WINGS

ESSAYS ON INVERTEBRATE CONSERVATION

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Forests and woodlands are valued worldwide for their environmental benefits and economic products. In this issue we explore three very different forest environments and the insects they support: old-growth coniferous forests in the Pacific Northwest, eastern broadleaf forests in New Jersey, and ancient woodlands in England.

Bees of the Eastern Forests

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People generally think of bees as creatures of open habitats, frequenting places with sunlight and plenty of flowers. And in general, that's probably true. But shouldn't there be some bee species that specialize on forest habitat? This is something I began wondering about more than fifteen years ago, when I was doing my first field work on native bees in New Jersey, a state that had once been blanketed in forest. In those studies, I found that the total number of bee species—and likewise the total number of individual bees—was roughly the same in landscapes that were largely forested as they were in deforested landscapes dominated by agriculture or suburban development. In fact, in one study, there were significantly more native bee species in the deforested landscapes. From an ecologist's point of view, this seemed odd, given that throughout most of recorded history, eastern North America was extensively forested.

Even though I found no evidence that bees as a whole benefited from the

New Jersey was once covered with forest, home to a community of bees adapted to a flora dominated by spring flowers. As the forest area shrank and the landscape became more open, the assemblage of bee species has changed too. Photograph by Nicholas A. Tonelli.

native type of vegetation, it seemed likely that the particular species found in the different habitats were different, and that, as forests were converted to human use, the loss of forest-associated species was compensated for with a gain in open-habitat species. I was curious about which species were the original forest bees—particularly because these species were likely the dominant native bee fauna in my study region prior to widespread deforestation by settlers. (The forest was largely intact until the mid-1600s, when two centuries of intense clearing for agriculture and towns began. More than half of the total forest area of the northeastern United States was lost during this period, with much of the rest cut over.) At the time I did this research, the habitat associations of most North American bee species, including the four hundred or so native to New Jersey, were unknown.

The opportunity to answer this question of the identity of the forest bee species came years later, when two excellent young scientists, Tina Harrison and Colleen Smith, working towards their PhDs in my research group at Rutgers University, studied native bees across New Jersey, Pennsylvania, and New York, and then published some of the first studies on forest bees. (Both received doctorates; Tina is now at the University of Louisiana and Colleen is at the University of Ottawa.) Tina designed a vast field-research project that allowed her to identify bees' habitat associations for the first time. A challenge for this type of work is that many bee species can readily fly a kilometer (six-tenths of a mile) or more while foraging; thus, the fact that a bee is found in a particular habitat type does not necessarily mean that it is dependent upon, or even associated with, that habitat. Tina got around this problem by choosing study sites in places where the surrounding landscape—defined as the land within fifteen hundred meters (nine-tenths of

Most sweat bees nest in the ground. The pure gold-green sweat bee (*Augochlora pura*) excavates its nests in rotting logs, a hint that it is a forest specialist. Photograph by Bryan E. Reynolds.

The common eastern bumble bee (*Bombus impatiens*) may be better able to adapt to a changing landscape than are many forest bees. Photograph by Bryan E. Reynolds.

a mile) of the site, an area of just over seven square kilometers (2.7 square miles)—was either predominantly (at least 80 percent) forested, predominantly agricultural, or predominantly urban and suburban development. Thus, at any site where she sampled bees, Tina could be reasonably certain that the bees she collected were associated with the surrounding habitat type. Almost all of the species that Tina and Colleen classified as forest associated were at least ten times as abundant in the forested landscapes as they were in agricultural and developed landscapes, and some species were up to three hundred times as abundant. In other words, these species are dependent on forests, and they are unlikely to persist in places where forests have been cleared.

Tina and Colleen found that roughly a third of all species that could be statistically analyzed—thirty-eight out of 118 species—were forest associated. Most of these species come from a small number of genera—*Andrena* (mining bees), *Nomada* (brood parasites of mining bees), *Colletes* (plasterer bees), *Osmia* (mason bees), *Bombus* (bumble bees), and *Lasioglossum* (sweat bees)—and often share some natural-history traits that match the seasonal timing of their habitat. In eastern deciduous forests there is a brief but intensive bloom of spring ephemeral wildflowers, as well as trees and shrubs, in April and May. This bloom ends by June when the trees leaf out and shade the forest understory.

A minority of forest-associated species—*Bombus* and some of the *Lasioglossum* species—are social, maintaining colonies in which multiple overlapping generations are raised throughout the spring and summer. These species have long flight seasons, and may use non-forest habitats once flowers are scarce in the forest. But most forest-associated bee species have short periods of adult

New Jersey's original forest has been fragmented and reduced by housing, industry, and agriculture. The community of bees that the landscape supports has also changed, with a shift away from forest-specialist species. Photograph by Dan Schenker.

activity and flight seasons corresponding to that period of brief springtime bloom; they emerge in March or April and disappear by June. As is typical of short-season species, three-quarters of these bees are solitary, with each female building her own nest in which she lays and provisions her eggs before she dies.

By comparison, a very different set of bee species are associated with the agricultural and suburban landscapes. These human habitats are dominated by species in the family Halictidae (sweat bees), and include many more social species with long flight seasons. As Tina put it in her published paper, "The dominant species in the native forest landscapes are solitary spring-flying bees and their associated brood parasites. In agricultural and urban landscapes these species are replaced by late-season bees from different phylogenetic lineages, many of which are social."

What about the bee species that are typical of open natural habitats, such as grasslands and meadows? We don't know for sure, because we couldn't study them. In the three-state region where we conducted our studies, there are no seven-square-kilometer areas where the landscape consisted predominantly of these habitats. They occur, but only at small scales. We suspect, however, that the bee species from our study system that once used open natural habitats, including the larger open areas created by Native Americans through burning, are found today in the disturbed open habitats created by agriculture and development. Places such as pastures, ag-

ricultural field margins, disused fields, residential yards, utility easements, and roadsides bloom throughout the summer and into fall, thus having seasonal timing very different from forests, but similar to that of open natural areas.

Once we knew the identities of the forest-associated bee species, we wanted to know how well they are persisting in today's fragmented and degraded forests. Colleen set out to answer this question in her PhD research. She worked in central New Jersey, a region densely populated not only with people but also with white-tailed deer, which degrade forests by browsing the understory wildflowers. In these heavily impacted areas she still found thirty-one of the thirty-eight forest-associated bee species, and forest species as a group were common across all of her forested study sites.

Interestingly, the forest bees and generalist bee species, which use both human habitats and forests, responded differently to forest size. Whereas the habitat generalists were similarly abundant in both large forests and smaller forest fragments, the forest bees were more abundant in the larger blocks of forest. This finding suggests that, as is the case for many other plants and animals that specialize on forest habitat, conserving large areas of forest is important for the wellbeing of forest bees.

Because their flight period coincides for the most part with the bloom of early-season trees and shrubs, forest bees are important pollinators of commercial fruits such as blueberries, apples, and cherries. Farmers have long been aware that honey bees, which originated in Africa or Asia, don't fly much in the cold, wet weather that typifies early spring in the Northeast. In contrast, the native forest bees are adapted to this climate, giving farmers an added incentive to manage for them.

Recent work led by Dr. James Reilly, a researcher in my lab group, found that wild bees are as important as honey bees in pollinating early-season fruit crops. Furthermore, these crops were often pollination-limited, meaning that they receive insufficient pollen to achieve full fruit set. This points to an opportunity to develop conservation and management guidelines for forest bee species, which could be useful for farmers seeking increased pollination.

Sadly, pollinator-habitat management as currently practiced in eastern North America is unlikely to support forest bees, for two reasons. First, it isn't done in the right place. The focus of management actions has been on enhancing pollinator habitat in open areas, such as agricultural fields and backyards, where forest-associated species are less likely to be found. Second, it focuses on the wrong time of year. The plants used to improve pollinator habitat in the eastern United States bloom in the summer, after most of the forest bees are no longer active.

The good news is that we have a wide-open opportunity to learn more about how we can manage forests to support our original native bee species.

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