumble bee habitat
Forests throughout the world are changing rapidly. For example, forests are affected by changing land use, climate change, invasive species, and fires (Lindenmayer et al. 2012, McDowell et al. 2020). Many of these changes are likely to affect the important roles that forests play in the lives of bumble bees, sometimes positively and sometimes negatively (table 1).

A common change in forests that could threaten bumble bees is the loss of understory flowers. For example, declines in floral resource availability in forests have been documented in Illinois, in the United States, driven in part by the loss of important spring flowering plants such as *Geranium maculatum* and *Hydrophyllum virginianum* (Burkle et al. 2013, Augspurger and Buck 2017, Mola et al. 2021). A decline in understory flowers may be caused by overbrowsing by deer or cattle grazing, canopy crowding, plant invasions, and other factors such as earthworm introductions. Overbrowsing by deer can reduce the abundance of understory herbs, as has been documented widely across the eastern United States (Frerker et al. 2014, Shelton et al. 2014) and Japan (Sakata and Yamasaki 2015). Although not as widely studied within woodlands, and seemingly with no studies focused on impacts on bees, cattle grazing can similarly decrease the abundance of native perennial wildflowers and increase exotic plant invasion (Pettit et al. 1995, Mabry 2002). Overbrowsing can reduce spring ephemeral availability and autumn flowering plants critical for fat acquisition by gynes before overwintering (Sakata and Yamasaki 2015). Restoration efforts aimed at reducing deer browse may be successful. In a study in grasslands, Nakahama and colleagues (2020) found the installation of deer fencing resulted in increased floral abundance and increased bumble bee and butterfly abundance and diversity within fenced areas about 3–8 years after installation. They caution, however, that other efforts to install deer fencing may be unsuccessful if the habitat has already been substantially degraded (Tamura 2010, Okuda et al. 2014). In those instances, deer fencing may need to be combined with additional efforts such as native plant seeding.

Encroachment from invasive shrubs can also reduce flower production within forests with downstream effects on pollinator populations (Miller and Gorchov 2004, McKinney and Goodell 2010, Hanula et al. 2016). The effects of invasive plants on pollinators can vary substantially according to the context of the invasion. Invasive plants may, at times, be the preferred floral resources of bumble bees (e.g., Gibson et al. 2019), but widespread invaders such as Chinese privet (*Lingustrum sinense*) and Amur honeysuckle (*Lonicera maackii*) can crowd forest understories and reduce total floral diversity or flowering duration even if the invader is a suitable food source itself (reviewed in Hanula et al. 2016). Experimental removal of invasive plants in these habitats can result in improved foraging conditions for bees and rapid recovery of bee communities (Hanula and Horn 2011). The net benefit of biomass removal on bumble bees may be highly context specific and requires careful consideration of the study system (Gibson et al. 2019).

Some human activities within forests such as limited logging can have positive impacts on bumble bee forager abundance by opening canopies and more closely approximating conditions within mature forests with well-established gap dynamics (Pengelly and Cartar 2010, Jackson et al. 2014, Proesmans et al. 2019, Lee et al. 2021). However, these same activities may have negative effects on the availability of microhabitats for nesting and overwintering; because of this, the net impact of long-term changes in forest dynamics are unknown. These effects are yet to be tested but provide clear research pathways for understanding how changing forest dynamics and associated management activities will affect bumble bee populations over the next several decades.

The direct and indirect negative impacts of pesticides, fungicides, and herbicides on bees are well documented (Lundin et al. 2015, McArt et al. 2017, Motta et al. 2018). Bees in agricultural landscapes may be exposed to pesticides directly, and drift carries different pesticides different distances from the places where they are applied (Hladik et al. 2016). Pesticide residues may reach forests via surface or subsurface water movement, airborne drift, or volatility. Movement of herbicides via volatiles is worthy of further consideration, because injury to plants up to 250 meters from application sites has been documented (Soltani et al. 2020). These herbicides could injure floral resources within forests resulting in reduced foraging opportunity for bees (Bohnenblust et al. 2016, Florencia et al. 2017). Previous work has suggested that forests may mitigate drift by capturing agrochemicals and reducing wind speeds (reviewed in Bentrup et al. 2019). However, the benefits of forests trapping these compounds are only positive if the forest is seen as matrix and not as primary habitat itself. If, instead, forests are bumble bee habitat these effects may be negative as drift or damage may concentrate in these areas. Future work investigating how forest habitat quality for bumble bee foraging, nesting, and overwintering is affected by drift from croplands is needed to understand how pesticides affect forests as bumble bee habitat. Overwintering may be of particular importance, because queens may come in direct contact with residues within soils for extended periods of time, which has been shown to negatively affect solitary bee development (Anderson and Harmon-Threatt 2019).

Several other factors change conditions within forests substantially and may affect bumble bee populations, but evidence is currently lacking to address this. Introduced European earthworms in hardwood forests of the Upper Midwest, in the United States, have resulted in changing soil and leaf litter conditions with negative consequences for understory forbs (Bohlen et al. 2004, Laushman et al. 2018) and possibly overwintering substrates. Besides direct losses of floral richness or abundance, shifting flowering phenology may also threaten resource availability, with advances in spring bloom documented widely (Kudo and Cooper 2019, Augspurger and Zaya 2020). Changing fire regimes, either reduced burning because of mesophication (Nowacki and Abrams 2008) or increased fire severity from climate warming and built-up fuel loads (Jolly et al. 2015), are also likely to affect bumble bee populations. Bumble bees often respond positively to fire in the short term, because of postfire bloom and increased canopy openness (Burkle et al. 2019, Galbraith et al. 2019, Mola et al. 2020b). However, direct mortality to queens and colonies also needs to be considered, especially

for species of conservation concern or in areas in which species are unlikely to be adapted to frequent or high-severity fires. Changes in forest structure may negatively affect the availability or suitability of nesting and overwintering substrates, although this is merely speculative as no research has been conducted on this to date. Understanding how past and continued changes in forest conditions affect foraging, nesting, and overwintering opportunities is critical, because we may overlook the role of forests in bumble bee life history if these conditions are sufficiently altered.

Incorporating forests into bumble bee monitoring and restoration

There has been a lack of emphasis on forest habitats for bumble bees within monitoring and restoration efforts. For the reasons outlined above, this likely limits the effectiveness of our conservation efforts. However, by explicitly incorporating forests into monitoring and restoration efforts we can further understand the role of forests in bumble bee biology and improve these habitats to support populations.

Several governmental and community science monitoring programs exist to attempt to locate bumble bees, often with a focus on rare or declining species. These efforts have proven critical in trends and locations of rare bumble bees (MacPhail et al. 2019). Some efforts are passive, such as iNaturalist or BeeSpotter, whose users upload their observations as species are encountered. Others are more directed with explicit sampling protocols. For example, the Nebraska Bumble Bee Atlas project encourages community scientists to survey for bumble bees by "survey[ing] for bumble bees at least twice between June and September" (www.nebraska-bumblebeeatlas.org/requirements-145172.html). The timing of these surveys is likely to miss most queens. Similarly, US Fish and Wildlife Service protocols to survey for the endangered rusty-patched bumble bee (*Bombus affinis*) intentionally avoid queens, thereby reducing observations within early season habitats such as forest canopies and understories (box 1). Of course, efforts such as this yield tremendous value for detecting species presence or persistence through time but may paint an incomplete picture of the importance of different habitat types to species by focusing predominantly on peak flight season. Given the lower numerical abundance of queens and early worker cohorts, and the difficulty of locating nests or overwintering queens, detectability of bumble bees within forests may be lower as well (Liczner and Colla 2019, Graves et al. 2020, Pugesek and Crone 2021). However, low numerical abundance should not be confused with low demographic importance, because these earliest individuals are key to colony establishment and success even long after the initial colony phases (Carvell et al. 2017, Woodard et al. 2019). Future monitoring and research efforts to explicitly include forests in search efforts along with a focus on early season surveys could greatly enhance our understanding of bumble bee habitat use.

Restoration programs or pollinator habitat creation efforts follow a similar pattern, with a strong focus on midsummer flowering resources (Dicks et al. 2015, Requier and Leonhardt 2020). Although many pollinator planting guides (examples at http://millionpollinatorgardens.org/resources) encourage the availability of floral resources all season long or encourage the use of trees or shrubs, this is generally not the focus of public-facing materials. Although pollinator plantings clearly increase peak season resources (Wood et al. 2018), greater consideration needs to be placed on nesting and overwintering habitat as well as resource availability during the tails of the season. The most cost-effective way to achieve this may be through the management and preservation of forested areas (Bentrup et al. 2019). Forest restoration is a costly and lengthy process, so protection of existing forests and restoration efforts targeted at reducing canopy crowding or the impacts of overbrowsing may be even more cost-effective means of increasing the services that forests provide to bumble bee conservation.

Promisingly, the management of forests for bumble bee populations is synergistic with other wildlife management goals and is often an unintended effect of other efforts (Williams 2011, Hanula et al. 2016). For example, in one study, forests that were managed for the red-cockaded woodpecker were also the most favorable long-term habitat for bees (Hanula et al. 2015). Similarly, management aimed at opening forest canopies to control pests and disease (Fettig et al. 2007, Simler-Williamson et al. 2019), is also likely to benefit bumble bees because favorable conditions for flowering are often found in mature forests with canopy gaps (Proesmans et al. 2019). However, changes in canopy cover from management activities can also affect forest floor temperatures, snowpack accumulation, and water infiltration and may influence the suitability of overwintering substrates (Varhola et al. 2010, Simler-Williamson et al. 2019), but this is yet to be studied for bumble bees or arthropods broadly and the directionality of the effects is unknown. Forest management efforts such as burning also seem compatible with bumble bee conservation goals as the effects of fire on bumble bees generally remains positive across a variety of habitats and species (reviewed in Carbone et al. 2019). Hedgerows, often containing woody plant species, have also been a mainstay of pollinator restoration efforts (Hannon and Sisk 2009). Forest edge plants can be favorable forage and may also serve multiple purposes in creating physical structure as well as providing protection from browsing mammals. For example, *Bombus dahlbomii* queens forage on Chilean box thorn (*Vestia foetida*) which is a noxious plant that can poison browsing mammals and so may provide protected forage (Polidori and Nieves-Aldrey 2015). Creative opportunities for managing habitat for bees may exist that make these efforts compatible with broader forest management goals.

Future research

There are many avenues of future research on the relationship between bumble bees and forests that are likely to be

Box 1. The potential of forests in conservation of the endangered rusty patched bumble bee (*Bombus affinis*).

In 2017, the rusty patched bumble bee (*Bombus affinis*) became the first bumble bee listed under the Endangered Species Act in the United States. *Bombus affinis* was once fairly widespread in North America but has suffered population declines and range contraction in the past few decades (Giles and Ascher 2006, Colla et al. 2012, Williams et al. 2014, USFWS 2019). As a sort of conservation flagship species for bees more generally, the development of this species' recovery plan presents an opportunity to "get it right" from the start and apply lessons learned as a model for other pollinator species that face similar threats.

Current conservation efforts by US Fish and Wildlife Service (USFWS), state, and local monitoring predominantly focus on mid-summer populations. For example, USFWS surveys "must be conducted between early June and mid-August, for the highest detection probability and to reduce potential impacts to *B. affinis* queens" (www.fws.gov/midwest/endangered/insects/rpbb/pdf/Survey_Protocols_RPBB_12April2019.pdf). Although this is a laudable goal to avoid negatively affecting queen nest establishment, it also means information on spring queens and early workers is underreported. Intentionally avoiding surveys during these times of the year leaves us without data-driven management actions and may be undervaluing the importance of woody land covers.

Earlier natural history surveys suggest *B. affinis* queens use a range of woody and nonwoody species early in the season. Fye and Medler (1954) document *B. affinis* queens using several fruit trees such as *Pyrus* and *Prunus* species as well as early flowering shrubs such as *Salix* and *Lonicera*. In a similar investigation, Macior (1968) documented 156 *B. affinis* queens foraging with more than half of them captured from *Berberis*, *Pyrus*, and *Lonicera*. In contrast, Wood and colleagues (2019) found only 14% of pollen species from museum specimens of *B. affinis* were from woody plant species. However, these samples had a median date of August 6th, which is relatively late in the flight season of *B. affinis* (Mola et al. 2021).

To extend on prior understanding and make use of limited data, we examined records compiled originally for Bumble Bees of North America (Williams et al. 2014) and updated annually by Dr. Leif Richardson to understand the potential importance of forests for this species recovery.

We found records of spring and early summer queens (April–June) foraging on 13 plant genera, of which 10 were associated with forest habitat (figure 1a). Two species of forest-associated flowering plants (*Dicentra cucullaria*, *Mertensia virginica*) account for nearly half of the observations (figure 1a) and are known to be especially early blooming (Mola et al. 2021). In contrast, gynes foraging between July and September were found on nine floral genera of which only two are primarily associated with forests, suggesting the importance of forests as forage habitat declines as the season progresses (figure 1b).
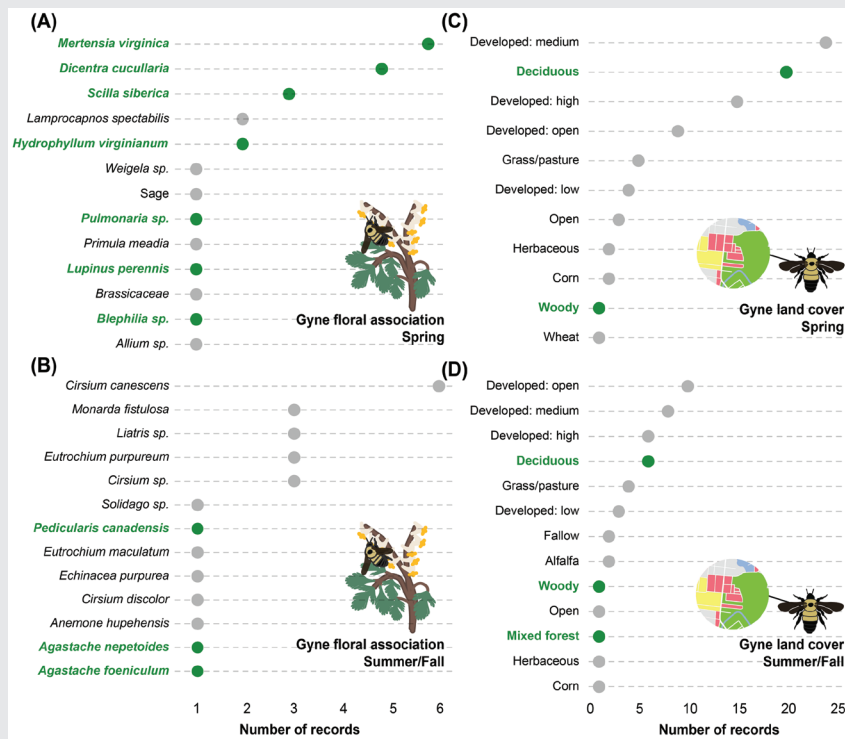

Figure 1. Landcover and floral associations of Bombus affinis *spring foundresses (panels (A) and (C)) and gynes (panels (B) and (D)). (A) Tally of landcover types within which each record of* B. affinis *spring foundresses was collected within the study region. (B) Tally of landcover types for* B. affinis *gynes (queen records after day of year 150). (C) Tally of floral species identified from photos of* B. affinis *foundresses. (D) Tally of floral species identified from photos of* B. affinis *gynes. Forest-associated plant species and land covers are colored green.*

Box 1. Continued.

We also examined land cover associations of queen records to assess habitat associations of *B. affinis*. In total, we overlaid 139 records with USDA Cropland Data Layer (NASS 2019) and extracted the landcover type each record was collected in. Although developed land cover types were the primary habitat association (figure 1c and 1d), as was expected given the dominance of community science records, deciduous forests were the second most common landcover (figure 1c and 1d).

The associations described in the present article are preliminary but suggest that the relationship between forests and *B. affinis* warrants rigorous scientific assessment, particularly to inform the species recovery plan and targeted conservation efforts. It seems unlikely a loss of forest plants was a driving factor in the decline of *B. affinis* (Mola et al. 2021), especially with other forest-associated species such as *B. vagans* remaining stable within the range. However, foraging associations from historical studies and from contemporary community science observations suggest that early season forest plants may be important areas of focus for habitat management. In addition, it is likely that nesting and overwintering habitat for *B. affinis* is favorable within forested landscapes, as was evidenced from several community science and anecdotal observations. Although data is limited at this time, the available evidence suggests that forests may play an important part in conservation and recovery planning for this endangered species.

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fruitful (box 2). Although many studies demonstrate a correlation between bumble bees and surrounding forest cover, few set out with this intention in mind. Future studies seeking to understand exactly why these correlations arise, either because of nesting, overwintering, or foraging habitat, across a variety of forest types could help land managers incorporate forests and woody habitats in species plans thoughtfully.

There is a pressing need to understand how changing conditions within forests from the threats discussed above are likely to affect bumble bees in the future and how management activities intended to counteract those threats will affect bumble bees. Of significant importance is likely to be the role of forests as thermal refugia under climate warming and understanding if, for example, species more reliant on open habitats may be more susceptible to the effects of warming as forests may offer refuge from heat waves and extreme weather events. Finally, perhaps underlying all these research needs, is greater capacity to study the role of forests in bumble bee biology. We argue above that our lack of understanding often comes from the difficulty of detecting bumble bees within forests (i.e., visual blockage, canopy foraging, time of year). Efforts to better coordinate community scientists, improve detection methods, and overcome the difficulty of identifying nesting and overwintering sites are all needed to improve our ability to study bumble bees within forested habitats.

Finally, although we review studies conducted in a wide range of forest types, there is also a strong bias toward research in temperate deciduous forests, predominantly in eastern North America, Europe, and Japan. A notable species lacking from our discussion is the tropical lowland rainforest specialist *B. transversalis*, which lives its entire life under deep canopy and makes use of twigs and leaves in its nest construction (Olesen 1989). Although it is an outlier in bumble bee life history, learning more about that species' origins and behaviors may reveal general patterns. Broadly, it remains to be seen whether the associations between bumble bees and woody habitats described in the present article are relevant to forest types, such as tropical montane forests, that are both understudied and important habitats for bumble bees.

Conclusions

In this article, we focused on the value of forests for fulfilling habitat requirements for bumble bees. However, it is important to note that these factors are not necessarily restricted to forests but are likely most often found within forests. For instance, orchards and gardens can also offer similarly early resources as natural or seminatural forest habitats (Watson et al. 2011, Nakamura and Kudo 2019, Nikkeshi et al. 2019). As we show in the case study with *B. affinis* (box 1), developed lands can offer substantial foraging opportunities for bumble bees and other studies demonstrate urban habitats can be suitable landscapes (McFrederick and LeBuhn 2006, Glaum et al. 2017, Reeher et al. 2020). In addition, nesting within anthropogenic habitats seems to be fairly common (Medler and Carney 1963, Liczner and Colla 2019). Overall, we have demonstrated that forests are often critical bumble bee habitat, but it may be possible that the benefits of forests are substitutable to some extent with other environments such as developed landcovers containing early season species or other types of early blooming natural habitats. We hope our perspective does not provide the idea that forests are *required* for bumble bees but instead that they offer a cost effective means to provide foraging, nesting, and overwintering habitats that are compatible with conservation goals of other organisms (Williams 2011, Bentrup et al. 2019) and may be overlooked in studies of bumble bee biology. A recurrent problem in bumble bee conservation is the lack of informed demographic models or an understanding of basic aspects of species biology (i.e., nesting and overwintering). Increasing our capacity to incorporate forests into these efforts is likely to produce rich data sets that better inform conservation efforts and lead to the development of useful demographic models.

Box 2. Future research themes toward understanding the role of forests in bumble bee conservation.

We provide brief topic areas and example questions although the list is not intended to be exhaustive. The future research needs in bumble bee forest ecology including the following:

1. **Basic relationships between forests and bumble bees**—relationships between forest or woodland cover and bumble bee population parameters, impacts of nesting and overwintering on colony abundance and survival

   • Are forests used as overwintering habitat for bumble bee queens?

   • What is the relationship between forest cover and colony abundance?

2. **Biotic interactions within forests**—interactions with microbiomes, disease transmission, and invasive species

   • Do forest flower nectar sources contain similar microbial communities as resources in open habitat?

   • Does the availability of forest flowers limit or encourage the spread of disease?

3. **Habitat complementarity and landscape context**—movements between forests and other habitats, seasonal resource use, comparisons of different forest types, contrasts of forests and open habitats, nutritional content of pollens in different habitats

   • What is the seasonal flowering profile of different forest types for bumble bees?

   • Do canopy and understory flowers offer similar or contrasting nutritional content?

4. **Changing forest conditions**—deer browse, fire, fragmentation, logging, and other threats and changes to forests in the modern world

   • How do changing fire regimes or mesophication affect the suitability of forests for nesting or overwintering?

   • Does disturbance from introduced organisms such as European earthworms in North America change nectar chemistry?

5. **Climate change**—microclimates, thermal refugia, shifting daily foraging phenology, impacts on nesting and overwintering, flowering phenology and resource quality

   • Does foraging on forest resources become more common compared with open habitat during extreme heat events?

   • How will changes in flowering phenology affect spring queen nest establishment?

6. **Forest management impacts**—effects of logging, target and nontarget restoration efforts, recreational ecology, successional stages

   • How do different timber harvest methods affect postharvest floral communities?

   • What management activities aimed at other species of concern have large positive or negative impacts on bumble bee populations?

7. **Monitoring, community science, detectability, and methodological constraints**—targeted forest bumble bee surveys, comparisons of detection between different forest types, tools and methods for locating nests and hibernacula within forests

   • Is bumble bee use of forest canopy underreported because of poor detection?

   • Can community science programs overcome gaps in our knowledge of early spring bumble bee foraging habitat?

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John M. Mola (jmola@usgs.gov; ORCID 0000-0002-5394-9071) and Ian S. Pearse (ORCID 0000-0001-7098-0495) are affiliated with the US Geological Survey, Fort Collins Science Center, in Fort Collins, Colorado, in the United States. Jeremy Hemberger (ORCID 0000-0003-3648-4724) is affiliated with the Department of Entomology and Nematology, at the University of California Davis, in Davis, California, in the United States. Jade Kochanski (ORCID 0000-0001-8693-2404) is affiliated with the Department of Integrative Biology and with the Department of Entomology at the University of Wisconsin Madison, in Madison, Wisconsin, in the United States. Leif L. Richardson (ORCID 0000-0003-4855-5737) is affiliated with the Xerces Society for Invertebrate Conservation, in Portland, Oregon, in the United States.