Fraxinus profunda

Pumpkin Ash

Oleaceae

Fraxinus profunda by Abel Kinser, 2022

***Fraxinus profunda* Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
Forests & Natural Lands
Office of Natural Lands Management
New Jersey Natural Heritage Program

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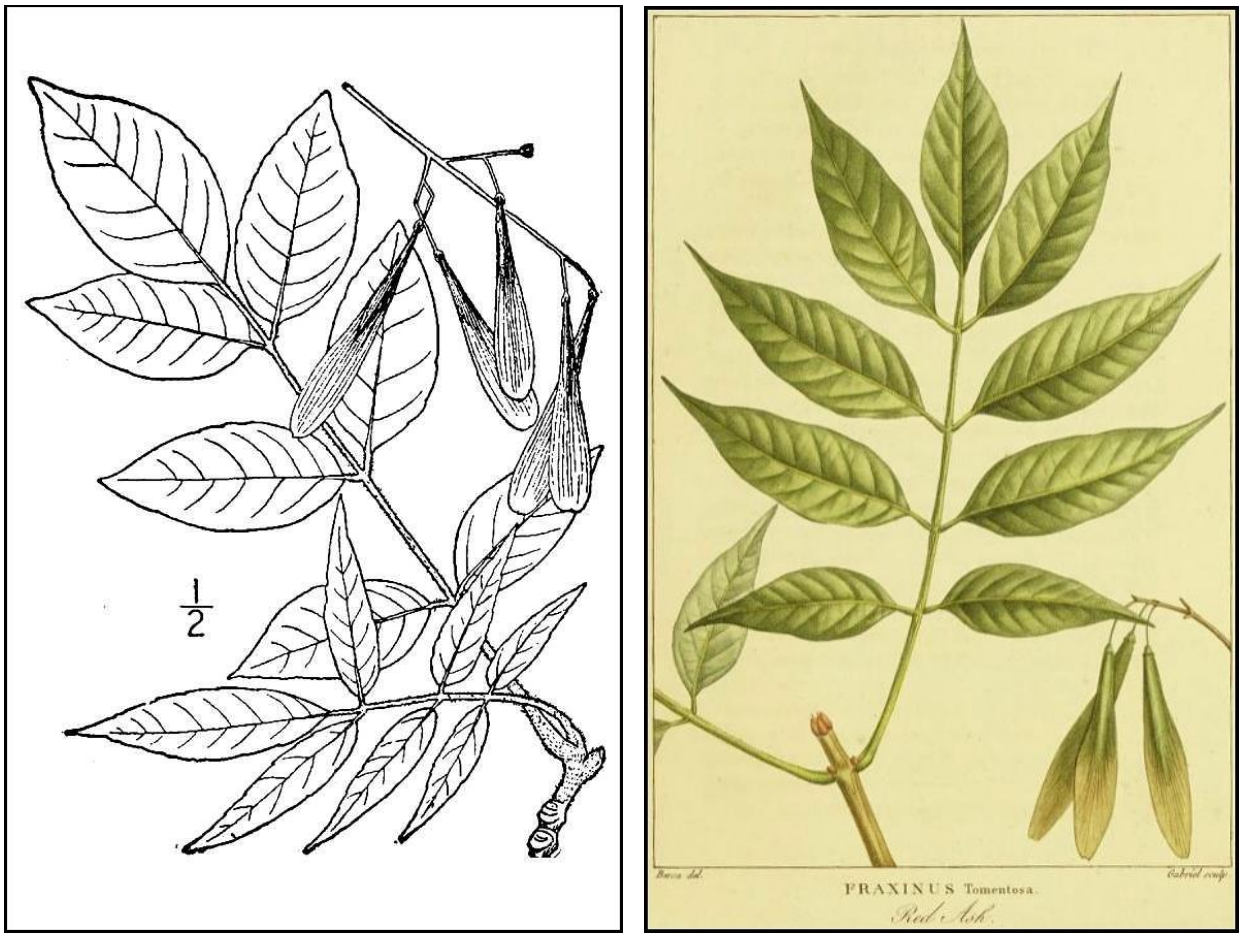
Life History

Fraxinus profunda (Pumpkin Ash) is a tree in the Oleaceae. The genus *Fraxinus* has been divided into a number of sections and *F. profunda* is included in Section *Melioides*. Species in that section are dioecious—meaning that individual plants are unisexual and produce either male or female flowers—and their flowers have sepals but lack petals. The compound leaves have 3–9 large leaflets and an unwinged rachis. All but two of the northeastern *Fraxinus* species (*F. nigra* and *F. quadrangulata*) were assigned to the same section (Dayton 1954, Miller 1955, Campbell 2017).



Left: Britton and Brown 1913, courtesy USDA NRCS 2024a. Right: Michaux 1813, courtesy of the John Carter Brown Library. Fernald (1938) cited the second image as a beautiful illustration of the species' foliage and fruit.

The members of section *Melioides* are similar in appearance and some of their morphological characteristics overlap, making identification challenging. In the past, *Fraxinus profunda* was alternately described as a variety of *F. americana* or *F. pennsylvanica* (see Synonyms section), and its status as a species was sometimes considered dubious (eg. Miller 1955, Wilson and Wood 1959). The discovery that *F. profunda* was polyploid led to the belief that it had originated via hybridization but after a close examination Hardin and Beckmann (1982) concluded that its micromorphological features did not support the hybrid origin theory. Pumpkin Ash was

previously thought to be hexaploid (Nesom 2014, Campbell 2017) but a recent genomic study determined that it was the only octoploid *Fraxinus* in North America (Whittemore et al. 2018). Among the species that occur in New Jersey, *F. profunda* appears to be most closely related to *F. pennsylvanica* (Wallander 2012).

Fraxinus profunda is a large tree: Exemplary individuals may be up to 40 meters tall and 1.73 meters in diameter at breast height (Harms 1965). The bases of the trees are often swollen or buttressed, as alluded to in the name 'Pumpkin Ash'. The bark is notably fissured and light grey or grey-brown in color. The twigs are round in cross-section and velvety during their first season. The pinnately-compound leaves usually have 7–9 stalked leaflets but leaves with as few as 3 or as many as 11 leaflets have occasionally been observed. The typical leaves are 20–45 cm long but like other members of the genus, *F. profunda* sometimes produces unusually large leaves—Craven (2008) reported leaf lengths of 48.8 cm and 51.9 cm for two individuals in Illinois. The leaflets are elliptic-ovate with acute tips, entire or slightly wavy-edged, 9–15 cm long, 3–7 cm wide, green on the upper side and slightly paler and pubescent below. The calyx of a pistillate Pumpkin Ash flower is four-parted and 3 mm in length, and the calyces persist at the base of the developing fruits. Ash fruits are single-seeded samaras (dry, indehiscent, and winged). *F. profunda* samaras are long relative to those of similar *Fraxinus* species, averaging 40–70 mm in length and 6–11 mm in width, and the bodies often become dark orange or reddish-brown at maturity. (See Fernald 1950, Dayton 1954, Gleason and Cronquist 1991, Craven 2008, Nesom 2010a & b.) Detailed descriptions of *Fraxinus* leaf morphology at the microscopic level are available in Hardin and Beckmann (1982) and Lawson et al. (2013).

Photos by Abel Kinser, 2022.

The habitats and vegetative characteristics of *Fraxinus profunda* and *F. pennsylvanica* overlap so the two species cannot be reliably distinguished at the sapling stage (Anderson et al. 2013). On average the leaves and samaras of *F. profunda* tend to be larger (Nesom 2014, Campbell 2017), but even when fruits are present identification may sometimes be difficult and the examination of multiple samaras is necessary due to variability. Snyder (1985) recorded lengths ranging from 6.5–7.5 cm in a New Jersey population. Craven (2008) recommended using a suite of features to make a species determination. The persisting calyces on *F. pennsylvanica* are smaller (1.0–1.5

mm) and the samara wings extend nearly to the base of the fruit bodies in contrast with those of *Fraxinus profunda* that arise from the upper end of the fruit body (Tiner 2009, Nesom 2010a). In the winter *F. profunda* has dark brown buds, obtuse terminal buds, and oblong leaf scars that form a 10–30 degree angle with the twigs while *F. pennsylvanica* has light brown buds, acute terminal buds, and semicircular leaf scars that nearly parallel the twigs (Whelden 1934).

Fraxinus profunda can reach reproductive maturity at an early age and ten-year-old trees have sometimes been known to bear fruit (Harms 1965). McCormac et al. (1995) observed that productivity is variable, with trees fruiting prolifically some years and hardly at all during other years. *Fraxinus* species in section *Melioides* typically begin to flower before the leaves have unfurled and that has been reported for *F. profunda* (Dayton 1954, Harms 1965); in Canada the flowers and leaves may emerge simultaneously (COSEWIC 2023). Throughout its range *Fraxinus profunda* flowers during April and May, develops samaras from August through October, and disperses seeds from October to December (Harms 1965, Craven 2008, COSEWIC 2023, NJNHP 2024, Weakley et al. 2024).

Pollinator Dynamics

Species in the genus *Fraxinus* exhibit a variety of pollination and breeding systems. About one third of the species are pollinated by insects and the balance are wind-pollinated. As with other members of the *Melioides* group, *Fraxinus profunda* is pollinated by wind (Wallander 2008). Fertilization in the species is likely enhanced by the absence of petals and the release of pollen before the leaves have expanded. Because *F. profunda* is dioecious self-pollination is not an option so seed production could be limited in low-density populations (Steven and Waller 2007).

Seed Dispersal and Establishment

Putnam et al. (1960) noted that *Fraxinus profunda* had excellent dispersal capabilities. Wind is the primary dispersal mechanism but some *F. profunda* seeds are also distributed by water (Harms 1965, Middleton 1999). The prominent wings on the fruits facilitate wind dispersal (Howe and Smallwood 1982) but may also help the seeds to float when they land in water. Harms (1965) indicated that *F. profunda* seeds can remain viable in water for several months, and also that they are often eaten by wood ducks and other birds. The dispersal of viable seeds following ingestion by waterfowl is well-documented, although results can vary depending on both plant species and seed retention time (Wongsriphuek et al. 2008, Farmer et al. 2017).

Many plants in the Oleaceae form seed banks, but those of *Fraxinus profunda* are probably short-lived because the propagules of most native northeastern ashes only remain viable for a few (3–4) years (Granger et al. 2017). *F. profunda* seeds germinate at the soil surface and they sprout readily when conditions are favorable—eg. on bare moist soil. Germination and establishment may be enhanced by a relatively open canopy but the seedlings are somewhat tolerant of shade and can generally flourish as long as the ground cover or overstory is not too dense (Putnam et al. 1960, Harms 1965). No reports of fungal associations in *F. profunda* were

found but arbuscular mycorrhizae have been documented in several other *Fraxinus* species that were examined, including *F. pennsylvanica* (Wang and Qiu 2006).

Habitat

Throughout its range *Fraxinus profunda* inhabits swamps, floodplains, and other wet lowland sites like old oxbows or vernal ponds (Fernald 1938, Harms 1965, McCormac et al. 1995, Rhoads and Block 2007, Liu 2017, COSEWIC 2023). Near the coast Pumpkin Ash may be found in freshwater tidal areas (Harms 1965, Tiner 2009, Anderson et al. 2013, Weakley et al. 2024). New Jersey habitats include a riverbank at the edge of a forested floodplain, a seepage area at the base of a ravine slope, and a remote swamp (Snyder 1985, NJNHP 2024).

Fraxinus profunda usually grows in loamy mineral soils with a layer of muck or shallow peat at the surface (Harms 1965). Surface water can be present well into the growing season or continuously throughout the year. *F. profunda* seedlings are tolerant of saturated soils and may even increase their growth in response to saturation. Older trees typically grow slowly in wet places and more rapidly in sites that are better drained (Mohlenbrock 1959, Hosner and Leaf 1962, Harms 1965). Generally speaking, *F. profunda* has intermediate light requirements and it may be found out in the open or in dense shade (Weakley et al. 2024). However, the species is most likely to thrive in shaded sites during the seedling stage and the trees become less tolerant of shading with age (Harms 1965, Granger et al. 2017).

In the south, *Fraxinus profunda* often grows in cypress-tupelo swamps where species such as *Taxodium distichum, Nyssa aquatica,* and *N. biflora* are characteristic (Thompson 1980, White 1983, Tiner 2009, Anderson et al. 2013). *F. profunda* may also occur in saturated or seasonally flooded forests where *Acer rubrum* and *Fraxinus pennsylvanica* are prevalent (Breden et al. 2001). Near the northern end of its range, Pumpkin Ash has been known to share habitat with trees like *Acer saccharinum, Gleditsia aquatica, G. triacanthos, Populus heterophylla, Quercus bicolor,* or *Q. palustris* (Mohlenbrock 1959, McCormac et al. 1995, COSEWIC 2023). *Acer negundo, Fagus grandifolia,* and *Liriodendron tulipifera* were noted as its associates at one New Jersey site (NJNHP 2024). In some locations *Fraxinus profunda* was identified as a dominant species in the canopy (Steury 1999, Breden et al. 2001, Anderson et al. 2013) or in the sapling layer (Granger 2017) but at other sites it was only a minor component of the forest (Boone 1983, McCormac et al. 1995).

Wetland Indicator Status

Fraxinus profunda is an obligate wetland species, meaning that it almost always occurs in wetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2024b)

FRPR

Coefficient of Conservancy (Walz et al. 2020)

CoC = 9. Criteria for a value of 9 to 10: Native with a narrow range of ecological tolerances, high fidelity to particular habitat conditions, and sensitive to anthropogenic disturbance (Faber-Langendoen 2018).

Distribution and Range

The global range of *Fraxinus profunda* is restricted to the eastern and central United States and Canada (POWO 2024). The map in Figure 1 shows the extent of Pumpkin Ash in North America. *F. profunda* is largely absent from the center of its depicted range: Occurrences are mainly located along the Atlantic and Gulf coasts in the east and the Mississippi and Ohio River watersheds in the west (McCormac et al. 1995, Nesom 2010a, Kartesz 2015). In Canada it is only known from southwestern Ontario (COSEWIC 2023).

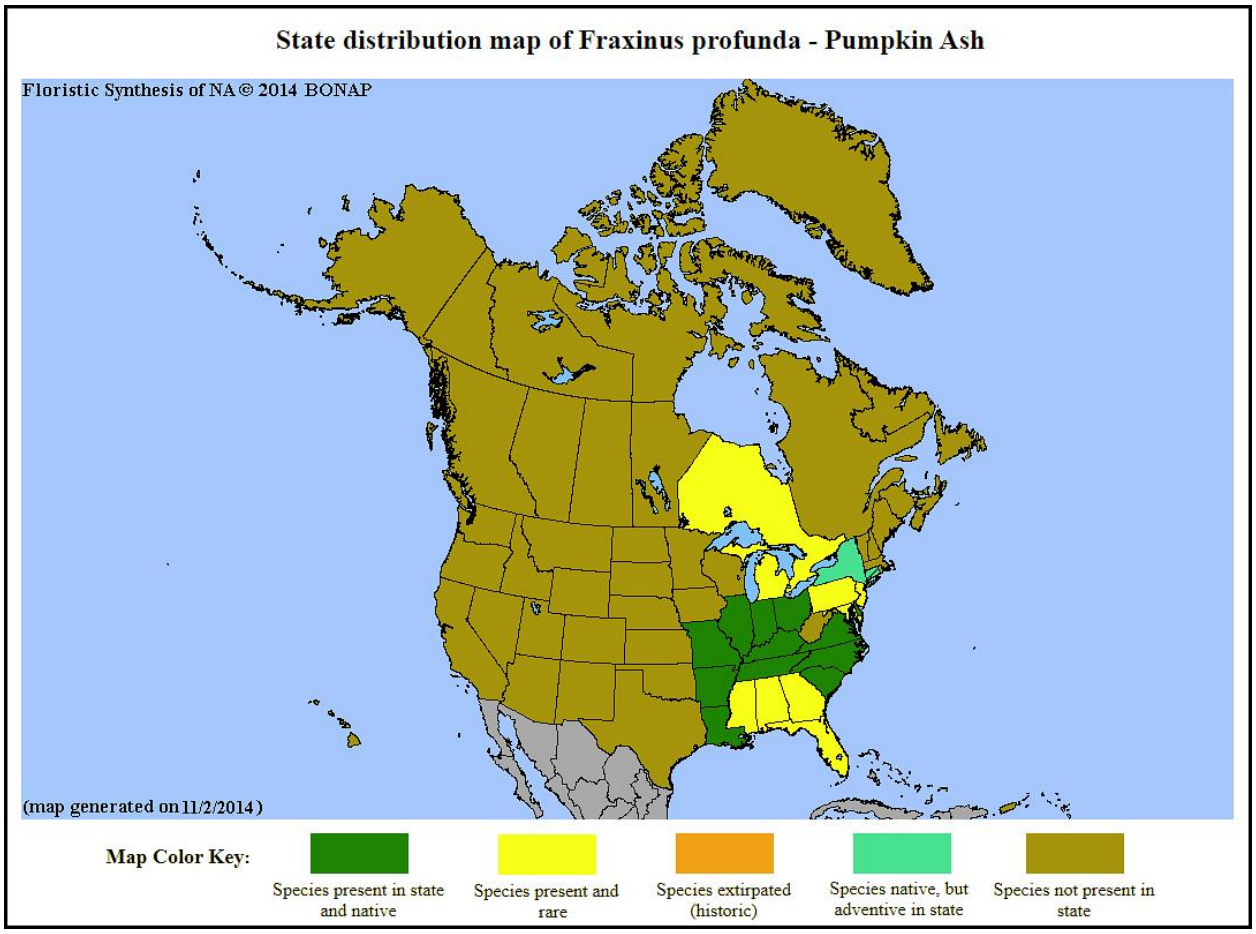


Figure 1. Distribution of F. profunda in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2024b) shows records of *Fraxinus profunda* in three New Jersey counties: Cape May, Monmouth, and Ocean (Figure 2). Specimens from Burlington and Sussex counties that are labeled as *F. profunda* are in the collection at the New York Botanical Garden

Steere Herbarium (Mid-Atlantic Herbaria 2024). The data include historic reports and do not reflect the current distribution of the species.

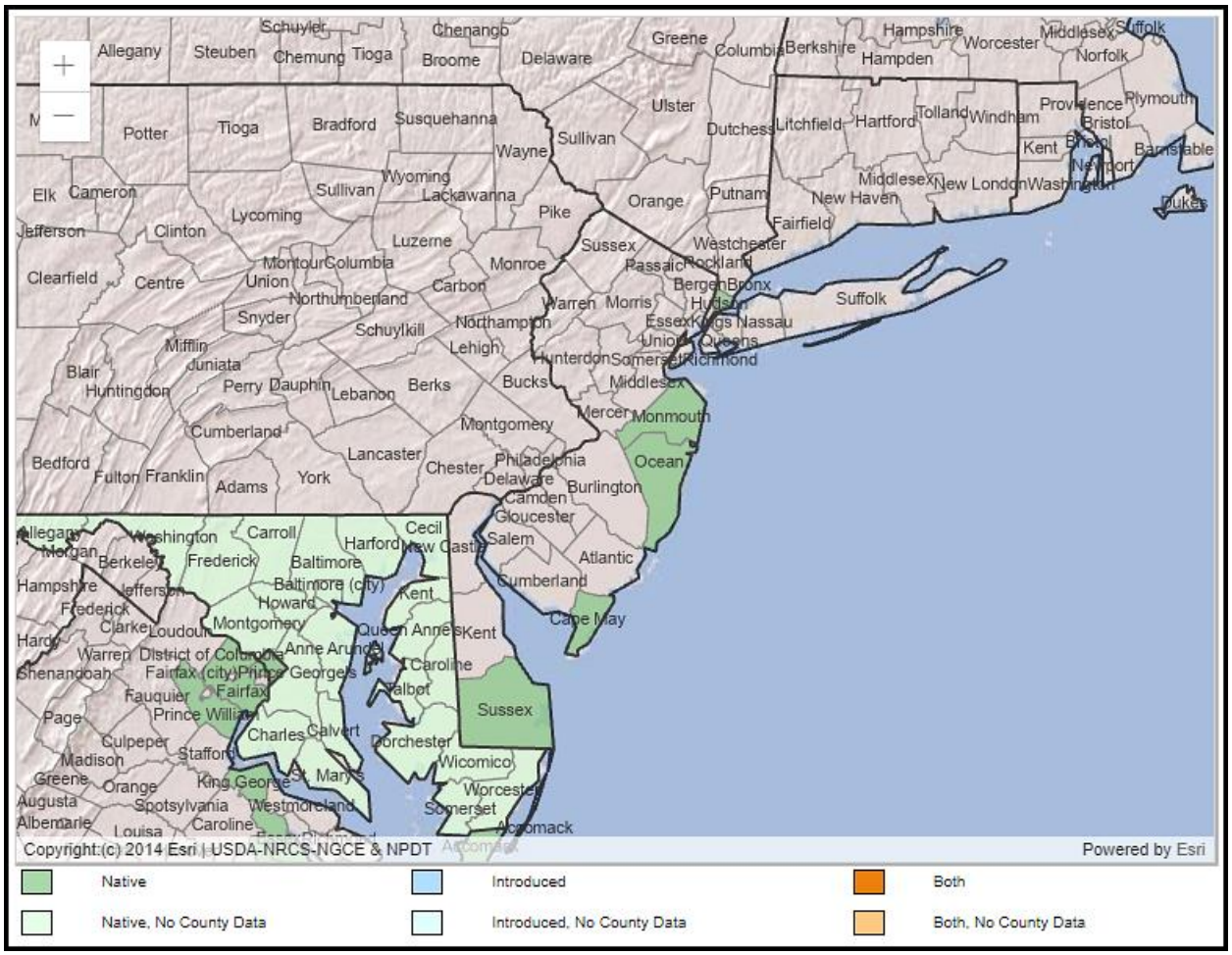


Figure 2. County records of F. profunda in New Jersey and vicinity (USDA NRCS 2024b).

Conservation Status

Fraxinus profunda is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors (NatureServe 2024). The map below (Figure 3) illustrates the conservation status of *F. profunda* throughout its range. Pumpkin Ash is vulnerable (moderate risk of extinction) in five states, imperiled (high risk of extinction) in one state, and critically imperiled (very high risk of extinction) in three states, the District of Columbia, and Ontario. *F. profunda* was designated as an endangered species in Canada in May 2022 (COSEWIC 2023) and it has been ranked as critically endangered on the IUCN Red List of Threatened Species since March 2017 (Westwood et al. 2017).

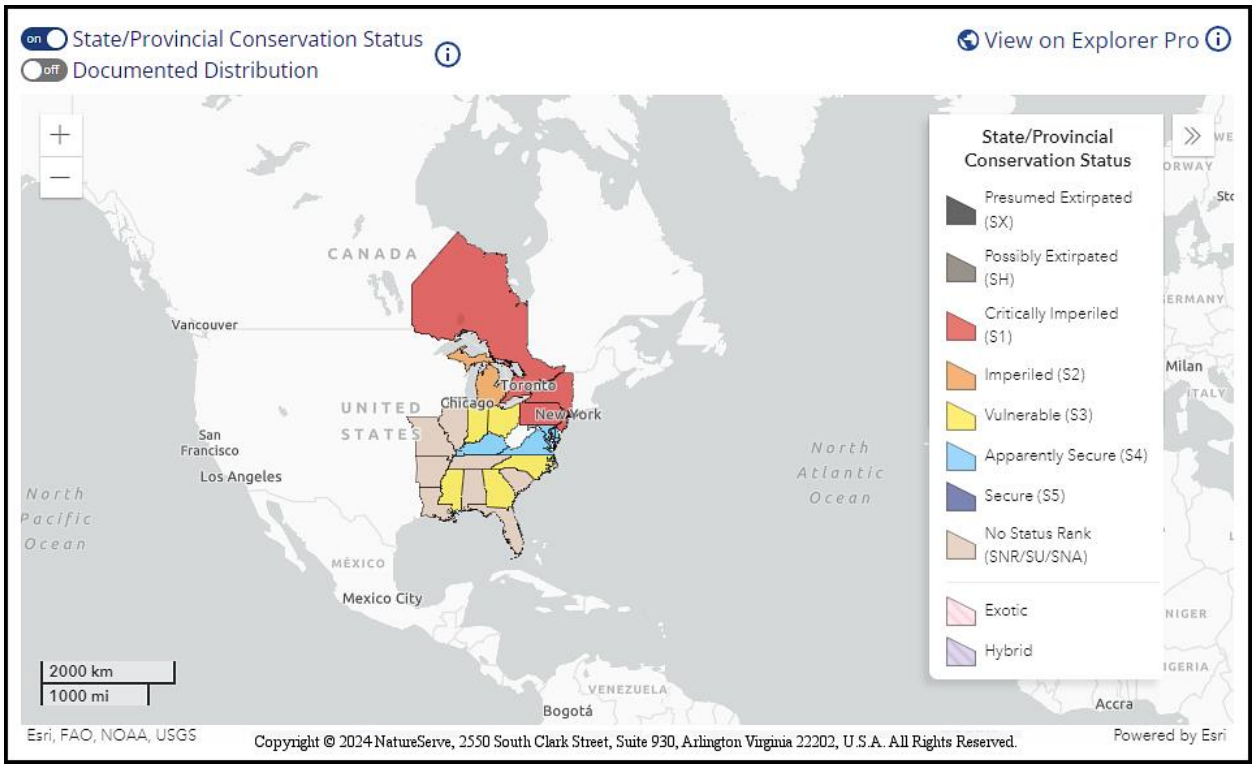


Figure 3. Conservation status of F. profunda in North America (NatureServe 2024).

New Jersey is one of the states where *Fraxinus profunda* is critically imperiled (NJNHP 2024). The S1 rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *F. profunda* is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to *F. profunda* signify that the tree is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

The earliest reports of *Fraxinus profunda* in New Jersey were from two locations in Gloucester County (Stone 1911) and Taylor (1913) noted that they were the only records of the species in the greater New York area outside of the New York Botanical Garden. According to Snyder (1985) those records, as well as some other reports from Burlington County, had been based on misidentified specimens of *Fraxinus pennsylvanica* var. *austinii*. Campbell (2017) cited Long's collection from Burlington County as an example of a specimen that appeared to be transitional between *Fraxinus profunda* and *F. pennsylvanica*, but Whittemore et al. (2018) asserted that any seeming intergradation between the two species was due to overlap in their ranges of variability. Material from New Jersey was not included in the latter study.

New Jersey's first confirmed occurrence of *Fraxinus profunda* was documented by David Snyder in Monmouth County during 1983 and within three years two additional populations of the species were found in Cape May and Ocean counties (Snyder 1985 & 1986, NJNHP 2024).

Those three occurrences were the only ones cited as extant by Breden et al. (2006) and they are the only populations currently tracked by the Natural Heritage Program (NJNHP 2024).

Threats

Throughout its range, a number of threats to *Fraxinus profunda* have been identified over the years. Habitat can become unsuitable as a result of hydrological changes, land conversion for agriculture, or the spread of invasive flora (Ormes et al. 2021, COSEWIC 2023). Logging may be a concern at some sites (COSEWIC 2023). Aust et al. (1997) found that *F. profunda* was relatively tolerant of mechanical wood harvesting practices but was nearly absent from sites where herbicides had been applied. White-tailed Deer (*Odocoileus virginianus*) consume young twigs and leaves, and can be a serious impediment to regeneration. *Fraxinus profunda* is also very susceptible to fire, and hot fires can consume large trees (Putnam et al. 1960, Harms 1965).

Harms (1965) noted that there were no documented concerns for *Fraxinus profunda* as a result of disease or insects, but that observation preceded the arrival of the Emerald Ash Borer (*Agrilus planipennis*) in North America. The Emerald Ash Borer (EAB) is a wood-boring beetle that requires species in the Oleaceae in order to complete its life cycle—the larvae feed on the cambium layer of mature trees and the resulting damage usually kills a host tree within 2–4 years. EAB was first detected on the continent in 2002. In 2014 it was discovered in New Jersey and by 2020 it had been documented in every county in the state. All of the native *Fraxinus* species in the United States are susceptible to the beetle, as is White Fringetree (*Chionanthus virginicus*), and Pumpkin Ash is one of the species that has been identified as highly vulnerable to infestation (Hausman et al. 2010, Liu 2017, NJDA 2024).

The threat to *Fraxinus profunda* from EAB is extensive and severe. More than 90% of an ash stand can be lost within five or six years of the initial infestation (Knight et al. 2010, Klooster et al. 2014, Steiner et al. 2019, COSEWIC 2023). It was initially thought that low-density stands of ash might be less attractive to EAB but Knight et al. (2013) found that mortality was actually more rapid due to higher concentrations of beetles on individual trees in the small populations. Many barriers to stand regeneration have been identified. Although *Fraxinus profunda* can readily establish seedlings its seed bank is short-lived and can rapidly become depleted in the absence of mature trees (Klooster et al. 2014). Seedlings and saplings are at risk from deer herbivory (Hausman et al. 2010). An ash regeneration study by Aubin et al. (2015) documented the presence of residual EAB populations that would attack saplings with stems as small as 2 cm in diameter, preventing the trees from reaching a reproductive age. High rates of stand mortality can alter site hydrology and increase the amount of light that reaches the forest floor, making the community more accessible to a suite of invasive plant species that hamper the establishment of *F. profunda* seedlings (Hausman et al. 2010, Knight et al. 2010, Granger 2017, Granger et al. 2017).

Climate Change Vulnerability

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Fraxinus profunda* populations to climate change. The species was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climactic conditions in accordance with the guidelines described by Young et al. (2016) and the state climactic computations by Ring et al. (2013). Based on available data Pumpkin Ash was assessed as Moderately Vulnerable, meaning that it is likely to show some decrease in abundance or range extent in New Jersey by 2050. Iverson and Taft (2022) concluded that there was not sufficient data to model the impacts of climate change on the species in Illinois.

Several factors may contribute to the vulnerability of *Fraxinus profunda* in New Jersey. Some of the effects of changing climactic conditions in the state include higher temperatures, shifting precipitation patterns that result in more intense storms and lengthier droughts, and rising sea levels along the coast (Hill et al. 2020). *F. profunda* is intolerant of drought and is moderately susceptible to dieback during periods of desiccation (Putnam et al. 1960, Harms 1965, Pijut 2005). Lawson et al. (2013) reported high stomatal density in Pumpkin Ash leaves, which likely contributes to its low drought tolerance. Severe tropical storms can also take a toll on the species. After Hurricane Andrew in 1992, *F. profunda* trees in hard-hit parts of Louisiana experienced some crown loss from the heavy winds. Although much of the damage was relatively minor, severe impacts were noted to trees at one third of the sites examined by Leininger et al. (1997). One of New Jersey's *F. profunda* populations is located in an area that could be susceptible to storm surge during Category 3 or higher intensity hurricanes (NJ Adapt 2024). Ormes et al. (2021) pointed out that any populations in freshwater tidal habitat could be jeopardized by rising seas and salt water intrusion. While EAB remains the primary threat to *Fraxinus profunda* throughout its range, additional stresses from climate change could hasten the demise of populations that are already under pressure.

Management Summary and Recommendations

Multiple management strategies have been employed in an effort to save populations of *Fraxinus profunda* and other native ash species throughout North America. An early attempt to control the spread of EAB by reducing ash tree density was unsuccessful because it increased the concentration of beetles on a smaller number of trees (Knight et al. 2013). The inoculation of individual trees with a chemical that deters EAB appears to be moderately effective where it has been tested but the process is labor-intensive and costly. Resources have also been invested in the identification of potential biological control agents, propagation efforts for eventual reintroduction, and genetic studies designed to facilitate regeneration and develop strains of *F. profunda* that are resistant to EAB (Stevens and Pijut 2012 & 2014, Liu 2017). One interim strategy being explored in Canada is the planting of alternate woody species in order to maintain healthy forest communities at sites where significant numbers of *Fraxinus* trees have been lost (Tidman 2020).

Only one of New Jersey's *Fraxinus profunda* populations has been monitored since the Emerald Ash Borer arrived in the state (NJNHP 2024) and updated status evaluations of the remaining two occurrences are needed. Frequent population appraisals were recommended by Ormes et al. (2021) in order to effectively assess the range-wide impacts of EAB on *F. profunda*.

Synonyms

The accepted botanical name of the species is *Fraxinus profunda* (Bush) Bush. Orthographic variants, synonyms, and common names are listed below (ITIS 2024, POWO 2024, USDA NRCS 2024b). Britton and Brown (1913) treated *Fraxinus profunda* and *F. michauxii* as distinct species. Fernald (1938) viewed them as conspecific and included both under the name *F. tomentosa*, which he credited to Michaux, but Little (1952) determined that Michaux's use of *F. tomentosa* was inconsistent with the rules of nomenclature and restored *F. profunda*. *Fraxinus profunda* is sometimes referred to as Red Ash but that name is also frequently applied to other *Fraxinus* species.

Botanical Synonyms	**Common Names**
Fraxinus michauxii Britton	Pumpkin Ash
Fraxinus tomentosa Michx. f.	
Fraxinus profunda var. *ashei* E. J. Palmer	
Fraxinus americana var. *profunda* Bush	
Fraxinus pennsylvanica ssp. *profunda* (Bush) A. E. Murray	
Fraxinus pennsylvanica var. *profunda* (Bush) Sudw.	
Calycomelia profunda (Bush) Nieuwl.	
Calycomelia tomentosa Kostel.	

References

Anderson, Christopher J., B. Graeme Lockaby, and Nathan Click. 2013. Changes in wetland forest structure, basal growth, and composition across a tidal gradient. The American Midland Naturalist 170(1): 1–13.

Aubin, I., F. Cardou, K. Ryall, D. Kreutzweiser, and T. Scarr. 2015. Ash regeneration capacity after Emerald Ash Borer (EAB) outbreaks: Some early results. The Forestry Chronicle 91(3): 291–298.

Aust, W. Michael, Stephen H. Schoenholtz, Thomas W. Zaebst, and Beth A. Szabo. 1997. Recovery status of a tupelo-cypress wetland seven years after disturbance: Silvicultural implications. Forest Ecology and Management 90: 161–169.

Boone, George C. 1983. Forest survey in Henstep Valley, Union County, Pennsylvania. Proceedings of the Pennsylvania Academy of Science 57(2): 201–203.

Breden, Thomas F., Yvette R. Alger, Kathleen Strakosch Walz, and Andrew G. Windisch. 2001. Classification of Vegetation Communities of New Jersey: Second iteration. Association for Biodiversity Information and New Jersey Natural Heritage Program, Office of Natural Lands Management, Division of Parks and Forestry, NJ Department of Environmental Protection, Trenton, NJ. 230 pp.

Breden, T. F., J. M. Hartman, M. Anzelone and J. F. Kelly. 2006. Endangered Plant Species Populations in New Jersey: Health and Threats. New Jersey Department of Environmental Protection, Division of Parks and Forestry, Office of Natural Lands Management, Natural Heritage Program, Trenton, NJ. 198 pp.

Britton, N. L. and A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada in three volumes: Volume II (Amaranth to Polypremum). Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 735 pp.

Campbell, Julian J. N. 2017. Green/Red and White Ashes (*Fraxinus* Sect. *Melioides*) of east-central North America: Taxonomic concepts and polyploidy. Phytoneuron 28: 1–36.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). Page updated May 18, 2023. *Fraxinus profunda* entry on Species at Risk Public Registry. Accessed June 2, 2024 at https://species-registry.canada.ca/index-en.html#/species/1540-1108

Craven, Brian W. 2008. The Impact Of Climate On The Leaf Characteristics Of Genus *Fraxinus*. Master's Thesis, Eastern Illinois University, Charleston, IL. 233 pp.

Dayton, William A. 1954. Some more notes on United States ashes (*Fraxinus*). Journal of the Washington Academy of Sciences 44(12): 385–390.

Faber-Langendoen, D. 2018. Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments. NatureServe, Arlington, VA. 52 pp.

Farmer, Jaime A., Elisabeth B. Webb, Robert A. Pierce II, and Kevin W. Bradley. 2017. Evaluating the potential for weed seed dispersal based on waterfowl consumption and seed viability. Pest Management Science 73(12): 2592–2603.

Fernald, M. L. 1938. Noteworthy plants of southeastern Virginia (continued). Rhodora 40(4): 434–459.

Fernald, M. L. 1950. Gray's Manual of Botany. Dioscorides Press, Portland, OR. 1632 pp.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Second Edition. The New York Botanical Garden, Bronx, NY. 910 pp.

Granger, Joshua J. 2017. Regeneration of Imperiled Hardwoods in the Eastern United States. Doctoral Dissertation, University of Tennessee, Knoxville, TN. 195 pp.

Granger, Joshua J., John M. Zobel, and David S. Buckley. 2017. Potential for regenerating major and minor ash species (*Fraxinus* spp.) following EAB infestation in the eastern United States. Forest Ecology and Management 389: 296–305.

Hardin, James W. and Robert L. Beckmann. 1982. Atlas of foliar surface features in woody plants, V. *Fraxinus* (Oleaceae) of eastern North America. Brittonia 34(2): 129–140.

Harms, W. R. 1965. Pumpkin Ash. In Russell M. Burns and Barbara H. Honkala (Technical Coordinators). Silvics of North America: Volume 2 Hardwoods. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington, DC. 1711 pp.

Hausman, Constance E., John F. Jaeger, and Oscar J. Rocha. 2010. Impacts of the Emerald Ash Borer (EAB) eradication and tree mortality: Potential for a secondary spread of invasive plant species. Biological Invasions 12: 2013–2023.

Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.

Hosner, John F. and Albert L. Leaf. 1962. The effect of soil saturation upon the dry weight, ash content, and nutrient absorption of various bottomland tree seedlings. Soil Science Society of America Journal 26(4): 401–404.

Howe, Henry F. and Judith Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology, Evolution, and Systematics 13: 201-228.

ITIS (Integrated Taxonomic Information System). Accessed May 31, 2024 at http://www.itis.gov

Iverson, Louis R. and John B. Taft. 2022. Past, present, and possible future trends with climate change in Illinois forests. Erigenia 28: 53–70.

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (http://www.bonap.net/tdc). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Kinser, Abel. 2022. Four photos of *Fraxinus profunda* from Illinois. Shared via iNaturalist at https://www.inaturalist.org/observations/126423209, licensed by https://creativecommons.org/licenses/by-nc/4.0/

Klooster, W., D. Herms, K. Knight, C. Herms, D. McCullough, A. Smith, K. Gandhi, and J. Cardina. 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biological Invasions 16: 859–873.

Knight, Kathleen S., Daniel A. Herms, John Cardina, Robert P. Long, Annemarie Smith, Joanne Rebbeck, Kamal J. K. Gandhi, Catherine P. Herms, and Wendy S. Klooster. 2010. When does Emerald Ash Borer (*Agrilus planipennis*) cause changes in light regimes and shifts in species composition? Summary of Organized Oral Session 56-6, from the 95th ESA Annual Meeting, Pittsburgh, PA. Available at https://eco.confex.com/eco/2010/techprogram/P22141.HTM

Knight, Kathleen S., John P. Brown, and Robert P. Long. 2013. Factors affecting the survival of ash (*Fraxinus* spp.) trees infested by Emerald Ash Borer (*Agrilus planipennis*). Biological Invasions 15: 371–383.

Lawson, Shaneka S., Paula M. Pijut, and Charles H. Michler. 2013. Species selection in hardwoods research: Variations in baseline physiological responses of select temperate hardwood tree species. Journal of Forestry Research 24(2): 285−292.

Leininger, T. D.; A. D. Wilson, and D. G. Lester. 1997. Hurricane Andrew damage in relation to wood decay fungi and insects in bottomland hardwoods of the Atchafalaya Basin, Louisiana. Journal of Coastal Research, 13(4): 1290–1293.

Little, Elbert E. 1952. Notes on *Fraxinus* (ash) in the United States. Journal of the Washington Academy of Sciences 42(12): 369–380.

Liu, Houping. 2017. Under siege: Ash management in the wake of the Emerald Ash Borer. Journal of Integrated Pest Management 9(1): 1–16.

McCormac, J. S., J. K. Bissell, and S. J. Stine. 1995. The status of *Fraxinus tomentosa* (Oleaceae) in Ohio with notes on its occurrence in Michigan and Pennsylvania. Castanea 60(1): 70–78.

Michaux, François-André. 1813. Histoire des arbres forestiers de l'Amérique septentrionale: Considérés principalement sous les rapports de leur usage dans les arts et de leur introduction dans le commerce, ainsi que d'après les avantages qu'ils peuvent offrir aux gouvernemens en Europe et aux personnes qui veulent former de grandes plantations. Volume 3. De l'Imprimerie de L. Haussmann et d'Hautel, Paris. Illustration courtesy of the John Carter Brown Library, Providence, RI.

Mid-Atlantic Herbaria. 2024. Accessed at https://midatlanticherbaria.org/portal/index.php on May 31, 2024.

Middleton, Beth. 1999. Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. Plant Ecology 146: 169–184.

Miller, G. N. 1955. The genus *Fraxinus*, the ashes, in North America, north of Mexico. Cornell University Agricultural Experiment Station, Ithaca, N.Y. Available at https://digital.library.cornell.edu/catalog/chla7251474_8573_002

Mohlenbrock, Robert H. 1959. A floristic study of a southern Illinois swampy area. The Ohio Journal of Science 59(2): 89–100.

NatureServe. 2024. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed May 31, 2024 at https://explorer.natureserve.org/

Nesom, Guy L. 2010a. Notes on *Fraxinus profunda* (Oleaceae). Phytoneuron 32: 1–6.

Nesom, Guy L. 2010b. *Fraxinus biltmoreana* and *Fraxinus smallii* (Oleaceae), forest trees of the eastern United States. Phytoneuron 51: 1–30.

Nesom, Guy L. 2014. Phylogeny of *Fraxinus* Sect. Melioides (Oleaceae): Review and an alternative hypothesis. Phytoneuron 95: 1–9.

NJ Adapt (New Jersey Climate Change Resource Center). 2024. Interactive map of flood hazard zones, accessed June 5, 2024 at https://www.njfloodmapper.org/

NJDA (New Jersey Department of Agriculture). 2024. Emerald Ash Borer. Accessed June 1, 2024 at https://www.nj.gov/agriculture/divisions/pi/prog/emeraldashborer.html

NJNHP (New Jersey Natural Heritage Program). 2010. Explanation of Codes Used in Natural Heritage Reports. Updated March 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2024. Biotics 5 Database. NatureServe, Arlington, VA. Accessed March 15, 2024.

Ormes, M., L. Morse, and A. Treher. 2021. *Fraxinus profunda* conservation status factors. NatureServe, Arlington, VA. Accessed May 31, 2024 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.132557/Fraxinus_profunda

Pijut, Paula M. 2005. Planting and care of fine hardwood seedlings: Native hardwood trees of the central hardwood region. FNR-218, Hardwood Tree Improvement and Regeneration Center, USDA Forest Service North Central Research Station, Purdue University, West Lafayette, IN. 16 pp.

POWO. 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed May 21, 2024 at http://www.plantsoftheworldonline.org/

Putnam, John A., George M. Furnival, and J. S. McKnight. 1960. Management and Inventory of Southern Hardwoods. Agriculture Handbook 181, U.S. Department of Agriculture, Washington, DC. 102 pp.

Rhoads, Ann Fowler and Timothy A. Block. 2007. The Plants of Pennsylvania. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.

Ring, Richard M., Elizabeth A. Spencer, and Kathleen Strakosch Walz. 2013. Vulnerability of 70 Plant Species of Greatest Conservation Need to Climate Change in New Jersey. New York Natural Heritage Program, Albany, NY and New Jersey Natural Heritage Program, Department of Environmental Protection, Office of Natural Lands Management, Trenton, NJ, for NatureServe #DDCF-0F-001a, Arlington, VA. 38 pp.

Snyder, David B. 1985. Additions to New Jersey's Flora. Bartonia 51: 95–98.

Snyder, David B. 1986. Rare New Jersey plant species rediscovered. Bartonia 52: 44–48.

Steiner, Kim C., Lake E. Graboski, Kathleen S. Knight, Jennifer L. Koch, and Mary E. Mason. 2019. Genetic, spatial, and temporal aspects of decline and mortality in a *Fraxinus* provenance test following invasion by the Emerald Ash Borer. Biological Invasions 21: 3439–3450.

Steury, Brent W. 1999. Annotated list of vascular plants from a nontidal barrier wetland along the Chesapeake Bay in Calvert County, Maryland. Castanea 64(2): 187–200.

Steven, Janet C. and Donald M. Waller. 2007. Isolation affects reproductive success in low-density but not high-density populations of two wind-pollinated *Thalictrum* species. Plant Ecology 190: 131–141.

Stevens, Micah E. and Paula M. Pijut. 2012. Hypocotyl derived in vitro regeneration of Pumpkin Ash (*Fraxinus profunda*). Plant Cell, Tissue and Organ Culture 108: 129–135.

Stevens, Micah E. and Paula M. Pijut. 2014. Agrobacterium-mediated genetic transformation and plant regeneration of the hardwood tree species *Fraxinus profunda*. Plant Cell Reports 33: 861–870.

Stone, Witmer. 1911. The Plants of Southern New Jersey. Quarterman Publications, Boston, MA. 828 pp.

Taylor, Norman. 1915. Flora of the vicinity of New York - A contribution to plant geography. Memoirs of the New York Botanical Garden 5: 1–683.

Thompson, Ralph L. 1980. Woody vegetation and floristic affinities of Mingo Wilderness Area, a northern terminus of southern floodplain forest, Missouri. Castanea 45(3): 194–212.

Tidman, David. 2020. Restoring Forest Cover and Enhancing Biodiversity of the Carolinian Forest in Ontario Affected by Ash Tree Decline from the Emerald Ash Borer. Conservation Halton Summary ENVS*6500, available at https://atrium.lib.uoguelph.ca/server/api/core/bitstreams/4fe7da3e-a18d-47c1-88a5-73b18f1e06f7/content

Tiner, Ralph W. 2009. Field Guide to Tidal Wetland Plants of the Northeastern United States and Neighboring Canada. University of Massachusetts Press, Amherst, MA. 459 pp.

U. S. Army Corps of Engineers. 2020. National Wetland Plant List, version 3.5. https://cwbi-app.sec.usace.army.mil/nwpl_static/v34/home/home.html U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2024a. *Fraxinus profunda* illustration from Britton, N. L. and A. Brown, 1913, An illustrated flora of the northern United States, Canada and the British Possessions, 3 vols., Kentucky Native Plant Society, New York, Scanned By Omnitek Inc. Image courtesy of The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC.

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2024b. PLANTS profile for *Fraxinus profunda* (Pumpkin Ash). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed May 31, 2024 at http://plants.usda.gov

Wallander, Eva. 2008. Systematics of *Fraxinus* (Oleaceae) and evolution of dioecy. Plant Systematics and Evolution 273: 25–49.

Wallander, Eva. 2012. Systematics and floral evolution in *Fraxinus* (Oleaceae). Belgishe Dendrologie Belge 2012: 39–58.

Walz, Kathleen S., Jason L. Hafstad, Linda Kelly, and Karl Anderson. 2020. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservancy (CoC) Values for Species and Genera (update to 2017 list). New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ.

Wang, B., and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16(5): 299–363.

Weakley, A. S. and Southeastern Flora Team. 2024. Flora of the Southeastern United States. Edition of March 4, 2024. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2023 pp.

Westwood, M., D. Jerome, S. Oldfield, and J. Romero-Severson. 2017. *Fraxinus profunda*. The IUCN Red List of Threatened Species. Accessed June 1, 2024 at https://www.iucnredlist.org/species/61919022/113525283

Whelden, C. M. 1934. Studies in the genus *Fraxinus*: I. A preliminary key to winter twigs for the sections *Melioides* and *Bumelioides*. Journal of the Arnold Arboretum 15(2): 118–126.

White, David A. 1983. Plant communities of the lower Pearl River basin, Louisiana. The American Midland Naturalist 110(2): 381–396.

Whittemore, Alan T., Julian J. N. Campbell, Zheng-Lian Xia, Craig H. Carlson, Daniel Atha, and Richard T. Olsen. 2018. Ploidy variation in *Fraxinus* L. (Oleaceae) of eastern North America:

Genome size diversity and taxonomy in a suddenly endangered genus. International Journal of Plant Sciences 179(5): 377–389.

Wilson, Kenneth A. and Carroll E. Wood, Jr. 1959. The genera of Oleaceae in the southeastern United States. Journal of the Arnold Arboretum 40(4): 369–384.

Wongsriphuek, Chanpen, Bruce D. Dugger, and Anne M. Bartuszevige. 2008. Dispersal of wetland plant seeds by Mallards: Influence of gut passage on recovery, retention, and germination. Wetlands 28(2): 290–299.

Young, Bruce E., Elizabeth Byers, Geoff Hammerson, Anne Frances, Leah Oliver, and Amanda Treher. 2016. Guidelines for Using the NatureServe Climate Change Vulnerability Index, Release 3.02, 1 June 2016. NatureServe, Arlington, VA. 65 pp.