Forest Diversity and Disturbance: Changing Influences and the Future of Virginia's Forests

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ABSTRACT

The Virginia landscape supports a remarkable diversity of forests, from maritime dune woodlands, swamp forests, and pine savannas of the Atlantic Coastal Plain, to post-agricultural pine-hardwood forests of the Piedmont, to mixed oak, mesophytic, northern hardwood, and high elevation spruce-fir forests across three mountain provinces in western parts of the state. Virginia's forests also have been profoundly shaped by disturbance. Chestnut blight, hemlock woolly adelgid, emerald ash borer, and other pests have caused declines or functional extirpation of foundation species. Invasive plants like multiflora rose, Oriental bittersweet, and Japanese stiltgrass threaten both disturbed and intact forests. Oaks and other fire-dependent species have declined with prolonged fire suppression, encouraging compositional shifts to maple, beech, and other mesophytic species. Agriculture has left lasting impacts on soil and microsite variations, and atmospheric nitrogen deposition has led to soil acidification, nutrient loss, and diversity declines. Future changes associated with climate warming are expected to influence species distributions and habitat quality, particularly for hemlock-northern hardwood and spruce-fir forests. These and other disturbances will continue to shape Virginia's forests, influencing species interactions, successional trajectories, and susceptibility to invasive plants and secondary stressors, and initiating broader impacts on forest diversity, ecosystem processes, and habitat resources for associated species and neighboring ecosystems.

DIVERSITY OF VIRGINIA'S FORESTS

Biodiversity losses affect ecosystems throughout the world, but forests have been particularly affected. Like most forests in eastern North America, those in Virginia have undergone centuries of change, shaped by natural and cultural disturbances. Pollen records suggest that Appalachian oak forests have changed more rapidly over

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the past 150 years than at any other time in the past 4,000 years (Delcourt and Delcourt 1998). Across Virginia, these rapid changes have resulted largely from agricultural clearing, timber harvesting, and burning; invasive species impacts; intensive herbivory by white-tailed deer; and atmospheric influences (Gilliam 2007; Fleming 2012). Habitat loss, degradation, and fragmentation are considered primary threats to forested ecosystems (Wilson and Tuberville 2003). In less than four decades, Virginia has lost more than 200,000 ha of forest. Annually, this includes an estimated 20,000 ha of forest loss and a comparable area of development throughout the state (Wilson and Tuberville 2003; VA-DOF 2014a). Non-native and invasive plants, insects, and pathogens further threaten Virginia's forests. Nearly half of the species listed as threatened or endangered under the U.S. Endangered Species Act are considered at risk because of non-native invasive species, with damage and control costs for invasive species in Virginia estimated at $1.4 to $3 billion per year (Pimentel et al. 2005).

Virginia leads the nation in vascular plant diversity and diversity of globally rare plants (13th and 14th, respectively) (Wilson and Tuberville 2003). Despite this remarkable diversity, or more likely because of it, Virginia has one of the highest plant and animal extinction rates in the country (8th in the U.S.). Much of Virginia's diversity results from variations in topography, regional climates, soils, and bedrock geology across more than 750 km from the Atlantic Ocean to the Appalachian Mountains, and numerous species at or near northern or southern geographic limits. Virginia spans seven of 20 major "ecoregions" (U.S. EPA 2013) and five major physiographic provinces (Woodward and Hoffman 1991; Fleming 2012) across the eastern U.S. Descriptions of physiographic provinces and associated natural communities used in this manuscript follow Fleming (2012), as presented in the *Flora of Virginia* (Weakley et al. 2012). The Atlantic Coastal Plain in far eastern Virginia makes up approximately one-fifth of the state. This province is dominated by maritime dune woodlands, scrub, and grasslands; tidal marshes; forested swamps; and pine savannas (Fleming 2012). Historically, much of the Coastal Plain was dominated by longleaf pine (*Pinus palustris*) forests and woodlands, with oaks, hickories, and other pine species of greater importance in the northern and inner Coastal Plain. Today, Coastal Plain forests are comprised largely of loblolly and shortleaf pines (*Pinus taeda, P. echinata*) or southern mixed hardwoods. Additional diversity occurs in maritime dune woodlands where live oak (*Quercus virginiana*) and other drought-tolerant coastal oaks and pines are common, and bottomland swamp forests of bald cypress (*Taxodium distichum*), swamp tupelo (*Nyssa aquatica)*, black gum (*N. biflora*), and red maple (*Acer rubrum*) (Fleming 2012; Fleming et al. 2016). West of the Coastal Plain, the Piedmont covers an additional 40% of the state's land area. These rolling, post-agricultural pine-hardwood forests are relatively low in diversity and dominated by mixed oaks, most notably white and black oaks (*Q. alba, Q. velutina*), and Virginia and shortleaf pines (*P. virginiana, P. echinata*). Successional forests include hardwoods such as sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), and hickories (*Carya* spp.).

Recognition of three distinct mountain provinces emphasizes the topographic and geologic diversity in western parts of the state. In the Ridge and Valley and the Blue

Ridge Provinces, mixed oak forests dominate drier sandstone ridges and upper slopes where American chestnut (*Castanea dentata*) once was common. Chestnut oak (*Q. montana*), white oak, red oak (*Q. rubra*), and hickories are especially common, with understory ericaceous or heath shrubs (esp. blueberries; *Vaccinium* spp.) on drier and more acidic sites. Mesophytic species increase on calcareous substrates, particularly in cool, moist valleys, and reach greatest importance in mesophytic cove forests in far western Virginia, in the Cumberland and Allegheny Mountains of the Appalachian Plateaus province. These mesophytic forests are considered a hotspot of temperate forest diversity and are dominated by an impressive variety of tree species, including sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), red and white oaks, tulip poplar, basswood (*Tilia americana* var. *heterophylla*), yellow buckeye (*Aesculus flava*), eastern hemlock (*Tsuga canadensis*), and magnolia (*Magnolia* spp.) (Woodward and Hoffman 1991; Fleming 2012). At higher elevations, dominance shifts to northern hardwoods such as sugar maple, American beech, black and yellow birches (*Betula lenta, B. alleghaniensis*), and hemlock. Unique montane forests occur on the highest peaks of the Blue Ridge, above 1,500 m, where spruce-fir (*Picea rubens-Abies fraseri*) forests become prevalent.

Forest disturbances and ecosystem responses are as varied as Virginia's forests themselves. Maritime forests and dune woodlands on the Coastal Plain are considered globally rare natural communities due to restricted range and threats from coastal development, erosion, and other natural and anthropogenic impacts on dune systems. Fire suppression is responsible for structural and compositional changes in fire-dependent coastal woodlands (Fleming et al. 2016). High elevation spruce-fir forests experience greatest threat from the balsam woolly adelgid (*Adelges piceae*), an introduced insect responsible for more than 90% mortality of Fraser fir (*Abies fraseri*), as well as atmospheric pollution and acid deposition, and historical impacts of logging and fire. Alluvial floodplain forests have a long history of agricultural clearing and logging, development, and hydrologic alteration. Moist, nutrient-rich floodplain soils also make these communities particularly susceptible to invasive plants (Spira 2011). Across nearly all parts of the state, vast pre-settlement forests have been largely cleared or degraded for anthropogenic land uses, particularly crops and grazing animals (Stephenson et al. 1993; Fleming 2012). Degradation of Appalachian rich cove forests is of particular concern due to their exceptional biotic diversity and richness of endemic species (Woodward and Hoffman 1991; Spira 2011). In this region, overharvesting also threatens commercially important forest herbs such as American ginseng (*Panax quinquefolius*) and black cohosh (*Actaea racemosa*), and, like floodplain forests, mesic conditions make these sites particularly susceptible to invasive plant encroachment.

LAND USE AND LEGACY EFFECTS

Native American settlements were documented in southeastern Virginia as early as 17,000 years ago, with small-scale agriculture and low-intensity fires increasingly used as management practices. As Native American populations expanded 8,500 to 4,000 years ago, agricultural clearing and burning became more widespread and intensive throughout the state (Egloff and Woodward 2006). Despite this, the Virginia landscape

was almost continuously forested when Europeans colonized in the early 1600s. As European settlements grew, forests were cleared rapidly, with nearly 50% of the state's forests were removed by the late-1800s (Fleming 2012). Intensive logging, agriculture, and burning, and opening of mountain regions for timber and coal extraction caused severe landscape degradation by the 1930s. By the mid-1900s, however, many farms were abandoned and much of the eastern landscape returned to forest. In Virginia, approximately 60% of uplands and 75% of remaining wetlands are now forested (Fleming 2012). As a result, eastern forests have been described as more natural today than at any other time in recent centuries (Foster et al. 2003).

Despite agricultural abandonment and reforestation in the early 20th century, today's forests are very different from those of the past. It is becoming clear that modern species distributions and ecosystem dynamics cannot be understood without considering this long-term history of anthropogenic land use, particularly agricultural history. These influences are especially apparent in the herbaceous layer, because of its responsiveness to site conditions and disturbance (Small and McCarthy 2005; Gilliam 2007). Flinn and Vellend (2005) suggest that differences in species composition, diversity, and soil characteristics in post-agricultural forests (compared to forests without agricultural history) may persist for centuries after land abandonment. Loss of diversity occurs through direct elimination of species during land clearing and reduced recruitment, often due to dispersal limitations and low fecundity of forest herbs. Encroachment of opportunistic species during forest recovery also impacts native diversity (Foster et al. 2003; Flinn and Vellend 2005). Cultivation (plowing) has been shown to homogenize upper soils layers, deplete nutrients and organic matter, and remove microsite variation (e.g., pit and mound topography created by tree falls) necessary for the germination of many forest herbs (Beatty 2003; Foster et al. 2003). Soil amendments produce lasting increases in pH and fertility and encourage competitive, nitrogen-demanding species (Foster et al. 2003; Flinn and Vellend 2005). These "legacies" or persistent influences of historical land use practices can equal or outweigh prevailing influences such as topography, soils, and modern disturbances.

Structurally and compositionally, today's forests also are very different from those of pre-settlement periods. Across the U.S., most forests (~85%) are less than 100 years old and just 0.1% are considered old-growth (> 200 years) (Gilliam 2007; Butler et al. 2015). In Virginia, youngest forests occur in the coastal plain and southern piedmont. Throughout the state, forests are highly fragmented, with just 20% in large, contiguous blocks (Fleming 2012; Rose 2013). A regional assessment of land cover change from 1973 to 2000 shows that forest regeneration has now slowed and forest cover is declining across the eastern U.S. (Drummond and Loveland 2010). In 2011, approximately 6.4 million ha in Virginia were forested – similar to 2001 forested area. However, more than 100,000 ha of forest has shifted to non-forested use. Development was responsible for the greatest net loss of forest, except in the inner coastal plain where losses stemmed largely from mechanical clearing for timber and agriculture (Drummond and Loveland 2010; Rose 2013). No major gains in forest area were reported across the region, although Rose (2013) noted that declines in agriculture

offset increases in development and clearing over the past decade. As a result of these land conversions, Virginia forests today are relatively even-aged and comprised largely of oak-hickory (*Quercus-Carya*), oak-pine, or loblolly-shortleaf pine (*Pinus taeda-Pinus echinata*) forest types. A sizable proportion of these forests lie in pine plantations (~13%, esp. loblolly pine) and early-successional pine or pine-hardwood stands (~10%), especially in the piedmont and coastal plain (Fleming 2012; VA-DOF 2014a).

FIRE HISTORY AND FOREST MESOPHICATION

Fire history also has played an important role in shaping eastern forests, including those in Virginia. For thousands of years, Native Americans used low-intensity surface fires to clear the landscape, prepare sites for crops, and encourage fruit production and wild game. This periodic burning and occasional lightning fires created a patchy landscape and strongly favored fire-tolerant trees such as oaks, American chestnut, and pines (Delcourt and Delcourt 1998; Brose et al. 2001). Fire also was key to the formation of open woodlands, savannas, and grasslands in Virginia (Fleming 2012). With European colonization, fires increased in frequency and severity. High-intensity stand-replacing fires became common in the late 19th and early 20th centuries as forests were cleared and burned. Railroads expanded access to forests in remote parts of the state and sparked frequent fires from coal or wood fuel ignitions. These intense fires continued to favor oaks, hickories, chestnut, and coastal fire-tolerant pines such as longleaf and shortleaf pines, and restricted mesophytic species such as beech and maples to moist and protected sites (Ware et al. 1993; Nowacki and Abrams 2008). Concern over the effects of these intense and unregulated fires led to extensive fire suppression campaigns (i.e., Smokey Bear) beginning in the mid-20th century. These efforts were highly effective, nearly eliminating fire from Virginia's natural and managed ecosystems over the next 100 years (Brose et al. 2001; Fleming 2012).

The role of fire in forest development in Virginia and neighboring regions has been well-documented. Studies of fossil pollen and charcoal by Delcourt and Delcourt (1998) illustrate the importance of Native American burning in expanding oak-chestnut forests across the southern Appalachians 3,000 to 1,000 years ago, particularly on ridgetops and upper slopes. Tree rings studies by Aldrich et al. (2014) in pine-oak forests of the Virginia Blue Ridge and Ridge and Valley Provinces report a relatively constant 6 to 8 year fire return interval from the late 1600s through European settlement and early industrialized logging and railroads. By the early 1900s, however, fire scars were almost entirely absent from these trees due to fire suppression efforts. Silver et al. (2013) found similar results in Virginia Ridge and Valley forests, with a typical fire return interval of 14 years from 1850 to 1930, followed by a period of marked fire suppression. In coastal plain forests on Virginia's Eastern Shore, Kirwan and Shugart (2000) reported negative correlations of American beech and red maple, species highly sensitive to fire, to soil charcoal and modeled fire frequencies. They concluded that beech and red maple dominance is indicative of long-term fire absence, whereas scarlet oak (positively correlated with fire history estimators) indicated a long-term history of fire in these coastal plain forests.

Fire prevention efforts beginning in the early 1900s led to dramatic structural and compositional changes in eastern forests. Open woodlands and savannas have been replaced by closed-canopy forests; fire-dependent species have been replaced by those sensitive to fire; and forest understories have become increasingly shaded, encouraging

shade-tolerant species (Brose et al. 2001). In Virginia, many fire-dependent communities are declining due to fire suppression, including Pond Pine (*Pinus serotina*) Woodlands and Pocosins and Pine / Scrub Oak Sandhills (historically dominated by longleaf pine) on the coastal plain and Pine-Oak / Health Woodlands in the Appalachian Mountains (Fleming 2012; Fleming et al. 2016). Nowacki and Abrams (2008) coined the term "mesophication" to describe the replacement of oaks, hickories, pines, and other fire-tolerant eastern forest trees by mesophytic and fire-sensitive species such as red maple, American beech, tulip poplar (*Liriodendron tulipifera*), black birch, and Eastern hemlock. These species create dense shade and cool, moist conditions less conducive to fire. These changes reduce oak regeneration and have resulted in widespread declines, particularly of white oak. Once the dominant species across much of the Central Appalachians, Abrams (2003) suggests that virtually no white oak regeneration has occurred in eastern forests over the past 100 years, and little to no regeneration has occurred in other upland oak species over the past 50 years. While oaks tolerate a wide range of growing conditions, higher light, shallow leaf litter, and periodic disturbance are needed for successful germination. In the absence of fire, white oak tends to be a poor competitor and generally gives way to more shade-tolerant species. In pre-settlement forests of Virginia, white oak was one of the most abundant forest species, representing an estimated 18 to 49% of forest cover, with secondary importance of red oak, American chestnut, chestnut oak, hickories, and pines. Today, white oak remains dominant (30% of forest cover) only on xeric, nutrient poor sites but is considerably less abundant (5-9%) on mesic sites (Abrams 2003).

Current forest inventory data emphasize this compositional shift to mesophytic species. Virginia forests contain a diversity of tree species, but just four: tulip poplar, loblolly pine, chestnut oak, and white oak – make up about 50% of the total forest volume (Rose 2013). Since 2001, tulip poplar has increased by more than 20% in Virginia forests. Loblolly pine has increased by 32%, with most increases in the coastal plain and eastern piedmont. Based on tree density (rather than volume), red maple and loblolly pine were by far the most abundant species in 2011, representing almost a quarter of all tree stems in Virginia forests (12% and 10%, respectively). Red maple and loblolly pine each had more than three times the density of the most abundant oaks (white oak = 3.5%, chestnut oak = 3%). These numerous small stems indicate that red maple and loblolly pine make up much of the regeneration layer in our forests (Rose 2013). Efforts to encourage regeneration of oaks and other fire-dependent species focus largely on prescribed burning. Fire has been very effective in restoring some fire-dependent natural communities, although there is little expectation that Virginia's natural areas will return to pre-settlement conditions (Wilson and Tuberville 2003; Fleming 2012).

DIRECT AND INDIRECT EFFECTS OF FOREST PESTS
Forests Pests and Pathogens

Exotic insect pests and fungal pathogens pose a serious threat to Virginia's forests and have been responsible for declines or functional extirpation of many forest species. American chestnut, eastern hemlock, and other forest dominants have been described as "foundation species" for their local abundance, importance to forest structure and microenvironments, and regulation of ecosystem processes for co-occurring species (Ellison et al. 2005). Effects of pests and pathogens on foundation species can be

particularly detrimental because of these broader ecosystem impacts. For example, American chestnut once comprised more than 50% of Appalachian forests on drier upland sites, but by the 1940s was largely eliminated by the chestnut blight (*Cryphonectria parasitica*) fungus (Paillet 2002). Today, chestnut occurs almost exclusively as an understory shrub and typically succumbs to the blight before reaching reproductive maturity, resulting in compositional shifts largely to oak or oak-hickory dominance. Compared to oaks, chestnut grows and takes up nutrients more quickly, leaves decompose more rapidly, and high tannin content results in slower wood decomposition. Thus, ecological consequences of losing American chestnut have included, changes in forest productivity, nutrient dynamics, and decomposition rates, as well as reduced quantity and quality of wildlife food. Altered nutrient dynamics also have influenced associated streams and macroinvertebrate and fish assemblages (Ellison et al. 2005).

Like American chestnut, eastern hemlock and Carolina hemlock (*Tsuga caroliniana*) may be functionally eliminated from our forest in coming decades due to an exotic pest. The hemlock woolly adelgid (*Adelges tsugae*; HWA), a Japanese insect, often kills adult trees within just four to ten years (McClure 1991). The HWA has spread to nearly every Virginia county in which eastern and Carolina hemlocks occur (piedmont and mountains) and has caused severe declines in hemlock populations (Fleming 2012; Rose 2013). Abella (2014) reported nearly 50% mortality of eastern hemlock in Shenandoah National Park from 1990-2000, with greater impacts in lower elevation forests. Krapfl et al. (2011) found significant but somewhat lower declines (11% mortality of canopy trees and 34% mortality of understory hemlocks) in higher elevation forests of Great Smoky Mountains National Park from 2003 to 2008-2009. Along streams in the Virginia Ridge and Valley province and West Virginia Appalachian Plateau, Martin and Goebel (2012) reported that hemlock remained dominant but both trees and saplings showed more than 50% defoliation, suggesting that complete mortality is likely within a few years. As one of the only evergreen trees in low- and mid-elevation Appalachian forests, hemlocks support unique ecosystem functions. Their foliage creates dense shade, cool moderate temperatures, and forms a thick layer of acidic and slowly decomposing leaf litter that influences water chemistry, temperature, and flow in associated streams. Hemlock forests also support unique assemblages of understory plants, invertebrates, birds, and mammals (Ellison et al. 2005; Abella 2014). With hemlock mortality, canopy gaps increase understory light availability, soil temperatures and nitrification rates, and decrease moisture (Jenkins et al. 1999), encouraging invasive plants such as Japanese barberry (*Berberis thunbergii*), Oriental bittersweet (*Celastrus orbiculatus*), tree of heaven (*Ailanthus altissima*), garlic mustard (*Alliaria petiolata*), and Japanese stiltgrass (*Microstegium vimineum*) – species typically absent from healthy hemlock forests (Small et al. 2005; Eschtruth et al. 2006; Martin and Goebel 2012). Former hemlock forests often shift to oak, birch, maple, and/or tulip poplar dominance, or thickets of rhododendron (*Rhododendrox maximum*) that are capable of inhibiting forest development. These new communities differ markedly from hemlock-dominated forests in structure, microclimate, nutrient dynamics, and habitat resources for associated species (Jenkins et al. 1999; Small et al. 2005).

Flowering dogwood (*Cornus florida*) has experienced severe declines due to dogwood anthracnose (*Discula destructiva*), a fungal disease. Dogwood anthracnose

was first recognized in Virginia in the early 1980s and currently affect dogwood trees throughout the central and southern Appalachians (Suchecki and Gibson 2008). Drought and powdery mildew also contribute to dogwood declines. In Virginia forests, dogwood declined more than 30% from 2001 to 2007, with an additional 25% through 2011 (Rose 2013). Higher elevation moist and shaded sites, including cove and alluvial forests, appear most heavily affected, many reporting more than 90% loss (Jenkins and White 2002; Holzmueller et al. 2006; Suchecki and Gibson 2008). Loss of dogwood as a subcanopy tree has the potential to reduce soil fertility and pH, as its leaf litter is an important contributor of soil calcium, and eliminate an important food source for many associated forest birds (Holzmueller et al. 2006).

The emerald ash borer (*Agrilus planipennis*; EAB), an Asian wood-boring beetle, is a more recent threat to Virginia forests and responsible for widespread declines in ash trees (*Fraxinus* spp.). Larval feeding interrupts sap flow, girdling and killing trees often within 2 to 4 years. Early infestation sites have shown up to 99% mortality of adult trees. All North American ash species are susceptible, including white (*F. americana*) and green ash (*F. pennsylvanica*), those most common in Virginia forests (Herms and McCullough 2014). In Virginia, EAB became established in 2008 and since has been discovered in 23 counties, primarily in central and northern parts of the state (VA-DOF 2014b). Like other forest pests, broader impacts of the EAB include canopy gap formation, increased understory light and reduced moisture levels and nitrification, increased woody debris, and facilitation of non-native invasive plants (Hausman et al. 2010; Herms and McCullough 2014). Ash mortality also is predicted to impact insect species that feed on ash trees, including more than 20 species of North American moths, butterflies, and leaf miners that rely on ash as a primary food source (Wagner 2007). Flower et al. (2013) also suggest substantial declines in regional forest productivity (30% or more) with ash mortality, at least in the short-term, during which time severely infected stands may function as carbon sources rather than sinks.

Other more recent or perhaps less well-known pathogens in Virginia forests include butternut canker disease (*Ophiognomonia clavigignenti-juglandacearum*), which has caused dramatic declines in butternut (*Juglans cinerea*), a species once widespread in the northeast and southward to northern and western parts of Virginia (Clark et al. 2008; Bower et al. 2014). By 1995, nearly 80% butternut mortality was reported in southeastern states, with complete elimination from North and South Carolina forests (Schlarbaum et al. 1998). Other pests not yet affecting Virginia forests but raising considerable concern include black walnut thousand cankers disease (*Geosmithia morbida*), a fungal pathogen spread by the walnut twig beetle (*Pityophthorus juglandis*) and first discovered in Virginia in 2011. Forest Inventory and Analysis data showed that black walnut populations in Virginia remained healthy, with stable crown conditions from 2000 to 2010 (Randolph et al. 2013). However, walnut mortality due to thousand cankers disease in western states and more recent outbreaks in Tennessee have led to careful monitoring and quarantines in Virginia.

Many other insect pests and pathogens threaten Virginia forests. Our intention is not to not present an exhaustive list here, but to emphasize the important role they may play in future Virginia forests. Lovett et al. (2006) suggest that these pests may be the primary driver of ecosystem change in coming decades. Gandhi and Herms (2010) say that these invaders have the potential to "unleash a diverse cascade of direct and indirect effects on ecosystem processes and ecological interactions that can alter

community composition and successional trajectories of eastern North American forests". Impacts common to many of these pests and pathogens include tree defoliation, stress, and mortality; increased size and frequency of canopy gaps; altered light, temperature, and moisture environments; increased woody debris; altered litter quality and nutrient cycles; changes in species interactions, composition, and successional trajectories; and facilitation of light-demanding and invasive species.

Non-Native Invasive Plants

Ninety non-native invasive plant species have been identified by the Virginia Department of Conservation and Recreation (VA-DCR) as ecological or economic threats to the Virginia's protected natural areas (Heffernan et al. 2014). These tend to be most abundant in forests of the Virginia piedmont and least in mountain provinces, particularly in the northern Ridge and Valley (Rose 2013). Thirty-eight of the invasive plants recognized by VA-DCR have an invasiveness rank of "high" for their widespread abundance, ability to invade relatively undisturbed habitats, and pronounced impacts on native species and ecosystem processes (Heffernan et al. 2014). Across Virginia, Japanese honeysuckle (*Lonicera japonica*), multiflora rose (*Rosa multiflora*), and tree-of-heaven are considered the most widespread and abundant invasive plant species (Robertson et al. 1994; Rose 2013). Others ranked as highly invasive across the state include shrubs such as autumn olive (*Elaeagnus umbellata*), Chinese privet (*Ligustrum sinense*), and Amur honeysuckle (*Lonicera maackii*); woody vines such as kudzu (*Pueraria montana* var. *lobata*) and Oriental bittersweet; and many herbaceous species, including garlic mustard and Japanese stiltgrass (Heffernan et al. 2014).

Invasive tendencies are much more common among shrubs and herbs, as these species tend to grow more rapidly with higher rates of vegetative and sexual reproduction. However, tree-of-heaven (high invasiveness rank) and princess tree (*Paulownia tomentosa*; medium invasiveness) are of particular concern in Virginia (Heffernan et al. 2014). Both have increased dramatically in Virginia forests in recent years (2007 to 2011: 16% and 14% increases) (Rose 2013). Tree-of-heaven is particularly problematic because of its ability to suppress resident species through allelopathy or chemical inhibition. In southwest Virginia, tree-of-heaven was found to have greater impact on native understory species than associated invasives, suggesting that it may facilitate the spread of other non-native plants (Small et al. 2010). Chemical inhibition also has been noted in garlic mustard, a common invader of moist forest understories in Virginia. Stinson et al. (2006) found that garlic mustard suppresses tree reproduction in beech-maple forests by interrupting beneficial seedling-mycorrhizal fungi associations, helping garlic mustard to invade relatively intact forests. Japanese stiltgrass, also prevalent in shaded and intact forest understories, alters soil chemistry and nutrient cycles and reduces habitat use by soil invertebrates (Ehrenfeld et al. 2001; McGrath and Binkley 2009). Additional species have been listed by the VA-DCR as "early detection species" – those not yet widespread in Virginia but highly invasive in similar habitats of the region (Heffernan et al. 2014). Wavy-leaved basket grass (*Oplismenus undulatifolius*), discovered just recently (late 1990s) in northern Virginia and Maryland, has been listed as a highly invasive early detection species. Predictive models suggest that, like garlic mustard and Japanese stiltgrass, basket grass has the potential to invade intact and deeply shaded forests and negatively affect understory diversity and ecosystem-level processes (Beauchamp et al. 2013).

Recent ecological studies have focused on understanding ecosystem characteristics that promote or inhibit "invasibility". In temperate forests, site disturbance is very often associated with invasive plant abundance. Numerous studies also suggest that forests or forest patches with greater light, moisture, and nutrients, and those with higher native plant diversity, are more susceptible to invasion (Levine and D'Antonio 1999; Stohlgren et al. 2003; Martin et al. 2008). Using Forest Inventory and Analysis (FIA) data from hemlock-white pine-northern hardwood forests in Pennsylvania, Huebner et al. (2009) found consistently higher invasive plant richness in younger, fragmented forests and those with higher soil pH (increasing availability of nutrients such as Ca, Mg, N) and native plant diversity. Lundgren et al. (2004) and Kelly et al. (2009) also reported increased richness and abundance of invasive plants in disturbed central hardwood and hemlock-northern hardwood forests of southern New England, particularly near roads and trails. Historical land use also appears to have lasting influences on invasive plant distributions. Post-agricultural forests typically support greater richness and abundance of invasive species than sites continuously forested over the past 100 to 150 years (Lundgren et al. 2004; Von Holle and Motzkin 2007; Mosher et al. 2009). Japanese barberry (*Berberis thunbergii*), a common invasive shrub in Virginia forests, seems particularly problematic in post-agricultural forests (DeGasperis and Motzkin 2007; Mosher et al. 2009).

Intact or undisturbed forests typically are thought to be more resistant to non-native plant invasions (Luken 2003). For example, McCarthy et al. (2001) reported no non-native species in an old-growth central Appalachian mixed-oak forest, despite dozens of invasive species in surrounding fields and edge habitats. Recent studies, however, suggest that many invasive species are common in intact, shaded forests and have pronounced impacts. Martin et al. (2008) identified 58 species of invasive plants with high shade tolerance in southern U.S. forests. While many also invade open habitats and disturbed forests, these species have the capacity to invade deeply shaded and intact forests. Of those species ranked as highly invasive and widespread in Virginia, Huebner (2003) found multiflora rose, Amur honeysuckle, Oriental bittersweet, and garlic mustard to occur frequently in closed-canopy forests, based on West Virginia herbarium records. Oriental bittersweet and Japanese stiltgrass were especially common in open, disturbed forests, and Morrow's honeysuckle (*Lonicera morrowii*) and Tartarian honeysuckle (*L. tatarica*) occurred in both forest environments. Habitat models for Oriental bittersweet in North Carolina mountains showed preference for mesic tulip poplar (non-oak) forests and sites with canopy and forest floor disturbance (McNab and Loftis 2002). In these forests, prolonged invasion of bush honeysuckles (e.g., *L. maackii, L. morrowii, L. tatarica*) and Oriental bittersweet has been shown to suppress native species, reducing richness and abundance of tree seedlings and understory herbs, and altering vegetation development patterns in developing forests (Fike and Niering 1999; Collier et al. 2002, Hartman and McCarthy 2008). Thus, it is clear that across Virginia's forests, non-native, invasive plants exert broad impacts on native species that range from direct competition for resources to indirect effects such as altered nutrient cycles, light environments, plant-pollinator interactions, and successional trajectories (Butler et al. 2015).

White-Tailed Deer and Forest Regeneration

From the 1930s to the 1990s, white-tailed deer (*Odocoileus virginianus*) populations across Virginia expanded from 25,000 to 900,000 deer – an increase of

3,500%! (Cote et al. 2004). Changes in land use, especially agriculture and forest fragmentation, loss of top predators, and reduced hunting have led to unprecedented increases in deer in eastern North America. Damage to forest plants from excessive herbivory has been shown to occur at densities as low as 4 deer / km^2 (10 / mi^2) (Alverson et al. 1988). In 1988, deer densities were reported at well over 12 / km^2 (30 / mi^2) in many parts of Virginia, most notably northern and southeastern regions (VD-GIF 2007). Populations throughout the state are estimated to be beyond forest carrying capacities, except in south central and extreme southwest counties. In managed forests of Virginia and elsewhere, excessive browsing also has been shown to reduce stand height and density and lengthen rotation periods, greatly reducing economic value of timber (Cote et al. 2004).

White-tailed deer have been described as keystone species or ecosystem engineers for their broad influences on forest structure, composition, and diversity (McShea and Rappole 1992; Baiser et al. 2008). Intense herbivory reduces growth, regeneration, and survival of preferred browse species, driving shifts in forest composition and successional pathways (Horsley et al. 2003; Baiser et al. 2008). Preferred species, including oaks and hemlock, are typically uncommon or absent from forest understories outside deer exclosures (McShea and Rappole 1992). There is particular concern for reestablishment of eastern hemlock following hemlock wooly adelgid attack, as seedlings are slow growing and especially susceptible to deer browse (Cote et al. 2004). In coastal oak-beech forests near Washington, D.C., Rossell et al. (2007) reported severe oak decline and predicted that continued deer browse will shift future forests almost exclusively to American beech. In mixed-hardwood forests on the Virginia coastal plain, Kribel et al. (2011) documented similar increases in beech and holly (*Ilex opaca*) and declines in red maple, dogwood, and other hardwoods, suggesting that these changes most likely were driven by selective deer browse. Similar studies in Appalachian forests found increases in American beech and reductions in red maple, sugar maple, white ash, and black cherry in response to excessive browse (Kain et al. 2011). Deer avoidance also has favored hay-scented fern (*Dennstaedtia punctilobula*) in many eastern forests (Horsley et al. 2003). Hay-scented fern is a strong understory competitor and has been shown to reduce germination and survival of red oak, white ash, and birch seedlings (George and Bazzaz 2003)

Plants with slow growth and reproductive rates such as spring ephemerals and other mature, mesic forest herbs and shrubs are particularly susceptible to herbivory, especially in spring and summer when herbaceous plants are a primary component of deer diets and most or all above-ground biomass is consumed. In Smoky Mountains National Park, Thiemann et al. (2009) reported severe declines in richness and cover of forest herbs, including complete loss of 46 species from sample plots. These changes occurred from the late 1970s to 2004, a period when peak deer densities reached 43 deer / km^2. Many forest herbs also delay flowering for several seasons after defoliation or shift to predominantly non-reproductive states. In Trillium (*Trillium* spp.), excessive browsing reduced average plant size, lowered survival rates, and delayed flowering for many years (Augustine and Frelich 1998). Similarly, Canada mayflower (*Maianthemum canadense*) was 40 times less likely to flower when exposed to deer browse (Cote et al. 2004). Furedi and McGraw (2004) found that deer eliminated more than half of all fruit-bearing American ginseng plants from West Virginia forests and consumed 50 to 100% of all seeds in some populations. As a result of deer browse and

intense wild harvest pressures, this and other economically valuable Appalachian medicinal herbs may be driven to extinction in the coming century.

Intensive deer browse can initiate far reaching, cascading effects in forested ecosystems. Through direct competition and habitat alteration, deer influence the abundance and distribution of associated animal species. Deer exclosure studies in Shenandoah National Park and elsewhere suggest that removal of understory vegetation increases light and habitat space, facilitating establishment of shade-tolerant invasive plants like garlic mustard, Japanese stiltgrass, and Japanese barberry (Rooney et al. 2004; Knight et al. 2009). Deer-assisted seed dispersal (on hair and hooves) and browse avoidance (preferential browsing on more palatable species) also facilitate spread of these invasives into forest understories. In turn, invasive plants limit regeneration of native trees and herbs through shading and other forms competitive exclusion. Understory removal also eliminates essential habitat resources and causes declines in ground- and midstory-nesting birds and understory insects and spiders (Cote et al. 2004; Baiser et al. 2008). In the fall, deer feed heavily on acorns and other fruits. Competition for food resources has been shown to limit small mammal and other wildlife populations in Virginia forests, particularly during poor mast years (McShea and Rappole 1992). Other broad-ranging ecosystem effects include reduced forest productivity and nutrient cycling, as preferred browse species often are those with nutrient-rich foliage. Remaining unpalatable species or plant components leave lower quality leaf litter for nutrient cycling through the forest ecosystem.

ACID DEPOSITION, CLIMATE CHANGE AND FUTURE FORESTS

Over the past century, industrial and agricultural emissions of nitrogen and sulfur oxides have greatly increased, altering global biogeochemical cycles and increasing concern for the effects of acid deposition on eastern forests. Though Clean Air Act regulations have reduced sulfur emissions and improved air quality in some regions, atmospheric nitrogen and associated deposition continue to increase in many northeast and mid-Atlantic forests (Erisman et al. 2013). Today, some historically nitrogen-limited forests show symptoms of "nitrogen saturation", the availability of nitrogen in excess of biological demand (Aber et al. 1998). Excess nitrogen has been linked to severe ecosystem changes, including increased nitrogen mineralization and nitrate leaching, soil acidification and nutrient loss (esp. calcium and magnesium), aluminum toxicity, and watershed eutrophication. Plant-mycorrhizal associations, important in nutrient absorption for many forest species, also typically decline with nitrogen enrichment (Pardo et al. 2011; Erisman et al. 2013).

Some of the most obvious effects of increased nitrogen deposition are changes in species composition, diversity, and overall forest declines (Bobbink et al. 2010). High elevation spruce-fir forests receive especially high levels of nitrogen deposition due to persistent cloud cover and wet and dry deposition. Effects include reduced tree growth, foliar nutrient imbalances and needle dieback, and increased susceptibility to secondary stressors such as insect pests and diseases, drought, and freezing or frost damage (Bobbink et al. 2010; Gilliam 2014). Fraser fir, a high elevation southern Appalachian endemic, has been largely eliminated from the canopy of these forests by the introduced balsam woolly adelgid and stress from chronic acid deposition (Stehna et al. 2013). Recent studies suggest that nitrogen deposition also negatively affects deciduous forests in the central and southern Appalachians (Boggs et al. 2005; Pardo et al. 2011).

Changes in species composition and reduced diversity have been noted repeatedly, as species adapted to nutrient-limited conditions are replaced by species capable of rapid nitrogen utilization or those less affected by soil chemistry and acidification. While specific influences vary, decreased growth and survival of chestnut oak, scarlet oak, yellow birch, and basswood have been reported in northern hardwood forests, as well as increases in faster-growing, mesophytic species such as red maple, black cherry, and invasive plant species (Pardo et al. 2011; Gilliam 2014). In Virginia, effects of increased nitrogen deposition have been well-documented in mountain forests. Piedmont and coastal plain forests receive lower levels of atmospheric nitrogen deposition and have had little associated study. It is expected, however, that eastern Virginia forests will respond to excess nitrogen in much the same way, with nitrate leaching and soil acidification, changes in foliar nutrient concentrations and increased susceptibility to secondary stress, and shifts in community composition and declines in species richness (Gilliam et al. 2011).

In a review of nitrogen saturated forests in eastern North America, Fenn et al. (1998) suggested that young, vigorously growing forests are most efficient in retaining excess nitrogen, whereas mature forests have relatively low nitrogen retention capacities. In addition, changes in composition and diversity tend to be most pronounced on nutrient-poor sites (Fenn et al. 1998; Bobbink et al. 2010). Forest understory communities are particularly sensitive to nutrient dynamics and have shown significant compositional shifts in response to excess nitrogen. Repeated nitrogen enrichment treatments in eastern deciduous forests have resulted in increased tree canopy cover, causing severe shading and reduced richness and abundance of understory herbs (Bobbink et al. 2010). Gilliam et al. (2011) found initial increases in understory herbaceous cover in central Appalachian forests, but again reported declines in species richness. As in the canopy, declines in herbaceous layer diversity were attributed to competitive exclusion by fast growing, nitrophilous or mesophytic species and non-native invasive species, reduced mycorrhizal associations, and increased susceptibility to disease and herbivory (Gilliam 2007; Gilliam et al. 2011).

Climate changes associated with increased nitrates, carbon dioxide, and other greenhouse gases have influenced Central Appalachian forests for decades and are expected to increase throughout this century. A recent climate change vulnerability assessment for central Appalachian forests suggests that regional temperatures will increase year-round, resulting in longer growing seasons and more frequent weather extremes (Butler et al. 2015). Decreased precipitation in summer months will increase the potential for drought-stress, and increased precipitation in winter will increase streamflow and flooding potential. Warming and drought impacts are expected to have greatest effects on northern hardwood, hemlock, and spruce/fir forest types, those typical of cool, moist environments, and reduce habitat quality for associated species such as beech, sugar maple, black cherry (*Prunus serotina*), red spruce, and balsam fir. The forest herbaceous layer also is expected to respond to climate changes, given its sensitivity to moisture and microclimatic variations, including perennial herbs of economic and cultural importance for medicinal use, foods, or crafts (i.e., non-timber forest products) (Butler et al. 2015; See McGraw et al. 2013 for detailed discussion of climate change and American ginseng.). Floodplain and riparian forests also are expected to be vulnerable. In contrast, drier, southern forest types such as dry and dry-mesic oak-hickory and oak-pine forests and woodlands are predicted to be least

vulnerable, with potential expansion of species such as shortleaf pine, southern red oak (*Q. falcata*), blackjack oak (*Q. marilandica*) post oak (*Q. stellata*), and shagbark and bitternut hickories (*Carya ovata, C. cordiformis*) under warmer and drier climate conditions (Butler et al. 2015).

Just as climates affect native species and forest communities, climate changes are expected to influence the distribution and overall impacts of forest pests and other disturbances. Warmer climates are likely to support range expansion for a number of invasive species, include some of Virginia's most problematic species (Dukes et al. 2009). For example, the hemlock woolly adelgid has been limited by winter temperature extremes. Expansion of this insect pest northward and into higher elevation sites is expected with warmer climates. Similar increases in geographic range and ecological impacts are predicted for beech bark disease, currently isolated to just a few Virginia forests, and forest tent caterpillars, responsible for severe defoliation of oaks, maples and other canopy species. Several invasive plant species also are predicted to expand with warmer temperatures, including Oriental bittersweet, tree of heaven, kudzu, privet, and bush honeysuckles (Dukes et al. 2009; Butler et al. 2015). More frequent and severe droughts also are expected to increase the intensity and frequency of wildfires, further influencing nutrient cycles, forest regeneration, and resulting successional pathways (Dale et al. 2001).

The composition and diversity of Virginia's forests reflect variations in topography, regional climates, and soil conditions across the state. However, our forests also have experienced, and are continuing to experience, natural and anthropogenic disturbances and subsequent successional changes. Agriculture, timber harvest, and shifting fire regimes have left lasting influences on vegetation and ecosystem properties. Oaks and other fire-dependent species have declined in many forests due to prolonged fire suppression, with compositional shifts to shade tolerant, mesophytic species. Forest fragmentation, exotic plants, insects, and pathogens, and intensive deer browse also shape forest regeneration and herbaceous layer diversity. And, climate changes are predicted to influence both native and invasive species and the timing of pest outbreaks. It is clear that to manage and conserve Virginia's forests in the future, we must work to understand the complex and synergistic effects that influence the remarkable diversity of our forest communities.

LITERATURE CITED

Abella, S. R. 2014. Impacts and management of hemlock woolly adelgid in national parks of the eastern United States. Southeastern Naturalist 13: 16-45.

Aber, J. D., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems: hypothesis revisited. BioScience 48: 921-933.

Abrams, M. D. 2003. Where has all the white oak gone? Bioscience 53: 927-939.

Aldrich, S. R., C. W. Lafon, H. D. Grissino-Mayer, and G. G. DeWeese. 2014. Fire history and its relations with land use and climate over three centuries in the

central Appalachian Mountains, USA. Journal of Biogeography 41: 2093-2104.

Alverson, W. S., D. M. Waller, S. L. Solheim. 1988. Forests too deer: Edge effects in Northern Wisconsin. Conservation Biology 2: 348–358.

Augustine, D. J. and L. E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12: 995-1004.

Baiser, B., J. L. Lockwood, D. La Puma, and M. Aronson. 2008. The perfect storm: Two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions 10: 275-285.

Beatty, S. W. 2003. Habitat heterogeneity and maintenance of species in understory communities. Pages 177-197 *in* F. S. Gilliam and M. R. Roberts (eds.), The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

Beauchamp, V. B., S. M. Koontz, C. Suss, C. Hawkins, K. L. Kyde, and J. L. Schnase. 2013. An introduction to *Oplismenus undulatifolius* (Ard.) Roem. & Schult.(wavyleaf basketgrass), a recent invader in Mid-Atlantic forest understories. Journal of the Torrey Botanical Society 140: 391-413.

Bobbink, R., K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J. Erisman, M. Fenn, F. Gilliam, A. Nordin, L. Pardo, and W. DeVries. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. Ecological Applications 20: 30-59.

Boggs, J. L., S. G. McNulty, M. J. Gavazzi, and J. M. Myers. 2005. Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests. Canadian Journal of Forest Research 35: 1901-1913.

Bower, J. E., S. Brosi, F. Ammer, C. J. Small, 2014. Health status of butternut (*Juglans cinerea*) in Maryland. M.S. Thesis, Applied Ecology & Conservation Biology, Frostburg State University, Frostburg, MD.

Brose, P., T. Schuler, D. van Lear, and J. Berst. 2001. Bringing fire back: The changing regimes of the Appalachian mixed-oak forests. Journal of Forestry 99: 30-35.

Butler, P. R., Iverson, L., Thompson, F. R., III, Brandt, L., Handler, S., and 43 others. 2015. Central Appalachians forest ecosystem vulnerability assessment and synthesis: A report from the Central Appalachians Climate Change Response Framework project. General Technical Report NRS-146. USDA. Forest Service, Northern Research Station, Department of Agriculture, Newtown Square, PA. 310 p.

Clark, S. L., S. L. Brosi, S. E. Schlarbaum, H. D. Grissino-Mayer. 2008. Dendrochronology of two butternut (*Juglans cinerea*) populations in the southeastern United States. Forest Ecology and Management 255: 1772-1780.

Collier, M. H. and J. L. Vankat. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. American Midland Naturalist 147: 60–71.

Cote, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics. 35: 113–147.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and B. M. Wotton. 2001. Climate change and forest disturbances. BioScience 51: 723-734.

DeGasperis, B. G. and G. Motzkin 2007. Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. Ecology 88: 3115-25.

Delcourt, P. A. and H. R. Delcourt. 1998. The influence of prehistoric human-set fires on oak-chestnut forests in the southern Appalachians. Castanea 63: 337-345.

Drummond, M. A. and T. R. Loveland. 2010. Land-use pressure and a transition to forest-cover loss in the eastern United States. BioScience 60: 286-298.

Dukes, J. S., J. Pontius, D. Orwig, J. R. Garnas, V. L. Rodgers, N. Brazee, B. J. Cooke, K. A. Theoharides, E. E. Strange, R. Harrington, J. Ehrenfeld, J. Gurevitch, M. Lerdau, K. Stinson, R. Wick, and M. P. Ayres. 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? Canadian Journal of Forest Research 39: 231-248.

Egloff, K. and D. B. Woodward. 2006. First People: The Early Indians of Virginia. University of Virginia Press, Charlottesville. 96 p.

Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecological Applications 11: 1287-1300.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, J. Mohan, D. A. Orwig, N. L. Rodenhouse, W. V. Sobczak, K. A. Stinson, J. K. Stone, C. M. Swan, J. Thompson, B. Von Holle, and J. R. Webster. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 9: 479-486.

Erisman, J. W., J. N. Galloway, S. Seitzinger, A. Bleeker, N. B. Dise, A. R. Petrescu, A. M. Leach, and W. de Vries. 2013. Consequences of human modification of the global nitrogen cycle. Philosophical Transactions of the Royal Society B: Biological Sciences 368: 20130116.

Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. Canadian Journal of Forest Research 36: 1435-1450.

Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemyer. 1998. Nitrogen excess in North American ecosystems: Predisposing factors, ecosystem responses, and management strategies. Ecological Applications 8: 706-733.

Fike, J. and W. A. Niering. 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. Journal of Vegetation Science 10: 483-492.

Fleming, G. P. 2012. The nature of the Virginia flora. Pages 24-75 *in* A. S. Weakley, J. C. Ludwig, and J. F. Townsend. Flora of Virginia. Botanical Research Institute of Texas Press, Fort Worth, TX.

Fleming, G. P., K. D. Patterson, K. Taverna, and P. P. Coulling. 2016. The natural communities of Virginia: Classification of ecological community groups.

Second approximation. Version 2.7. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, VA.

Flinn, K. M. and M. Vellend. 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3: 243-250.

Flower, C. E., K. S. Knight, M. A. Gonzalez-Meler. 2013. Impacts of the emerald ash borer (*Agrilus planipennis* Fairmaire) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biological Invasions 931-944.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. BioScience 53: 77-88.

Furedi, M. A. and J. B. McGraw. 2004. White-tailed deer: Dispersers or predators of American ginseng seeds? American Midland Naturalist 152: 268-276.

Gandhi, K. J. K, and D. A. Herms. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biological Invasions 12: 389-405.

George, L. O. and F. A. Bazzaz. 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. Pages 265-282 *in* F.S. Gilliam and M.R. Roberts (eds.), The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845–858.

Gilliam, F. S. 2014. Nitrogen biogeochemistry research at Fernow Experimental Forest, West Virginia, USA: Soils, biodiversity and climate change. Ch. 29, Pages 267-278 *in* M. A. Sutton, et al. (eds.), Nitrogen Deposition, Critical Loads and Biodiversity. Springer Science, New York, NY.

Gilliam, F. S., C. L. Goodale, L. H. Pardo, L. H. Geiser, and E. A. Lilleskov. 2011. Eastern temperate forests. Ch. 10, Pages 99-116 *in* L. H. Pardo, M. J. Robin-Abbott, C. T. Driscoll (eds.), Assessment of Nitrogen Deposition Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States. General Technical Report NRS-80. USDA Forest Service, Northern Research Station, Newtown Square, PA.

Hartman, K. M. and B. C. McCarthy. 2008. Changes in forest structure and species composition following invasion by a non-indigenous shrub, Amur honeysuckle (*Lonicera maackii*). Journal of the Torrey Botanical Society 135: 245-259.

Hausman, C. E., J. F. Jaeger, and O. 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.

Heffernan, K., E. Engle, C. Richardson. 2014. Virginia Invasive Plant Species List. Virginia Department of Conservation and Recreation, Division of Natural Heritage. Natural Heritage Technical Document 14-11. Richmond.

Herms, D. A., D. G. McCullough. 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. Annual Review of Entomology 59: 13-30.

Holzmueller, E., J. Shibu, M. Jenkins, A. Camp, A. Long. 2006. Dogwood Anthracnose in eastern hardwood forests: What is known and what can be done? Journal of Forestry 104: 21-26.

Horsley, S. B., S. L. Stout, D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13: 98-118.

Huebner, C. D. 2003. Vulnerability of oak-dominated forests in West Virginia to invasive exotic plants: Temporal and spatial patterns of nine exotic species using herbarium records and land classification data. Castanea 68: 1-14.

Huebner, C. D. R. S. Morin, A. Zurbriggen, R. L. White, A. Moore, and D. Twardus. 2009. Patterns of exotic plant invasions in Pennsylvania's Allegheny National Forest using intensive Forest Inventory and Analysis plots. Forest Ecology and Management. 257: 258-270.

Jenkins, M. A. and P. S. White. 2002. *Cornus florida* L. mortality and understory composition changes in western Great Smoky Mountain National Park. Journal of the Torrey Botanical Society 129: 194-206.

Jenkins, J., J. D. Aber, and C. D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. Canadian Journal of Forest Research 29: 630-645.

Kain, M., L. Battaglia, A. Royo, and W. P. Carson. 2011. Over-browsing in Pennsylvania creates a depauperate forest dominated by an understory tree: Results from a 60-year-old deer exclosure. Journal of the Torrey Biological Society 138: 322-326.

Kelly, A, C. J. Small, G. Dreyer. 2009. Vegetation classification and invasive species distribution in natural areas of southern New England. Journal of the Torrey Botanical Society 136: 500-519.

Kirwan, J. L. and H. H. Shugart. 2000. Vegetation and two indices of fire on the Delmarva Peninsula. Journal of the Torrey Botanical Society 127: 44-50.

Knight, T. M., J. L. Dunn, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29: 110-116.

Krapfl, K. J., E. J. Holzmueller, and M. A. Jenkins. 2011. Early impacts of hemlock woolly adelgid in *Tsuga canadensis* forest communities of the southern Appalachian Mountains. Journal of the Torrey Botanical Society 138: 93-106.

Kribel, J., K. B. Kolman, and S. Ware. 2011. Rapid change in sapling and seedling layers in an otherwise stable hardwood forest: An effect of deer browsing. Castanea 76: 140-148.

Levine, J. M. and C. M. D'antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87: 15–26.

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56: 395-405.

Luken, J. O. 2003. Invasions of forests of the eastern United States. Pages 283-301 *in* F. S. Gilliam and M. R. Roberts (eds.), The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York, NY.

Lundgren, M., Small, C. J., Dreyer, G. D. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeastern Naturalist 11: 313-332.

Martin, K. L., and P. C. Goebel. 2012. Decline in riparian *Tsuga canadensis* forests of the central Appalachians across an *Adelges tsugae* invasion chronosequence. Journal of the Torrey Botanical Society 139:367–378.

Martin, P. H., C. D. Canham, and P. L. Marks. 2008. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment 7: 142–149.

McCarthy, B. C., C. J. Small, and D. L. Rubino. 2001. Composition, structure and dynamics of Dysart Woods, an old-growth mixed mesophytic forest of southeastern Ohio. Forest Ecology and Management 140: 193-213.

McClure, M. S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environmental Entomology 20:258-64.

McGrath, D. A. and M. A. Binkley. 2009. *Microstegium vimineum* invasion changes soil Chemistry and microarthropod communities in Cumberland Plateau forests. Southeastern Naturalist 8: 141-156.

McGraw, J. B., A. E. Lubbers, M. Van der Voort, E. H. Mooney, M. A. Furedi, S. Souther, J. B. Turner, and J. Chandler. 2013. Ecology and conservation of ginseng (*Panax quinquefolius*) in a changing world. Annals of the New York Academy of Sciences 1286: 62-91.

McNab, W. H. and D. L. Loftis. 2002. Probability of occurrence and habitat features for Oriental bittersweet in an oak forest in the southern Appalachian mountains, USA. Forest Ecology and Management 155: 45-54.

McShea, W. J. and J. H. Rappole 1992. White-tailed deer as keystone species within forested habitats of Virginia. Virginia Journal of Science 43: 177-186.

Mosher, E. S., J. A. Silander, Jr., A. M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biological Invasions 11: 2317-2328.

Nowacki, G. J. and M. D. Abrams. 2008. The demise of fire and "mesophication" of forests in the Eastern United States. BioScience 58: 123-138.

Paillet, F. L. 2002. Chestnut: History and ecology of a transformed species. Journal of Biogeography 29: 1517-1530.

Pardo, L. H., M. E. Fenn, C. L. Goodale, L. H. Geiser, C. T. Driscoll, E. B. Allen, J. S. Baron, R. Bobbink, W. D. Bowman, C. M. Clark, B. Emmett, F. S. Gilliam, T. L. Greaver, S. J. Hall, E. A. Lilleskov, L. Liu, J. A. Lynch, K. J. Nadelhoffer, S. S. Perakis, M. J. Robin-Abbott, J. L. Stoddard, K. C. Weathers, and R. L. Dennis. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecological Applications 21: 3049-3082.

Pimentel, D., R. Zuniga, D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273-288.

Randolph, K. C., A. K. Rose, C. M. Oswalt, and M. J. Brown. 2013. Status of black walnut (*Juglans nigra* L.) in the eastern United States in light of the discovery of thousand cankers disease. Castanea 78: 2-14.

Robertson, D. J., M. C. Robertson, T. Tague. 1994. Colonization dynamics of four exotic plants in a northern Piedmont natural area. Bulletin of the Torrey Botanical Club 121: 107-118.

Rooney, T. P., S. M. Wiegmann, D. A. Rogers, D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology 18: 787-798.

Rose, A. K. 2013. Virginia's Forests, 2011. Resource Bulletin SRS–197. USDA Forest Service, Southern Research Station, Asheville, NC. 92 p.

Rossell, Jr., C. R., S. Patch, and S. Salmons. 2007. Effects of deer browsing on native and non-native vegetation in a mixed oak-beech forest on the Atlantic coastal plain. Northeastern Naturalist 14: 61-72.

Russell, F. L., D. B. Zippin, N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: A review. The American Midland Naturalist 146: 1-26.

Schlarbaum, S. E., F. Hebard, P. C. Spaine, and J. C. Kamalay. 1998. Three American tragedies: Chestnut blight, butternut canker, and Dutch elm disease. In: K. O. Britton, Ed. Proceedings of the 1997 Exotic Pests of Eastern Forests Conference. U.S. Forest Service and Tennessee Exotic Pest Plant Council 45-54.

Silver, E. J., J. H. Speer, M. Kaye, N. J. Reo, L. F. Howard, A. K. Anning, S. W. Wood, and H. M. Wilbur. 2013. Fire History and Age Structure of an Oakpine Forest on Price Mountain, Virginia, USA. Natural Areas Journal, 33(4): 440-446.

Small, C. J. and B. C. McCarthy. 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. Forest Ecology and Management 217: 229-243.

Small, M. J., C. J. Small, and G. D. Dreyer. 2005. Changes in hemlock-dominated forests following woolly adelgid infestation in southern New England. Journal of the Torrey Botanical Society 132: 458-470.

Small, C. J., D. C. White, B. Hargbol. 2010. Allelopathic influences of the invasive tree of heaven (*Ailanthus altissima*) on a native and a non-native herb. Journal of the Torrey Botanical Society 137: 366-372.

Spira, T. P. 2011. Wildflowers and Plant Communities of the Southern Appalachian Mountains and Piedmont. The University of North Carolina Press, Chapel Hill. 521 p.

Stehna, S. E., M. A. Jenkins, C. R. Webster, S. Josed. 2013. Regeneration responses to exogenous disturbance gradients in southern Appalachian Picea-Abies forests. Forest Ecology and Management 289: 98-105.

Stephenson, S. L., A. N. Ash, and D. F. Stauffer. 1993. Appalachian oak forests. Pages 255-304 *in* W. H. Martin, S. G. Boyce, and A. C. Echternacht (eds.), Biodiversity of the Southeastern United States: Upland Terrestrial Communities. John Wiley, New York.

Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G. Hallett, D. Prati, and J. N. Klironomos. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. Public Library of Science (PLoS) Biology 4:727-731.

Stohlgren, T. J., D. T. Barnett, and J. T. Kartesz. 2003. The rich get richer: Patterns of plant invasions in the United States. Frontiers in Ecology and the Environment 1: 11-14.

Suchecki, P. F. and D. J. Gibson. 2008. Loss of *Cornus florida* L. leads to significant changes in the seedling and sapling strata in an eastern deciduous forest. Journal of the Torrey Botanical Society 135: 506-515.

Thiemann, J. A., C. R. Webster, M. A. Jenkins, P. M. Hurley, J. H. Rock, and P. S. White. 2009. Herbaceous-layer impoverishment in a post-agricultural southern Appalachian landscape. American Midland Naturalist 162: 148-168.

U.S. Environmental Protection Agency (US EPA). 2013. Level III Ecoregions of the Continental United States (map), Revised April 2013. National Health and Environmental Effects Research Laboratory, Corvallis, Oregon, U.S. EPA. https://pubs.usgs.gov/tm/04/c03/virtual_CD/useco.pdf

Virginia Department of Forestry (VA-DOF). 2014a. 2014 State of the Forest: Annual Report on Virginia's Forests. VDOF P00129. Virginia Department of Forestry, Charlottesville, VA.

Virginia Department of Forestry (VA-DOF). 2014b. Forest Health Review. Virginia Department of Forestry. 12/2014. Virginia Department of Forestry, Charlottesville, VA.

Virginia Department of Game and Inland Fisheries (VD-GIF). 2007. Virginia Deer Management Plan (2006-2015). Wildlife Information Publication No. 07-1, VA Department of Game and Inland Fisheries, Richmond, VA.

Von Holle, B. and G. Motzkin. 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. Biological Conservation 136: 33-43.

Wagner, D. L. 2007. Emerald ash borer threatens ash-feeding Lepidoptera. News of the Lepidopterists' Society 49: 10-12.

Ware, S., C. C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: The former longleaf pine forest. Pages 447-493 *in* W. H. Martin (ed.), Biodiversity of the Southeastern United States: Lowland Terrestrial Communities. John Wiley & Sons, Inc., New York, NY.

Weakley, A. S., J. C. Ludwig, and J. F. Townsend. 2012. Flora of Virginia. Botanical Research Institute of Texas Press, Fort Worth, TX.

Wilson, I. T. and T. Tuberville. 2003. Virginia's Precious Heritage. Natural Heritage Technical Report 03-15. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, VA.

Woodward, S. L. and R. L. Hoffman. 1991. The nature of Virginia. Pages 21-41 *in* K. Terwilliger. Virginia's Endangered Species. The McDonald & Woodward Publishing Company, Blacksburg, VA.