THE ECOLOGICAL ROLE OF AMERICAN ELM (*ULMUS AMERICANA* L.) IN FLOODPLAIN FORESTS OF NORTHEASTERN NORTH AMERICA

Christian O. Marks[1]

Abstract.—Before Dutch elm disease, the American elm (*Ulmus americana* L.) was a leading dominant tree species in the better drained parts of floodplain forests where flooding occurs about 1 percent of the time. Although still common in these habitats today, *U. americana* now rarely lives long enough to reach the forest canopy because elm mortality rates increase sharply with tree size. This article reviews the impact that the loss of American elm due to Dutch elm disease has had on floodplain forests, helps provide a clear rationale for restoring this iconic species in the wild, and also provides quantitative benchmarks against which to measure progress. *Fraxinus* L. species are ecologically the most similar species to *U. americana*, but *Fraxinus* trees are now also threatened because of the spread of the invasive emerald ash borer. This new threat to floodplain forests of northeastern North America adds urgency to the need to develop more disease tolerant selections of *U. americana* and plant them into floodplain habitats.

Introduction

The loss of native elms from cities and villages across Europe and North America in the wake of the nonnative Dutch elm disease (DED) and the aesthetic impacts of that loss on the traditional landscape has received much public attention (Campanella 2011, Richens 1983). This cultural loss has been the primary motivation behind past efforts to breed more disease-resistant elms and manage the pathogen and its vectors (Dunn 2000, Smalley and Guries 1993). However, the impact of DED on wild elm populations in their native habitats is an equally important part of this story because any durable restoration requires that elms can co-evolve with the pathogen, which they can only do in the wild. Here, my aim is to show the impact that DED has had on native elm populations and their habitats in North America, focusing on American elm (*Ulmus americana* L.), the most widespread and common of the native North American elm species. To this end, I will present a synthesis of pertinent results from my own research in Connecticut River floodplain forests and published ecological research from across the native range of *U. americana*.

A review of a species' ecology is integral to its restoration for several reasons. First, given the many other threats affecting most ecosystems and the limited resources available for conservation, one needs a compelling rationale why restoring this particular species is a priority (Marks and Van Driesche 2016). For example, a key question to investigate is if natural selection has already increased the disease tolerance of the wild population to the level where demographic rates and elm forest structure are recovering unassisted by a breeding program. Second, when implementing a restoration, one should have a clear idea of what one is attempting to restore, including quantitative pre- and post-disturbance reference points against which to evaluate progress (e.g., Hanberry et al. 2012). Third, the leading cause of failure in plant reintroductions is that environmental conditions at reintroduction sites were inappropriate (Godefroid et al. 2011). This observation highlights the need for accurate quantitative measurements of species habitat requirements and preferences.

[1] Floodplain Forest Ecologist, The Nature Conservancy, 136 West Street, Northampton, MA, 01060, USA. To contact, email at cmarks@tnc.org.

Knowing well the ecology of American elm is all the more critical because it is a foundation species in river floodplains. A foundation tree species is a dominant canopy species whose architecture defines forest structure and whose traits control ecosystem dynamics and processes (Ellison et al. 2005). I will review the evidence that American elm was a codominant canopy species of floodplain forests of major rivers in the northeastern and prairie regions of North America before the spread of DED, as well as exploring the ecological role of American elm in those forests. Specifically, the review shows that the loss of American elm likely changed not just the composition of floodplain forests but also their structure, successional dynamics, and ecosystem processes. This finding lends support to the argument for investing in a disease-tolerance breeding and planting program to restore the wild population of American elm.

Distribution

The range of *U. americana* includes most of eastern North America (Bey 1990), but its relative abundance varies substantially across that range. Based on maps of the U.S. Forest Service's Forest Inventory and Analysis plot data, *U. americana* and the other native elm species have their greatest importance in the midwestern states in an area that roughly corresponds to the tallgrass prairie region, as well as in the Mississippi River alluvial plain, around Lake Erie and Lake Ontario, and into the Hudson River Valley (U.S. Forest Service, n.d.). Today, these regions are associated with intensive cultivation of corn, soybeans, and other agriculture (Hanberry et al. 2012). This association implies that like agriculture, elms are attracted to the most fertile soils. Maps of soil pH confirm that this region has soils with generally higher pH than the rest of eastern North America (U.S. Forest Service, n.d.). The distribution of highest *U. rubra* Muhl. abundance is even more strongly skewed toward this region of higher pH soils (U.S. Forest Service, n.d.). Up to the present, efforts to select disease tolerant elms from the native elm populations have been based mainly in northeastern North America where DED has occurred the longest. The observation that elm was historically also very abundant in the floodplain forests of the prairies and the Mississippi River alluvial plain suggests that exploration of these regions for exceptionally large surviving native elms may result in the discovery of additional disease tolerant selections (Whittemore and Olsen 2011).

Habitat and Succession

The Society of American Foresters lists *U. americana* as either a codominant or a commonly associated tree species in eight of its forest cover types (Table 1). What these forest types have in common is that they typically have seasonal flooding. Flooding acts not only as a periodic stress in creating hypoxic conditions in the soil, but also delivers sediments and nutrients with the floodwaters (Adair et al. 2004, Steiger and Gurnell 2003). Although all of these forest types occur on riverine floodplains, the black ash-American elm-red maple type can also occur in other types of swamps (Rudolf 1980).

A closer examination of Table 1 reveals that the elm-associated floodplain forest cover types actually represent different phases or regional variations on the same successional sequence (Table 2). This successional sequence starts with the formation of sand or gravel bar habitat in response to lateral river channel migration. Pioneer trees like *Salix* L. species and *Populus deltoides* W. Bartram ex Marshall are first to colonize the bars but are soon joined by *Acer saccharinum* L., which becomes dominant as the shorter-lived *Salix* and *P. deltoides* begin to die off (Table 2). Over time, sediments continue to accrete on the bar and annual flooding becomes less prolonged. On these older and better drained floodplain surfaces, the pioneer tree species are gradually replaced by *Fraxinus pennsylvanica* Marshall and *Ulmus americana*, two tree species that have both sufficient flood and shade tolerance to survive in the understory of the floodplain

Table 1.— Description of Society of American Foresters (SAF) forest cover types where American elm (*Ulmus americana*) is either a co-dominant species or a commonly associated species (Eyre 1980)

Number	Name	Description
39	Black ash – American elm – red maple	Most northern type of elm forest occurring well into the boreal region. It is found in swamps, gullies, and small depressions of slow drainage and along sluggish streams. Ash predominates on sites with higher pH whereas red maple predominates on more acidic sites, while American elm tends to grow on somewhat better drained sites.
61	River birch – sycamore	Floodplain forest type that may include American and slippery elms further back from the river. River birch is more dominant on streams flooded with acidic water because it is more tolerant of dissolved aluminum than other floodplain tree species.
62	Silver maple – American elm	Following cottonwood and willow in first bottoms of major rivers or pioneer community on abandoned floodplain fields. Relative proportion of maple to elm depends on history of stand.
63	Cottonwood	Characteristic of fronts and banks of most major streams. Cottonwood dominates the pioneer stage, but American elm can be an associated species in later stages.
65	Pin oak – sweetgum	A floodplain forest type with intermediate levels of flooding. American elm is one of many possible associated species.
93	Sugarberry – American elm – green ash	Major river floodplains at intermediate elevations in the floodplain. Appears to be long term in the successional scale because all type species are shade tolerant when small and reproduce readily.
94	Sycamore – sweetgum – American elm	River fronts in the first bottoms of major rivers, the banks of smaller rivers and large creeks that flood, and occasionally branch heads and coves of small creeks. Sites are rich with moderately good drainage and have adequate moisture throughout the growing season. Succeeds cottonwood on riverfront sites, but may be a pioneer forest on heavily cutover sites or old agricultural fields in floodplains. Where there are frequent flood disturbances, it may represent a persistent subclimax, but the climax will be swamp chestnut oak, cherrybark oak, or sweetgum – willow oak.
95	Black willow	Characteristic of fronts and banks of most major streams. Black willow is a temporary pioneer type. Cottonwood is the most common associate but American elm can be an associate in later stages. With succession, black willow is replaced by the silver maple – American elm type in the central region and by the sycamore – sweetgum – American elm type in the southern region.

Table 2.— Succession sequences of floodplain tree species on point bars and channel bars of major rivers. Sequences are inferred from transects across bar surfaces of increasing age (and elevation).

Successional sequence	Study location	Reference
Salix eriocephala – S. nigra – Populus deltoides – Acer saccharinum – Fraxinus pennsylvanica – Ulmus americana	Connecticut River in Massachusetts	Marks et al. 2014
Salix nigra – Acer negundo – A. saccharinum – Ulmus americana – Fraxinus nigra	Connecticut River in Vermont	Marks et al. 2014
Salix interior – S. nigra – Betula nigra – Fraxinus pennsylvanica – Ulmus americana – Celtis occidentalis	Chippewa River in Wisconsin	Barnes 1985, 1991
Salix amygdaloides – Populus deltoides – Acer negundo – Fraxinus pennsylvanica -Ulmus americana – Quercus macrocarpa	Missouri River in North Dakota	Johnson et al. 1976

forest (Table 2). The *F. pennsylvanica* - *U. americana* dominance will continue until sediments accrete to the point that the flood-intolerant tree species that dominate the surrounding upland forests can colonize (e.g., *Acer saccharum* Marshall, *Tilia americana* L., *Quercus rubra* L., etc.) (Marks et al. 2014). Regional variations on this successional sequence are related to differences in the species pool associated with climate and soil pH. For example, on the drier western edge of its range, *U. americana* may be codominant with *Acer negundo* L. instead of *A. saccharinum* (Weaver et al. 1925, Wiebe and Shadick 2011). In riparian forests along medium and higher gradient streams and rivers, the pioneer tree species that *U. americana* eventually replaces can be *Platanus occidentalis* L. or on more acidic streams *Betula nigra* L. (Marks et al. 2014, McClelland and Ungar 1970, Oosting 1942). In particular, in the southern part of the *U. americana* range there are many more floodplain tree species such as *Celtis laevigata* Willd. and especially *Liquidambar styraciflua* L. that are associated with *U. americana* (Hanberry et al. 2012). Regardless of these regional variations, *U. americana* consistently appears to be most abundant in the better drained, older parts of forested point bars, riverine islands, and active floodplains where flooding is less frequent than in the *Salix*- and *P. deltoides* -dominated pioneer habitats but still frequent enough to prevent invasion by upland tree species (Marks et al. 2014). That transition zone where *U. americana* is most abundant occurs where flooding happens about 1 percent of the time (i.e., 4 days/year, on average) (Marks et al. 2014).

In the Connecticut River basin, the habitat of *U. rubra* is more restricted than that of *U. americana*. This fact may be underappreciated because even researchers have sometimes erroneously identified *U. americana* as *U. rubra*. Specifically, unlike *U. americana*, *U. rubra* appears to be generally restricted to higher floodplain terraces that do not flood every year (Curtis 1959, Marks et al. 2014). Moreover, within the Connecticut River watershed, *U. rubra* was further restricted to those high terraces that had the highest soil pH (Marks, unpublished data). The distribution of *Celtis occidentalis* L. was similarly restricted to sites with high soil pH, and is consequently a good indicator species for *U. rubra* habitat. The observation that *U. rubra* can be found on much drier sites outside riparian areas, particularly those of limestone origin (Cooley and Van Sambeek 1990), further emphasizes the importance of soil pH for this species.

A quantitative way to determine which tree species are most similar to native elm species ecologically is to review studies that did ordinations of floodplain forest species composition on multiple environmental gradients. Such ordinations show that *F. pennsylvanica* is ecologically the most consistently close to *U. americana,* and *C. occidentalis* the closest to *U. rubra* (Cowell and Dyer 2002, Meitzen 2009, Townsend 2001, Turner et al. 2004). The close ecological similarity of *F. pennsylvanica* implies that in many floodplain forests it has been able to replace *U. americana* in the canopy, thereby mitigating the impact of DED on these forests. Unfortunately, large numbers of mature *Fraxinus* trees are now also being lost across northeastern North America due to the invasive emerald ash borer (*Agrilus planipennis* Fairmaire 1888) (Flower et al. 2013, Knight et al. 2013). Although this pest will further impact late successional floodplain forests, the prospect of planting disease-tolerant selections of *U. americana* into large canopy gaps created by dead *Fraxinus* offers some hope for the ecological recovery of these forests (Knight et al. 2012).

It is interesting to observe that the European sister species of the North American elms have very similar habitat affinities (Richens 1983). *Ulmus laevis*, like *U. americana,* is primarily a species of floodplain forests where it replaces *Salix* and *Populus* pioneer species to become codominant with an ash species (*Fraxinus excelsior* L.) and *Quercus robur* L. (a sister species of *Q. bicolor* Willd.) in the later part of floodplain succession (Carbiener and Schnitzler 1990, Ellenberg 1988, Karpati and Toth 1961, Loiseau 1997, Margl 1973, Passarge 1956, Schnitzler 1995). *Ulmus glabra* Huds., like *U. rubra* flourishes on rich high floodplain terraces and in

ravines, but also occurs in some upland forests, principally on calcareous soils (Ellenberg 1988, Grime et al. 1988, Richens 1983, Schnitzler 1995). The *Ulmus*-related genera of *Planera* J. F. Gmel. and *Celtis* are likewise associated with floodplains and rich calcareous soils, respectively (Burns and Honkala 1990). This close ecological similarity implies a high level of niche conservatism in the family Ulmaceae. More importantly, the observation that all of these habitats have a high nutrient availability suggests that soil nutrient availability is of fundamental importance to the Ulmaceae.

Much prime elm habitat has been lost to clearing for agriculture because agriculture also prizes rich alluvial soils (Gerrard 1987). The construction of dams and levees has resulted in further losses of floodplain forest habitat (e.g., Johnson and Waller 2012, Johnson et al. 2012, Knutson and Klaas 1998). The increasing rarity of floodplain forests is making their protection and restoration a priority for both private and public conservation organizations (e.g., Hanberry et al. 2012, Nislow et al. 2010). The restoration of riparian buffers along streams in intensively cultivated agricultural fields is also a priority for the USDA Natural Resource Conservation Service programs. These parallel restoration efforts in prime elm habitat provide an opportunity for collaboration that could greatly augment capacity to implement plantings with disease tolerant selections of native elms across their range.

Dominance

The dominant plant species most strongly influence ecosystem processes like productivity, transpiration, and nutrient cycling. The tree species that have been abundant in a given region for a longer time also tend to have the most insect species associated with them (Southwood 1961). These plant species that dominate ecosystem structure and processes have been dubbed "foundation species" (Ellison et al. 2005). Given their large influence on ecosystem processes and structure, it has been argued that foundation species should be of greatest conservation concern when new threats, such as introduced pests and pathogens, emerge (Ellison et al. 2005).

Although never as common in eastern North America as dominant upland trees such as those in the genera *Quercus, Fagus* L., *Acer, Tsuga* Carrière, or *Pinus* L. (Thompson et al. 2013), *Ulmus* was frequently a dominant or codominant canopy tree species in its primary bottomland habitats before the spread of DED. For instance, in southern Ontario, *U. americana* was the leading dominant in forests of wet sites (Maycock 1963). In Connecticut River floodplain forests, *U. americana* was noted to be codominant with *A. saccharinum* (Nichols 1916). Even today, *U. americana* is second only to *A. saccharinum* in abundance in Connecticut River floodplain forests (Table 3). *U. americana* is also the most widespread, occurring in all floodplain forest types throughout the Connecticut River basin (Table 3). Floodplain forests in southern Quebec were likewise co-dominated by *A. saccharinum* and *U americana* before DED (Tessier et al. 1981). On the Upper Mississippi River, *U. americana* was codominant with *A. saccharinum* and *F. pennsylvanica*, and continues to be the second or third most abundant tree species (De Jager et al. 2012, Knutson and Klaas 1998). *U. americana* was dominant in some floodplain forests of the Wabash, Tippecanoe, and White Rivers in Indiana (Lee 1945, Lindsey et al. 1961), and continues to have very high densities in some Wabash River floodplains forests (Lindsey 2013). *U. americana* was also codominant in floodplain forests on major rivers in Wisconsin prior to the spread of DED, and continues to be one of the most common tree species in those floodplain forests (Curtis 1959, Hale et al. 2008, Johnson and Waller 2012, Turner et al. 2004). In floodplain forests of major rivers in Illinois, *U americana* was also codominant, especially in the more northern parts of the state and on the drier older parts of the floodplain (Hosner and Minckler 1963, Telford 1926, Thone 1922, Turner 1936). In the later stages of succession, *U. americana* was also codominant in floodplain forests in the western part of its

Table 3.— Composition of Connecticut River floodplain forests (Marks et al. 2014). Common species are listed in order of decreasing abundance. Uncommon species that were less than 0.5 percent of the trees are not included. Relative abundance measure used is frequency (i.e., percentage of all trees that belong to that species). Distribution refers to how widespread the tree species is measured as the percentage of (103) study sites where the species occurred in either the tree or in the shrub layer data. Species codes and nomenclature follows the USDA plants database (NRCS 2012).

Species scientific name	Species code	Relative abundance (% trees)	Distribution (% sites)
Acer saccharinum	ACSA2	23.93	71
Ulmus americana	ULAM	12.68	90
Acer rubrum	ACRU	8.48	60
Fraxinus pennsylvanica	FRPE	6.19	59
Acer saccharum	ACSA3	4.41	53
Acer negundo	ACNE2	4.27	49
Prunus serotina	PRSE2	3.77	64
Populus deltoides	PODE3	2.90	40
Carya cordiformis	CACO15	2.46	66
Platanus occidentalis	PLOC	2.27	35
Lindera benzoin	LIBE3	2.14	38
Carpinus caroliniana	CACA18	2.00	39
Quercus palustris	QUPA2	1.75	37
Pinus strobus	PIST	1.65	33
Fraxinus americana	FRAM2	1.59	50
Salix nigra	SANI	1.55	21
Alnus incana ssp. rugosa	ALINR	1.54	50
Quercus rubra	QURU	1.24	54
Tilia americana	TIAM	1.21	46
Viburnum lentago	VILE	0.97	36
Carya ovata	CAOV2	0.79	29
Tsuga canadensis	TSCA	0.68	17
Ilex verticillata	ILVE	0.66	34
Fagus grandifolia	FAGR	0.64	33
Ulmus rubra	ULRU	0.64	15
Betula lenta	BELE	0.62	19
Fraxinus nigra	FRNI	0.62	14
Rhus typhina	RHTY	0.57	17

range, including in Oklahoma (Bruner 1931, Collins et al. 1981, Hefley 1937, Little 1938, Rice 1965), Nebraska (Albertson and Weaver 1945, Weaver et al. 1925), North Dakota (Johnson et al. 1976), and Saskatchewan (Harms and Baker 1998, Wiebe and Shadick 2011). Even in the Lower Mississippi River Valley in southeastern Missouri where there are more competing species than further north, native elms were the most frequently recorded floodplain trees after *Liquidambar styraciflua* in General Land Office Surveys from the 19th century (Hanberry et al. 2012). Before DED arrived, *U americana* was sometimes also codominant in swamps in northeastern North America often with *Fraxinus nigra* Marshall and *Acer rubrum* L., (e.g., Barnes 1976, Meilleur et al. 1994). From this literature review we can conclude that before the spread of DED, *U. americana* was a codominant or even the most dominant canopy tree species in many floodplain forest stands across northeastern North America and westwards along the major rivers of the prairies.

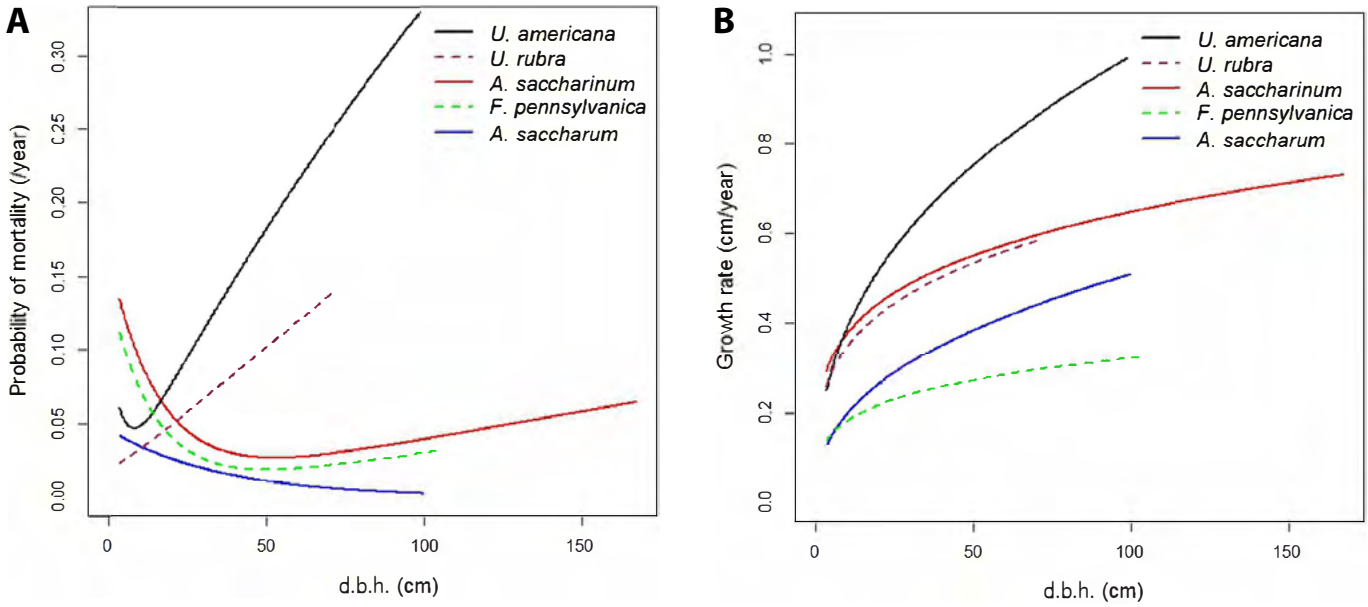

Figure 1.—Maximum likelihood estimates of size dependent average mortality (A) and diameter growth rates (B) for native elms and other common floodplain tree species of the Connecticut River Valley (Marks and Canham 2015). D.b.h. is the diameter at breast height. The study included more than 1,800 *U. americana* trees distributed across 90 floodplain forest sites from southern Connecticut to northern New Hampshire. Note that high growth rates are in part because floodplain species are fast growing, but also in part because floodplains have highly productive soils.

Demographic Decline

The first pandemic of Dutch elm disease in North America began with the arrival of the pathogen *Ophiostoma ulmi* (Buisman) Melin & Nannf. (1934) around 1927 (Brasier 2000). It was followed by a second pandemic caused by a more virulent strain of the pathogen *O. novo-ulmi*, likely starting in the 1940s (Brasier 2000). This second strain quickly became dominant and has now spread across almost the entire native range of American elm killing millions of trees (Brasier 2000). Unlike mature elms, elm seedlings are often spared. Seed production in American elm may begin as early as age 15 (Bey 1990). Around the same age, the probability of mortality due to DED begins to rise (Fig. 1A). Consequently, some of these small elms may produce another generation of seedlings before they are killed by DED, even if they do not have any significant tolerance to the disease. Therefore, although the average size of elm trees is expected to be much smaller after the arrival of DED, the number of elm trees may not decline as much. There is even the possibility of the number of elm trees increasing on some sites because each elm tree occupies less space. In other words, the initial demographic response to DED may differ depending on tree size class. Longer term, these population dynamics must result in a strong natural selection for earlier reproduction and/or increased ability to avoid and/or survive DED infection, potentially countering or even reversing a decline in the wild elm population depending on the amount of genetically-based variation available and its heritability. Thus data on the population trends in the wild population are highly pertinent to informing the prospects and necessity of disease tolerance breeding programs.

There is no systematic long-term monitoring program specifically designed for assessing elm population trends across the range of *U. americana*. However there have been several studies investigating the initial response of formerly elm-dominated forests to DED-induced elm mortality. The general pattern appears to be that there was a dramatic decline in total elm basal area in the affected stands as mature elms die from DED, but the response in the sapling and

small tree layer seems to be variable. Where elms were more dominant, larger canopy gaps resulted in more light, which allowed gaps to be invaded by shrubs (Dunn 1986, Huenneke 1983). Since that time, most of these shrub filled gaps have probably undergone succession back toward tree dominance, although there are no published followup studies. In other sites, canopy gaps created by elm mortality were filled by competing tree species even in the initial response, but there are also sites where sapling regeneration was mostly elms (Barnes 1976, Grittinger 1978, McBride 1973, Parker and Leopold 1983, Richardson and Cares 1976). Longer term studies of floodplain forests have also shown a dramatic decline in the number of large elms and total elm basal area, but a variable response in the seedling layer (Hale et al. 2008, Johnson and Waller 2012, Johnson et al. 2012, Knutson and Klaas 1998).

Demographic models of tree species allow investigating size dependent effects on mortality rates, which are clearly important in DED. In Connecticut River floodplain forests, where DED has occurred everywhere since the 1950s, both *U. americana* and *U. rubra* now have rapidly increasing mortality rates as a function of tree size (Fig. 1A). These mortality rates for mature elms are much higher than the mortality rates of similar sized trees of other species growing at the same sites (Fig.1A). Even though the high growth rate of elms can compensate somewhat for their high mortality rates (Fig. 1B), between the years 2008 and 2013 the population of modeled 30 cm (1 foot) d.b.h. elm trees in Connecticut River floodplain forests declined by 6.5 percent and 3.1 percent per year for *U. americana* and *U. rubra,* respectively (Marks and Canham 2015). The long-term rate of decline in the elm population may well be less severe than the measured rate from this relatively short study period because elm mortality may occur in waves (Brasier 1986). Likewise, it is possible that natural selection has increased the average disease tolerance in this elm population since the arrival of DED, but these high mortality rates especially for trees over 30 cm diameter at breast height (d.b.h.) (Fig. 1A) imply that the level of disease tolerance is still far from sufficient to allow native elms to reclaim their former role as codominant trees in the canopy of Connecticut River floodplain forests.

Forest Structure

"The well-known umbrella shape of the typical, planted, roadside elm is maintained to a large degree by the elm that grows in forest stands. The interlacing of the branches of adjacent trees occurs only near the top of the canopy, and conveys a strong resemblance to the arched vaulted ceiling of a cathedral" (Curtis 1959). Pictures of elm-dominated floodplain forests from before the arrival of DED are hard to find, but there are a few journal articles with black and white photos from the western part of the *U. americana* range (Albertson and Weaver 1945, Bruner 1931, Hefley 1937, Weaver 1960, Weaver et al. 1925). Here, I have included some color photos of elm-dominated floodplain forests on the Red River in eastern Saskatchewan, where DED did not arrive until after the year 2000 (Figs. 2-5). These color photos help convey the majesty of elm forests before the spread of DED.

The mounting risk of elm mortality due to DED with increasing tree size (Fig. 1A) has resulted in elms larger than 60 cm (2 feet) d.b.h. becoming rare in floodplain forests (Fig. 6). The few remaining elms that are larger usually occur in locations outside the floodplain where they are more than 90 m (300 feet) away from the nearest other remnant elms thereby reducing their chance of being visited by the bark beetles that spread DED. For instance, measurements in a Michigan elm forest in the wake of the initial wave of DED showed that elm mortality was highest in the lowland pockets where elm density was greatest (Richardson and Cares 1976). Due to this intense exposure to DED in floodplain forests where elms are most abundant, the size structure of the elm population in these forests has been dramatically reduced. Whereas in the 19th century elms were reported to be the largest trees in Massachusetts (Emerson 1887),

Figure 2.—Photo of the Rendek Elm Forest Sanctuary taken in the 1990s before the arrival of Dutch elm disease on the site around 2001. At the time the photo was taken, the canopy of this floodplain forest on the Red Deer River in eastern Saskatchewan was still dominated by *U. americana* (Harms and Baker 1998, Wiebe and Shadick 2011). Photo by Karen Wiebe, University of Saskatchewan, used with permission.

Figure 3.—Photo of the Rendek Elm Forest Sanctuary taken in the 1990s before the arrival of Dutch elm disease on the site around 2001. At the time the photo was taken, the canopy of this floodplain forest on the Red Deer River in eastern Saskatchewan was still dominated by *U. americana* (Harms and Baker 1998, Wiebe and Shadick 2011). The dominant fern in the forest understory is *Matteuccia struthiopteris*. Photo by Karen Wiebe, University of Saskatchewan, used with permission.

Figure 4.—Photo of floodplain forest dominated by *U. americana* on the south bank of the Red Deer River, Saskatchewan, about 800 m (0.5 miles) due west of the Manitoba border. The photo was taken on 24 July 1997, before Dutch elm disease arrived in this forest. The dominant fern in the forest understory is *Matteuccia struthiopteris*. Photo by Richard Kerbes, SOS Elms Coalition, Saskatoon, Saskatchewan, used with permission.

Figure 5.—Photo of floodplain forest dominated by *Ulmus americana* on the south bank of the Red Deer River, Saskatchewan, about 800 m (0.5 miles) due west of the Manitoba border. The photo was taken on 24 July 1997, before Dutch elm disease arrived in this forest. Photo by Richard Kerbes, SOS Elms Coalition, Saskatoon, Saskatchewan, used with permission.

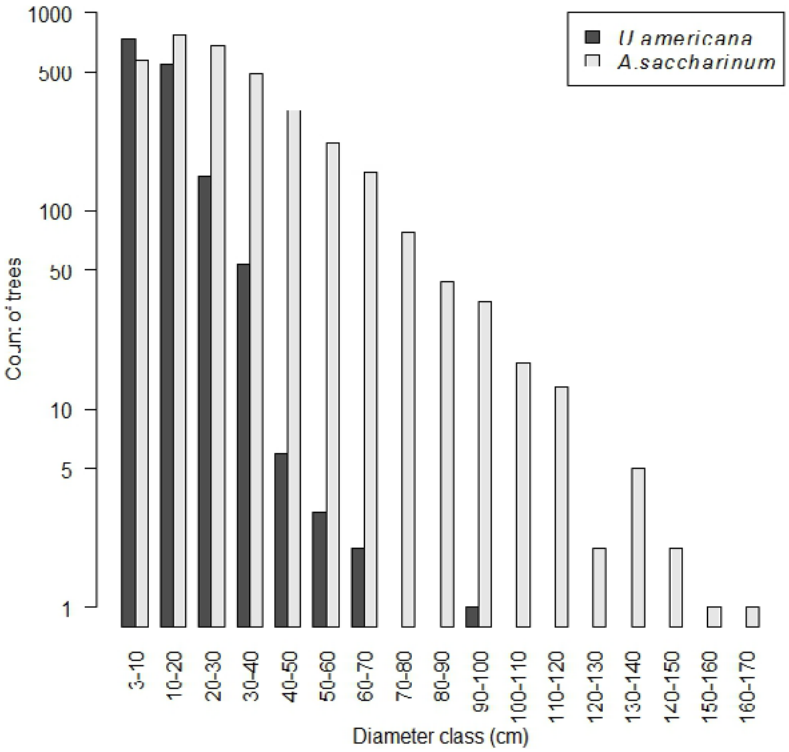

Figure 6.—Comparison of current tree size distributions for *U. americana* and *A. saccharinum*, the two most common floodplain tree species in the Connecticut River watershed. Size data were measured on the same sites for both species (Marks and Canham 2015). The one elm with a d.b.h. over 90 cm (3 feet) has died of DED since these data were collected.

today the silver maples (*A. saccharinum*) in Connecticut River floodplain forests are more than double the size of the elms (Fig. 6). Large reductions in the size distribution of floodplain forest elms have been measured across the elm range (Barnes 1997, Johnson and Waller 2012, Knutson and Klaas 1998, Richardson and Cares 1976). The 60 cm (2 feet) upper limit to the post-DED elm tree size distribution from the Connecticut River (Fig. 6) is remarkably consistent with these studies from other parts of the elm range. This observation suggests that exceptional native elms that have survived long enough to reach a size substantially larger than 60 cm (2 feet) d.b.h. despite the likely frequent past exposure to bark beetles in floodplain forest may well possess elevated tolerance to DED.

Given that the primary impact of DED on elm forests has been a dramatic reduction in the size of elms, it is a helpful point of reference for restoration to review the size and age that native elms can reach in the absence of DED. Specifically, a key question is if the rate of survival in a restored native wild elm population is sufficiently high that some elms will achieve a similar size and longevity as before the arrival of DED. My collaborators and I have been searching for the largest surviving elms in the Connecticut River, Housatonic River, and Lake Champlain valleys over the last 9 years to help identify native elms that may have elevated tolerance to Dutch elm disease. Based on our measurements of more than 250 exceptionally large elms scattered across this region, maximum d.b.h. are in the range of 92 to 184 cm (3 to 6 feet) and maximum heights are close to 33 m (110 feet) for both *Ulmus americana* and *U. rubra*. An inspection of state and national champion tree databases reveals that these maximum sizes are typical across eastern North America, although in exceptional cases *U. americana* can exceed 255 cm (8.5 feet) d.b.h. and 44 m (145 feet) in height, while the largest *U. rubra* recorded are over 225 cm (7.5 feet) d.b.h. and 37 m (125 feet) tall. Historic measurements of notable trees in Massachusetts and Connecticut from before the arrival of DED also record the largest individuals of *U. americana* at over 8 foot d.b.h. (Emerson 1887, Matthies 1934). The somewhat smaller maximum tree sizes among champion *U. rubra* compared with champion *U. americana* may be more of a consequence of there being far fewer *U. rubra* than *U. americana* trees (i.e., one is less likely to find an exceptional individual in a smaller sample). Whenever we have seen mature *U. rubra* and *U.*

americana growing together, trees of the two species were similar in height. Variation in height is much greater when comparing forest-grown and open-grown elms. Based on my measurements, forest-grown *U. americana* that live long enough to reach the canopy of floodplain forests can exceed 30 m (100 feet) in height while the range of heights for exceptionally large surviving open-grown *U. americana* is wider and less tall (65-90 feet or 20-27 m). Forest grown elms usually have a long main trunk before the first branching (Fig. 7), whereas open-grown elms often begin branching close to the ground to extend their crown out to the sides (Fig. 8). Likewise, there is geographic variation in tree size. We noticed that elms are shorter in the much colder northern part of the Connecticut River watershed than in the southern part of the watershed. There is probably more size variation across the broader range of *U. americana*. Although maximum diameters can be just as large in the western part of the *U. americana* range (e.g., Bronaugh 1993), elm canopy heights are notably less tall in the western-most part of the range and on drier sites (Albertson and Weaver 1945, Bey 1990).

U. americana was a long-lived species prior to the spread of DED, often reaching 175 to 200 years, with some trees older than 300 years (Bey 1990). Reports of elm ages for notable trees of Connecticut from before the arrival of DED are consistent with this range in longevity (Matthies 1934). I found a few measurements on ages of champion *U. americana* that also support this range in longevity. One measurement of a champion (6 foot or 185 cm d.b.h.) *U. rubra* in Vermont was around 150 years old when it died (exact age was not possible to determine because of decay) (Gus Goodwin, personal communication). Thus, exceptionally large elms may not be as old as they appear because elms can grow very quickly (Fig. 1B).

Figure 7.—Photo of an exceptionally large surviving American elm (*Ulmus americana*) in a Connecticut River floodplain forest in West Springfield, MA. This elm is 77 cm (>2.5 feet) d.b.h. and over 32.5 m (~110 feet) tall, and displays a straight trunk that is unbranched for at least the first 20 m (~65 feet), as is typical of forest-grown elms. The surrounding canopy trees are silver maple (*Acer saccharinum*). Photo by Christian O. Marks, The Nature Conservancy, used with permission.

Figure 8.—Photo of a lone, exceptionally large surviving American elm (*Ulmus americana*) on the bank of the Allagash River in northern Maine. This tree displays the tendency of many open-grown elms to start branching not far above the ground. Photo by Deborah Gardner, Mahoosuc Guide Service, used with permission.

Functional Traits

Elm species have unique traits that allow us to readily identify them in the field such as the alternating reddish-brown and cream-colored layers in the bark of *U. americana* (Wojtech 2011). Mature *Ulmus americana* and *U. laevis* also develop more pronounced buttress roots than other temperate trees, which helps identify them and adds to their aesthetic appeal (Richens 1983). Elm wood is also notoriously difficult to split because of its cross grain, a wood property that was sought after by wheelwrights (Richens 1983). Although these elm traits have utility for people and may well have some adaptive value to the trees in their native habitats, here I am concerned with traits that are functional in the sense that they affect ecosystem processes (*sensu* Garnier et al. 2016). Specifically, from a conservation perspective, a species loss is particularly consequential if that species possesses functional traits that differ substantially from the species that replace it. For example, the deciduous tree species that are replacing the evergreen conifer eastern hemlock (*Tsuga canadensis* (L.) Carrière) that have died due to invasive hemlock wholly adelgid have very different leaf traits than *Tsuga* and do not cast shade that is nearly as dark (Ellison et al. 2005).

Several primary axes of plant functional trait variation have been proposed (Westoby et al. 2002). Specifically, the leaf economics spectrum has been identified as a primary axis of functional trait variation globally (Wright et al. 2004). On this spectrum, leaf designs range from species with thick, tough, well-defended, long-lived leaves that have low metabolic rates and associated nitrogen content, to species with the opposite leaf attributes (Grime et al. 1988, Onoda et al. 2011, Reich et al. 1998b). These leaf traits have a strong influence on decomposition rates, and their palatability for herbivores, and consequently also on nutrient cycling (Cornelissen et al. 1999, Cornwell et al. 2008, Grime et al. 1988, Grime et al. 1996, Janzen 1974). Another important spectrum of trait variation is represented by the growth-survival tradeoff in trees, where fast-growing, short-lived species tend to have less dense wood with fewer defensive compounds than slow-growing, long-lived species (Wright et al. 2010). Wood density and tree longevity have obvious effects on forest carbon sequestration. Combining all of these traits, into a single global fast-slow economics spectrum for plants has been proposed (Lambers and Poorter

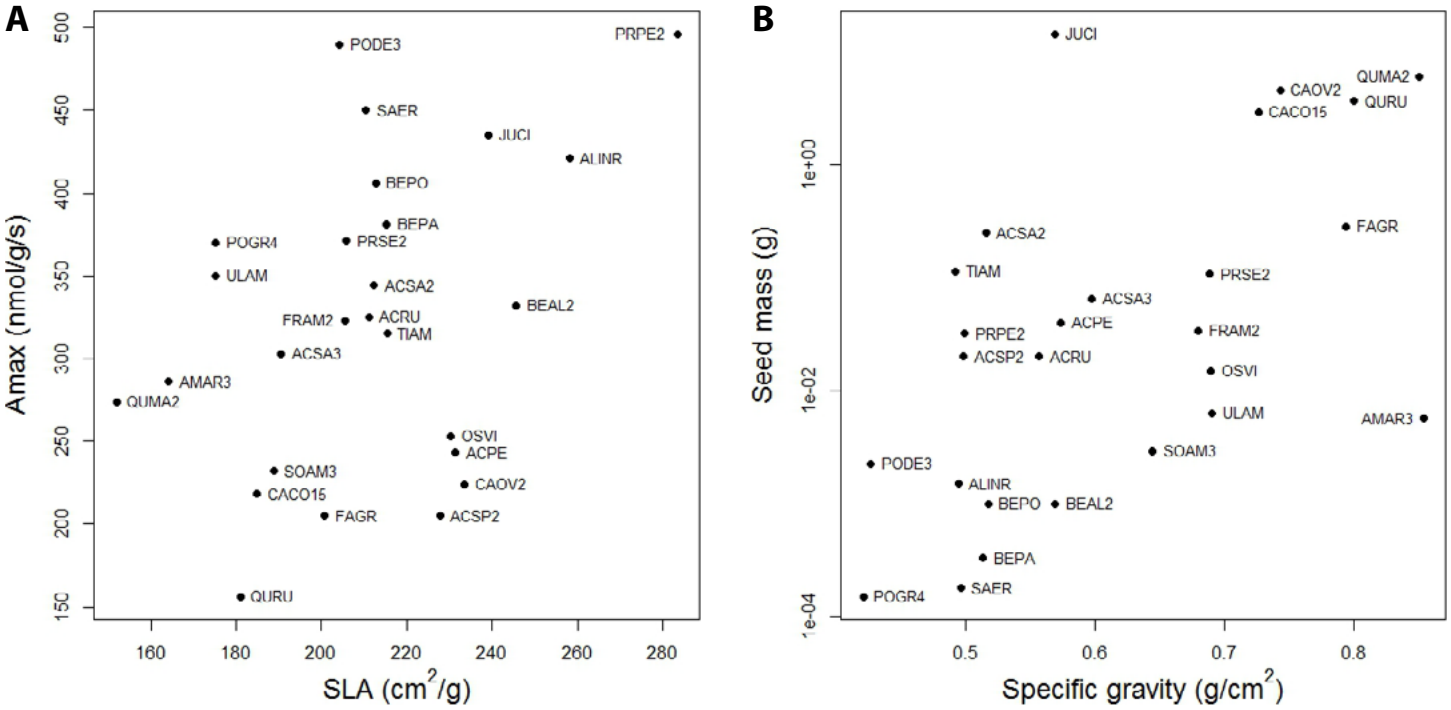

Figure 9.—Bivariate plots of functional trait values for 26 temperate deciduous forest tree and large shrub species from northeastern North America. (A) Data for maximum photosynthetic rate (Amax) and specific leaf area (SLA) are from Marks and Lechowicz (2007). There is a marginally significant positive relationship between Amax and SLA (p= 0.05806, adj. r^2= 0.1059); (B) Seedling wood specific gravity values are unpublished data from the experiment in Marks and Lechowicz (2007), and seed mass data were taken from the literature (Hewitt 1998, Young and Young 1992). There is a significant positive relationship between the log-transformed seed mass and wood specific gravity (p= 0.002827, adj. r^2= 0.287). The species acronyms in the plots are as follows: ACPE = *Acer pensylvanicum* L., ACRU = *Acer rubrum* L., ACSA2 = *Acer saccharinum* L., ACSA3 = *Acer saccharum* Marshall, ACSP2 = *Acer spicatum* Lam., ALINR = *Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen, AMAR3 = *Amelanchier arborea* (Michx. f.) Fernald, BEAL2 = *Betula alleghaniensis* Britton, BEPA = *Betula papyrifera* Marshall, BEPO = *Betula populifolia* Marshall, CACO15 = *Carya cordiformis* (Wangenh.) K. Koch, CAOV2 = *Carya ovata* (Mill.) K. Koch, FAGR = *Fagus grandifolia* Ehrh., FRAM2 = *Fraxinus americana* L., JUCI = *Juglans cinerea* L., OSVI = *Ostrya virginiana* (Mill.) K. Koch, PODE3 = *Populus deltoides* W. Bartram ex Marshall, POGR4 = *Populus grandidentata* Michx., PRPE2 = *Prunus pennsylvanica* L. f., PRSE2 = *Prunus serotina* Ehrh., QUMA2 = *Quercus macrocarpa* Michx., QURU = *Quercus rubra* L., SAER = *Salix eriocephala* Michx., SOAM3 = *Sorbus americana* Marshall, TIAM = *Tilia americana* L., ULAM = *Ulmus americana* L.. Species codes and nomenclature follows the USDA plants database (NRCS 2012).

2004, Reich 2014). A third important functional trait tradeoff is between producing many small seeds that can disperse to a wider surrounding area or producing fewer but larger seeds with more stored maternal reserves to support survival and establishment of the developing seedlings (Foster and Janson 1985, Leishman et al. 2000). Seeds are an important source of food for birds and mammals, with large "mast" seeds being especially valued by wildlife (Leishman et al. 2000). In forests, these plant functional trait spectra tend to follow succession from small-seeded, fast-growing pioneers to larger-seeded, slow-growing climax species (Reich et al. 1998a, 1998c).

A comparison of 26 temperate deciduous tree species from northeastern North America shows that *U. americana* falls near the middle of the trait range on this functional trait spectrum (see ULAM in Fig. 9). Not surprisingly, *Fraxinus*, which is most like elm in terms of habitat preferences and successional status, is also very close to elm on the functional trait spectra (compare FRAM2 to ULAM in Fig. 9A and 9B). Other species that frequently co-occur with *U. americana,* such as *A. saccharinum* and *A. rubrum*, likewise have similar functional trait values (see ACSA2 and ACRU, respectively, in Fig. 9A and 9B). Therefore, we should not expect a large impact on ecological function where elm was replaced in the forest canopy by these ecologically and functionally similar species following the spread of Dutch elm disease.

It is important to note that leaf traits, seed size, and wood specific gravity are not the only functionally important traits of trees. Loss of elms as codominant canopy trees may have affected ecological functions in floodplain forests in more subtle ways. For instance, a relatively

unique trait of elms is that their seeds ripen in late spring, a time when there are few other seeds available to granivorous birds and mammals. Although *A. saccharinum* and *A. rubrum* also produce their seeds in late spring, *Fraxinus* and most other northeastern North American tree species produce their seeds later in the year (Young and Young 1992). Another potentially unique characteristic of elms is that their wood is reputed to have exceptional resistance to decay when in continuous contact with water (Richens 1983). Given that the wood of fallen riparian elms will frequently end up in the water and that logs provide ecologically important habitat structure in stream channels (Collins et al. 2012, Schenk et al. 2014), decay resistance of submerged wood could be a functionally significant trait. Unfortunately, I do not know of any studies comparing durability of elm logs with logs of other species in streams. Studies comparing decomposition rates of logs on the ground showed that under those circumstances elm logs decay relatively quickly but decay rates of submerged logs could be substantially slower (Vrška et al. 2015).

Food Web

Farmers have fed elm leaves to their livestock since prehistoric times because of the relatively high palatability of elm (Grime et al. 1988, Richens 1983). As is typical of palatable plants, elm leaves have a low carbon-to-nitrogen ratio (C:N), a high pH, and decompose quickly (Ellenberg 1988). In the Connecticut River floodplain, beavers cut trees in the following order of frequency: *Salix, Populus, Fraxinus, Ulmus, Acer* (Marks and Canham 2015). My observations of vole girdling of tree seedlings planted in floodplains suggest that this rank order of genus preferences extends to rodent species other than beavers. In North America, there are more than 500 species of insects that are thought to be intimately associated with elm by either breeding, feeding, ovipositing, or hibernating in elms (Hoffmann 1942). Comparisons of tree genera for the number of insect species that feed on them show that *Ulmus* is ranked near the median both in eastern North America (Tallamy and Shropshire 2009) and Europe (Southwood 1961). Although counterintuitive, palatable plants like elm are actually expected to have fewer herbivorous insect species feeding on them because production of defensive compounds that reduce palatability evolve in response to more intensive insect feeding (Wratten et al. 1981). Nevertheless, native plants have many more caterpillars and other insects feeding on them than nonnative species (Burghardt et al. 2010, Southwood 1961). Thus the loss of large numbers of native elms and their frequent replacement by nonnative trees in cities may have had a significant impact on abundance of butterflies and moths as well as the success of nesting birds that prey on caterpillars (Burghardt et al. 2009).

Perhaps more important than the number of herbivores supported by elm is the number of insects that are specialized to elms as their primary host, because these species would be most threatened by a loss of elms (Table 4). In the case of the double-toothed prominent caterpillar

Table 4.—Preliminary list of caterpillars native to eastern North America that are specialized on *Ulmus* as their primary or even their exclusive host plant (Wagner 2010)

Common name	Species name	Type of caterpillar
Ochre dagger moth	*Acronicta morula*	Moth
Ruddy dagger moth	*Acronicta rubricoma*	Moth
Delightful dagger moth	*Acronicta vinnula*	Moth
Four-horned sphinx	*Ceratomia amyntor*	Moth
Double-lined prominent	*Lochmaeus bilineata*	Moth
Double-toothed prominent	*Nerice bidentata*	Moth
Question mark	*Polygonia interrogationis*	Butterfly

(*Nerice bidentata* Walker) this specialization appears to go beyond diet; the characteristic double-toothed dorsal keel of this caterpillar mimics the edge of an elm leaf (Wagner 2010). Insect species specialized to elms as their host have so far not been reported as threatened due to DED. This finding is not surprising, given that elm trees are still frequent in floodplain forests even if the total basal area of *Ulmus* trees has declined precipitously. However, these elm-specialist species could become threatened in the future should native elms continue to decline.

Ulmus americana and *U. rubra* are the first trees to flower in the spring, closely followed by *Acer rubrum* and *A. saccharinum* (Heinrich 1976, Marks unpublished data). The elms flower before leaf out when there is often still snow on the ground in New England. Although elms are primarily wind pollinated, their flowers are sometimes visited by insects, especially bees (Richens 1983). Likewise, herbivorous insects and their avian predators are attracted to the developing seeds of these tree species in early spring when most other trees are still bare. The early greening of floodplain trees may be one of the reasons that songbirds follow major rivers on their spring migration (Gauthreaux and Belser 2003, Kirsch et al. 2013).

Unlike most upland tree species whose seeds ripen in the summer or fall, the seeds of many floodplain tree species ripen in the spring to time their dispersal to coincide with the receding waters of the spring freshet. The order of floodplain tree seed dispersal roughly corresponds to the elevation of their preferred habitat. Specifically, *U. americana* seeds ripen first because they prefer the most well-drained parts of the active floodplain. They are followed by *A. rubrum* and *A. saccharinum*. Last of the spring seed producing trees are *P. deltoides* and *Salix* species because they are specialized to colonizing the most flood prone surfaces on new bars (Marks, unpublished data). Both avian and small mammal granivores consume elm seeds (Dulamsuren et al. 2009; Erritzoe 2010; Hulme and Hunt 1999; Perea et al. 2013, 2014; Venturas et al. 2014). Given that winter caches of seeds may be depleted by spring and few other plants produce seed at that time of year, elm seed could be locally important to granivore populations.

Conclusions and Perspectives

The greatest impact of DED on American elm has been on the population of canopy trees (i.e., trees >30 cm or >1 foot d.b.h). Unlike smaller elm trees, the number of elms that live long enough to reach the floodplain forest canopy have become rare (Fig. 6) because elm mortality rates increase dramatically with tree size (Figure 1A). One cannot talk about a recovery in the floodplain elm population until the *U. americana* mortality rate for canopy tree elms has come down to the range of mortality rates for other tree species (i.e., 3 to 5 percent/year). In controlled tests, currently the most disease-tolerant selections of *U. americana* can have a mortality rate as low as 4 percent after infection with the DED pathogen (e.g., Beier et al. 2017, this proceedings; Flower el al. 2017, this proceedings; Townsend and Douglass 2001), which implies that reaching the goal of an eventual recovery of the elm canopy tree population is plausible.

Ulmus americana fulfills the primary criterion of foundation species by having been a leading dominant of many forests, in this case floodplain forests of northeastern North America, the Mississippi Alluvial Valley, and along the rivers of the prairies. However, the loss of *U. americana* as canopy trees probably has not had as large of an effect on ecosystem processes and higher trophic levels as the loss of some other foundation species because the tree species that have replaced elms are ecologically and functionally very similar to elm. In particular, *A. saccharinum, A. rubrum*, and *Fraxinus* species, especially *F. pennsylvanica,* have similar functional traits and habitat preferences. Such ecological redundancy of tree species increases the resiliency of forests to disturbances, in this case, recovery of ecosystem processes and forest structure following the loss of canopy elms due to DED. However, with the invasive emerald ash borer now spreading

across the region and killing millions of *Fraxinus* trees, any "ecological insurance" from species redundancy has been used up in the region's floodplain forests. The reintroduction of canopy elms by planting disease tolerant *U. americana* selections in floodplain forests across the region to replace the *F. pennsylvanica* that have died would be a timely conservation action to help these increasingly rare communities recover some ecological resiliency (e.g., Knight et al. 2017, this proceedings).

The preferred habitat of elms are rich soils, in the case of *U. americana*, typically alluvium in the better drained parts of active floodplains (i.e., in the transition from dominance by floodplain pioneer tree species like *P. deltoides* and *A. saccharinum*, to upland tree species like *A. saccharum* and *Tilia americana,* which occurs where flooding happens around 1 percent of the time). Forests on relatively flat ground with rich soils such as many floodplain forests have been extensively cleared for agriculture. With a growing concern over stream water quality impacts of intensive agriculture, there are conservation programs that plant riparian buffers on streams passing through crop fields and pastures. This restoration of riparian buffers provides an opportunity to reintroduce native elms to these prime elm habitats by planting disease tolerant selections of *U. americana* (e.g., Knight et al. 2017, this proceedings).

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