


# Forests are critically important to global pollinator diversity and enhance pollination in adjacent crops

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## ABSTRACT

Although the importance of natural habitats to pollinator diversity is widely recognized, the value of forests to pollinating insects has been largely overlooked in many parts of the world. In this review, we (i) establish the importance of forests to global pollinator diversity, (ii) explore the relationship between forest cover and pollinator diversity in mixed-use landscapes, and (iii) highlight the contributions of forest-associated pollinators to pollination in adjacent crops. The literature shows unambiguously that native forests support a large number of forest-dependent species and are thus critically important to global pollinator diversity. Many pollinator taxa require or benefit greatly from resources that are restricted to forests, such as floral resources provided by forest plants (including wind-pollinated trees), dead wood for nesting, tree resins, and various non-floral sugar sources (e.g. honeydew). Although landscape-scale studies generally support the conclusion that forests enhance pollinator diversity, findings are often complicated by spatial scale, focal taxa, landscape context, temporal context, forest type, disturbance history, and external stressors. While some forest loss can be beneficial to pollinators by enhancing habitat complementarity, too much can result in the near-elimination of forest-associated species. There is strong evidence from studies of multiple crop types that forest cover can substantially increase yields in adjacent habitats, at least within the foraging ranges of the pollinators involved. The literature also suggests that forests may have enhanced importance to pollinators in the future given their role in mitigating the negative effects of pesticides and climate change. Many questions remain about the amount and configuration of forest cover required to promote the diversity of forest-associated pollinators and their services within forests and in neighbouring habitats. However, it is clear from the current body of knowledge that any effort to preserve native woody habitats, including the protection of individual trees, will benefit pollinating insects and help maintain the critical services they provide.

*Key words:* Anthophila, bees, ecosystem services, agriculture, deforestation, hover flies, Syrphidae.

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## I. INTRODUCTION

*What we are doing to the forests of the world is but a mirror reflection of what we are doing to ourselves and to one another* (Maser, 1989, p. 229)

A growing body of evidence indicates that insect populations are in steep decline in both temperate and tropical regions (Sánchez-Bayo & Wyckhuys, 2019; Janzen & Hallwachs, 2021), raising concerns about the long-term health and sustainability of both natural and anthropogenic areas. Extensive and long-term reductions in pollinators are particularly concerning (Burkle, Marlin & Knight, 2013; Barendregt *et al.*, 2021; Forister *et al.*, 2010; Powney *et al.*, 2019; Ulyshen & Horn, 2023) considering that these organisms are estimated to pollinate nearly 90% of flowering plant species worldwide (Ollerton, Winfree & Tarrant, 2011) and account for 35% of global crop production by volume (Klein *et al.*, 2007). High pollinator diversity not only improves crop yields (Klein, Steffan-Dewenter & Tscharntke, 2003; Campbell *et al.*, 2022) but also provides the functional redundancy needed to compensate for losses of individual species, including managed honey bees (*Apis mellifera* L.) (Ricketts, 2004; Garibaldi *et al.*, 2013; Winfree *et al.*, 2007b). Because pollinator declines pose serious threats to food security (Klein *et al.*, 2007) as well as the reproductive success of native plants (Vamosi *et al.*, 2006; Cunningham, 2000), there is great interest in research aimed at understanding the major drivers behind these losses. Many factors are thought to be contributing to the loss of pollinators including pesticide use, pathogens, climate change, and the introduction of non-native species (Barendregt *et al.*, 2021; Vanbergen, 2013). However, the loss and degradation of natural habitats is probably the single most important factor (Wilcove *et al.*, 1998; Ellis *et al.*, 2010; Brown & Paxton, 2009; Ollerton *et al.*, 2014). Because many

landscapes are, or will soon be, dominated by anthropogenic land uses, there is a recognized need for research focused on the conservation value of remnant patches of native vegetation (Ellis *et al.*, 2010).

It is well established that natural and semi-natural areas play a large role in sustaining pollinating insect populations and their services in mixed-use landscapes (Kennedy *et al.*, 2013). However, the value of forests to these organisms remains underappreciated compared to more open habitats such as grasslands and meadows. In fact, some researchers have even suggested that forests provide suboptimal habitats for pollinators based on lower capture rates relative to adjacent open habitats (Wagner, Metzler & Frye, 2019; Mandelik *et al.*, 2012; Hoehn, Steffan-Dewenter & Tscharntke, 2010; Hagen & Kraemer, 2010). While the abundance of bees and other pollinators may sometimes be lower in forests than in other habitats, an increasing body of literature, reviewed herein, indicates that forests are not only of critical importance to global pollinator diversity (Rivers-Moore *et al.*, 2020; Mola *et al.*, 2021; Alison *et al.*, 2022; Maurer *et al.*, 2022) but also contribute importantly to pollination services in adjacent habitats (Ricketts *et al.*, 2004).

Because forests have dominated a large fraction of Earth's land area for hundreds of millions of years, far preceding the origins of angiosperms and pollinating insects (Willis & McElwain, 2002; van der Kooi & Ollerton, 2020), it is unsurprising that they are important to global pollinator diversity. At the end of the last glacial maximum (~10,000 years ago) forests covered approximately 40% of global land area (Ritchie & Roser, 2021). Although roughly a third of that forest cover has since been lost, due primarily to human activities within the past 300 years, roughly 27% of the global land area remains forested (Ritchie & Roser, 2021). In some regions, forest loss has been far more extensive than these

global estimates suggest, particularly within urbanized or intensive agricultural production landscapes where forests are typically limited to small fragments or narrow corridors bordering fields, streams, or roads (Proesmans *et al.*, 2019; Zelaya *et al.*, 2018; Franceschinelli *et al.*, 2017; Lentini *et al.*, 2012). Moreover, most remaining forests have changed substantially in their structure and/or composition due to logging practices, fragmentation, altered fire regimes, the intentional planting of exotic tree species, and the introduction of other non-native organisms (e.g. invasive woody shrubs, insect pests, and diseases). As forest loss and degradation continue throughout much of the world (Hansen *et al.*, 2013; Ellis *et al.*, 2010), especially in the tropics, there is an urgent need to understand better the interactions between forests, pollinator diversity, and the vital ecosystem services they provide.

## II. AIMS AND SCOPE

Our goal in this review is to provide evidence highlighting the importance of forests to pollinating insects and their services based on the existing literature. To be as inclusive as possible, we adopt broad definitions of ‘forest’ and ‘pollinator’. First, we recognize that the term ‘forest’ covers an exceptional diversity of ecosystems that are physically dominated by trees, ranging from closed-canopy stands consisting of several to hundreds of tree species per hectare (Phillips *et al.*, 1994), to open woodlands that are maintained by frequent fire or grazing. Additional variability in forest composition and structure comes from differences in stand size, successional stage, and management history. Thus, for the purposes of this review, we consider any grouping of trees – regardless of age, size, origins, and spacing – to be a forest. While we acknowledge that individual trees are not forests in the typical use of the word, we feel it is important to include them in this review as they occupy one extreme along the forest size gradient and are important elements in many landscapes. How the value of forests to pollinators may differ among regions, forest types, or management histories is beyond the scope of this review, although we touch on these topics briefly (e.g. see Sections VIII.5 and XI). However, we do distinguish between ‘native’ and ‘non-native’ forests, with the former consisting primarily of tree species native to a particular region and the latter referring to plantations of exotic tree species (e.g. *Eucalyptus*) introduced from other regions.

With respect to our definition of ‘pollinator’, we do not limit this review to bees, which are considered the most effective pollinators in many ecosystems (Willmer, Cunnold & Ballantyne, 2017). Instead, we recognize the role that all flower-visiting insects may play in pollination (Rader *et al.*, 2016) and therefore include findings from other taxa when possible. We acknowledge that vertebrates including bats and birds are also important pollinators in

many systems (Ratto *et al.*, 2018) but do not consider them here. While we refer to flower visitors as ‘pollinators’ throughout this review, it is well known that not all visits to flowers result in pollination and few studies establish the actual contributions of individual taxa to pollination. For example, some taxa visit plants only for nectar and rarely transfer pollen (Epps, Allison & Wolfe, 2015; Parker, Williams & Thomson, 2016). Moreover, many non-bee pollinators, cleptoparasitic bees, and some bee groups (e.g. Hylaeinae and Euryglossinae) are less hairy and carry very little pollen externally whereas other bees engage in nectar-robbing behaviour (Irwin *et al.*, 2010).

The degree to which individual pollinator taxa depend on, or benefit from, forests varies greatly and remains poorly understood for many species. Following Smith *et al.* (2021), we use the term ‘forest associated’ to refer to species that are thought to depend on forests for their survival. While these species may not be strictly confined to forests, they require resources found only in forests at some stage of their life cycle. This can include both specific floral resources or nesting resources such as hollow trees or dead wood. We also follow Smith *et al.* (2021) in defining a ‘habitat generalist’ as a species that might be found in or benefit from forests without requiring them for population persistence.

As the global literature on forests and pollinators is far too vast to provide an exhaustive overview of current knowledge in a single article, we have three distinct objectives in this review. First, we clarify the critical role forests play in supporting world pollinator diversity by describing the unique floral and non-floral resources upon which a large fraction of species depend (Section IV), show that forests support a distinct pollinator fauna (Section V), and describe how these species can be lost from extensively deforested regions (Section VI). Second, we explore the effects of forest cover (Section VIII) and fragmentation (Section IX) on pollinator diversity within both forests and adjacent land uses, and we identify factors likely to contribute to conflicting results among studies. Finally, we investigate the relationship between forest cover and crop productivity and consider the amount and spacing of forests needed to optimize pollination services in mixed-use landscapes (Section X). Ultimately, our goal for this review is to increase awareness about the critical role forests play in conserving pollinators and their services as well as to identify key knowledge gaps and priorities for future research. Table 1 provides a summary of topics covered in this article along with suggestions for future work.

## III. DIVERSITY AND LIFE HISTORIES OF POLLINATING INSECTS

While a detailed description of the diversity and biology of pollinators can be found elsewhere (Danforth, 2007; Danforth, Minckley & Neff, 2019; Larson, Kevan & Inouye, 2001), it is worth briefly summarizing the major

Table 1. Summary of topics discussed in this review with suggestions for future research.

Topic	Consideration	Suggestions for future research	Section in text
Forest resources important to pollinators	Flowers provided by forest trees, shrubs, and herbs	How important are trees, including wind-pollinated species, to forest pollinator communities? Which species are dependent on tree pollen? Under what conditions are these pollens selected or preferred? What is their nutritional quality?	IV.1
	Honeydew as an energy source	How important are honeydew and other non-floral sugar sources to the energy budgets of forest pollinators at different times of the year?	IV.2
	Plant resins used in nesting	What are the resin requirements of forest bees and where are they primarily sourced?	IV.2
	Nest and overwintering sites	Which species of ground-nesting bees prefer to nest in forests and where are these nests located? What is the relative value of fallen <i>versus</i> standing dead wood to pollinator taxa including cavity-nesting bees? How does climate impact nesting availability and longevity? How important are extreme weather events and wildfire in creating and destroying nest sites?	IV.3
	Physical structures	To what extent do forests improve foraging habitats by providing protection from wind? How important are forests and trees as mate-finding landmarks? How do they act as transit corridors and promote connectivity between patches?	IV.4
Contribution of forests to regional and global pollinator diversity	Forest-dependent pollinators	What proportion of pollinator diversity is dependent on forests? How does this vary depending on region and forest type? How are pollinators vertically distributed in forests across space and time? How important are canopy resources to pollinator diversity?	V
Pollinator regime shifts	Loss of forest-associated pollinators from highly deforested landscapes	What proportion of forest cover is needed to maintain forest-associated pollinator diversity?	VI
Benefits of diverse landscapes	Some loss of forest cover is not necessarily bad for pollinators	Which land uses benefit pollinators through enhanced habitat complementarity? Which land uses have negative effects?	VII
Effect of forest cover on pollinator diversity	Spatial scale of analysis	What spatial scale best predicts the relationship between forest cover and pollinator diversity? How does this relationship differ between small and large scales? Note: studies designed to avoid correlations between scales are especially desirable.	VIII.1
	Focal taxa	How do responses to forest cover vary among functional and taxonomic groups?	VIII.2
	Landscape context	How does the habitat in which sampling takes place affect the relationship between forest cover and pollinator diversity? How does the surrounding matrix impact results?	VIII.3
	Temporal context	What are the peak seasons of forest pollinator activity in different regions and forest types? Note: because forest pollinator communities are often highly seasonal, sampling should be conducted throughout the season.	VIII.4
	Forest type and disturbance history	How does the value of forests differ among regions and forest types? What is the relative value of old-growth <i>versus</i> secondary forests to these insects? How does selective timber harvest impact the value of forests as sources of food and nesting resources? Can ecological forestry provide resources to pollinators by, e.g. adding early successional habitat, maintaining tree diversity, assisting with climate resiliency, and enhancing structural diversity and deadwood habitat?	VIII.5
	External stressors	How will climate change affect the importance of forests to pollinators? Which pollinator taxa are expected to benefit from future climate change, and which are expected to incur negative impacts?	VIII.6

(Continues on next page)

Table 1. (Cont.)

Topic	Consideration	Suggestions for future research	Section in text
Effect of forest fragmentation	Patch number	How does patch number impact pollinator diversity and abundance across the landscape? Does patch number impact resilience to future changes (e.g. climate change, habitat destruction, and invasive species)? Note: to isolate the effects of patch number or other fragmentation metrics, researchers are encouraged to control for forest amount and quality when designing experiments.	IX.1
	Patch size	Which pollinator taxa are most dependent on large forest patches? Do life-history traits predict which pollinators will respond most strongly to changes in patch size? Does patch size influence spillover and movement of taxa between forest and non-forest habitats?	IX.2
	Patch shape and edge effects	What are the relative benefits of edge <i>versus</i> interior habitats to foraging and nesting pollinators? Which pollinator taxa will be resilient or vulnerable to patch shape and edge effects?	IX.3
	Isolation	What is the optimal distance between forest patches? How do small patches, hedgerows and individual trees enhance matrix permeability? How does isolation impact metapopulation dynamics and gene flow?	IX.4
Spillover of pollinators from forests into crops	Contribution of forest pollinators to crop pollination	For which crop species does proximity to forests enhance yield? What is the optimal amount and arrangement of forests within agriculturally dominated landscapes that maximize economic benefit while also enhancing pollinator diversity?	X
Challenges facing land managers	The number and complexity of threats facing remnant forests continue to grow	What are the species-specific responses of pollinators to management activities relative to their specific resource requirements?	XI

groups of pollinators and key life-history characteristics that differentiate them. A great diversity of insects visit flowers (Kitching *et al.*, 2007), but, because bees are particularly well adapted for collecting and transporting pollen (Danforth, 2007), they are the most important pollinators in most ecosystems. However, non-bee taxa are known to be the primary pollinators of many plants (Silberbauer-Gottsberger & Gottsberger, 1975; Ssymank *et al.*, 2008; Sakai *et al.*, 1999; Mayfield, 2005; Appanah, 1981; Appanah & Chan, 1981; Epps *et al.*, 2015) and play an important supplemental role for many others. For example, in a review of past studies, Rader *et al.* (2016) reported that non-bees account for 25–50% of all flower visits and increase fruit set beyond that achieved by bees alone. Although the relative importance of non-bee groups varies depending on region and plant species, taxa within the orders Diptera (flies), Lepidoptera (moths and butterflies), and Coleoptera (beetles) play key roles in many systems. Flies are generally considered the second most important pollinator group after bees, with the contributions of species in the families Syrphidae (hover flies) and Bombyliidae (bee flies) and the superfamily Muscoidea being especially noteworthy (Larson *et al.*, 2001; Moquet *et al.*, 2018). Within the Lepidoptera, moths are among the most important pollinators in tropical forests where they pollinate many plant species with nocturnal flowering periods (Bawa, 1990; Silberbauer-Gottsberger & Gottsberger,

1975; Nilsson *et al.*, 1987), and are the primary pollinators of many tree species and other plants (Haber & Frankie, 1989). Beetles were among the earliest pollinators of angiosperms and are likely the fourth most important group of pollinating insects globally after bees, flies, and moths (Bawa, 1990). Although some researchers have questioned their effectiveness at cross-pollination, their importance as pollinators of numerous economically useful plants demonstrates that they can perform this role (Irvine & Armstrong, 1990). Indeed, the importance of beetles to pollination in forests is likely greatly underestimated and may be highest in places such as tropical Australia where they may pollinate, depending on forest type, up to a quarter of all plant species (Irvine & Armstrong, 1990).

Several life-history differences between bees and other pollinating insects have important implications for conservation efforts. The first concerns larval diets and nesting locations. Whereas bees require floral resources (i.e. pollen and nectar) as both adults and larvae (Michener, 2007), the immature stages of other flower-visiting insect taxa feed on a wide variety of non-floral substrates, including the leaves or stems of living plants, dead wood, fungi, and insect prey [Moquet *et al.* (2018) and references therein]. As a consequence, such species often require multiple habitats to satisfy both larval and adult resource requirements. However, it should be noted that bee taxa that require specific habitats

for nesting (e.g. dead wood, tree cavities) can also require different habitats depending on the stage of development. A second important difference between bees and other pollinating insects is that bees are central-place foragers, meaning that they return to their nest or, in the case of certain males, some other previously occupied space after foraging (Roubik, 1989). As a result, most species forage within relatively small areas and few are likely to fly more than 1–2 km from their nest (Roubik, 1989). By contrast, most other pollinating taxa abandon their eggs after laying them and are therefore less restricted in their movement (Haber & Frankie, 1989).

#### IV. FORESTS PROVIDE UNIQUE RESOURCES TO POLLINATORS

Forests provide pollinators with a wide variety of flowers, nesting sites, and other resources that are generally absent from other land cover types (Fig. 1). Many pollinators depend on one or more of these resources, and are thus considered forest associated, whereas others may benefit from forests without requiring them (*sensu* Smith *et al.*, 2021). Because these resources are unevenly distributed within the three-dimensional space between the forest floor and the top of the canopy, pollinators also exhibit uneven distributions across this vertical gradient (Ramalho, 2004; Bawa *et al.*, 1985; Appanah, 1981; Bawa, 1990). However, given the logistical challenges of accessing the canopy, our understanding of pollinator diversity and ecology near the ground far exceeds what is known from the upper reaches of forests (Ulyshen, Soon & Hanula, 2010; Dorey, 2021; Urban-Mead *et al.*, 2023). With this limitation in mind, we briefly summarize current knowledge about the importance of both floral and non-floral (e.g. honeydew, resin, nesting and overwintering habitats, and structural features) resources to pollinator diversity in forests.

##### (1) Floral resources

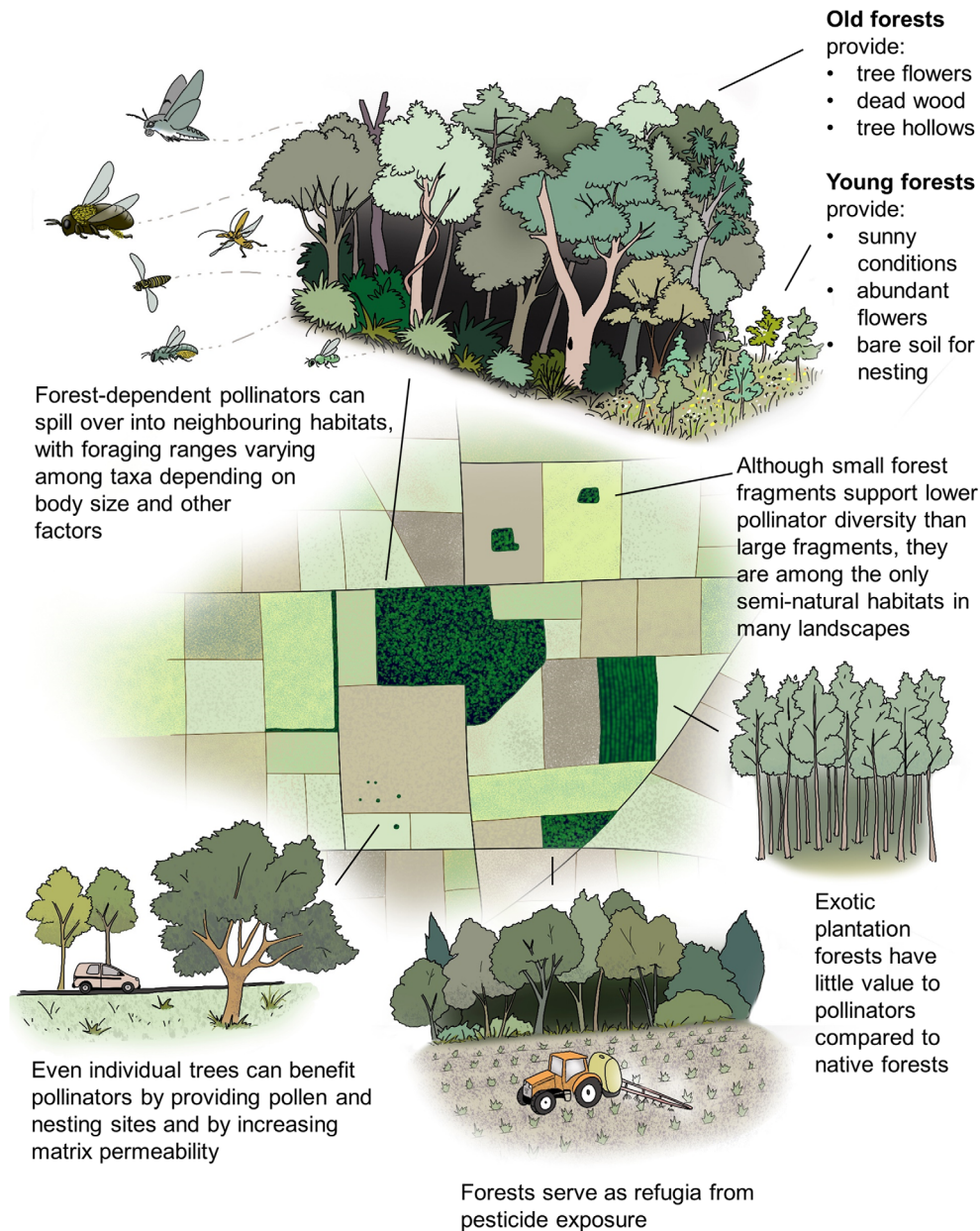
Flowers can be found throughout the forest canopy but are often concentrated in the uppermost and lower layers. In most forests, mass-blooming trees create highly heterogeneous resource landscapes both within and between years (e.g. Frankie *et al.*, 1997). This is especially true in tropical forests where the vast majority of tree species rely on animal pollinators. In Costa Rica, for example, Bawa *et al.* (1985) estimated that >97% of rainforest trees are animal pollinated, with large bees playing a particularly important role. In Brazil, stingless bees (*Meliponini*) alone visit 40–90% of all tree species (Kerr, Carvalho & Nascimento, 1999). Some bee species are known to specialize on flowers of particular tree species. In the Australian tropics, for instance, Dorey (2021) rediscovered a bee species that had not been collected for nearly a century and exclusively found it on the flowers of two tree species. Although the proportion of

wind-pollinated tree species generally increases with distance from the tropics, animal-pollinated trees are still common in many temperate forests. For example, in eastern North American forests, 20–60% of tree species, depending on the forest type, rely on animals for pollination (Regal, 1982). In temperate systems, many genera of insect-pollinated trees are recognized as important early-spring resources (Bertrand *et al.*, 2019; Allen & Davies, 2022; Urban-Mead *et al.*, 2023) and seed set in some tree species (e.g. *Prunus serotina* Ehrh. in North America) may even be pollinator limited (McLaughlin *et al.*, 2022). The proportion of animal-pollinated tree species does not fully capture the importance of trees to pollinators, however. Wind-pollinated trees are also increasingly recognized as pollen sources for bees (Kraemer & Favi, 2005; Splitt *et al.*, 2021; Saunders, 2018; Urban-Mead *et al.*, 2023; Fig. 2A), although the conditions under which such pollen is preferred or nutritionally beneficial remain largely unknown (Wood *et al.*, 2021; Roulston, Cane & Buchmann, 2000). However, some research suggests that tree-derived pollen may be more nutritious to some bees than the pollen of herbaceous plants (Wood *et al.*, 2021). Additionally, marked inter-annual fluctuations in fruiting (i.e. masting) is a common phenomenon among trees (e.g. oaks) in temperate regions. Because this is in part driven by differences in flower production between years (Sork & Bramble, 1993), masting trees may contribute to inter-annual fluctuations in tree-associated pollinator populations.

Flowers are typically rare in the shrub and herb layers beneath closed-canopy forests, being much more common in early-successional stands, areas of canopy disturbance (e.g. treefall gaps) (Ulyshen *et al.*, 2022a), or neighbouring open habitats (Mathis *et al.*, 2021, 2022). This is especially true in conifer-dominated forests that develop closed canopies (Wray & Elle, 2015). Closed-canopy temperate deciduous forests exhibit strong patterns with respect to the seasonality of flowering, with most plants (including overstorey trees) blooming in early spring before canopy closure (Schemske *et al.*, 1978; Heinrich, 1976). In northern temperate systems dominated by broadleaved trees, spring-blooming herbaceous plants (‘ephemerals’) provide a unique and brief period of flower availability prior to canopy closure (Motten, 1986). These herbs support several species of putative floral resource specialists (Fowler, 2016), as well as generalists, such as bumble bees (*Bombus* spp.) which rely on nectar resources for successful nest establishment (Mola *et al.*, 2021).

##### (2) Non-floral plant resources: honeydew and resin

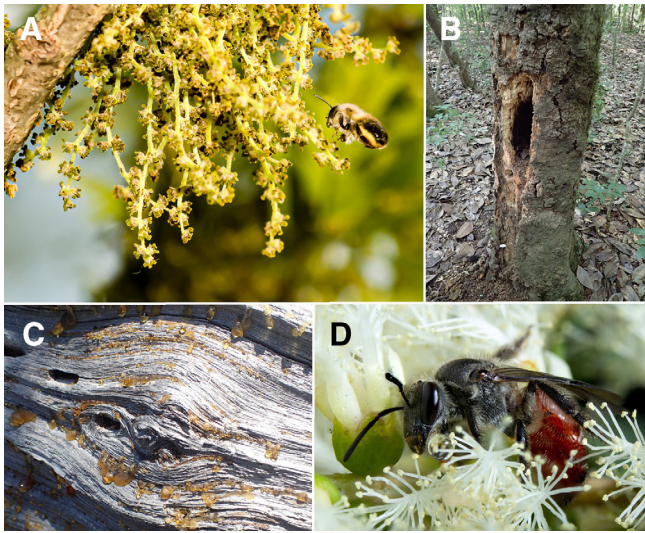
With >30% of bee species globally depending on them, the conservation value of non-floral plant resources has been increasingly recognized in recent years (Requier & Leonhardt, 2020; Chui, Keller & Leonhardt, 2022). Although many non-floral resources are used by pollinators, honeydew and resins are of particular importance to pollinators in forests. Honeydew is a sugary secretion excreted by sap-sucking scale insects, treehoppers, aphids, and other



**Fig. 1.** Forests are an important part of mixed-use landscapes worldwide where they enhance regional pollinator diversity as well as pollination services in adjacent habitats.

hemipterans (Crane & Walker, 1985). A large number of bees are known to collect accumulations of honeydew from leaves and other surfaces, or directly from the secreting insects (Roubik, 1989). Interestingly, pines (*Pinus* spp.) and firs (*Abies* spp.) are among the many tree taxa that provide honeydew (Crane & Walker, 1985; Gounari *et al.*, 2021), illustrating that even conifers can be a source of sugars to pollinators in forests. This has been particularly well documented in honey bees for which honeydew can exceed nectar in importance (Gounari *et al.*, 2021). Indeed, honeydew is so important to honey production in some regions that

beekeepers intentionally move their hives to take advantage of this resource, and forest managers may even consider honeydew when planning timber harvest schedules (de-Miguel, Pukkala & Yeşil, 2014). Honeydew collection is also known from other social bees including bumble bees [Cameron, Corbet & Whitfield (2019) and references therein], stingless bees (dos Santos *et al.*, 2019; Koch, Corcoran & Jonker, 2011), and a wide variety of solitary bee species and other insects (Konrad *et al.*, 2009; Meiners *et al.*, 2017; Gardner-Gee & Beggs, 2013). Indeed, spraying diluted honey onto foliage to simulate natural honeydew has been



**Fig. 2.** Forests are an important source of floral and nesting resources for pollinators. (A) Wind-pollinated trees, such as this oak, can be important sources of pollen for many bees (photograph: Tom Kimmmerer). (B) Hollow trees, such as this magnolia, and dead wood provide essential habitat for many pollinators including bees, flies and beetles (photograph: Michael Ulyshen). (C) Resin collected from both living and dead trees is used by many bees for nest construction (photograph: Michael Ulyshen). (D) Mass-flowering trees, such as this *Melaleuca* in Australia, are major sources of flowers to pollinators in forests (photograph: James Dorey).

shown to be an effective method for sampling bees in tropical forests (Salmah, Inoue & Sakagami, 1990; Liow, Sodhi & Elmqvist, 2001). While honeydew is thought to be less nutritious (Wäckers, van Rijn & Heimpel, 2008) and less preferred by pollinators than nectar (Konrad *et al.*, 2009), there is a growing awareness that it may be a critical resource during times of floral scarcity or drought (Gardner-Gee *et al.*, 2014; Meiners *et al.*, 2017). Ulyshen *et al.* (2010) proposed the use of honeydew as an explanation for high numbers of bees captured in the canopy of a temperate deciduous forest in Georgia, USA, in mid-summer when no trees were blooming. Similarly, Gagliardi & Wagner (2016) speculated that a suspected canopy-specialist butterfly species in North America uses honeydew or other non-floral sugar sources when nectar is unavailable.

Other important forest resources used by bees include resins (Fig. 2C), an umbrella term often used to include plant exudates such as sap, gum, and latex (Chui *et al.*, 2022). Resins are most typically used by bees in the families Apidae and Megachilidae and are primarily used for nest waterproofing and moisture management, or directly as nest-building material – usually mixed with pebbles or other small aggregates. In addition to their antimicrobial and antiparasitoid properties, resins provide chemical and visual camouflage and physical defence (e.g. entombing invading hive beetles in resin) (Chui

*et al.*, 2022). We note that many of the trees used by bees for resins are similar to those used to acquire honeydew and include many wind-pollinated species, such as conifers (Chui *et al.*, 2022), providing additional evidence that trees not traditionally thought to be important to pollinators can provide important resources to these insects.

### (3) Nesting and overwintering resources

Many pollinator taxa depend on forests for nesting resources that are not found in other land cover types. Forest type, species composition, disturbance history, and age can influence the availability of suitable nest sites. For example, old forests provide a number of resources that are rare or absent from younger forests, such as the large hollow trees used by many stingless bees in the tropics (Roubik, 1983; Salmah *et al.*, 1990). Other saproxylic resources, such as standing dead trees, rotting logs, and water-filled tree holes, also tend to be more readily available in old forests (Fig. 2B). In addition to providing structures for bee nesting (e.g. wood-boring beetle galleries in standing dead trees) (Westerfelt *et al.*, 2015; Stockhammer, 1966), such habitat elements support a wide range of flower-visiting flies and beetles which include many highly effective yet generally underappreciated pollinators (Rader *et al.*, 2016). Despite the known importance of dead wood to insect biodiversity (Ulyshen, 2018), correlative work evaluating how pollinator diversity is influenced by the amount of deadwood have yielded mixed results, with some studies finding positive relationships (Galbraith *et al.*, 2019a; Loy *et al.*, 2020; Vázquez *et al.*, 2011) and others finding no relationship (Herrault *et al.*, 2016; Urban-Mead *et al.*, 2021). One possible explanation for such inconsistencies is that pollinator taxa may not necessarily respond to deadwood at the scale at which measurements are made.

The value of forests to pollinators that nest in or near the soil varies considerably among taxa. Many species of *Andrena*, *Nomada*, *Colletes*, and other ground-nesting bees are commonly found in forests (Smith *et al.*, 2021; Batra, 1980), and dense leaf litter on the forest floor, particularly on well-drained slopes, can provide preferred cover for bumble bee nesting and overwintering (Mola *et al.*, 2021). Accumulations of leaf litter are thought to benefit overwintering bumble bees by buffering against cold weather and other environmental extremes (Williams *et al.*, 2019). At one temperate location, bumble bees nesting in forests exhibited higher reproductive output than those nesting nearby in meadows (Pugesek & Crone, 2021). In tropical forests, soils are often too moist for ground nesting, leading bumble bees in lowland areas to nest near the ground beneath roots or other vegetation (Roubik, 1989). Young or recently disturbed forests, such as those frequently subjected to prescribed fire (Ulyshen *et al.*, 2021), may provide better conditions for soil-nesting bees than closed-canopy stands, although completely open habitats may provide the best conditions for some species (Dorey *et al.*, 2021). Interestingly, the soil exposed on the root plates of fallen trees can provide valuable nesting substrates for some bees (Campbell *et al.*, 2017).



#### (4) Physical structures

The physical presence of forests, or specific physical structures, can benefit pollinators in a variety of ways. For example, there is growing recognition that forests can be important even to non-forest species by providing shelter from climatic extremes, including drought and strong winds, and thus have the potential to buffer the effects of climate change for some pollinator taxa (Dover, Sparks & Greatorex-Davies, 1997; Oliver, Brereton & Roy, 2013; Ganuza *et al.*, 2022). Both nesting and foraging bumble bees are thought to benefit from the cooler and less windy conditions provided within and adjacent to forests [Mola *et al.* (2021) and references therein]. Although little studied, the crowns of dominant trees can also be aggregation sites for males of some species which, among other landmarks, act to facilitate mate finding and reproduction (Roubik, 1989).

### V. FORESTS SUPPORT A DISTINCT POLLINATOR FAUNA

Although it has long been known that many pollinator taxa are adapted to the unique floral and nesting resources provided by forests, only recently have efforts been made to quantify the proportion of forest-associated species. This contrasts with better-studied taxa, such as birds, for which forests are required by >60% of species (Buchanan, Donald & Butchart, 2011). The best such estimate for pollinators comes from the northeastern USA where approximately 32% of analysed bee species are associated with forests while the rest are either habitat generalists (31%) or are associated with anthropogenic habitat (37%) (Smith *et al.*, 2021; Harrison, Gibbs & Winfree, 2018). The proportion of bee species in tropical regions that depend on forests has not, to our knowledge, been quantified. However, certain diverse tropical taxa, such as stingless bees (Salmah *et al.*, 1990; Roubik, 1983, 1989) and orchid bees (Aguiar *et al.*, 2015; Cândido *et al.*, 2018; Carneiro *et al.*, 2022), are strongly associated with forests. Although garnering less research attention than bees, and less formally quantified than the approach taken by Smith *et al.* (2021), other pollinator taxa exhibit similar patterns of forest dependency. Many hover flies and flower-visiting beetle taxa, for instance, nest in dead wood and are therefore strongly reliant on forests (Ulyshen, 2018; Alison *et al.*, 2022). Much like the patterns exhibited by bees, studies on these taxa show strong differences in community composition between forests and open habitats (Allison *et al.*, 2019; Branquart & Hemptinne, 2000).

Comparisons between forests and other land cover types often capture the importance of forests to local and regional pollinator diversity (Gutiérrez-Chacón, Dormann & Klein, 2018; Ganuza *et al.*, 2022; Kuussaari *et al.*, 2007; Tylianakis, Klein & Tscharrntke, 2005; Alison *et al.*, 2022; Ferreira *et al.*, 2022) but this is not always the case. Indeed, many studies comparing the total richness or abundance of

species from different land cover types have reported significantly lower numbers in forests compared to other land uses, leading some authors to conclude that forests are less important to pollinator diversity than flower-rich open habitats (Wagner *et al.*, 2019; Mandelík *et al.*, 2012; Hoehn *et al.*, 2010; Hagen & Kraemer, 2010). There are three main reasons why the value of forests to pollinators is sometimes overlooked. First, because forest pollinator communities tend to exhibit distinct seasonality (see Section VIII.4), failing to take time of year into account can yield erroneous conclusions about the diversity of pollinators in forests (Wagner *et al.*, 2019; Tylianakis *et al.*, 2005). Second, whether sampling takes place at the forest edge, where flowers and pollinators can be more concentrated throughout much of the year, or in the forest interior can strongly affect the diversity of pollinators reported (Alison *et al.*, 2022; Allen & Davies, 2022). Similarly, sampling only near the forest floor may produce misleading results given the known importance of both temperate and tropical forest canopies to pollinators, a widely recognized limitation of past research on pollinators in forests (Hagen & Kraemer, 2010; Nery *et al.*, 2018; Hall *et al.*, 2019; Hoehn *et al.*, 2010; Liow *et al.*, 2001; Allen & Davies, 2022). Researchers are increasingly aware of this shortcoming (Milam *et al.*, 2022) and are developing standardized methods for sampling pollinators within and above forest canopies (Ulyshen, Horn & Hanula, 2020a; Urban-Mead *et al.*, 2021; Cunningham-Minnick *et al.*, 2022, 2023).

Finally, decisions about how to analyse diversity data can result in contrasting conclusions about the value of forests to pollinators. Because pollinators are often less abundant in forests than in open areas with greater flower availability, it is important to control for sampling effort (i.e. rarefaction) or completeness (Chao & Jost, 2012) when comparing species richness among habitats. When this is done, richness is commonly found to be higher or similar in forests when compared to other land uses (Lentini *et al.*, 2012; Collado, Sol & Bartomeus, 2019). Moreover, differences in the number of species found in forests and other habitats are not as informative as differences in species composition. Indeed, most studies find that forests support compositionally distinct communities when compared to open habitats (Mallinger, Gibbs & Gratton, 2016; Escobedo-Kenefic *et al.*, 2020; Winfree, Griswold & Kremen, 2007a; Allen *et al.*, 2019; Alison *et al.*, 2022; Ferreira *et al.*, 2022) and pollinators in forests exhibit greater habitat specificity than those found in other land cover types (Tylianakis *et al.*, 2005; Collado *et al.*, 2019).

### VI. EXTENSIVE DEFORESTATION RESULTS IN POLLINATOR REGIME SHIFTS

It is well established that landscape changes can result in altered pollinator communities (Rader *et al.*, 2014; Lichtenberg, Mendenhall & Brosi, 2017) and this appears to be particularly the case following the conversion of forests

to other land uses. Although many forest-associated bees can be found foraging in non-forested habitats, and some species are favoured by particular crops (Benjamin, Reilly & Winfree, 2014), these species generally do not persist in extensively deforested areas, a pattern observed in both temperate and tropical regions (Harrison *et al.*, 2018; Kerr *et al.*, 1999; Brown, Barton & Cunningham, 2020; Liow *et al.*, 2001; Burkle *et al.*, 2013). Using mammal data, Pardini *et al.* (2010) demonstrated that high levels of deforestation can result in a 'regime shift' where forest-associated species are lost to the point that patch area and management efforts have little influence on the greatly diminished species pool. They further demonstrated stronger effects for forest-associated species than for habitat generalists which, by definition, are less reliant on forest patches. A growing body of evidence indicates that similar regime shifts occur among pollinators at high levels of deforestation where forest-associated species are lost and, in some cases, replaced by habitat generalists (Kerr *et al.*, 1999; Collado *et al.*, 2019; Harrison *et al.*, 2018; Hall *et al.*, 2019; Liow *et al.*, 2001; Burkle *et al.*, 2013). For example, Burkle *et al.* (2013) reported less than half the number of bee species remaining in an area of Illinois, USA, compared to 120 years previously. The authors noted that, over this time period, most forests and prairies in their study had been converted to agriculture and forest-associated taxa such as *Nomada* and species in the family Megachilidae were disproportionately missing. Similarly, Harrison *et al.* (2018) concluded that forest-associated taxa such as *Andrena*, *Nomada*, and *Osmia* were missing from anthropogenic habitats in the northeastern USA. In other studies, such as in agricultural areas of Australia and Mexico, similar regime shifts are suspected but cannot be confirmed due to an absence of information about the pollinator fauna prior to extensive forest clearance (Hall *et al.*, 2019; Jha & Vandermeer, 2010). Likewise, Liow *et al.* (2001) caught fewer forest bee species in the highly transformed landscapes of Singapore and peninsular Malaysia compared to the diversity known from Borneo. They further noted that the fauna captured in Singapore, the most deforested region investigated in that study, was distinct from nearby peninsular habitats and expressed concern that remnant forests in such places may lack the pollinators needed by patches of regenerating forest. This concern is well founded considering that species-rich tropical forests are particularly prone to pollen limitation due to high levels of competition for pollinators by plants (Vamosi *et al.*, 2006). Although it remains unclear how much forest cover is needed to prevent major losses of forest-associated pollinator diversity, regime shifts appear particularly likely after the extent of forest cover on the landscape drops below 20% based on studies from parts of Mexico (<15%), Australia (17%), Brazil (6%), and Singapore (3%) (Hall *et al.*, 2019; Jha & Vandermeer, 2010; Kerr *et al.*, 1999; Liow *et al.*, 2001). On the other hand, some forest loss, as discussed in the following section, can increase landscape pollinator diversity, especially when forest conversion results in greater habitat complementarity.

## VII. DIVERSE LANDSCAPES CAN ENHANCE POLLINATOR DIVERSITY

Because forests support distinct pollinator assemblages, including many specialist species that depend on them for floral resources, nesting/breeding substrates, or for shelter (see Section V), they are critically important to sustaining regional and global pollinator diversity (Collado *et al.*, 2019; Salmah *et al.*, 1990; Brown & Albrecht, 2001; Ferreira *et al.*, 2022). Recent work from Germany, for example, confirms that landscapes with a higher proportion of forests have more heterogeneous pollinator communities (i.e. greater beta diversity) and, consequently, greater gamma diversity (Ganuza *et al.*, 2022). The conversion of forests to early seral stages (e.g. through logging, pest outbreaks, fire, etc.) or to other land uses is not necessarily detrimental to pollinator diversity, however. On the contrary, many pollinators readily move between different habitats (Blitzer *et al.*, 2012) and it is widely accepted that landscape diversity promotes biodiversity, with patchworks of forests, agriculture, and other habitats supporting higher pollinator diversity than landscapes dominated by any single land cover type (Mandelik *et al.*, 2012; Krauss, Steffan-Dewenter & Tschardt, 2003; Oliver *et al.*, 2010; Brown *et al.*, 2020; Nery *et al.*, 2018; Montagnana *et al.*, 2021). Diverse landscapes are thought to promote habitat complementarity, ensuring floral and nesting resource availability across the landscape and throughout the year (Mallinger *et al.*, 2016; Mandelik *et al.*, 2012; Nery *et al.*, 2018; Moquet *et al.*, 2018; Mola *et al.*, 2021; Maurer *et al.*, 2022). Because peak flowering often occurs at different times in forests in comparison to crops and other land uses, for instance, forests can help sustain pollinator populations during periods of flower scarcity elsewhere (Urban-Mead *et al.*, 2023). Moreover, many forests provide floral resources, as well as non-floral sugar sources such as honeydew (see Section IV), throughout the year, thus providing greater continuity in resource availability than is typical of many crops and other anthropogenic habitats (Lentini *et al.*, 2012; Ferreira *et al.*, 2022). Conversely, floral resources provided by non-forested habitats can sustain pollinators during periods of low flower availability in forests. It is well established that many pollinator taxa depend on specific forest microhabitats, like dead wood, for larval development and on flower-rich open habitats as adults and, therefore, are expected to benefit from a mix of forests and open habitats (Moquet *et al.*, 2018; Klein *et al.*, 2003).

Although non-forested areas have the potential to boost pollinator diversity in mixed landscapes, some may have negative effects. Meadows or pastures with higher proportions of forbs and native grasses generally provide an abundance of floral resources and support a high diversity of pollinators (Nery *et al.*, 2018; Ulyshen *et al.*, 2022a; Mandelik *et al.*, 2012) whereas agricultural habitats can vary widely in their effects on pollinators, as influenced by the quality and timing of floral resources provided by particular crops, as well as the extent to which chemicals are used to control

weeds and insect pests. For instance, organic orchards and agroforestry (Steffan-Dewenter, 2003; Klein *et al.*, 2002; Bentrup *et al.*, 2019) can be expected to provide better habitat for pollinators than more intensively managed systems such as row crops.

### VIII. LOCAL EFFECTS OF FOREST COVER ARE SCALE, TAXON, AND CONTEXT DEPENDENT

As discussed in the preceding two sections, some forest loss can benefit landscape pollinator diversity but too much can result in the near elimination of forest-associated species. Thus, a key question for conserving pollinators in mixed-use landscapes is: how much forest cover is needed, and in what configuration, to provide for both forest-associated species and those which benefit from other land-use practices? Researchers exploring the relationship between forest cover and pollinator diversity have typically approached this question in two ways. First, many studies have evaluated how pollinator diversity in agriculture or other anthropogenic habitats changes with distance from the forest edge (Ricketts, 2004; Aguiar *et al.*, 2015; Klein *et al.*, 2003; Blanche, Ludwig & Cunningham, 2006). Although these studies typically fail to take the surrounding landscape into account – including the potential influence of other more distant forest patches – they provide valuable insights into the distance at which forest pollinators can move into adjacent habitats (i.e. spillover; see Section X). The second approach has involved testing the influence of proportional forest cover on pollinator diversity at one or more spatial scale(s) based on aerial imagery. Although most studies from this latter group support the conclusion that forests benefit pollinator diversity (Rahimi, Barghjehveh & Dong, 2022), others report conflicting results. Even studies conducted within the same region, such as the northeastern USA, have reached divergent conclusions about the importance of forests to pollinator diversity (Collado *et al.*, 2019; Wagner *et al.*, 2019; Winfree *et al.*, 2007a). In this section we explore several factors likely to contribute to these contrasting results. These are spatial scale, focal taxa, landscape context, temporal context, forest type and disturbance history, and external stressors.

#### (1) Spatial scale

The spatial scale at which forest cover most strongly affects pollinator diversity, whether positively or negatively, has important implications for conservation efforts. However, this is likely to vary among taxa depending on their foraging range and dispersal capabilities, landscape context, and even the response variable being measured. Because studies that examine a single spatial scale risk missing important effects, comparisons at multiple scales are needed to determine which scale correlates most strongly with a specific response, i.e. the ‘scale of effect’ (Holland, Bert & Fahrig, 2004). In some cases, opposite conclusions can be reached about the

relationship between forest cover and pollinator diversity depending on the scale investigated. In the southeastern USA, for example, Janvier *et al.* (2022) found urban bee diversity to be negatively related to the amount of forest within the surrounding 250 m but positively related to forest cover at ~2 km. Similarly, in Brazil, Montagnana *et al.* (2021) reported a positive effect of forest cover on bee diversity at large scales (5 km) but found landscape heterogeneity to be more important at the local scale (1 km). Moreover, in a study of European hover flies, Moquet *et al.* (2018) found adult habitat availability (floral density) to be more relevant at local scales whereas larval habitat availability (e.g. forest proximity) was more relevant at the landscape scale. Taken together, such findings support the idea that forests play an important role in enhancing pollinator diversity regionally (e.g. by providing habitats and resources essential to forest-associated species) but may have neutral or negative effects more locally if other land uses happen to provide better foraging habitat.

Most studies have found that bee communities generally respond most strongly to forest cover at scales between 300 and 2000 m (Taki, Kevan & Ascher, 2007; Winfree *et al.*, 2007a; Watson, Wolf & Ascher, 2011; Gutiérrez-Chacón *et al.*, 2018; Landaverde-González *et al.*, 2017; Janvier *et al.*, 2022; Park *et al.*, 2015; de Sousa *et al.*, 2022; Campbell *et al.*, 2022). Smaller species are generally thought to respond to smaller scales than larger species due to differences in foraging range and dispersal ability (Kendall *et al.*, 2022). In Greece, for example, Tscheulin *et al.* (2011) found conifer forest area to be an important predictor of small and large bee abundances at 250 m and 1000 m, respectively. Some researchers select spatial scales for analysis based on the typical flight distances of bees. For example, Benjamin *et al.* (2014) studied the effects of land cover on bees within 300 m and 1500 m radii which represented the typical flight distances for small and large bees, respectively. Although body size has been a reliable predictor of scale of effect in many studies (Tscheulin *et al.*, 2011; Franceschinelli *et al.*, 2017), some large bees respond to forest cover at smaller scales than predicted from body size (Gutiérrez-Chacón *et al.*, 2018; Benjamin *et al.*, 2014; Carneiro *et al.*, 2022). Moreover, some studies have found small bees to transfer pollen over longer distances than expected (Jha & Dick, 2010). Therefore, testing multiple scales is warranted regardless of a taxon’s expected flight capabilities.

Although much less studied than bees, the scale of effect varies among other pollinator taxa as well. In Canada, for instance, Holland *et al.* (2004) found the spatial scale at which different species of cerambycid beetles (including many flower-visiting taxa) responded most strongly to forest cover ranged from 20 to 2000 m. Although some hover fly species are capable of foraging over many kilometres (Lander, Boshier & Harris, 2010) and migrating individuals can transport pollen hundreds of kilometres (Wotton *et al.*, 2019), most are thought to respond to resource availability, including forest cover, within a few hundred metres. In Spain, Baz & Garcia-Boyer (1995) found forest area within a 1 km radius to be a positive predictor of butterfly diversity in forest

fragments. Most recently, in Brazil, Campbell *et al.* (2022) found forest cover within 400 m to best explain the richness of flower-visiting insects in açai palm (*Euterpe oleracea* Mart.) plantations. These results suggest that bees and non-bee pollinators generally respond to forest cover at similar scales, although with considerable variation among taxa.

Efforts to determine the relative importance of different spatial scales to pollinators are often complicated by land-use activities that may be correlated across scales (Steffan-Dewenter *et al.*, 2002; Ferreira *et al.*, 2015; Carneiro *et al.*, 2022). In one of the few studies designed to control for this issue, Benjamin *et al.* (2014) specifically selected blueberry (*Vaccinium corymbosum* L.) fields at which land cover at the local (300 m) and landscape (1500 m) scales were not correlated. They found that when landscapes were less dominated by agriculture (i.e. with greater forest cover), large bee abundance was high regardless of local conditions. However, when agriculture dominated the broader landscape, local land use had a stronger impact on the abundance of large bees. By ensuring that land cover attributes were uncorrelated between local and landscape scales, that study provided particularly strong evidence that even local efforts to maintain or restore forests and other natural habitats (e.g. at scales relevant to individual farms) can have measurable benefits to pollinators and their services. We suggest that more such work take this approach to disentangle these effects.

## (2) Focal taxa

The perceived value of forests to pollinators depends, in large part, on the taxa being investigated, and their associated traits. Although the responses of bees or other pollinators are often analysed in aggregate, such analyses risk underestimating the value of forests to pollinators. Among bees captured in forests in the northeastern USA, for instance, Smith *et al.* (2021) found forest associates to benefit from forest cover while habitat generalists were unaffected. They reported twice as many forest-associated bees and 20% more species in areas of greatest forest coverage compared to the least-forested areas in that study. Similarly, in Belgium, Moquet *et al.* (2018) demonstrated the value of analysing groups of hover flies with similar ecological traits separately rather than analysing all taxa combined. In that study, aphidophagous species were more affected by landscape structure (e.g. distance to forests) than saprophagous taxa, possibly because the adult and larval stages of aphidophagous species require different habitats and are therefore more dependent on landscape heterogeneity. It is clear from some taxa, such as bumble bees (Mola *et al.*, 2021), that even certain genera exhibit considerable inter-specific variability in sensitivity to forest cover. Such patterns underscore the importance of trait- or species-level analyses.

For bees, one of the best predictors that a species is sensitive to forest cover is nesting above ground (Brown *et al.*, 2020), particularly in tree cavities or dead wood. Throughout the tropics, for example, eusocial stingless bees

depend largely, although not entirely, on trees for nesting (Salmah *et al.*, 1990; Roubik, 1983, 1989). This group is particularly sensitive to the amount of forest cover (Brosi, 2009a; Salmah *et al.*, 1990; Brown & Albrecht, 2001; Gutiérrez-Chacón *et al.*, 2018; Ricketts, 2004; Heard & Exley, 1994; Klein *et al.*, 2003; Campbell *et al.*, 2022) to the point that they are largely extirpated from the most extensively deforested areas. In Brazil, for example, Kerr *et al.* (1999) estimated that 95% of stingless bee species had been lost from the São Paulo area where only 6% of the original forest cover remains. In addition to relying on forests for nesting sites, large colonies of stingless bees are also expected to benefit from the short but concentrated blooming periods of many tree species coupled with the year-round availability of flowers, a continuity of resources often absent from crops and other anthropogenic habitats (Gutiérrez-Chacón *et al.*, 2018; Ricketts, 2004; Brosi, 2009a; Ramalho, 2004). Differences in foraging strategies among stingless bees, despite similarities in nesting, are thought to make some species more sensitive to forest loss than others (Lichtenberg *et al.*, 2017). Thus, variable responses can even be expected within a closely related group of forest-associated species.

By contrast, nesting below ground is considered a defining feature of bees adapted to open habitats in many systems and, as a group, ground-nesting bees are less sensitive to forest cover (but see Section IV.3). In Colombia, Gutiérrez-Chacón *et al.* (2018) found that although overall bee richness and abundance were positively correlated with forest cover, ground-nesting species did not respond to the proportion of forests at any spatial scale and were capable of nesting in the bare soil provided by pastures. Brown *et al.* (2020) similarly found ground-nesting bees to be positively associated with pasture cover in Australia whereas species nesting above ground were associated with forest. In another Australian study, Lentini *et al.* (2012) noted that some of the smallest ground-nesting bees captured, with estimated foraging ranges of only 20–62 m, occurred far from forest remnants, indicating the ability to nest within fields near retained trees or other untilled areas. Finally, in Costa Rica, Lichtenberg *et al.* (2017) found that ground-nesting stingless bees as well asinquilines of ants or termites were more capable of persisting in deforested landscapes. Within forests, ground-nesting bees may rely on recently burned areas (Ulyshen *et al.*, 2021), canopy gaps resulting from tree falls, or other disturbed areas (Rivers *et al.*, 2018b), although it should be noted that some species regularly nest or overwinter in closed-canopy forests beneath a covering of leaf litter (Batra, 1980; Mola *et al.*, 2021). For example, in temperate regions, bumble bees are known to nest at the edge of forests, along hedgerows or in the forest interior (Osborne *et al.*, 2008; Liczner & Colla, 2019; Williams *et al.*, 2019; Pugsek & Crone, 2021; Mola *et al.*, 2021). It should also be stressed that the preferred nesting conditions for many forest-associated ground-nesting bees remain unknown and should be the focus of future investigations.

Another factor likely to influence the perceived importance of forests to pollinators is body size. Because, as mentioned in Section VIII.1, small-bodied bees and other

insects have shorter foraging ranges than larger species (Kendall *et al.*, 2022), they may be more sensitive to loss of forest cover. Indeed, this has been documented among stingless bees in Central and South America (Mayes *et al.*, 2019; Lichtenberg *et al.*, 2017; Campbell *et al.*, 2022) and is consistent with research from other systems showing that small-bodied bees are particularly vulnerable to habitat loss (Jauker *et al.*, 2013). The limited dispersal abilities of small-bodied pollinators means that their association with forests can be overlooked if sampling takes place far from the forest edge. For example, Ricketts (2004) found that forests greatly increased native bee richness and pollination 50 m from the forest edge but found no such effect at 800 or 1600 m in Costa Rican coffee (*Coffea* spp.) crops. Similarly, in Indonesia, Klein *et al.* (2003) reported a steep decline of forest-associated social bee species with distance from the nearest forest in Sulawesi, with the number approaching zero as the distance exceeded approximately 1 km. Similar results were reported for nitidulid beetles on custard apple (*Annona squamosa* L. × *A. cherimola* Mill. hybrids) in tropical Australia which sharply decreased in abundance and richness with distance from rainforests (Blanche & Cunningham, 2005). Large bees with the largest foraging range have the potential to travel much larger distances from forests than small bees. In the study by Ricketts (2004), honey bees, which were presumably nesting in the remaining forest patches, were the primary pollinators of coffee at locations 800 and 1600 m from the forest edge. The foraging range of honey bees likely explain why many studies fail to show a strong relationship between honey bee abundance and forest cover (Heard & Exley, 1994; Park *et al.*, 2015), although the presence of commercial hives may also contribute to these patterns (Brown *et al.*, 2020). Similarly, some hover fly species are known to forage over many kilometres and may be less sensitive to forest proximity than species with more limited foraging ranges (Lander *et al.*, 2010).

### (3) Landscape context

The perceived value of forests to pollinators can be strongly influenced by where sampling takes place within a landscape. Studies of pollinator diversity in open habitats, which are likely to be dominated by habitat generalists or those favouring anthropogenic disturbance, may not detect an influence of surrounding forest cover (Schüepp *et al.*, 2011; Mallinger *et al.*, 2016), especially if sampling is done far from the nearest forest or if the region has been largely deforested. A meta-analysis by Ricketts *et al.* (2008), for instance, reported an exponential decline in pollinator richness with distance from forests and other natural habitats, with richness dropping to half of its maximum at a distance of 1500 m. Thus, if pollinators are sampled too far from forests, the benefits of forests can be missed.

At the other extreme, efforts to sample pollinators within or near forests with a large proportion of forest-associated species may be more likely to detect positive correlations between forest cover and diversity (Taki *et al.*, 2007;

Proesmans *et al.*, 2019; Gutiérrez-Chacón *et al.*, 2018; Ferreira *et al.*, 2022; Campbell *et al.*, 2022). However, not all studies support this conclusion. For example, Winfree *et al.* (2007a) reported a negative relationship between forest cover and the abundance and species richness of bees in forests of the northeastern USA, while agriculture and low-density development both exhibited a positive relationship. Moreover, work by Nery *et al.* (2018) in Brazil suggested that forest cover may have a positive effect on bee diversity in open habitats but a negative effect in forests, although the effects were weak. Such findings may reflect the importance of landscape heterogeneity to pollinator diversity. For example, in the extensively forested landscape studied by Winfree *et al.* (2007a), the movement of bees from agricultural and developed areas into forests may have boosted bee abundance and richness relative to sites more dominated by forests. Consistent with this, Ferreira *et al.* (2022) captured more bee species at the edge of soybean [*Glycine max* (L.) Merr.] fields and Amazon rainforests than in either of the adjacent habitats in Brazil. However, the extent to which bees and other pollinators move from anthropogenic habitats into forests remains largely unknown (Blitzer *et al.*, 2012). Finally, as discussed above (Section VIII.2), analysing the results for forest-associated species and habitat generalists separately may better capture the benefits of forest cover to pollinator diversity.

### (4) Temporal context

Differences in the seasonality of blooming and emergence of associated pollinators between forests and other habitats likely account for some of the mixed results among previous studies. Season of sampling is an especially important consideration in temperate deciduous forests where most plants bloom early in the spring before leaf expansion (Heinrich, 1976). Because forest-associated bees exhibit similar phenological patterns, studies focused on spring-active bees may be more likely to detect positive effects of forest cover on bee populations than those sampling later in the season (Taki *et al.*, 2007; Watson *et al.*, 2011). In the northeastern USA, for example, Harrison *et al.* (2018) found forest bee activity to be largely concentrated in the spring months coinciding with the peak flowering time for most forest plant species, whereas bee numbers were low in the spring and did not peak until mid-summer months in agricultural and urban environments. Interestingly, that study found no overall differences in abundance or richness between forest and non-forest habitats after pooling data across sampling periods. Similar results were reported by Wray & Elle (2015) in oak savannas in Canada and by Grundel *et al.* (2010) in Indiana, USA. Similarly strong seasonal patterns have been reported from tropical forests, arising from seasonal changes in rainfall which, in turn, affect floral resource availability (Tylianakis *et al.*, 2005; Hagen & Kraemer, 2010). It is clear from such studies that sampling in only one season might overlook the importance of forests to pollinators at other times of the year. Although less well-studied than bees,

different seasonal patterns may also be exhibited by other pollinator taxa. In the Netherlands, for example, Barendregt *et al.* (2021) found hover fly abundance to exhibit a bimodal pattern, with a spring peak followed by a larger summer peak several months later. Thus, regardless of focal taxon, sampling throughout the year will help ensure a more accurate representation of forest pollinator diversity.

### (5) Forest type and disturbance history

It should be stressed that a tremendous variety of ecosystems are classified as ‘forest’ and that some of these ecosystems are inherently of greater value to pollinators than others. Although a complete accounting of this topic is beyond the scope of this review, it is worth briefly summarizing broad patterns likely to affect the relationship between forest cover and pollinator diversity. First, the diversity and composition of tree species is known to affect forest pollinator diversity (Jha & Vandermeer, 2010; Traylor *et al.*, 2022) and closed-canopy forests dominated by conifers are typically of lower value to pollinators than forests consisting of diverse combinations of flowering trees (Tscheulin *et al.*, 2011; Wray & Elle, 2015; Mola *et al.*, 2021). Such patterns suggest that forest cover may be more important to pollinators in some regions than others, a notion consistent with work showing that the responses of bee communities to land-use change varies significantly among geographic regions (De Palma *et al.*, 2016). Similarly, monocultural plantation forests, especially those composed of non-native species such as *Eucalyptus* or oil palm (*Elaeis guineensis* Jacq.), provide very little benefit to pollinators compared to native forests and may even be worse than deforested habitats (Aguiar *et al.*, 2015; Eltz *et al.*, 2002), although the physical presence of such stands may still provide some benefit (see Section IV.4). Plantation forests are often characterized by low-quality forage, a depauperate plant fauna, and an absence of suitable nesting sites. Wu *et al.* (2019) reported negative effects of mixed-species plantation forests on bees in China and stressed the importance of afforestation efforts to plant native rather than exotic species. In Indonesia, Power, Nielson & Sheil (2022) found a positive relationship between flower visitation by bees and proximity to remnant rainforests but nearby oil palm plantations provided no such benefit.

Even within the same forest type, as discussed below, differences in forest age and management/disturbance history can have important implications for pollinator diversity. Regarding forest age, many studies report greater diversity of hover flies and beetles from old forests due to the greater availability of dead wood and other microhabitats used for nesting (Proesmans *et al.*, 2019; Salmah *et al.*, 1990; Herrault *et al.*, 2016). By contrast, forest age appears to be less important for bees (Ulyshen, Pokswinski & Hiers, 2020b; Rasmussen, 2009; Dixon *et al.*, 2022), except for stingless bees and other taxa dependent on large trees for nesting (see Section IV.3), and many researchers stress the value of early-successional stands that provide an abundance of flowers prior to canopy closure (Taki *et al.*, 2013; Roberts,

King & Milam, 2017), especially in intensively managed conifer systems (Rivers & Betts, 2021). In the northeastern USA, Smith *et al.* (2021) reported no significant effect of forest age, measured as the proportion of older growth forests within a 500 m radius, on the richness of forest-associated or habitat-generalist bees. The abundance of habitat-generalist bees decreased with forest age, however, possibly due to the negative relationship between floral resource availability and forest age reported in that study.

Finally, management activities (e.g. timber harvest, prescribed fire, etc.) or natural disturbances (e.g. wildfire) that result in more open forest conditions or more early-successional habitat increase flower density near the ground (Hoehn *et al.*, 2010; Lindh, 2005) and generally benefit pollinators (Rivers *et al.*, 2018a,b; Hanula, Ulyshen & Horn, 2016; Grundel *et al.*, 2010; Galbraith *et al.*, 2019b). Some authors have even suggested that a history of fire suppression may have contributed to declines in pollinator numbers in some regions (Hanula, Horn & O’Brien, 2015). However, the effects of anthropogenic and natural disturbances on pollinators remain poorly understood, with a particular need for more information on species-level responses in relation to specific habitat requirements (see Section XI).

### (6) External stressors

External stressors can also affect the relationship between forest cover and observed pollinator diversity. For example, Ganuza *et al.* (2022) found mean annual temperature and proportion of forest to have an interacting effect on the gamma diversity of German butterflies. Forest cover promoted butterfly diversity in warm regions while the opposite pattern was observed in comparatively cool regions. Such findings suggest that forests may become increasingly important to pollinator diversity under climate change. Forests may also mitigate the negative effects of insecticides on pollinators. In New York, Park *et al.* (2015) found that the negative relationship between pesticides and bees decreased as the proportion of forests and other natural habitats increased. This was attributed to forests either providing more resources or serving as refugia from pesticide exposure. Similarly, in lulo (*Solanum quitoense* Lam.) crops of the Colombian Andes, Obregon *et al.* (2021) found the negative effects of imidacloprid on bee abundance and richness to be lessened by a high proportion of natural habitat in the surrounding landscape. However, natural habitats had no buffering effect at the highest pesticide concentrations, suggesting that high pesticide use is harmful regardless of landscape context. Additionally, landscapes with few forests or natural habitats need more insecticides for pest control (Meehan *et al.*, 2011). Hence, protecting forests might simultaneously buffer pollinators from the negative impacts of pesticides and decrease production costs by reducing the amount of pesticides required.

Although beyond the scope of this review, it should be noted that a wide variety of biotic agents also have the potential to degrade the quality of forests for pollinators. For

example, Sakata & Yamasaki (2015) found that deer caused bumble bees to decline in Japanese forests by severely reducing the coverage of autumn-flowering plants. Additionally, many invasive species, including various exotic plants, insects, and pathogens, continue to reduce the value of forests to pollinators. For example, by preventing native tree regeneration, some native shrubs threaten the future of forest cover in some regions (Ulyshen *et al.*, 2020b). Unfortunately, such problems only add to the list of challenges facing land managers (see Section XI).

## IX. FOREST FRAGMENTATION HAS VARIABLE EFFECTS ON POLLINATORS

Although the extent to which landscapes are forested can strongly influence pollinator diversity (see Section VIII), forest fragmentation can have additional independent effects beyond those of forest cover. As forest fragmentation continues throughout the world, particularly in the tropics (Fischer *et al.*, 2021), there is an urgent need to understand better how these changes affect pollinator communities. However, measuring such effects is challenging because fragmentation metrics are often highly correlated with both habitat amount and quality (Holzschuh, Steffan-Dewenter & Tscharrntke, 2010; Fahrig, 2017; Wang, Blanchet & Koper, 2014). Efforts to disentangle these effects suggest that habitat fragments contribute more to biodiversity than is often assumed, possibly through greater habitat diversity, increased functional connectivity, positive edge effects, enhanced landscape complementarity, or other mechanisms (Fahrig, 2017). Because few studies addressing the effects of forest fragmentation on pollinator diversity have controlled for the confounding effects of forest area (Hadley & Betts, 2012), the results from the existing literature must be interpreted with caution. With this limitation in mind, below we briefly consider how forest patch number, size, shape, and isolation are likely to affect the diversity of pollinators. Although most studies cited here, unless otherwise indicated, did not control for forest area, they still provide important insights into the effects of forest fragmentation on pollinator diversity.

### (1) Patch number

One simple measure of fragmentation is the number of forest patches for a given total area of forest. In Brazil, de Sousa *et al.* (2022) reported a negative relationship between orchid bee richness and the number of forest patches within the surrounding 500 m after controlling for the amount of forest. This suggests that landscapes with more extensive patches of forest may support higher bee diversity than an equivalent area of fragmented forest although such patterns will likely depend on the spatial scale under consideration as well as the size of the fragments.

### (2) Patch size

It is well accepted that biodiversity typically increases with patch size, a pattern often attributed to larger habitat patches containing a greater variety and availability of resources (Herrault *et al.*, 2016). While research on the diversity and abundance of pollinators in forests – including bees, hover flies, and butterflies – largely supports this expectation (Aguirre & Dirzo, 2008; Calvillo *et al.*, 2010; Nemésio & Silveira, 2007; Aizen & Feinsinger, 1994; Smith & Mayfield, 2018; Brosi, 2009b; Baz & Garcia-Boyero, 1995; Herrault *et al.*, 2016), the effects appear to be strongest when patches are more isolated (Storck-Tonon & Peres, 2017). This might be because the confounding effects of surrounding forest cover are minimized when patches are more isolated.

Some taxa appear to be more sensitive to patch size than others. Unsurprisingly, forest-associated bees are impacted more than generalists and some highly competitive taxa, such as honey bees, can become more dominant in smaller forest fragments (Aizen & Feinsinger, 1994; Brosi *et al.*, 2008). Several studies suggest that effects of forest patch size may vary between ground- and cavity-nesting bees (Neame, Griswold & Elle, 2013), with cavity-nesting species being particularly sensitive. For example, Brosi *et al.* (2008) found stingless bees that nest in tree cavities to be favoured by larger forest fragments in Costa Rica. This group is sensitive to the availability of large trees throughout the tropics (Samejima *et al.*, 2004) and because such trees experience higher mortality near forest edges (Laurance *et al.*, 2000), small fragments likely provide less suitable habitat. However, bees that nest in smaller cavities may be less sensitive to fragment size (Stangler, Hanson & Steffan-Dewenter, 2015). In Brazil, for example, Montagnana *et al.* (2021) found forest patch size to be the least relevant variable in explaining the diversity of bees and wasps in trap nests. Orchid bees are another group of tropical bees that are strongly associated with forests and sensitive to patch size (Brosi, 2009b). However, the strong flight capabilities characteristic of orchid bees allow them to move readily between fragments and their ability to use resources along forest edges likely reduces many negative effects of fragmentation (Brosi, 2009b).

The size of forest patches may have important implications for the pollination rates of plants within the forest patches as well as those in adjacent habitats. In Australia, Cunningham (2000) reported lower reproductive success for two plant species in linear forest fragments than in nearby large forest patches. Similarly, Aizen (1994) reported negative effects of fragmentation on the reproductive success of several forest plants in Argentina. However, other insect-pollinated plants appear to be less sensitive to fragmentation, possibly because pollinator numbers are not reduced enough to limit pollen transfer (Aguirre & Dirzo, 2008) or because primary pollinators readily disperse long distances across the landscape. Interestingly, Huais *et al.* (2020) suggested that forest-associated bees may disperse farther into adjacent soybean fields from large patches than from small patches.

While the literature generally supports the conclusion that large fragments host a more diverse forest-associated pollinator fauna than small fragments, these insects are also likely to benefit from the retention of even the smallest patches (Benedick *et al.*, 2006; Power *et al.*, 2022). In fact, several small patches may be of even greater conservation value than equivalent areas within larger patches (Fahrig, 2017), as there may be greater species turnover across several small patches than within a single large patch. Moreover, a recent meta-analysis found the presence of trees and woody shrubs to be one of the best predictors of pollinator diversity in gardens (Majewska & Altizer, 2020). In addition to providing a dense supply of flowers when in bloom, trees and other woody plants may also benefit pollinators by providing shelter and shade (Majewska & Altizer, 2020; Donkersley, 2019; Dover *et al.*, 1997). Hedgerows of flowering woody shrubs are known to provide important resources to pollinators (Hannon & Sisk, 2009) and even solitary trees can act as important stepping stones for long-distance pollen movement, a particularly important function for endangered trees (Lander *et al.*, 2010). Supporting this idea, Manning, Gibbons & Lindenmayer (2009) suggested that scattered trees facilitate movement of organisms across the landscape and may be particularly important to species adapting to climate change. Furthermore, Lentini *et al.* (2012) reported a positive correlation between bee diversity in agricultural areas and the number of retained trees within a 100 m radius. However, isolated trees experience elevated mortality and poor recruitment, similar to the higher rates of tree mortality observed at forest edges (Laurance *et al.*, 2000). Bee diversity in agricultural areas will likely be reduced as these ‘living dead’ trees are lost from the landscape.

### (3) Patch shape and edge effects

In addition to the size of forest patches, patch shape can also influence pollinator diversity. Shape has been commonly quantified using the ratio of perimeter: area (Baz & Garcia-Boyero, 1995) or, to make the metric more independent of patch area,  $\text{perimeter}^2:\text{area}$  (Brosi, 2009b). Patches that are more circular in shape are generally thought to be of greater conservation value due to reduced edge effects (Diamond, 1975). While the results from some pollinator studies support this expectation, such as butterflies associated with forest fragments in Spain (Baz & Garcia-Boyero, 1995), findings from other studies are less clear. For example, in Poland, Sobieraj-Betlińska, Szefer & Twerd (2023) found no difference in the richness or abundance of bees collected in linear *versus* non-linear woodlots in agricultural areas after controlling for area, isolation, and other factors. In Costa Rica, Brosi (2009b) found that although patch size was a positive predictor of orchid bee abundance and richness (marginally), both metrics were higher in patches with more edge relative to area. It is possible that perimeter: area ratio becomes detrimental to these insects beyond a certain point, however, as Nemésio & Silveira (2010) found that

fragments with larger core areas sustained orchid bee communities better in Brazil. One benefit of more elongated forest patches with greater perimeter: area ratios is that they can be encountered more readily by dispersing organisms. This was proposed by Griffin & Haddad (2021) as one explanation for why patches of longleaf pine (*Pinus palustris* Mill.) forests with winged extensions were more readily colonized by an experimentally released species of megachilid bee than were rectangular patches of the same area in South Carolina, USA.

The proportion of forest area consisting of edge habitat (defined as the area within 100 m of an edge) continues to increase and is expected to reach 50% in tropical regions by 2100 (Fischer *et al.*, 2021). Thus, there is a great need to understand the relative value of these areas to pollinators. Numerous studies, in addition to the work on orchid bees described above, have reported pollinators benefiting from forest edges. For example, studies from both temperate and tropical forests show that forest edges can provide warm and dry conditions favourable to both ground- and cavity-nesting bees (Proesmans *et al.*, 2019; da Rocha-Filho *et al.*, 2017; Stangler *et al.*, 2015). Many species nest more readily at the forest edge than in the interior although other taxa exhibit the opposite pattern (da Rocha-Filho *et al.*, 2017). However, the value of forest edges to pollinators may diminish with time, because edges experience greater tree mortality (Laurance *et al.*, 2000), are more prone to invasion by non-native plants (Brothers & Spingarn, 1992), and are more exposed to human activities and associated pollutants (Magura, Lövel & Tóthmérész, 2017).

### (4) Isolation

Biodiversity is generally expected to be lower in isolated habitat patches than in well-connected patches. Not only does isolation create a barrier to immigration, it also increases the likelihood of local populations going extinct over time. Although a number of studies have reported negative effects of isolation on pollinator diversity in forests (Benedick *et al.*, 2006; Storck-Tonon & Peres, 2017), others have reported only weak (Brosi, 2009b) or neutral effects. Such inconsistencies likely result from differences in the degree of isolation among studies, differences in foraging ranges among pollinators, and the quality of the matrix between forest patches (i.e. its permeability). For example, stronger effects of isolation have been reported for orchid bees when forest patches are separated by water (Storck-Tonon & Peres, 2017) than when they are separated by more hospitable matrices like fields (Brosi, 2009b). Encouragingly, efforts to create or protect key features such as hedgerows and scattered trees can facilitate the movement of pollinators (and transported pollen) through the matrix, thereby enhancing connectivity and preserving biodiversity in fragmented landscapes (Griffin & Haddad, 2021; Cranmer, McCollin & Ollerton, 2012; Townsend & Levey, 2005; Tewksbury *et al.*, 2002).



## X. SPILLOVER OF POLLINATORS FROM FORESTS BOOSTS YIELDS IN MANY ADJACENT CROPS

As summarized in the previous sections, forests are critically important to regional pollinator diversity and often enhance the diversity of flower-visiting insects in adjacent land uses. Many crops provide large but typically brief pulses of floral resources that can attract and benefit a range of pollinators from the surrounding landscape, including those associated with forests. As crop production is often limited by a lack of pollinators (Reilly *et al.*, 2020), the movement or ‘spillover’ of pollinators from natural habitats, including forests, into neighbouring crops (Blitzer *et al.*, 2012) generally enhances pollination services (Garibaldi *et al.*, 2011; Power *et al.*, 2022; Eeraerts, 2023). However, as discussed below, the economic benefits of forests and associated pollinators depend on a variety of factors including the forest dependency and foraging ranges of the species involved.

The strongest examples of agriculture benefitting from forest-associated pollinators come from the tropics where stingless bees are important to >60 crops, providing a service worth billions of dollars annually [Brosi (2009a) and references therein]. The value of these and other forest-associated bees to coffee production has been especially well documented. For instance, in Brazil, De Marco & Coelho (2004) found forest fragments and their associated pollinators to increase coffee production by nearly 15%. Similarly, in Costa Rica, Ricketts *et al.* (2004) found coffee yield to increase by 20% within about 1 km of forest, with an estimated annual value to a single farm of US\$60,000. Although less studied than coffee, many other crops are known similarly to benefit from forests and their associated pollinators. These include macadamia (*Macadamia integrifolia* Maiden & Betche) and longan (*Dimocarpus longan* Lour.) in Australia (Blanche *et al.*, 2006), *Solanum quitoense* in Colombia (Obregon *et al.*, 2021), cashew (*Anacardium occidentale* L.) in Brazil (Freitas *et al.*, 2014), *Jatropha curcas* L., a biofuel crop, in Mexico (Romero & Quezada-Euán, 2013), mango (*Mangifera indica* L.) in South Africa (Carvalho *et al.*, 2010), oilseed rape (*Brassica napus* L.) in Brazil (Halinski *et al.*, 2020), grapefruit [*Citrus X paradisi* Macfad. (pro. sp.)] in Argentina (Chacoff & Aizen, 2006), and aubergine (*Solanum melongena* L.) in Kenya (Gemmill-Herren & Ochieng’, 2008). In Brazil, Halinski *et al.* (2020) suggested spillover of pollinators from forests into oilseed rape may increase profits by more than US\$800 per hectare compared to the areas most isolated from forests. Thus, it is clear from this large and growing body of literature that protecting forests can have major economic benefits and is important for both sustainable agriculture and for providing pollination services to native plants. In light of such patterns, researchers are increasingly calling for the protection of forest patches to boost crop yields on farms (Halinski *et al.*, 2020; Power *et al.*, 2022; Marks *et al.*, 2022; Eeraerts, 2023).

While there are clear benefits of forest cover to some crops, this is not always the case. In Mexico, for example,

Landaverde-González *et al.* (2017) found that although bee diversity was positively correlated with forest cover, forest cover reduced chili (*Capsicum chinense*) pollination. This finding was attributed to a bee species (*Lasioglossum* sp.) that is particularly important to chili pollination yet strongly associated with non-forested habitats. Similarly, in Costa Rica, Mayfield (2005) reported no relationship between proximity to forest and the diversity of flower visitors on oil palm. In fact, flies exhibited greater visitation rates farther from forests, possibly because predation pressure was higher near forests than in the interior of palm plantations. The results from other crops are less clear. For instance, although soybean flower visitation by bees has been shown to decrease with distance from forests (Monasterolo *et al.*, 2015; Huais *et al.*, 2020), yield appears to increase with distance (Huais *et al.*, 2020; Zelaya *et al.*, 2018). As suggested by Zelaya *et al.* (2018), this apparent contradiction may be unrelated to pollination, resulting instead from competition for water or sunlight between soybeans and trees near the forest edge.

Even in crops benefitting from forest pollinators, the benefits will be limited to areas within the foraging ranges of the species involved. As discussed in Section VIII.1, small-bodied taxa may not forage beyond a few hundred metres of the forest edge whereas larger species may travel up to several kilometres (Ricketts, 2004; Halinski *et al.*, 2020). Even feral honey bees, which are among the least sensitive bees to forest fragmentation (Heard & Exley, 1994; Park *et al.*, 2015; Ricketts, 2004; Monasterolo *et al.*, 2015), have been found to decline at distances >500 m from the forest edge (Chacoff & Aizen, 2006). A meta-analysis by Ricketts *et al.* (2008) reported that while pollinator richness drops to half its level at 1500 m from the edge of forests or other natural habitats, the decline of flower visitation is steeper, halving at a distance of ~700 m. Thus, forests can be expected to provide the greatest economic benefit when they are regularly interspersed within the agricultural matrix. Indeed, Winfree *et al.* (2007b) suggested one reason watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] fields in New Jersey received more than sufficient pollination was that all were within 300 m of forests, even in areas with relatively low forest cover. Interestingly, the analysis by Ricketts *et al.* (2008) also detected a much steeper decline of bee richness from the forest edge in tropical than in temperate regions, with the points of 50% decline being about 600 m and 1300 m, respectively. Possible explanations for this pattern include the especially strong dependence on forests by stingless bees in the tropics, greater availability of floral resources in tropical landscapes creating less incentive for long-distance dispersal, and more extreme environmental conditions (e.g. higher temperatures) in tropical landscapes (Ricketts *et al.*, 2008). Whatever the underlying mechanism, these results suggest that tropical crop production may be especially sensitive to forest cover, and particularly for crops pollinated by stingless bees.

Honey bees are major pollinators of many crops and may buffer against declines of native pollinator diversity with

distance from forests. Indeed, as reviewed by Ricketts *et al.* (2008), some studies found no decline in crop yield with increasing distance from natural habitats despite strong declines in bee richness or flower visitation across the same gradient. The authors suggested this may be due to honey bees providing adequate pollination far into fields where native bee abundance is low. This is an important consideration as it suggests forests and their associated native pollinators may provide an even more critical compensatory mechanism in the event of honey bee declines than currently recognized. It also suggests that the existing literature may underestimate the importance of forest proximity to crop production, and that growers would benefit from supporting native pollinator diversity found in forests and other natural habitats adjacent to production areas.

## XI. LAND MANAGERS FACE A COMPLEX MIX OF ONGOING AND EMERGING CHALLENGES

Although beyond the scope of this review, it is worth briefly mentioning the many ongoing and emerging challenges facing forests and associated pollinator communities. In addition to the loss, fragmentation and degradation of forests, climate change and invasive species promise to have dramatic effects on the structure and composition of forests. Indeed, in some regions, these forces threaten the future of forest cover itself (Davis *et al.*, 2019; Ulyshen, Horn & Hanula, 2022b). As native forest cover continues to decline in many regions, questions about how best to manage remnant stands will only become more urgent. Regarding pollinator conservation, it is critically important to develop a better understanding of the nature of pollinator–forest associations. We need to know not only which species depend on forests, but also the floral and nesting resources required by these species. Research focused only on differences in total pollinator abundance or species richness among different forest types or conditions runs the risk of managing for habitat generalists at the expense of forest specialists. For example, it is common knowledge that open forests are characterized by greater herbaceous flower availability as well as greater flower-visiting insect activity (Hanula *et al.*, 2016). However, the effects on rarefied species richness (i.e. controlling for abundance, see Section V) may yield opposing results (Hanula *et al.*, 2015), especially if the management tool used to create open conditions removes important floral or nesting resources required by some species. Prescribed fire, for example, is a very effective tool for reducing forest basal area but also results in dramatic changes in tree composition (Pellegrini *et al.*, 2021), with poorly understood effects on pollinator community composition. The loss of certain flowering trees from the overstorey or important nesting (e.g. dead wood) or overwintering (e.g. leaf litter) substrates may have deleterious impacts on some taxa, including rare species. Such effects might be missed if researchers only focus on coarse abundance and richness metrics. Thus, only by

understanding species-level responses can optimal and adaptive management strategies be developed to ensure that suitable habitats are available for the entire suite of species endemic to an area.

## XII. CONCLUSIONS

(1) Even though research on forest pollinators has been largely confined to the two-dimensional space characterized by the forest floor – largely overlooking the complex, resource-rich, and biodiverse canopy – it is still abundantly clear from the literature that forests are critically important to supporting global pollinator diversity. It is also evident that forest-associated pollinators are not only important to the reproductive success of forest plant species, but also to the production of many insect-pollinated crops. Indeed, as substantiated by the large body of work summarized in this review, the effects of forest loss and degradation on pollinators are not limited to biological interactions within forests but often impact adjacent areas, including many of the crops on which humans depend for food and livelihood.

(2) There is evidence to suggest that a certain amount of forest loss can be beneficial to regional pollinator diversity if the new land uses enhance habitat complementarity across the landscape. However, too much forest loss can have strong negative effects on forest-associated taxa and we should expect that any major habitat alterations will create associated changes in species composition. Identifying the threshold at which forest loss results in detectable reductions in pollinator diversity should therefore be a priority for future research. Because extensive losses of forest-associated pollinators are commonly observed below 20% forest cover (Section VI), a reasonable initial goal for conservation, given current information, is to ensure that a minimum of one fifth of the landscape remains forested in regions where forests naturally dominate. Studies aimed at better developing this target (e.g. Eeraerts, 2023), which may vary regionally and depending on forest type, are urgently needed.

(3) While maintaining adequate forest cover can prevent major losses of pollinator diversity, restoration efforts will be needed to recover diversity in the most extensively deforested areas. Encouragingly, pollinators readily colonize newly created woodlands (Fuller *et al.*, 2018) and region-wide increases in forest cover have been shown to benefit pollinator diversity in a historically forested landscape (Smith *et al.*, 2021). However, restoration of the most degraded landscapes will likely face challenges. Theory suggests that the effects of patch size and isolation are unlikely to appear – especially for highly mobile taxa – until a large proportion of the habitat has been lost (Andrén, 1994). However, beyond a certain point, biodiversity may be too degraded to benefit from efforts to restore or improve habitats (Pardini *et al.*, 2010; Tschardtke *et al.*, 2005; Herrault *et al.*, 2016). Such patterns suggest that extensive deforestation will not only result in large losses of pollinator diversity

but will also greatly reduce the effectiveness of conservation programs aimed at recovering these species and the services they provide.

(4) Although the benefits of large intact forest patches to biodiversity are well known, there are also benefits of protecting smaller tracts throughout the landscape. Among these are the economic benefits from the spillover of forest-associated pollinators into neighbouring crops. It is clear from many studies that the benefits of forest-associated pollinators to crop yield diminish and eventually disappear beyond a few hundred metres of the forest edge. This suggests that conservation efforts that seek to maintain forest patches at regular spacings will achieve the greatest economic benefit. Although many questions remain about the amount and spatial configuration of forests needed to protect biodiversity and ensure the sustainable provision of pollination services, any effort to protect forest patches or otherwise improve matrix permeability is likely to provide long-term benefits.

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