IMPACTS OF OAK DECLINE, GYPSY MOTH, AND NATIVE SPRING DEFOLIATORS ON THE OAK RESOURCE IN VIRGINIA

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Abstract—The oak-hickory and oak-pine forest types dominate much of the southern landscape. In the Blue-Ridge and Appalachian Mountains of western Virginia, oak as a percentage of total forest volume can be as high as 60 percent. Much of this forest type is represented by older aged cohorts with little potential for oak regeneration to replace declining codominants. Oak decline is a prevalent natural phenomenon across the landscape, brought about by aging cohorts growing on poor sites, and exacerbated by inciting factors such as recurring drought and insect defoliation events. In Virginia, the gypsy moth (*Lymantria dispar* L.) has been the primary spring defoliator of oaks since the mid-1980s, although outbreak populations have been moderated since the mid-1990s by the gypsy moth fungus, *Entomophaga maimaiga*. In addition, several native defoliators have produced periodic outbreaks since the 1950s, particularly the fall cankerworm. The fall cankerworm (*Alsophila pometaria*) is the most common native defoliator of Virginia's oaks, producing outbreaks somewhere in the State about every 5 years for the last 65 years or so. According to detailed historical records, these outbreaks seem to be getting worse in terms of acres impacted by defoliation. Other native defoliators have also had periodic outbreaks over this time period, albeit less frequently than the fall cankerworm. These include the forest tent caterpillar (*Malacasoma disstria*), variable oakleaf caterpillar (*Lochmaeus manteo*), linden looper (*Erannis tiliaria*), oak leaf tier (*Croesia semipurpurana*), and half-winged geometer (*Phigalia titea*). Collectively, these insects produce recurring stresses on the oak resource that, in concert with periodic drought stress, could significantly exacerbate ongoing decline and punctuate mortality events.

INTRODUCTION

The oak-hickory and oak-pine forest types collectively represent a major proportion of total forest area across much of the southern region of the United States, particularly across the Southern Appalachians, Cumberland Plateau, and portions of the Piedmont (Conner and Hartsell 2002). Oak (*Quercus* spp.) is an essential resource in these regions, representing a major proportion of many forest canopies. These trees provide high-quality wood products and an essential food source for many wildlife species via regular acorn (mast) crops. Furthermore, with over 30 species across the Southern United States, many of which become large and/or relatively long-lived, oaks significantly improve forest biodiversity. Indeed, over 500 species of Lepidoptera (moths and butterflies) feed on oak leaves as caterpillars, which are a major food source for most resident and migrant bird species as well as other animals (Tallamy and Shropshire 2009).

Unfortunately, the long-term health and condition of the oak resource may be under threat in some regions. Canopy oaks are increasingly in older age cohorts (80+ years), which inevitably results in accelerating rates of decline and mortality (Oak and others 1996, 2016). In addition, more punctuated mortality events can be triggered by environmental conditions such as drought or defoliation (Manion 1991). In concert, many oak-dominant forests lack sufficient oak regeneration to replace mature trees as they die off (Dey 2014, Rose 2008). The low regeneration potential of oak across many landscapes is due to a multitude of factors such as: 1) competition with more shade-tolerant species in dense understories, such as red maple (*Acer rubrum*) or blackgum (*Nyssa sylvatica*); 2) competition with more shade-intolerant species in open stands, such as birch (*Betula* spp.) or tulip poplar (*Liriodendron tulipifera*); 3) lack of appropriate management (prescribed burning, selection thinning) and/or conditions ideal for oak survival, such as intermediate light levels in the understory; and 4) heavy pressure from deer browse (McShea and others 2007, Woodall and others 2010). Currently, annual volume increment of most major oak species is either slowly increasing or static (Miles 2014), but these trends are expected to reverse as growth rates of aging tree cohorts begin to slow down and

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mortality rates increase. A lack of regeneration in many areas means oak-dominant canopies will not replace themselves over time without appropriate management.

OAK DECLINE

Due to the abundance and aging cohort of oaks in the Southern Appalachians, oak decline is a prevalent condition across this landscape. Decline is broadly defined as a gradual failure in health of a forest, stand, or tree resulting from a combination of biotic and abiotic factors in which no single agent is responsible. In some cases, the key factors associated with decline are unknown or difficult to determine; in other cases decline is fairly predictable and can be thought of as a mechanism of succession, especially in older, senescent stands. Oak decline falls into the latter category. Symptoms of declines can include reduced growth, foliage tufting, epicormic branching, small or chlorotic leaves, twig and branch dieback, asymmetrical crowns, premature fall coloration in hardwoods, degeneration of roots and mycorrhizae, and depletion of food reserves (Manion 1991).

The decline process can be separated into 3 phases, based on Paul Manion's forest decline concept (Manion 1991): 1) predisposing factors, 2) inciting factors, and 3) contributing factors. Predisposing factors are typically associated with site characteristics – poor soils with low fertility or moisture holding capacity, aspect and elevations that expose trees to challenging environmental extremes, and vegetative composition. The age of the trees is also a predisposing factor. As the term implies, trees facing these conditions are 'predisposed' to later health problems. Inciting factors can be one-time or multiple, repeated disturbances, biotic or abiotic, that can further weaken trees and accelerate the decline process. Examples of inciting factors can include drought, late frost, and insect and disease outbreaks. This discussion will focus on gypsy moth (*Lymantria dispar* L.) and other insect defoliators as major inciting factors in the oak decline process in Virginia. Finally, contributing factors are typically biotic agents that, once established in the tree, lead directly to mortality. Contributing factors are normally ubiquitous and non-aggressive insects or pathogens that are only able to exploit trees that are in a weakened condition. Examples of contributing factors to oak decline are various wood boring insects such as two-lined chestnut borer (*Agrilus bilineatus*) and red oak borer (*Enaphalodes rufulus*), ambrosia beetles, carpenterworms, and fungi such as *Armillaria* root disease and *Hypoxylon* canker. The latter pathogens are found in most hardwood forests where they fester for many years without causing problems, but can be 'released' when trees are under stress. Drought conditions are the most common stress on the landscape, and the visible appearance of hypoxylon canker on hardwood stems is a reliable indicator of drought stress (Oak and others 1996, Starkey and Oak 1989). Oaks make up as much as 56 percent of the forest volume in the northwestern parts of Virginia, and from 18–35 percent of the resource in other areas (Miles 2014). With the decline of aging cohorts of oaks and associated stressors being a prevalent force, the majority of trees dying across the Commonwealth are oaks.

Tree species in the red oak group may be more vulnerable to decline compared to the white oak group. In part, this may be due to red oaks' greater abundance on poor, rocky soils at higher elevations (Oak and others 2016, Spetich and others 2016). Red oaks also differ significantly in wood structure compared to white oaks in that they lack tyloses, which are bladder-like extensions of parenchyma cells that project themselves into adjacent wood vessels. By essentially 'plugging' the pits in between wood cells, tyloses help limit water loss and also facilitate the compartmentalization of decay in trees in response to injury and pathogen invasion. Thus, red oaks as a group can generally be said to be less drought-resistant and more susceptible to pathogen invasion compared to white oaks (Oak and others 1996).

SPRING DEFOLIATORS

Our focus is on gypsy moth, fall cankerworm, and other spring defoliators that utilize oak species as major hosts. Gypsy moth, as an invasive species, is the most problematic since repeated, severe defoliation events over successive years are more common than with native defoliators who have a co-evolved natural enemy complex in place that reacts more quickly to outbreak populations of its prey with a strong density-dependent response. However, several other native defoliators periodically reach outbreak populations and can cause significant damage to the oak resource (Asaro and Chamberlin 2015). These include the fall cankerworm (*Alsophila pometaria*), forest tent caterpillar (*Malacasoma disstria*), variable oakleaf caterpillar (*Lochmaeus manteo*), linden looper (*Erannis tiliaria*), half-winged geometer (*Phigalia titea*), and oak leaf tier (*Croesia semipurpurana*). All these defoliators feed during the spring, which is the most damaging time of year for trees to lose leaf tissue (Coulson and Witter 1984). Refoliation depletes a tree's nutritional and energy reserves which compromise other necessities such as chemical defense and energy storage. However, it would be more energetically expensive for trees to lose leaves early in the growing season and not replace them, foregoing photosynthesis for most of the season. By contrast, trees that lose leaf tissue during the second half of the growing season have already begun storing energy reserves via photosynthesis, and will often not expend vital energy reserves putting out a new crop of leaves prior to fall (Houston and others 1981). The pivot point that determines if a tree will leaf out again after being defoliated depends on the tree species and other physiological conditions. From an evolutionary standpoint, spring defoliation allows these insects to exploit newly emergent oak leaves when tannin content is at its lowest. Tannins interfere with efficient digestion and absorption of vital nutrients, so by avoiding them, these insects experience increased nutritional gain and fecundity. This is thought to be the primary reason that many spring defoliators exhibit eruptive population dynamics compared to those that feed later in the growing season (Bernays 1981, Feeny 1970, Feeny and Bostock 1968).

We summarized the outbreak activity of all spring defoliators of oak since 1953 in Virginia utilizing records from quarterly and annual reports by forest health specialists within the Virginia Department of Forestry. Where outbreak maps were absent, we used narrative descriptions of approximate areas and acres defoliated if sufficient detail was provided to reconstruct the event spatially and temporally. Additional details on data collection methodology are provided in Asaro and Chamberlin (2015).

GYPSY MOTH OUTBREAK HISTORY IN VIRGINIA

The gypsy moth was introduced into Massachusetts in 1869 and has been spreading south and west ever since (Liebhold and others 1989). Adult moths reached northern Virginia in the late 1960s, but the first major defoliation wasn't reported until 1984 (Davidson and others 2001). As of 2018, gypsy moth has infested most of the State, with only extreme southwest Virginia escaping major defoliation to date. The outbreak history of gypsy moth in Virginia spans the years 1984–2017 and can be broken out into four major periods separated by years with non-damaging populations (fig. 1): 1) 1984–1995 – the initial wave, 2) 2000–2003, 3) 2005–2009 and 4) 2015–the present. The initial wave of gypsy moth had the most devastating impact, resulting in a cumulative total of 4.3 million acres of heavy defoliation across much of northern Virginia over 12 years. In 1996, the sudden appearance and first known epizootic of the gypsy moth fungus (*Entomophaga maimaiga*) occurred, crashing the population abruptly (Asaro and Chamberlin 2015, Hajek 1995). *Entomophaga maimaiga* is not density dependent (as are the gypsy moth virus and other natural enemies) so therefore does not change the cyclical nature of gypsy moth populations (Allstadt and others 2013, Liebhold and others 2013). However, the fungus is more active and impactful during wet spring weather, where rain splash can disperse fungal spores from infected larvae to other actively feeding larvae (Hajek 1999, Reilly and others 2014). This is perhaps why subsequent gypsy moth outbreak periods never reached the severity of the initial wave – the 2000–2003 period impacted 644,000 cumulative acres, the 2005–2009 period 234,000 acres, and the current period from 2015 to the present <50,000 acres so far (fig. 1). Successive years of very dry spring weather can lead to more significant outbreaks once again, but this has not occurred in Virginia since 2008.

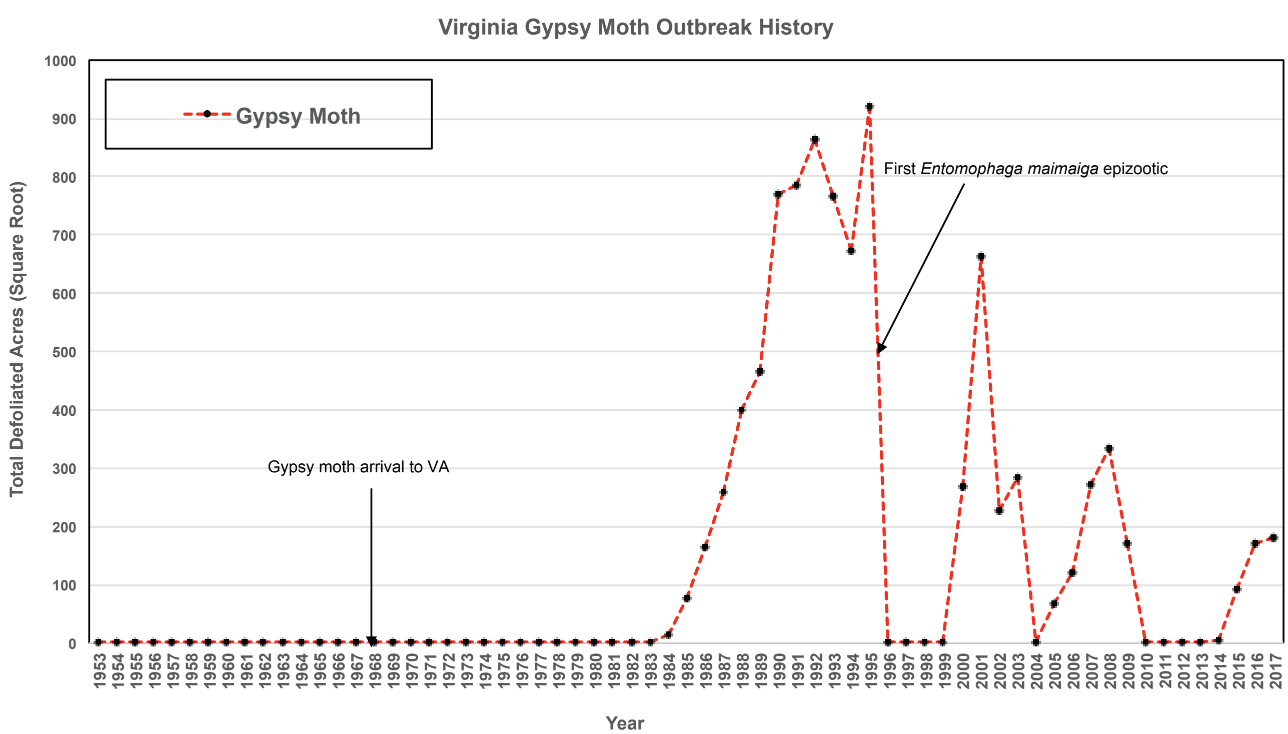

Figure 1—Outbreak history of gypsy moth in Virginia expressed in terms of annual defoliated acres by year. Note: values for total defoliated acres were square-root transformed so that extreme highs and lows are visible on the same graph.

Nonetheless, the impact of all this cumulative defoliation by gypsy moth has been significant, particularly along the Blue Ridge and Appalachian mountain chains spanning down the western spine of Virginia. Many locations experiencing successive years of heavy to severe defoliation were on Federal lands such as the George Washington National Forest and Shenandoah National Park. The signs of past gypsy moth outbreaks can still be seen in these areas today, with standing dead oak trees that persist for years littered across the landscape (Asaro and Chamberlin 2015). Although gypsy moth can feed on hundreds of different species of trees and shrubs,[1] oaks are most preferred and, where they are abundant, most likely to suffer mortality compared to other species (Liebhold and others 1994). These same areas were already major centers of oak decline prior to the arrival of gypsy moth due to a combination of high oak volumes, maturing stands, and high-elevation sites where trees grow in challenging conditions (poor, drought-prone soils and high exposure to climatic extremes) (Oak and others 1996). Waves of drought and gypsy moth defoliation have exacerbated oak decline where it was already occurring. Some of the poorest sites along ridges are typically the hardest hit, although species like chestnut oak that are highly competitive on these poor sites are likely to successfully regenerate. In contrast, more mesic sites on lower slopes and coves, when defoliated, can suffer losses to higher value species such as white (*Q. alba*) and northern red (*Q. rubra*) oaks. Oaks are less competitive on more mesic sites without appropriate levels of disturbance or management. In addition, nonnative invasive plants are increasingly invading and overtaking sites when sudden canopy losses increase light levels to the understory (Asaro and Chamberlin 2015). Finally, heavy deer browse in many areas can often prohibit the establishment of oak seedlings and saplings, even if other conditions for oak regeneration are favorable (McShea and others 2007). Therefore, without intervention, many locations seeing rapid loss of mature oak canopy will likely transition to other forest types dominated by species such red maple, tulip poplar, or sweet birch (*B. lenta*). As gypsy moth inevitably advances southward along the Appalachian Mountains, and westward across Tennessee, Kentucky, and into the Ozark Mountains of Missouri and Arkansas, similar ecological shifts in oak species abundance may be anticipated (Spetich and others 2016).

OUTBREAK HISTORY OF FALL CANKERWORM AND OTHER NATIVE DEFOLIATORS

The fall cankerworm, so named due to the fall activity of adult moths, has been the most common native defoliator of oak across Virginia over the last 60 years (see footnote 1, Asaro and Chamberlin 2015). Adult females are wingless, and upon emerging from pupation sites in the ground, will climb up the tree to mate. Egg masses are placed on bark surfaces of the main stem, branches, and twigs during the late fall or winter months. Fall cankerworm caterpillars hatch in early spring during or just after bud-break, earlier than gypsy moth (Drooz 1985). Outbreak populations in Virginia have been occurring somewhere in the State approximately every 5 years since the 1950s (fig. 2, Asaro and Chamberlin 2015). If we assume that historical records are reasonably accurate as to acres impacted, then outbreaks appear to be getting worse since 1980 compared to the previous 30 years (fig. 2). Although natural enemies, including an egg parasitoid, are effective in suppressing outbreak populations within a year or two (Butler 1990, Fedde 1980), substantially more acres appear to be defoliated with each new outbreak (fig. 2). For example, since 2002, fall cankerworm has defoliated more cumulative acres (almost 600,000) than the gypsy moth (365,000). The reasons for this trend are unclear, and much more research on population dynamics of this defoliator is warranted. Recurring populations within the same general areas are a hallmark of this pest, perhaps due to the limited ability of the flightless female moths to disburse long distances. Fall cankerworm can also be a recurring, persistent problem in urban areas such as Charlotte, NC, Richmond, VA, and the Washington, DC suburbs in northern Virginia (Ciesla and Asaro 2013).

Long-term impacts to the oak resource are generally considered minor due to the short-term nature of most fall cankerworm outbreaks (1–2 years), compared to gypsy moth (3–5 years). Like gypsy moth, fall cankerworm has a very broad host range but prefers oaks where they are abundant (Ciesla and Asaro 2013). However, near complete defoliation of oaks over 2 years is not uncommon among ridgetop environments and more mesic habitats. These disturbances, when combined with older age cohorts, severe drought events, and ongoing oak decline can lead to significant canopy loss, although the degree to which this occurs has not been properly documented (Crow and Hicks 1990). Similar arguments can be made for other native defoliators of oak in Virginia. Although major outbreaks of forest tent caterpillar, linden looper, variable oak leaf caterpillar, oak leaf tier, and half-winged geometer have been much less frequent than fall cankerworm over the last 60 years (fig. 2, Asaro and Chamberlin 2015), one or two severe oak defoliation events at the right place and time can theoretically precipitate significant canopy loss. For example, two major outbreaks of the variable oakleaf

[1] Asaro, C. 2005-2014. Forest health review. Virginia Department of Forestry, Charlottesville, VA. http://www.dof.virginia.gov/infopubs/index.htm.

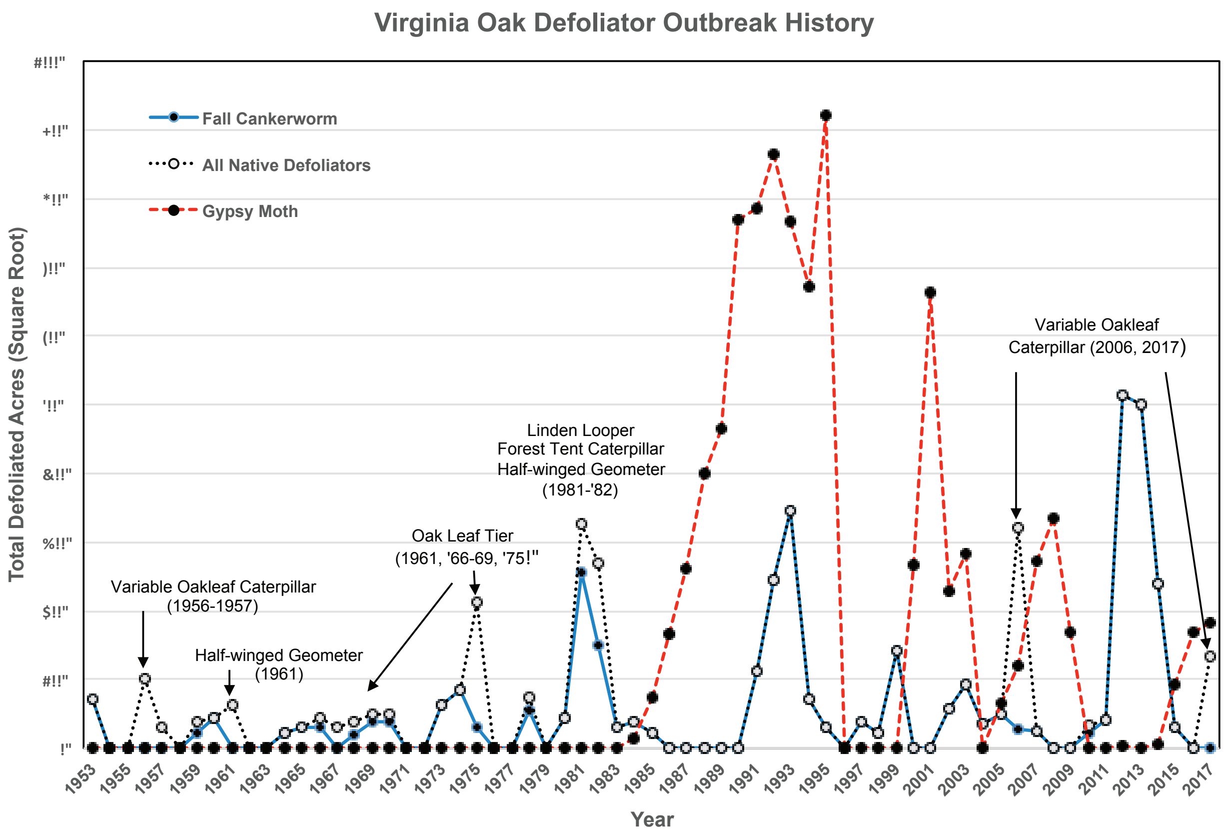

Figure 2—Outbreak histories for several major spring defoliators of oak forests in Virginia expressed in terms of annual defoliated acres. The solid (blue) line represents annual fall cankerworm defoliation, the dashed (red) line represents annual gypsy moth defoliation, and the dotted (black) line represents a combination of annual defoliation by all native defoliators, including fall cankerworm. Several other important species are highlighted above areas of peak activity. Note: values for total defoliated acres were square-root transformed so that extreme highs and lows are visible on the same graph.

caterpillar,[2] which has a strong preference for white oak and has two generations per year, have occurred across many forested areas around Richmond in 2006 and 2017 (fig. 2, see footnote 1). In between those events, across the same area, a historic fall cankerworm outbreak occurred from 2012–2014 impacting over 250,000 acres for 2 successive years (fig. 2, Asaro and Chamberlin 2015). Although oak mortality following these defoliation events has been poorly documented, such concerns may be warranted given the overall condition of the oak resource, as described previously.

CONCLUSIONS

Beyond the impacts to Virginia's oaks by the gypsy moth, the frequency and severity of native defoliator outbreaks on this resource may be unappreciated. It seems probable that all of these defoliators, combined with other stressors, will continue to exacerbate oak decline in many areas, although more research to quantify defoliator impacts is needed. It's also worth continuing to monitor native defoliator outbreaks, especially if they are becoming more frequent, extensive, and severe over time. According to U.S. Forest Service Forest Inventory and Analysis data, oak volumes in Virginia continue to increase due to the abundance of maturing and mature age cohorts. However, this trend is expected to level off and then decline as mature trees continue to die off, and the potential for recruitment of oak seedlings/saplings into the canopy seems to be diminishing in many areas. Long term, this could have significant implications for forest biodiversity since oaks generally increase the diversity of insect fauna (moth caterpillars), birds, and wildlife dependent on regular mast crops. The prevalence of nonnative invasive plants and high deer populations across Virginia mean that there may be fewer opportunities for oaks to regenerate successfully even if the right balance of favorable disturbance or silvicultural prescriptions exist.

Across the Appalachians, chestnut blight eliminated the most common hardwood species during the early 20th century, which suddenly provided an ideal opportunity

[2] Chamberlin, L.A. 2016-2018. Forest health review. Virginia Department of Forestry, Charlottesville, VA. http://www.dof.virginia.gov/infopubs/index.htm.

for oaks, which were already prevalent, to increase in dominance (McCormick and Platt 1980, Woods and Shanks 1959). It may be that oaks in some areas are simply too abundant to be sustainable and that spring defoliators that prefer oaks are likewise more prone to outbreaks. Where unsustainable oak volumes currently exist, defoliation events in concert with other stressors associated with decline will inevitably act as a ‘correction mechanism,’ and new forest assemblages with less oak will be the result.

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