The Value of Forests to Pollinating Insects Varies with Forest Structure, Composition, and Age

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Abstract

Purpose of Review Forests play an essential role in conserving pollinating insects and supporting pollination services in mixed-use landscapes and are particularly important to species that require resources restricted to forests. However, some forests provide higher quality habitat for these organisms than others. The primary objectives of this article are to 1) review how pollinator communities are influenced by changes in forest structure, composition, and age, 2) explore how these patterns differ between conifer and broadleaf forests, and 3) provide recommendations for managers interested in optimizing forest conditions for pollinating insects.

Recent Findings Although biodiversity generally increases as forests mature and become more structurally and compositionally complex, patterns exhibited by pollinating insects vary depending on forest type and prevailing disturbance regimes. For example, conifer forests can either sustain pollinator diversity comparable to open habitats or experience reduced pollinator diversity depending on the openness of the canopy. In broadleaf forests, pollinator diversity often increases with age (following the stem exclusion stage) and increasing tree diversity, and diversity in these areas can exceed what is observed in open habitats even under closed-canopy conditions. Such patterns likely reflect the importance of flowering broadleaf trees to pollinators, including many forest-dependent species, and suggest that optimal management practices for conserving pollinators differ between conifer and broadleaf forests.

Summary We conclude that: 1) the quality of forests to pollinating insects is a function of forest structure and composition as mediated by forest age and disturbance history and 2) best management practices need to be developed separately for conserving pollinators in conifer and broadleaf forests. Research aimed at better understanding the value of different broadleaf tree taxa to pollinators, especially forest-dependent species, is needed.

Keywords Bees · Early seral forests · Forest canopy · Forest succession · Mature forests · Nesting resources

Introduction

Recognition that forests are important to pollinating insects (hereafter 'pollinators') has been building for decades [1–5], and interest in this topic has surged over the past several years [6••, 7, 8•, 9••, 10]. Far from providing suboptimal conditions for these organisms as suggested by some authors, it is now clear that forests support a large fraction of pollinator diversity endemic to many regions [11••]. Forests not only play a key role in maintaining regional pollinator diversity but they also promote pollination in adjacent land uses including many crops [11••], sometimes with substantial economic benefits [12, 13•].

To fully understand the value of forests to pollinators, it is first necessary to distinguish forest-dependent species from those that use forests opportunistically [14]. Forest-dependent species require resources restricted to forests at some point during their life cycle. Although such resources often include the flowers of trees or other forest plants, they can also include other plant structures, such as leaf or stem material used for food (e.g., by lepidopteran larvae), and substrates or microhabitats used for nesting or breeding (e.g.,

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dead wood, hollow trunks, or tree cavities). By contrast, pollinators that are habitat generalists can persist in landscapes devoid of forests yet may still make use of forest resources to meet their life history needs.

Recent work suggests that approximately a third of bee species are associated with forests in the northeastern U.S. [9••]. Work from other regions indicates that extensive deforestation results in the replacement of forest-dependent pollinators by habitat generalists or species favored by anthropogenic disturbances [15–19]. Moreover, beyond a certain level of forest loss, such 'regime shifts' are expected to be difficult to reverse even with major restoration efforts [11••]. Therefore, it is urgent to determine how much forest cover is needed to conserve forest-dependent pollinators [7, 11••, 20, 21]. There is an equally important need to understand how the structure, composition, and age of forests affect pollinators.

As forest succession proceeds, forest structure and composition change and the canopy can, depending on tree composition, become an increasingly important source of flowers and other resources for pollinators. Changes in structure with time depend largely on prevailing disturbance regimes which vary with region and forest type, topography, climate, human activity, among other factors [22, 23]. Whereas some mature forests are characterized by mostly closed canopies, others are not. More open structures occur in mature forests when disturbances kill sufficient numbers of dominant and co-dominant trees [24, 25]. Changes in forest composition include the predictable succession of tree species (e.g., shade-tolerant taxa replacing shade-intolerant taxa) as well as pests, diseases, natural disturbances, and management activities that select for a subset of tree species. While it is clear that pollinators respond to structural and compositional changes in forests, as reviewed here, inconsistent findings among studies suggest that such effects vary with forest type. Most notably, open stand conditions appear to be particularly important to pollinators when forests are dominated by trees that provide few floral resources [26, 27••, 28••].

The objectives of this article are to 1) provide a brief overview of global changes in forest cover, structure, composition, and age, 2) review how pollinator communities are affected by forest structure, composition, and age, 3) explore how these patterns may vary among forest types, particularly gymnosperm- vs. angiosperm-dominated forests (hereafter conifer vs. broadleaf, respectively), and 4) provide recommendations for managers interested in optimizing forest conditions for pollinator conservation. Efforts to define the term 'forest' are challenged by the variability in forest structure and composition observed globally. Therefore, to be as inclusive as possible we use the term 'forest' to refer to any ecosystem consisting of arborescent woody plants, regardless of their size or spacing. We adopt a similarly broad definition of 'pollinator' to refer to any flower-visiting insect that

has the potential to contribute to pollination. Although most of the literature on insect pollinators has focused on bees, non-bee insects can enhance pollination beyond what can be achieved by bees alone and are the primary pollinators of many plant species [5, 29]. Finally, this review aims to be global in coverage but we note that most recent research on these topics comes from work conducted in North America and Europe.

Global Changes in Forest Structure, Composition, and Age

Forests throughout the world continue to experience changes in structure, composition, and age, with important implications for biodiversity. Globally, forests encompass ~31% (~4.1 billion ha) of land area [30] with tropical forests representing the largest proportion (45%), followed by boreal (27%), temperate (16%), and subtropical (11%) forests. The amount of forest has been declining globally although the rate of decline (net forest loss) has slowed to ~4.7 million ha yr^{-1} [30]. This trend is influenced by many factors, including declines in deforestation rates in some countries and natural expansions of forests in others. Most recently, there have been several regional, national, and global initiatives to plant more trees, such as the The Trillion Tree Campaign which aims to plant one trillion trees worldwide as a nature-based solution to combat climate change [31].

While the loss of forests, such as through agricultural expansion [32], poses a major threat to global biodiversity, forest degradation, defined as the loss of key forest attributes that reduce the capacity of a forest to provide goods, services, and biodiversity [33], is also of concern, particularly in tropical regions [34]. Forest degradation often occurs in addition to forest loss, but this is not always the case. In the U.S., for example, forest cover has remained relatively stable over the past century [35] but a variety of forces are acting to reshape the structure and composition of these forests. These include non-native species, climate change, urbanization, and expansion of the wildland-urban interface (i.e., where houses and other developments meet or mix with undeveloped natural areas) [36–38].

Globally, old forests tend to be concentrated in regions that are cold and dry or warm and wet, whereas those of intermediate ages span large climatic gradients [39]. In North America, forests in the southeastern U.S. and in parts of central Canada are relatively young, reflecting the effects of industrial forest practices in the southeastern U.S. and the frequency of natural disturbances in central Canada [40]. A recent inventory in the U.S. found 64% of the ~58.4 million ha of forest managed by the USDA Forest Service were mature or old-growth [41]. Young forests (≤30 yrs old) comprise ~25% of forests in the U.S. whereas very old

forests (≥ 200 years old) comprise ~ 4% (calculations based on USDA Forest Service Forest Inventory and Analysis data, for all ownerships).

Climate changes driven by anthropogenic forces–including warming and altered precipitation patterns–can have direct and indirect effects on forests. Warming alters the phenology of vegetation (e.g., the timing of flowering and leaf out) and competitive relationships among species [42] and influences functional diversity, which has been shown to affect the vigor, growth, and survival of trees in some forest types [43, 44]. Many indirect effects of climate change are mediated through changes in the frequency and severity of disturbances that shape forest ecosystems by driving changes in vegetation growth, mortality, regeneration, and recruitment. Globally, approximately 98 million ha of forest were impacted by wildfire in 2015 [30], with more than two-thirds occurring in Africa and South America. Insects, diseases, and severe weather events damaged ~ 40 million ha of forests in 2015 [30], mainly in temperate and boreal regions. In western North America, tens of millions of ha were impacted by bark beetle (Curculionidae: Scolytinae) outbreaks during 2000–2020 due, in part, to warming and drought with billions of trees killed [45]. Exotic, invasive insects and diseases have greatly altered the structure and composition of some forests and are a growing conservation concern [46]. Invasive tree diseases, including chestnut blight and Dutch elm disease in North America (caused by *Cryphonectria parasitica* and *Ophiostoma ulmi*, respectively), have threatened the existence of entire tree genera. With climate change, novel forest ecosystems are becoming increasingly prevalent and characterized by forest conditions, environmental drivers, and disturbance regimes with no or few past analogs [47]. Continued warming and changes in precipitation patterns are expected to amplify interactions among forest disturbances. However, vulnerability of the world's forests varies due to differences in biophysical conditions, disturbances, and local and regional variations in climate [48].

Humans play a significant role in determining the distribution, structure, composition, and age of forests. Numerous social and economic drivers influence how, when, and where forests are managed for goods and services, with each of these decisions having the potential to affect pollinator conservation. Seventy-three percent of the world's forests are publicly owned, with the share of publicly owned forests declining globally since 1990 [20]. In the U.S., more than half of forest land is privately owned; most private ownership occurs in the eastern U.S. with most western U.S. forests publicly owned. Increases in landowner turnover rates, parcellation of forest properties, and forest fragmentation are important conservation concerns (due to habitat loss, among other factors) in the eastern U.S. and likely to intensify in the future [49]. Globally, tropical forests experienced the

most fragmentation between 2000 and 2020. However, 75% of the world's forests experienced a decrease in fragmentation between 2000 and 2020, including highly fragmented temperate and subtropical regions in northern Eurasia and southern China [50]. In the future, forest landowners and natural resource managers will be increasingly challenged to maintain forests and associated goods and services, including pollination services, in the face of environmental and socioeconomic changes.

Forest Structure

Forest structure–the horizontal and vertical arrangement of both living and dead vegetation–plays an important role in determining the amount and distribution of floral resources and breeding substrates used by pollinators. Here, we address the following three topics: 1) benefits and drivers of canopy openness, 2) effects of the shrub layer, and 3) the availability and suitability of breeding substrates. Although we discuss the effects of forest structure and composition on pollinators separately here, it should be noted that neither can be fully understood in isolation and the relative importance of each can be hard to disentangle [51].

Open canopies have increased floral herb abundance and diversity in the understory [52] and can have microclimates (e.g., temperature and soil moisture) that improve nesting habitat and enhance foraging conditions for pollinators [53–55]. The amount and diversity of floral resources in forests are highly linked to pollinator abundance and species richness [56, 57], including bees and wasps [58–62], flies [63], beetles [64], and butterflies [65]. Both natural disturbances and forest management activities can help maintain open canopies and enhance floral resource availability. The most common forest management treatments that increase canopy openness and floral resource availability in the understory include mechanized tree harvest and prescribed burning. Pollinator communities tend to respond positively to tree removal, especially in conifer forests where herbaceous floral diversity usually increases the first few years following thinning [27••, 66, 67]. For example, Davies et al. [68•] found that bee diversity and numbers of plant-bee interactions were greater in thinned versus unthinned ponderosa pine (*Pinus ponderosa*) stands in Colorado, U.S. Forest thinning in this system resulted in enhanced canopy openness and floral abundance in the understory, which were correlated with native bee abundance and diversity [68•]. In Europe, maintaining open habitats within forests (e.g., glades and clearings) and thinning forest stands is recommended to reverse recent declines in butterfly diversity [69]. Although thinning tends to benefit herbaceous floral abundance in the understory, thinning in some systems, such as tropical or temperate broadleaf forests, may reduce floral

resources for pollinators if it includes the removal of flowering trees or shrubs [70, 71].

Fire also creates more open canopies and increases floral abundance and diversity [72–75]. Some studies have shown that floral resources increase in response to the more open conditions following low-severity burns in both conifer and broadleaf forests, and that this results in higher pollinator diversity [76, 77•]. However, benefits of prescribed fire to floral and pollinator diversity tend to decline over time, sometimes within just a few years [78•]. For example, Gelles et al. [76] found that the highest floral diversity occurred one year after prescribed fire in ponderosa pine forests in Colorado whereas no difference in bee diversity was observed between burned and unburned stands after three years. In the U.S., a combination of mechanical thinning and prescribed fire has been shown in several studies to result in higher diversity of herbaceous plants and pollinators in temperate broadleaf and conifer forests [72, 77•, 79•, 80].

Both native and non-native species can form dense shrub layers that reduce the availability of flowers near the forest floor. Invasive non-native flowering plants can outcompete native plant species [81, 82] and may provide resources primarily for generalist and/or exotic pollinator species [83, 84]. Managing the shrub layer may help restore native plant and pollinator communities and their interactions [83, 85•, 86] (Fig. 1 D, E). However, this may not be the best course of action for flowering native shrubs [78•] and there is a shortage of research on the short and long-term consequences of removing invasive flowering species from forests [87–90].

In addition to floral resources, pollinators require nesting and overwintering sites which vary by taxa. Most bee species are ground-nesters and generally prefer exposed, malleable, dry soils at warm microsites with high light availability [91, 92]. While some forest bees are known to nest beneath leaf litter [93], the amount of bare soil is often positively correlated with abundance of ground-nesting bees [92]. This relationship has rarely been studied in forests, but in the southeastern U.S. prescribed fire has been shown to favor ground-nesting bees in pine (*Pinus* spp.) forests, likely via increases in bare soil [94, 95•], and soil-nesting bees declined with increasing depth of duff in broadleaf and conifer forests [96]. This trend seems to extend to other forest types [97, 98]. It is likely that most disturbances that create patches of bare soil could benefit bees that nest below ground. For example, thinning of the forest canopy can also promote bare soil, immediately via ground disturbance during harvesting and later through reduced litter deposition over time, and increase the amount of light reaching the forest floor with benefits to ground-nesting bees [55]. However, fire can compact soils which could limit the ability of bees to excavate nests [77•] and the extensive use of heavy (logging) equipment may have a similar effect [99], although this is not always the case [98].

Other pollinators, including many beetles (e.g., Cerambycidae, Scarabaeidae, Mordellidae) and hover flies (Syrphidae) require decaying wood for larval development, including that provided by tree hollows [100, 101]. While more structurally complex forests are hypothesized to increase nesting opportunities and larval feeding sites for pollinators [6••, 77•, 102, 103], relatively few studies have explicitly examined the effects of forest structure on nesting resources for pollinators. Abundance of dead wood (i.e., snags, stumps, and coarse woody debris) has been repeatedly linked to increases in cavity-nesting bees across a wide range of global forest types [6••, 79•, 96, 97, 104–106]. This may also be true for hoverflies and saproxylic beetles which also benefit from structural mosaics, increased canopy cover, and the presence of old and decadent trees [105, 107, 108]. Although some disturbances (e.g., high-severity wildfire) might be expected to reduce the availability of dead wood, several studies have found that woody debris and nesting opportunities for bees increase after severe wildfires [66, 79•, 109]. The effects of more exposed conditions on the suitability of breeding substrates for saproxylic pollinators probably vary among taxa. Although many beetle species that nest in dead wood benefit from sun exposure [110], more open conditions may negatively affect species dependent on wetter microhabitats, including many fly taxa [111–113]. More research is needed to clarify these relationships.

Forest Composition

In addition to defining which floral and nesting resources are available, the composition of forest vegetation also determines how such resources are distributed across space and time. For example, forest canopies can either represent zones of floral abundance or scarcity depending on the overstory tree community. Moreover, climatic adaptations can result in forest plant assemblages characterized by highly seasonal periods of blooming [17, 114]. Here, we review four topics of particular relevance to managers: 1) the relative value of forests dominated by conifers vs. broadleaf trees, 2) the relationship between pollinator diversity and tree diversity, 3) the conservation value of plantation forests, and 4) the effects of non-native plants, insects, and pathogens on forest pollinators.

The first trees were gymnosperms and their descendants still dominate about 32% of global forest cover [115]. They remain particularly widespread at high latitudes and high elevations, as well as in regions experiencing frequent fire. Conifer forests are characterized by relatively low plant diversity, especially in the canopy, although some open fire-maintained forests (e.g., longleaf pine, *Pinus palustris*) have some of the highest understory plant diversity outside of the tropics, including many endemic species [116].
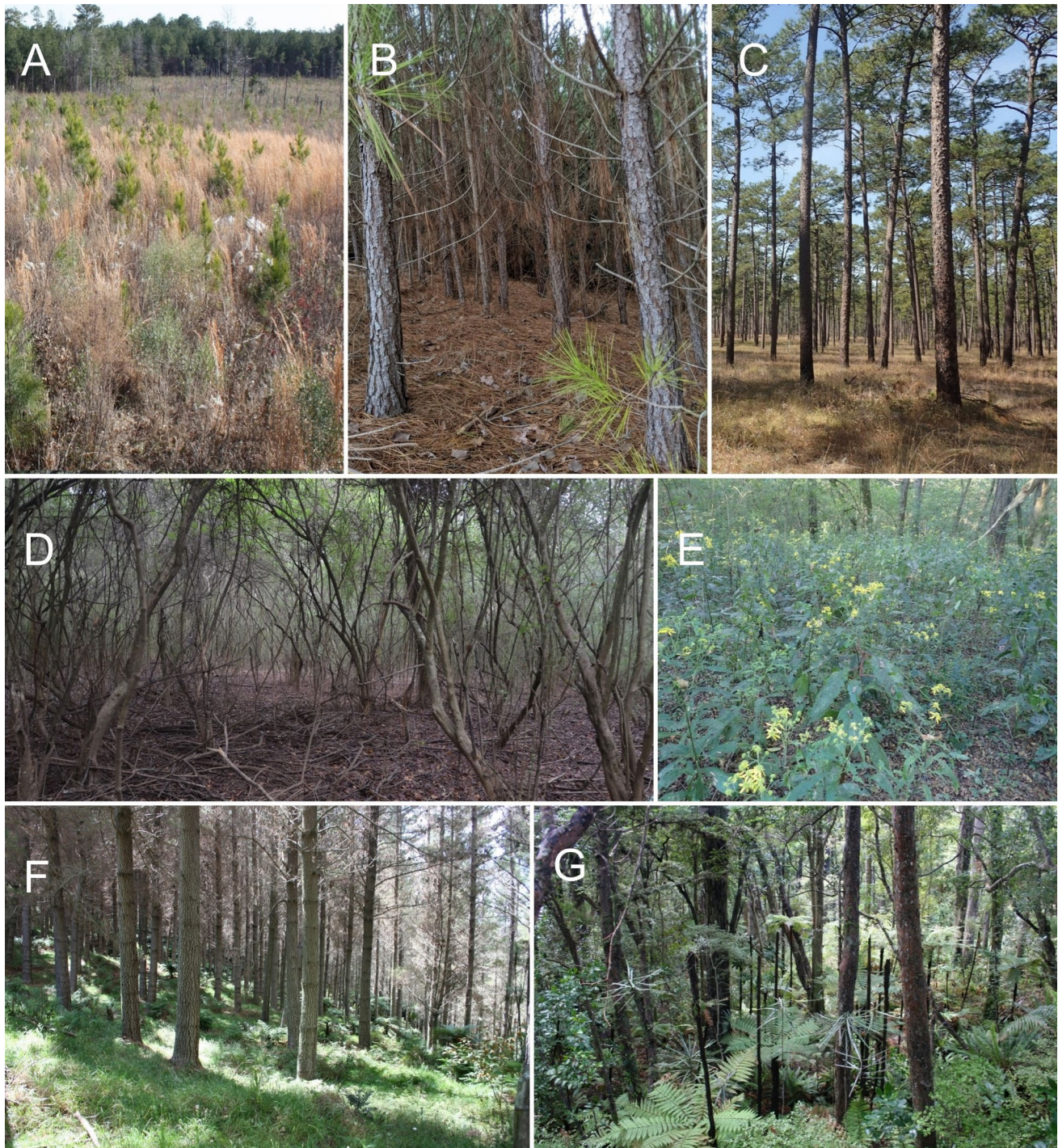
Fig. 1 Pollinator diversity changes with forest age, often declining as young stands (**A**) develop into dense stands (**B**) during the stem exclusion phase [26]. Pollinator diversity can then increase as forests mature, especially if fire or other disturbances maintain open under-stories (**C**) [26] or if floral resources are provided by the overstory trees [120]. Midstory thickets formed by invasive shrubs such as Chinese privet (*Ligustrum sinense*) (**D**) can greatly reduce floral resource availability near the forest floor [85•]. Efforts to eradicate such plants benefit flowering plants in the understory (**E**) as well as pollinators [85•]. Plantation forests such as this Monterey pine (*Pinus radiata*) plantation in New Zealand (**F**) are less structurally and composition-ally complex than native forests (**G**), with important implications for biodiversity (photos taken by Michael Ulyshen)

By contrast, the canopies of broadleaf forests commonly consist of dozens to hundreds of tree species per ha [117], including both insect- and wind-pollinated taxa. The few comparisons of pollinator diversity between conifer- and broadleaf-dominated forests suggest diversity tends to be higher in broadleaf forests. For example, this was shown for butterflies in India [118], and, more recently, work from the southeastern U.S. (where both forest types occur naturally) found that bee diversity is negatively correlated with the amount of pine forest in the surrounding landscape [119] as well as the proportion of pine locally [120]. Such findings may reflect differences in pollen quality between coniferous and broadleaf trees. Although a number of studies have reported conifer pollen on bees or in their nest provisions [121, 122••], this is typically in very small quantities [123] and may represent contamination rather than active collection [124]. Furthermore, other work suggests conifer pollen may be a less nutritious and less preferred resource than that of many angiosperm taxa [125]. Despite evidence that conifers provide less favorable floral resources to pollinators than broadleaf trees, it is important to stress that the value of conifer forests is mediated by canopy openness. As discussed in the previous section, open conifer forests are characterized by abundant floral resources in the understory and support diverse pollinator assemblages [126]. Moreover, in regions where both open conifer forests and broadleaf forests occur together, such as the southeastern U.S., the two forest types support distinct pollinator communities [119], indicating that both are important to regional diversity.

The relationship between overstory tree diversity and pollinator diversity remains understudied. Several studies reported no strong relationship between tree diversity and the richness of cavity-nesting bees [62, 127]. However, few bee species were collected in those studies and more comprehensive sampling efforts suggest tree diversity may indeed be important to bee diversity. In England, for example, the presence of flowering *Acer pseudoplatanus* greatly increased bee activity in the forest canopy [128•]. In forests of Ohio and Indiana, U.S., Cunningham-Minnick and Crist [83] reported a positive correlation between spring bee diversity and the diversity of woody plants. Moreover, in the southeastern U.S., Traylor et al. [120] found bee diversity to be positively correlated with the number of insect-pollinated broadleaf tree species nearby. Similar patterns were reported for hoverflies in a beech (*Fagus*) forest in France [107]. Although this question has not, to our knowledge, been specifically tested for other groups of pollinating insects, the diversity of beetles generally increases with increasing tree species diversity [129] and this is also likely to be the case for Lepidoptera given their host specificity as larvae. For pollen-limited tree species, pollinator abundance and diversity may be critical for maintaining fruit and seed set [130].

Planted forests cover ~ 294 million ha of which 131 million ha (~ 3% of global forest cover) consist of plantations focused on the production of goods (wood or fiber) or providing ecosystem services such as protection from desertification, wind, soil degradation, or other concerns [30]. Because the total area of plantation forests continues to increase, often replacing native forests or naturally treeless habitats, there is an urgent need to better understand how they affect biodiversity [30, 131, 132]. Globally, the most widely planted tree genera are *Pinus*, *Cunninghamia*, *Eucalyptus*, *Populus*, and *Acacia* [133]. In some parts of the world, such as North and Central America, plantations consist mostly of native species (e.g., *Pinus*) whereas in other areas, such as South America and New Zealand, most plantations consist of introduced species (e.g., *Eucalyptus*, *Pinus radiata*) [30] (Fig. 1F). Despite supporting pollinators in some landscapes, there is agreement among studies that intensively managed non-native plantations harvested on short rotations are typically of limited benefit to pollinators [134]. This is true even when the planted trees produce flowers likely to attract pollinators. For example, poor seed production observed in both *Eucalyptus* and *Acacia* plantations suggests inadequate flower visitation, possibly resulting from pesticides or cultivation practices that reduce foraging or nesting resources within and around plantations [135]. Moreover, as with any monoculture, the benefits of flowering plantation trees are limited to the flowering period of that individual species, which may be short-lived. Thus, it is critical to provide other sources of flowers nearby. This can include preserving semi-natural habitats and native trees [136–139], planting a mix of tree species [134], maintaining unplanted open spaces [140], harvesting in ways that result in uneven-aged stands [141], and employing thinning practices that increase the availability of flowers in the understory of forest plantations [142, 143].

The intentional or accidental introduction of non-native plant species has led to marked alterations of forest composition worldwide. In addition to the 44% of all plantation forests consisting of introduced species [30], many other non-native species of trees, shrubs, grasses, and herbs are naturalized or invasive. Furthermore, introduced insects and pathogens have caused strong changes in overstory tree composition, including the extirpation of mass-flowering trees (e.g., American chestnut, *Castanea dentata*) that were historically of great importance to pollinators [144]. While the effects of some introduced plants may be neutral or even positive [145, 146], others, such as certain woody shrubs, negatively affect native plants in the understory [147] and can pose a threat to entire forest ecosystems by preventing tree regeneration [85•]. Controlling such species is critical to restoring conditions for pollinators in invaded forests.

Forest Age

Forests undergo pronounced changes in both structure and composition as they age with a general trend toward greater complexity. As traditionally understood, there are four main stages of forest development [148]. These are the stand initiation stage, the stem exclusion stage when trees compete for space, the understory reinitiation stage when forest herbs and shrubs return to the understory, and the old growth stage when overstory trees begin to die. For the purposes of this review, it is helpful to add a fifth stage, marking the maturity and flowering of overstory trees, which occurs between the stem exclusion stage and the old growth stage. In addition to flowering forest trees and other plants, there is a proliferation of nesting and breeding microhabitats, such as tree hollows and dead wood, as trees age, senesce, and die. In most forests, natural disturbances result in an uneven age structure including patches of early successional habitat at landscape scales.

Comparisons of pollinator diversity among forests of different ages suggest conifer- and broadleaf-dominated forests exhibit different patterns due to variation in both disturbance regimes and availability of resources within the forest canopy. In conifer systems managed with regular prescribed fire (e.g., every few years), pollinator diversity appears to be unrelated to forest age [28••, 149, but see 150]. For example, Dixon et al. [28••] found no significant difference in bee richness among restored pine savannas across a gradient of stand ages (5–15, 15–30, 20–50, 50–75, and 75–100 yrs) on the southeastern U.S. Coastal Plain that were burned at two-year intervals. However, the same study [28••] and work by Hanula et al. [26] found bee diversity to be significantly lower in denser unburned pine stands compared to fire-maintained pine savannas. In Japan, Taki et al. [67] reported steep declines in bee richness with age in conifer plantations and Zitomer et al. [27••] reported similar results from northwestern North America where bee diversity declined by almost 50% for every five years since anthropogenic disturbance (i.e., clearcut harvest) in early successional, intensively managed Douglas-fir (*Pseudotsuga menziesii*) stands. Together, these studies suggest that conifer forests are of limited value to pollinators unless overstory tree density is reduced by fire or other disturbances (Figs. 1 A-C, Fig. 2). They also lend support to the idea that conifer trees provide insufficient floral rewards within the canopy to compensate for shaded understories. It is possible that old conifer forests characterized by uneven-aged structure and more canopy openings provide value to pollinators [150], consistent with the U-shaped curve described by Hilmers et al. [151], but more research is needed to evaluate this idea.

Unlike conifer forests, the canopies of broadleaf forests become increasingly valuable sources of floral resources as
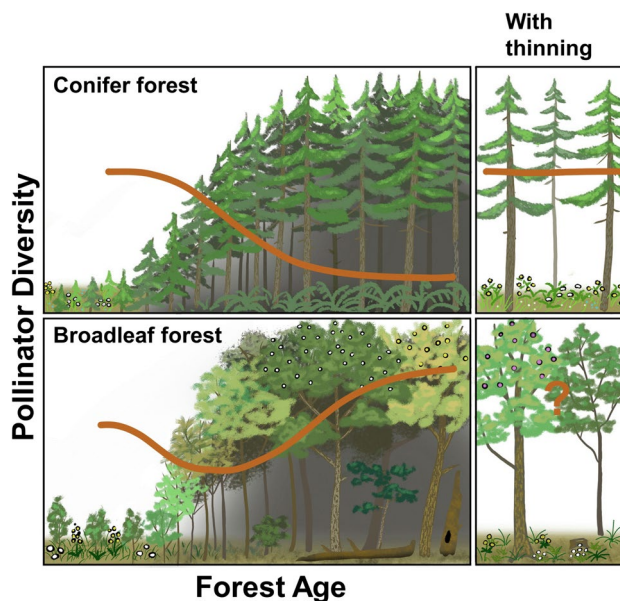
Fig. 2 Hypothesized relationships between pollinator diversity and forest age predict strong differences between conifer- and broadleaf-dominated forests. In the absence of disturbances, pollinator diversity in conifer forests declines rapidly with canopy closure and as the amount of light reaching the forest floor decreases [27••]. Reductions in conifer density–such as achieved with prescribed fire, thinning, or natural senescence–can restore pollinator diversity to levels comparable to that observed in more open habitats [26, 28••, 150, 151]. Although pollinator diversity declines similarly with time in young broadleaf forests [152•], it can increase as broadleaf trees mature and begin to flower, sometimes exceeding the diversity observed in open habitats [26]. This subsequent increase likely results from both the production of flowers in the canopy as well as nesting or breeding microhabitats essential to some forest-dependent pollinators. How pollinators may respond to thinning in broadleaf forests remains unknown. However, it is possible that reduced tree diversity and more xeric conditions may have a negative impact on some forest specialists. Given these differences, it is also hypothesized that a smaller proportion of pollinators in conifer forests are forest-dependent compared to broadleaf forests

trees age and begin to flower [122••]. Therefore, closed-canopy broadleaf forests can support high pollinator abundance and diversity, including many forest specialists. This may help explain why Taki et al. [67] reported higher pollinator diversity in mature broadleaf forests than in conifer forests of the same age in Japan. As in conifer forests, pollinator diversity declines from the open stand initiation stage to the stem exclusion stage when few flowers are available in the understory or canopy [67, 152•]. However, there is some support for the hypothesis that pollinator diversity increases as broadleaf trees mature and begin to produce flowers, and can reach levels exceeding what is observed in open habitats [26] (Fig. 2). In the southeastern U.S., Traylor et al. [120] reported that nearly half of the bee species examined were favored by older forests with a lower proportion of pine

(primarily *Pinus taeda*) in the canopy. Similar patterns are observed in tropical rainforests where diverse assemblages of stingless bees depend on old trees with cavities for nesting [153]. Thus, the relationship between pollinator diversity and forest age is hypothesized to differ between broadleaf and conifer forests (Fig. 2).

Another important consideration concerns changes in the composition of pollinator communities as forests age. Although little studied, pollinator composition can be expected to change strongly as forests transition from the youngest and most open stages to mature forests with flowering overstory trees and microhabitats required by forest-dependent species for breeding. While a considerable fraction of bee species in conifer forests depend on tree-derived resources (e.g., dead wood or resin) for nesting [126], the fact that conifer pollen is of comparatively limited value [124, 125] suggests that fewer pollinator species are dependent on conifer forests than on broadleaf forests. There is a strong need for research on changes in pollinator community composition as forests age, particularly work aimed at distinguishing between forest-dependent species and habitat generalists.

The differences described above regarding effects of forest age in broadleaf versus conifer forests have important implications for managers. Based on the information currently available, a stronger case can be made for prescribed burning or mechanically thinning to improve pollinator habitat in conifer forests as they age than in broadleaf forests. While thinning or burning broadleaf forests can be expected to increase floral resources near the ground, and this will likely favor many pollinator species, it is unclear how any associated changes in overstory tree diversity and composition may affect forest-dependent pollinators in these systems. Although a growing number of studies suggest the canopies of broadleaf forests are important to maintaining diverse pollinator assemblages, including forest-dependent species [10, 122••, 154•], much more research in this area is needed to anticipate how changes to the canopy are likely to impact this fauna at different stages of succession.

Discussion

As we have shown, forest structure, composition, and age are highly interrelated and strongly influence the diversity and composition of pollinator assemblages. In many parts of the world, human activities are resulting in forests that bear little resemblance to historical conditions. Such changes can have negative outcomes for pollinators, particularly for forest specialists. For example, many countries in South America and Asia have implemented subsidies and other incentive programs for establishing forest plantations [155]. The displacement of older and more diverse native forests by plantation monocultures of non-native tree species represent a loss of resources critical to native pollinator diversity. Other negative effects of human activities in forests include the alteration of historic disturbance regimes, such as fire exclusion, which has negative consequences for many plant species and pollinators that are adapted to disturbance. Fortunately, steps can be taken to help remedy the situation. Below we highlight some general recommendations for managers interested in improving conditions for pollinators in forested landscapes and provide suggestions for future research.

It is clear that the complexity of both forest structure and composition promotes insect diversity, including pollinators, with forest-dependent species benefiting the most. Most forests naturally become more structurally and compositionally complex as they age, although plant diversity can peak at mid-successional stages [156], with some critical resources being largely restricted to older forests [157]. While some of these resources, like large hollow-bearing trees and dead wood, can be found in younger forests and occasionally in other land cover types, older forests provide the critical benefit of ensuring temporal continuity in the availability of these resources. Thus, the conservation of old forests, where possible, will help ensure adequate resource availability for many sensitive species over time and space [158].

One characteristic typical of older forests is an uneven-aged stand structure maintained by regular natural disturbances such as wind events, wildfires, and outbreaks of forest insects and diseases [157]. Such disturbances are critical for maintaining forest biodiversity [156], so management that permits or emulates such disturbances at historic levels should improve conditions for pollinators. For example, the value of mature pine forests in the southeastern U.S. to pollinators is largely a function of fire frequency. Forests that burn infrequently tend to have higher tree densities as well as thicker understories that have fewer flowering species and low pollinator abundance and diversity [26]. By contrast, frequently burned forests have greater floral resource availability and more pollinators near the forest floor [26, 28••]. Timber harvest can also benefit pollinators by creating areas of good forage. Even clearcutting can benefit forest-dependent species provided there is suitable forest cover nearby [20]. Thus, it is important to ensure adequate availability of key resources throughout the landscape at appropriate temporal and spatial scales. For example, because most stingless bee species in the tropics nest in large cavity-bearing trees [159, 160], which are more common in older forests, it is important to incorporate old forests in management plans for this group.

Forests at stand initiation, understory reinitiation, and old growth stages of forest dynamics [148] often provide the greatest concentration of flowers within the herbaceous layer. Floral resources and pollinator diversity often decline from stand initiation to stem exclusion and will either remain low or increase

during understory reinitiation depending on the resources provided by the maturing trees in the canopy and on stand openness [161]. Maintaining open conditions may be more critical for pollinators in conifer forests than in broadleaf forests which often include mass-flowering canopy trees. While it may be possible that managing for more open canopies will benefit pollinators in all forest types, it remains poorly understood how practices that favor certain tree species over others, such as selective harvests or prescribed fire, may affect pollinator diversity within the canopies of mixed broadleaf-dominated forests. Future research aimed at clarifying the importance of different overstory tree species to forest-dependent taxa, as well as their response to alternative management actions, would be beneficial. There is a particularly strong need for more pollinator research in broadleaf forests.

A guiding principle in forest management is to mimic the disturbance regime to which an ecosystem is adapted. In some cases, conifer forests commonly experience more frequent or more widespread disturbances than broadleaf forests, such as wildfire or insect outbreaks. Disturbances are also common in broadleaf forests but often result in localized canopy gaps that arise from small-scale tree mortality events. Small clearings within regions extensively covered by broadleaf forests can be especially important to pollinators [78•], especially during times of the year when floral resources within closed-canopy forests are lacking. It is possible that more widespread thinning operations in broadleaf forests could continue to provide adequate resources for forest-dependent species while also improving conditions for habitat generalists. However, this should not be based on patterns observed in conifer forests given the many dissimilarities between these forest types (Fig. 2).

In plantations, incorporating native tree species and, when possible, planting a combination of tree species, can be expected to be of greater benefit to pollinators than monocultures of non-native tree species. As with any other crop, the negative effects of plantations on pollinators can also be ameliorated by protecting patches of native forests or other semi-natural habitats at regular intervals across the landscape [139].

Conclusions

As forest loss and degradation continue throughout much of the world, there is an urgent need to understand and satisfy the resource requirements of species endemic to each region. Because pollinators are essential to global food security, it is in our best interest to protect them and the ecosystems upon which they depend. Although the abundance and diversity of pollinators are declining in many parts of the world [162], including in some forests [163], steps can be taken to improve conditions for these organisms. It is particularly important to recognize that there is no substitute for semi-natural areas, and it is imperative that an adequate amount of such areas is conserved if we are to minimize local losses of endemic species. While targets remain poorly defined [21], a number of studies suggest strong declines in forest-dependent pollinators can be expected at < 20% native forest cover [15, 18, 19, 164] and that considerably more than that is needed to avoid declines in some taxa [20]. Such targets need to be developed separately for different regions and forest types and depending on conservation priorities.

It should be stressed that the amount of forest cover necessary to support endemic pollinator diversity will depend on the quality of forests for pollinator foraging and nesting. Native forests can generally be expected to be of greater value to pollinators than plantations of non-native tree species. Furthermore, the value of native forests to pollinators can be reduced through alterations of historic disturbance regimes, addition of invasive species, removal of hollow, moribund, or otherwise unmarketable trees, elimination of dead wood, and other interventions that result in less structurally and compositionally complex systems. Thus, in addition to protecting adequate forest cover, managers should be mindful of forest quality when working to conserve native pollinators in forests.

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Compliance with Ethical Standards

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