Dead treetops, their bare branches curving upward, stood dark against a blue sky. Only a few years before, these had been towering, vibrant ash trees, playing a vital role in riparian forest ecosystems of northwest Ohio. Then, the emerald ash borer (*Agrilus planipennis*), a shiny green beetle whose voracious maggot-like larva feeds just beneath the bark of the trees, swept through the forests leaving death and destruction in its wake.

The emerald ash borer, or EAB, is native to eastern Asia. There, it has little impact on Asian ash species, which are able to mount defenses against the larvae. But in the late 1990s, it was accidentally introduced to North America, arriving near Detroit, Michigan, on wooden shipping material. When EAB reached the nearby forests, it encountered North American ash species that had no co-evolutionary history with the pest and almost no defense. The insect was inadvertently spread by people, moving on firewood, logs and even vehicles. Now, it occurs in 35 U.S. states and five Canadian provinces.

Our job was to monitor the effects of this invasive pest, including the decline and death of the ash trees, and the cascading effects of the sudden loss of these tree species on their forest ecosystems.

EAB impacts on forests come in three phases. The first is the initial infestation, when EAB first arrives in a new area and begins to infest the ash trees. Trees begin to slowly decline and die. Once the EAB population has increased to high levels, the second phase — rapid tree mortality — begins. Finally, after all the
trees are dead, the aftermath phase begins. As the forest goes through these stages, different impacts unfold in a somewhat predictable fashion. At each stage, the changes wrought by EAB impact wildlife species, especially in sites where ash trees dominate.

Those impacts depend on the type of forest habitat. Several ash species grow in the region currently infested by the emerald ash borer, and each inhabits a different type of forest ecosystem and plays a different role in those forests. Black ash trees (*Fraxinus nigra*) are abundant in northern forested wetlands. Green ash trees (*F. pennsylvanica*) often blanket riverbanks and floodplains. White ash trees (*F. americana*) grow mixed with many other hardwood species in upland forests.

### The initial infestation

It's often difficult to tell when EAB first enters a forest and begins infesting the trees. For some trees, it can take a few years for the EAB population to expand enough to start causing problems. Exponential growth of the EAB population soon leads to many dying and dead trees, but some still remain healthy. Many of the affected trees are still alive during the initial infestation, as EAB larvae feed beneath the bark, but the tunnels they create block the flow of sugars and water through the tree. Their canopies thin. Dead branches appear — more and more each year.

Other plant species begin to claim the newly available sunlight, water and nutrients, and they can grow rapidly. While some of these species are native trees, others may be invasive shrubs (*Hoven et al. 2017*), which can quickly crowd out the rest. In forested wetlands, where the trees act like straws, constantly sucking up water during the growing season, the water table may begin to rise as dying ash forests take up less and less water (*Slesak et al. 2014*). High water tables can hinder future regeneration and growth of ash and other native trees and plants (*Kolka et al. 2018*).

The nutritious EAB larvae just beneath the bark are an easily accessible meal for woodpeckers. They quickly home in on this new food source and focus most of their feeding activity on infested ash trees. During the early infestation period, woodpecker feeding holes and EAB’s characteristic D-shaped exit holes are sometimes the only signs of the invasive insect’s presence. Sometimes woodpeckers peck small holes in the bark to get at the larvae just beneath. Other times they remove large patches of the outer bark from the ash tree, leaving the light tan inner bark — a phenomenon called “blonding.” When scientists examined Breeding Bird Survey and Christmas Bird Count data, they found that winter populations of five woodpecker species, as well as nuthatches (*Sitta* sp.), increase after EAB infests an area (*Koenig and Leibhold 2017*). Woodpeckers can eat up to 85 percent of the EAB larvae in a tree, but by the time the woodpecker eats a larva, it has already done significant damage to the tree (*Flower et al. 2014*).
The red-bellied woodpecker is one of several species that feed on emerald ash borer larvae.

The ovenbird nests in mature forest habitat while its fledglings use early-successional habitat.

Rapid mortality

The second stage of EAB impact is marked by rapid ash tree mortality as most of the remaining large ash trees die. While occasional ash mortality occurs throughout its range due to other factors (for example, black ash decline in northern Minnesota), EAB causes widespread, high levels of ash mortality. EAB is only able to feed on ash species (and white fringe tree [Chionanthus virginicus], a less common forest tree in the same family as ash [Olacaceae], and possibly commercial olive trees, which don’t grow in the range that EAB currently infests). Once the ash trees are killed, the invasive insects have nothing left to eat. After an EAB population reaches its peak, it rapidly crashes as its food source is eliminated. Rather than disappearing completely, however, a small number of EAB persist in most sites, likely feeding on smaller ash trees that were previously too small to attract the beetles’ notice.

The loss of ash trees directly impacts the insects and animals that eat them. The nutrient-rich leaves of ash trees may be consumed on the tree or once they fall to the forest floor or into streams. Forty-three insect species are specialists that feed predominately on ash. Many other insects consume ash in addition to other tree species (Gandhi and Herm 2010). These insects provide a critical, high protein food source for nesting birds to feed their rapidly growing young. Leaf litter on the forest floor decomposes or is consumed by herbivores or detritivores, and the nutrients are replenished in the upper layers of the soil. In streams and wetlands, the leaf litter is eaten by invertebrates like snails and caddisfly larvae, which are then eaten by predators, including amphibians, fish and crayfish.

The winged samaras, or seeds, of ash trees, aided by wind dispersal, foster regeneration away from the parent tree. Produced in great numbers every four to 10 years during mast years, these fruits also serve as a wildlife food source. Several animal species are known to feed on ash seeds, including squirrels, mice, ducks, turkeys and other birds. The impacts of the loss of this food source are not known.

Standing dead ash trees, known as snags, provide habitat for many animals, including cavity-nesting birds, bats and insects. Several bat species, including the endangered Indiana bat (Myotis sodalis), roost in cavities and beneath the loose bark of dead trees (Menzel et al. 2001). While there may be temporary benefits from the increase in the number of snags caused by EAB, in the long term, the loss of the ash trees will mean fewer ash snags in the future. Native insect larvae feeding on the dead trees may support larger-than-usual winter woodpecker populations. Dead ash wood rapidly becomes brittle; tree limbs and whole trees fall, producing a pulse of coarse woody debris that provides habitat for another suite of forest animals. Salamanders and small mammals find refuge in the cool, protected areas in and beneath fallen logs. Dead wood falls into rivers, creating many kinds of habitats, including pools, slow flowing areas and side channels. The creation of complex habitat structure allows many fish species to live in the rivers and provide spawning areas. In the surrounding floodplain, high water washes the branches and logs into piles and logjams.
The nutrient cycles, hydrology and temperature of some habitats may quickly change as the remaining ash trees rapidly die (Kolka et al. 2018). Trees that shade streams and rivers help keep the water temperature cool during hot summer days. In northern forested wetlands formerly dominated by black ash trees, the altered hydrology may convert areas to more open habitat with shrubs and herbs replacing the trees. As the ash trees die, aquatic habitats may quickly change, impacting the species that live there (Youngquist et al. 2017).

**The aftermath**

After the ash trees have died, the final stage of EAB impact begins. In the aftermath of EAB, other plant species replace the ash trees, and the new habitats that emerge will determine the suitability of the site for different species of wildlife. Different outcomes are expected in different places. Some sites may change very little. Others experience drastic changes. Many bird species select certain types of forest habitat based on the structure — the vertical arrangement of vegetation — rather than the tree species present. Some inhabit open forests with large trees. Others occupy dense early-successional habitat. Some reside in forests with many layers of vegetation. Ovenbirds (*Seiurus aurocapilla*), red-eyed vireos (*Vireo olivaceus*), scarlet tanagers (*Piranga olivacea*), wood thrushes (*Hylocichla...*)

The shaded area on this map shows counties confirmed to be infested by EAB as of December 2018 (USDA APHIS PPQ). The highlighted county is where ash mortality from EAB first occurred (Siegert 2014). Magenta-colored counties represent EAB Regulated Areas of Canada. The dots show the most recent complete inventory data for U.S. Forest Inventory and Analysis plots with ash surveyed during 2004-2017 (different states have different measurement cycles; Texas data is 2004-2015, while other states' cycles start in 2009 or later and end in 2015-2017). Because a small proportion of plots were measured as long as a decade ago, current mortality may be greater than what is shown on this map. The green dots are plots where dead ash trees represent no more than 10 percent of all standing trees (of all species), while the other colors show increasing importance of ash mortality. We used the importance value, which takes into account both the size and the number of standing dead ash trees relative to other trees in the plot, because it is a good proxy for the impact of ash mortality in that forest habitat. This map does not include dead ash trees that had already fallen. Ash mortality may be due to EAB or to other causes.
USDA Forest Service Technician Tim Fox uses a slingshot to collect ash seeds from a black ash tree as part of a strategy to combat the effects of emerald ash borer.

Researcher Rachel Kappier (right) measures the trunk diameter of a surviving ash tree.

mustelina), hooded warblers (Wilsonia citrina) and worm-eating warblers (Helmitheros vermivorum) use different habitat types at different life stages. They may use old forests with large trees for nesting, and early-successional forests for fledglings to feed (Vitz and Rodewald 2006, Chandler et al. 2012). Forests with a variety of successional stages may be important for the survival of young birds of these species. As the ash trees die, the structure of forest habitats changes, and the bird species assemblages are likely to change as well.

Within 10 years, the ash snags fall and the fallen wood decays on the forest floor, providing habitat for different suites of animals and insects in later stages of decay. Belowground, changes occur as well. Forests with ash trees have different soil microbial communities than other forests. Once the ash trees die, the soil bacteria and fungus species may shift just as the aboveground plant communities change. The implications of these changes are not well understood, but morel mushroom hunters are concerned. Their prized mushrooms often grow near mature ash trees.

**Coping with EAB**

What can be done to prepare for and mitigate the effects of EAB on forest ecosystems and the wildlife they support? Experiments and studies throughout the range of North American ash species are testing planting methods and different replacement tree species and have led to recommendations for managers. A forest inventory will determine how much ash and other desirable and undesirable species are present in the forest. In areas with invasive plants, removing them before the ash trees die may help prevent them from spreading. In forests dominated by ash, especially northern black ash ecosystems, underplanting or replanting native trees may be necessary to maintain forest cover and hydrology (Iverson et al. 2015).

Although much of the ash situation seems gloomy, we and other Forest Service scientists have been working to understand and mitigate the EAB problem, and there are several recent rays of hope. Native parasitoid insects, as well as released Asian parasitoid insects, may prove to be an effective biocontrol. By killing EAB eggs and larvae, these tiny wasps (which do not sting humans) may help reduce populations of EAB and protect smaller ash trees that are growing to replace the lost large trees (Duan et al. 2018).

While surveying dying ash stands, we have found some native white ash and green ash trees that survived the EAB infestation and appear healthy. Using genetically identical copies of these trees produced through grafting, painstaking experiments have looked at how EAB adults react to the foliage and what happens to EAB larvae when eggs are placed on the trees.

Forest Service scientists have shown multiple ways these trees are able to resist EAB (Koch et al. 2015).
Some are actually able to kill EAB larvae that try to feed on them! The most promising trees are being used in a tree-resistance breeding program, with the goal of producing ash trees that can be used in restoration and reforestation efforts that will be able to survive EAB. Insecticides are now available that provide excellent protection for landscape trees, although continued treatment is necessary as EAB persists in the landscape.

The genetic diversity of ash is being studied and preserved through seed collection and insecticide protection of some populations. Ash seeds from hundreds of trees across North America have been collected and preserved in climate-controlled, long-term storage facilities for future research and restoration.

Efforts to slow the spread of EAB — including public campaigns to stop the movement of firewood, targeted infested tree removal and deployment of lethal trap trees to slow the increase of EAB populations in new outlier infestations — will buy more time for the development of tactics to respond to EAB. Over the long term, integrated pest management, where managers use site-specific combinations of different strategies, will allow forest owners and managers to prepare for, mitigate and manage the effects of EAB on their forests (Liu 2018) and the wildlife species that depend upon them.

Kathleen S. Knight is a research ecologist with the USDA Forest Service Northern Research Station.

Charles E. Flower is an ecologist with the USDA Forest Service Northern Research Station.

Mark D. Nelson is a research forester with the USDA Forest Service Northern Research Station.