Relating eastern hemlock (*Tsuga canadensis*) ecosystem services to stand attributes in the Catskills

Jonathan Rosenthal

Radka Wildova, PhD.

Ecological Research Institute, Kingston, NY

Final version, March 2017

Ecological Research Institute

CRISP Catskill Regional Invasive Species Partnership

Executive summary

We performed a literature review aimed at identifying services provided by eastern hemlock stands, and the stand attributes that affect the capacity to provide these services. We present this information after first providing an overview of overall considerations in prioritizing stands for conservation, including practical aspects of conservation as well as relevant aspects of the ecology of the eastern hemlock and its major pest, hemlock woolly adelgid (HWA). Particularly important services identified include: stream flow regulation; nutrient retention; microclimate maintenance; provision of favorable habitat for brook trout; provision of important habitat for bird, mammal, and salamander species; recreational, aesthetic, and property value benefits; educational and research opportunities; and not to be overlooked, the service of simply being hemlock, an iconic presence in eastern forests. In some cases, occurrence of rare plants might also provide a rationale for conservation of particular stands. The long-term conservation of hemlock in the Catskills for all of these purposes requires maintenance of adequate genetic diversity, for which strategic recommendations are made. Finally, we make recommendations on how the information contained in this report can be used to proceed in prioritizing stands for conservation.

Table of Contents

I. Background, methodological approach, and rationale

This report was prepared by the Ecological Research Institute (ERI) on behalf of the Catskill Regional Invasive Species Partnership (CRISP) to assist in its efforts to develop a scheme for prioritizing regional eastern hemlock (*Tsuga canadensis*) stands for protection from the hemlock woolly adelgid (*Adelges tsugae*). Specifically this report:

(1) summarizes and synthesizes the available information on:

a. the services potentially provided by eastern hemlock stands in the Catskills; and
b. the influence of stand attributes on provision of these benefits; and

(2) suggests how this attribute information can then be employed to prioritize stands likely to provide the desired services, while also taking account of:

a. practical aspects that would affect the feasibility of conserving particular stands; and
b. the need to conserve adequate landscape-level hemlock genetic diversity.

In preparing this report, we performed an exhaustive search of the relevant literature and also had lengthy conversations with three of the leading researchers on eastern hemlock ecology: Dr. Charles Canham and Dr. Gary Lovett, both of the Cary Institute of Ecosystem Studies, and Dr. David Orwig, of Harvard Forest, each of which were helpful in characterizing the current state of knowledge of hemlock's ecosystem roles.

Extensive research has been published on various aspects of the ecological consequences of the invasion by HWA, some of it directly addressing the issues covered in this report, but much more of it touching on these topics only indirectly. Therefore, we have attempted, wherever possible, to stitch together information from multiple sources in order to help answer key questions. Wherever there are gaps in knowledge, we have noted these, both to make the limitations of our current understanding explicit and to encourage future research that will fill these gaps.

Ongoing communication from CRISP'S coordinator, John Thompson, has been essential in making us aware of the hemlock conservation efforts that have been underway in the CRISP region. Indeed, our report represents just one step in the ongoing efforts of CRISP to craft appropriate management responses to the HWA invasion. Thus, it draws upon previous initiatives, including the report "Facilitating management of hemlock woolly adelgid in the Catskill Mountains" by Zimmerman and Snider (2014), and in particular the "CRISP Hemlock Conservation Workshop" on October 6th, 2016, in which one of us (Wildova) participated along with a wide range of scientists, resource managers, educators, and others involved in shaping CRISP's regional approach to hemlock conservation. Among other products, this workshop yielded lists of services potentially provided by the area's hemlock forest and of stand attributes that can influence these services and/or the stands' prospects for conservation.

In generating the present report, we have been guided largely by these lists, because they enumerate issues that have already been identified as potentially important by CRISP partners. However, we have in some cases modified the lists to streamline the presentation of issues and also to include some aspects of stand characterization and/or potential services that were not originally included.

As mentioned above, although our primary focus is identifying potential hemlock forest services and the likely influence of stand attributes on provision of these services in the CRISP region, we place this in the context of other considerations, including the prospects for successful conservation of stands. These prospects would be influenced by various stand attributes, most especially the stands' current health status. The likelihood of achieving actual protection against HWA should be a threshold issue, because if a stand's conservation is impossible or impractical, then it would be a wasted effort to prioritize it for conservation, no matter its potential value. A thorough exploration of the technical determination of suitability for HWA management is beyond the scope of the present report, however, and this issue is covered only briefly, to provide context for the other considerations in stand conservation prioritization.

In using the information contained in this report to conduct stand conservation prioritization, it will become apparent that stand attributes that are favorable for provision of some services might be unfavorable for provision of others. Therefore, as part of its prioritization process, CRISP will need to determine the relative importance of different services, which may be done on a stand-by-stand basis.

Crucially, using any assessment of hemlock ecosystem services in prioritizing stands for conservation requires consideration of the alternative states of a site currently occupied by hemlock, because some of these states may furnish some of the hemlock's ecosystem services to some degree. Indeed, the impacts of HWA on forest structure and composition can be seen as consisting of two phases which temporally overlap and are closely linked. The first is the deterioration and death of the hemlocks in a stand, whereas the second is the growth of a replacement forest type. Although the first process generally results in some loss of ecosystem services, some services are restored in some fashion as new vegetation is established and proliferates. This has three important implications for hemlock stand conservation prioritization. First, it is a misleading oversimplification to assume that because hemlocks provide a particular service, the loss of the hemlock stand will result in long-term loss of the service. Second, the time horizon relevant to the desired outcomes must be clearly identified, regarding whether short-term disruption of services can be tolerated. Third, in deciding whether a hemlock stand needs to be conserved, some prediction will need to be made whether the services ultimately provided by the replacement vegetation will be sufficient.

Consideration of the alternative states of sites and the services provided by replacement vegetation should not detract from the appreciation of eastern hemlock as a species that is quite remarkable in many ways, that does provide some unique services and especially a unique overall package of services. In the following section, we provide a brief overview of this species, and the features that make it particularly important.

II. Eastern hemlock – a brief introduction

T. canadensis is a remarkably distinctive inhabitant of eastern forests, with traits that enable it to drive ecosystem processes where it occurs, not only providing unique physical structure, but, among other things, altering the microclimate, hydrology, and nutrient cycling. Indeed, based on the extent to which eastern hemlock essentially defines the ecosystems in which it is prevalent, it has been recognized as a foundation species, suggesting that its loss would have profound impacts.

Eastern hemlock is notable among trees of eastern N. America for its potential longevity (almost 1000 years, maturing at 250-300 years and typically living 400 years) and size (up to 200 cm DBH and 50 m tall, typically approaching 100 cm DBH and 30 m tall) (Godman and Lancaster 1990). While these attributes certainly contribute to its influence on ecosystems, much of the distinctiveness of hemlock forest can be attributed to its foliage's ability to photosynthesize efficiently even in dense shade. This enables the trees, unlike other conifers, to retain the foliage even on their lowest branches – giving hemlock stands unique structure that influences their interactions with wildlife. Moreover, the shade produced by the dense canopy is reinforced by the multiple sub-canopy layers of foliage, resulting in the forest floor being dimly light (receiving only 1% of the sunlight available above the canopy). This translates into a cooler microclimate in summer, with understory air temperature 3-4 deg. C lower in hemlock story than in the air layer immediately above the canopy (Hadley 2000); this is considerably cooler than in other forest types. In the winter, hemlock's dense foliage has the opposite effect, ly making the microclimate beneath it warmer than in other areas.

Hemlock's foliage even affects the ground beneath the trees even after it has fallen, as its chemistry makes hemlock's leaf litter decompose very slowly, an effect enhanced by the cool summertime microclimate. As a result, a thick layer of litter accumulates.

Indeed, many of the features of hemlock forest can be characterized as slow, with this description fitting not only the rates of nutrient cycling and soil water withdrawal, but also individual tree growth, with their size a testament to their longevity. Their longevity, in turn, translates into stability over a time scale of centuries, but hemlock processes and characteristics also confer ecosystem stability over shorter time scales, with properties such as water usage and shading showing much less seasonal variation than hardwoods, and soil and air temperature buffered somewhat against both seasonal and daytime variation.

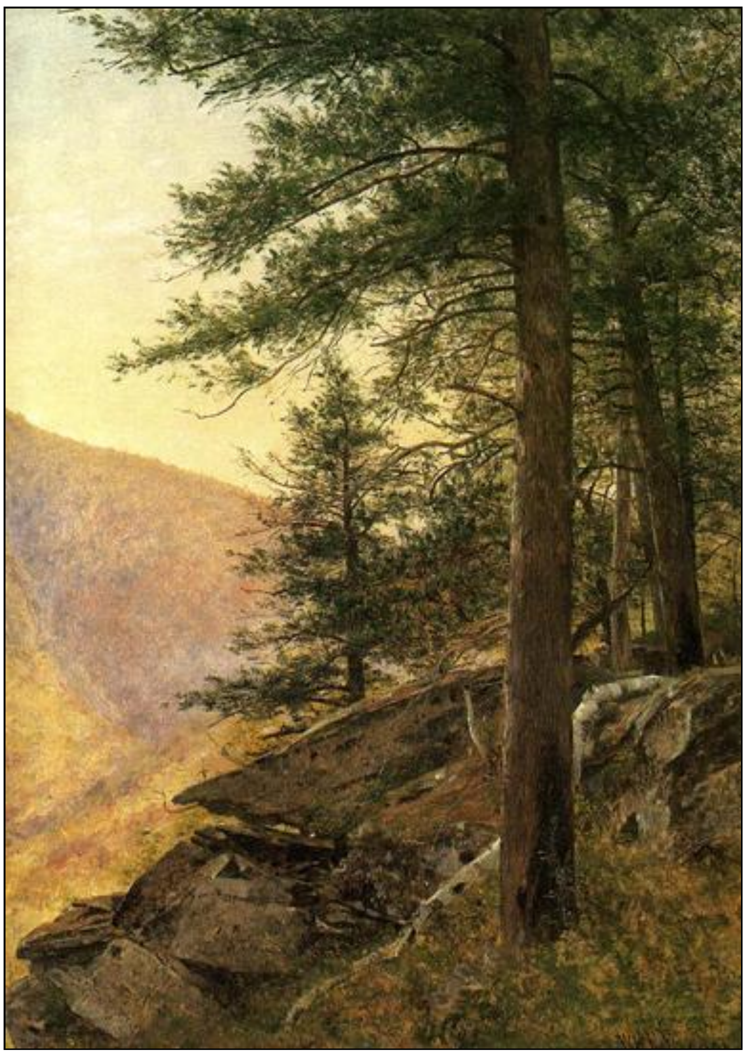

Figure 1. Hemlocks in the Catskills. Thomas Worthington Whittredge (1820 – 1910).

While eastern hemlock's ecosystem effects can be measured scientifically, some of them can also be readily appreciated simply by experiencing the distinctive conditions that one finds inside a hemlock stand. Stands are cool, dimly-lit, sheltered from excessive wind, rain, and sun, with an open understory (due primarily to the low amount of light reaching the forest floor) and a thick, soft carpet of litter underfoot. These qualities make for a unique and even inspirational visitor experience. Indeed, hemlocks have been singled out by such quintessential American writers as Henry David Thoreau, Emily Dickinson, Ernest Hemingway, and Robert Frost (Levis 2014) and celebrated by painters of the Hudson River School (Fig. 1).

Nevertheless, the area currently occupied by eastern hemlock is only a small fraction of what it had comprised at the time of European settlement. Hemlock, along with other forest, was cleared for agricultural use of the land, and then suffered particular depredation due to the use of its tannin-rich bark in the hide-tanning industry. The Catskills, in particular, were a major center of this industry, with only small pockets of old-growth hemlocks left behind, typically at sites that were so inaccessible as to make tree felling and stripping impractical. In addition, sites that were never entirely cleared still persist in the form of primary growth, and more widely hemlock has recolonized some of its former territory as second growth.

One thing we have learned from the re-establishment of hemlock forest since the turn of the 20th century (and also from studying the recovery of hemlock forest after a pre-historic die-off in 4,800 years ago), is that hemlock recolonizes areas slowly. This is not surprising given their very slow growth rates and relatively local seed dispersal. However, given the threat that they are currently facing, especially from hemlock woolly adelgid, their slow population recovery means that an emphasis must be placed on identifying and conserving important hemlock stands, before they are wiped out.

III. New York State community types in which hemlock is important

In contrast to the southern portion of its range, i.e., the southern Appalachians, where eastern hemlock occurs almost exclusively at elevations of 610 to 1520 m (2,000 to 5,000 ft) and is largely restricted to north and east slopes, coves, and cool, moist valleys (Godman and Lancaster 1990), in the north it occurs from sea level to 910 m (3000 ft), and is found in a much broader range of topography, including ravines, and swamp edges. The New York Natural Heritage Program recognizes three major ecological communities in the state that are dominated by hemlock: hemlock-northern hardwood forest; hemlock-hardwood swamp; and rich hemlock-hardwood peat swamp. Of these communities, hemlock-northern hardwood forest is widely represented in the Catskills, whereas hemlock-hardwood swamp occurs at only two locations and hemlock-hardwood peat swamp is absent.

IV. Relevant aspects of hemlock woolly adelgid ecology

The hemlock woolly adelgid (HWA), *Adelges tsugae* (Homoptera: Adelgidae), is a small, aphid-like insect native to Asia and likely western North America, mirroring the distribution of its secondary host, hemlock (*Tsuga*) species (Havill et al. 2006). It was accidentally introduced into eastern North America, where it was first documented in Richmond, Virginia in 1951 (Suoto et al. 1996), eventually spreading to at least 17 states in the eastern United States. Early in the history of the HWA's occurrence in the eastern U.S., its spread was slow and may have been limited by low hemlock density around the introduction site (McClure et al. 2001, Morin et al. 2009). In recent decades, HWA has spread more rapidly (Morin et al. 2009), initially northward along the Atlantic coast and, more recently, towards the southwest along the Appalachian Mountains. In the southeastern and Mid-Atlantic states, hemlock stands have rapidly succumbed to infestation and have not regenerated (Ford and Vose 2007, Nuckolls et al. 2009), likely due both to the fact that HWA has been longer established there and also because these areas largely lack the cold weather that typically inhibits HWA population growth and therefore spread.

The heart of the range of hemlock is in Pennsylvania, New York, and New England, where HWA infestation and its impact on hemlock stands have been more variable. There, hemlock mortality associated with HWA establishment can range from almost none to 95% (Orwig and Foster 1998, Bair 2002, Mayer et al. 2002). Moreover, whereas at southern sites it typically takes 5 years for trees to die after initial infestation, in the north trees typically survive 10 to 15 years, although some trees have lived with infestation for over 30 years (Orwig et al. 2002). The huge losses already experienced to the south of our region add to the imperative to conserve hemlock forest here, where there are still sizable numbers of relatively healthy trees, and where the typically slower mortality provides a greater window of opportunity to save them.

In the Catskills, HWA was first detected in the late 1990s, and hemlock decline has been detected ever since. In particular, hemlock mortality increased significantly from 0.4% in 2001 to 9% in 2012, and landscape-level assessment of hemlock heath decline in the Catskill Park using remote sensing revealed a drop from 59% of hemlocks being healthy in 2001 to only 16% in 2012 (Hanavan et al. 2015). A field survey in 2014 (Zimmerman and Snider 2014) also showed severe hemlock decline in the southeastern Catskills. Knowing how long it takes infestation to spread within this region, and how long it takes infested trees to decline and die are important to stand prioritization for two reasons: (1) letting us know how much time we have available to act; and (2) because the time course of decline and death are likely to influence the ecosystem consequences of infestation, knowledge of this time course would enable better consideration of the consequences of acting vs. not acting to conserve particular stands.

As mentioned above, HWA's population growth, spread rate, and lethality all tend to be lower in the North than the South. For example, HWA spread rate has been estimated to be 20.4 km/yr in the South and 8.9 km/yr in the North (Morin et al. 2009). Also in the South, e.g., North Carolina eastern hemlock mortality rates reached 84% eight years after the first signs of infestation (Ford et al. 2012), whereas in contrast in New Jersey, hemlock mortality rates reached 19% and in Pennsylvania 54% nine years after infestation (Eschtruth et al. 2006). Local environmental stressors are more important in the North because in the South trees decline rapidly regardless of particular location (Trotter and Shields, 2009). In addition, HWA's population dynamics as well as its impacts on trees also show relationships to particular environmental variables at both the site and individual tree level – although, to complicate things – the reliability of these trends also shows regional variability.

At the tree level, stressed trees such as overtopped ones have showed 70% mortality compared to healthy, dominant trees which showed only 15% mortality (Orwig and Foster 1998, Eschtruth et al. 2006, Rentch et al. 2009). Although all trees are attacked regardless of size/age, small trees die more quickly (within 2 years) than large healthy trees (within 4-15 or more years) (McClure et al. 1991). The abundance of hemlock in the forest is not a significant factor for hemlock HWA driven mortality suggesting that hemlock mixed in hardwood stands are just as susceptible to infestation as hemlock-dominated stands (Orwig et al. 2002, Evans et al. 2011).

Drought, in particular, has been identified as a particularly important environmental driver making hemlock more vulnerable to HWA. Thus, HWA-infested hemlock stands on drier south- and southwest-facing slopes or on steeper slopes have shown higher mortality rates and poorer health (Royle and Lathrop 1997, Bonneau et al. 1999, Orwig et al. 2002, Rentch et al. 2008, and for detailed results from the Catskills see Pontius 2006). Not all variation in HWA-eastern hemlock outcomes is necessarily due to environmental variables, however, as "lingering" hemlock trees that have remained healthy long after their neighbors have succumbed to HWA apparently have some resistance, although it remains to be seen to what extent this is heritable (Ingwell and Preisser 2011).

One factor that we believe may have the potential to significantly affect hemlock health in the Catskills, but which has received relatively little attention, is elongate hemlock scale (EHS), *Fiorinia externa*, another invasive insect pest, which often co-occurs with HWA in hemlock stands. Research we have performed at Mohonk Preserve, on the nearby Shawangunk Ridge (Nunn et al. unpubl.), suggests that EHS has a greater impact than HWA on hemlock health there. This would be in accordance with findings from Black Rock Forest in Orange County, New York (Danoff-Burg and Bird 2002). New York State is a particular hotspot for EHS, given that it was first introduced to N. America in New York City in 1908 (Preisser et al. 2008), and since then has progressed through much of the Hudson Valley and surrounding areas with its highest densities within 200 miles radius of New York City (Danoff-Burg and Bird 2002) [1]. Thus, EHS, its effects on hemlock, and its interactions with HWA might be particularly important here.

Not much is actually known about EHS interactions with HWA. One study (Miller-Pierce and Preisser 2012) found that HWA populations were 45% lower if they settled on trees that had already hosted EHS for two years, but not vice versa. However, the performance of the trees first infested with EHS was not better than those infested only with HWA (in fact it was poorer, but not significantly so). Moreover, in this study, hemlock performance did not differ significantly between trees infested only with EHS and only with HWA. Additionally, a study of long-term coexistence of EHS and HWA showed declining HWA densities and increasing EHS densities (Preisser et al. 2008). Based on these findings, we believe that more study of the direct and indirect interactions between these two pests and the implications of strategies aiming to control only one of them should be studied further, to help anticipate likely outcomes from particular HWA control strategies. For example, Raupp et al. (2008) showed that imidacloprid, a primary agent against HWA, does not seem to be very effective against EHS, raising the question of how its application will over the long term influence the impacts of this pest on hemlock. We are fortunate, however, in that data from Hanavan et al. (2015) and Zimmerman and Snider (2014) offer a baseline that can be used to evaluate to some degree the interaction between EHS and HWA and the correlations of each pest with hemlock decline in the Catskills (combined data would offer information from 58 sites).

V. Ability to generalize about hemlock ecosystem services and HWA impacts across space and time

In reviewing the relevant literature, it readily became apparent that whereas some of the ways in which eastern hemlock interact with their co-occurring biota and their physical environment – and thus the services the hemlock provide – are consistent throughout their range, others show considerable regional variation. This should not be surprising, given that there are differences in the flora and fauna between, for example, Maine and Kentucky, and more fundamentally, there are also differences in key environmental variables such as temperature. These differences largely explain divergent outcomes of studies, showing for example different effects of hardwood replacement of hemlock on groundwater discharge. Similarly, regional differences in flora lead to disparate successional trajectories, and as a consequence, disparities in within-stand microclimate attributes. Because of these differences, we place greater emphasis on studies done within the Northeast, as the systems they describe will tend to be most similar to those in the Catskills.

Another issue that arises is how current ecosystem behavior would change with a changing climate, meaning that we should not assume that system responses observed now for a given location would be quantitatively or perhaps even qualitatively similar in the future. This calls for modeling (with all of its inherent limitations) responses given different climate change scenarios. Also, to some extent, as the climate warms, some of the southern findings that are not now applicable to our region may serve as predictors of long-term outcomes here.

[1] New York has the unwanted distinction of being the state in which the greatest number of forest pest species has first occurred (Liebhold et al. 2013).

In addition to relevant studies coming from geographically disparate sites, there is also range in the types of studies from which we have drawn information. They include, for example, reports on biota or environmental variables from hemlock and/or hardwood sites (i.e., sometimes intended as comparative studies, but often just descriptions of one of these two broad community types), comparative studies across hemlock sites experiencing different levels of HWA infestation, and experimental studies in which hemlock trees are girdled to simulate die-off due to HWA infestation. Each of these types of studies can yield important insights, but each also has its limitations.

VI. Hemlock decline and forest succession

Needle fall due to HWA typically takes place over the course of several years, thus yielding "gradual gaps" (Jenkins et al. 1999). Moreover, even after a hemlock tree dies it typically takes eight to ten years (Baiser et al. 2014) before it falls (although branches and limbs fall off earlier and produce large amounts of woody debris on the ground (Orwig 2002)). During hemlock decline and accompanying increase of light in the stands, hardwood species respond by rapidly increasing their growth rates (see Orwig 2002, based on observations six years after HWA arrival).

In a long-term study, Small et al. (2005) found that in stands in SE Connecticut where hemlock originally formed 40% of the total basal area, after 15 years of HWA infestation, hemlock basal area decreased by 70%, with black oaks (*Quercus velutina*, *Q. coccinea*, and *Q. rubra*) increasing their total canopy basal area by about 50%, with American beech and black birch (*Betula lenta*) also showing particularly large increases. These species as well as black cherry and others quickly filled gaps resulting from hemlock loss. Total sapling density increased by a factor of 70 over this period, principally comprising sassafras and red maple. In another study, also in Connecticut (Orwig 2002), "dense carpets of black birch seedlings" established rapidly, and within six years grew into sapling thickets. Moreover, hardwoods at the sites were to increase their radial growth in response to hemlock loss (Orwig 2002). Black birch was the main replacement species in yet another study in Connecticut (Ingwell et al. 2012).

Black birch has also been found to be the prevalent replacement for hemlock in various studies done in Massachusetts (e.g., Raymer et al. 2013, Stadler et al. 2005). Black birch is likely associated with dying hemlock not only because of the increased light availability, but also because it is nitrophilous, and can take advantage of the increase in available nitrogen (Stadler et al. 2005). Kizlinski et al. (2002) found that the understory at their study sites in Massachusetts and Connecticut mostly comprised birch and red maple seedlings. A study (Ribbons 2014) across a latitudinal gradient ranging from Tennessee to Maine (including one site in/near the Catskills) found red maple seedlings to be particularly prominent in dead hemlock stands.

In the Catskills, Hanavan et al. (2015) reported high densities of moosewood maple saplings and black birch at sites with high hemlock mortality. However, in another study in the Catskills, this one using girdling to cause hemlock mortality intended to simulate HWA-induced decline and death, moosewood maple and yellow birch were well represented in the understory and responded strongly to hemlock mortality (Yorks et al. 2003).

A simulation study (Jenkins et al. 2000, parameterized in NW Connecticut) that used the SORTIE model to predict long-term (i.e., after 500 years) replacement forest species composition in response to hemlock die-off predicts that it will depend both on the other tree species already present and on the percentage of hemlock killed off. In particular, if 100% mortality is reached, all stands would eventually be completely replaced by American beech, but if this is absent, yellow birch would completely take over if initially present.

Because hemlock decline and death from HWA typically result in replacement by hardwoods, many studies that have attempted to assess the long-term impacts of hemlock loss have employed comparisons between healthy hemlock stands and hardwood stands. One factor that could affect hinder the succession of hemlock by hardwood forest (see Kizlinski et al. 2002; Yorks et al. 2003), or at least change the successional trajectory by affecting competitive hierarchies (Eschtruth et al. 2008), is deer herbivory pressure. Thus, deer management can be especially important for hemlock stands that are not prioritized for conservation, so that they can quickly return to closed-canopy forest (it can also be important for conserved hemlock forest, to prevent elimination of seedlings).

VII. Practical considerations of hemlock stand conservation prioritization

As mentioned above, prioritizing stands for conservation must take account not only of the relative services they provide, but also of the feasibility of the desired outcome. The most fundamental limiting factor is whether the stands are still in a state of health that permits any effective HWA control method to prolong its persistence. Beyond that, however, are considerations of whether it would be both practical and desirable to use a particular control method – even if it would be potentially effective – on the given stand. For example, one question would be whether the trees are sufficiently accessible to use enable use of that method, and another would be whether use of that method at the location would result in any adverse impacts. Because we are not experts on pesticide application or issues such as toxicity or potential for environmental contamination and they are beyond the scope of this report, we will not attempt to delve into them.

The question of whether there will be adequate funding to enable conservation of particular stands and – closely related to that – whether there is sufficient political will were identified by the "CRISP Hemlock Conservation Workshop" as factors to be considered in stand prioritization. One approach to these questions, discussed below, is to do public opinion research and then prioritizing stands based on the services that are most popular. Another approach, not mutually exclusive of the first, is to do outreach and education of the public and decision-makers in order to make them better informed and potentially more appreciative of services that may be poorly known or understood.

In the following section, we go through the list of potential hemlock ecosystem services, reviewing the evidence for each, discussing their likely importance in the Catskills, and suggesting which stand attributes would affect mediate the stand's ability to provide those services.

VIII. Eastern hemlock ecosystem services in relation to stand attributes – insights for stand prioritization

Time and again when discussing ecosystem services with forest ecologists, we were told that the most indispensable service that eastern hemlock provides is simply being hemlock. By this it was meant that although hemlock provides a wide range of services, many of these could be provided to some extent by other species, but this would not make up for the loss of hemlock itself, an iconic species. Nevertheless, the other services provided by hemlock stands, both directly and indirectly not only provide additional justification for their conservation, but should also be taken into account in conservation prioritization. In this overview, we examine all the ecosystem service which have been suggested as potentially emanating from hemlocks, and propose stand attributes that likely affect stand provision of those services. We begin with the service directly constituted by the continued persistence of viable hemlock populations in our region – continuing to be a living, sustainable part of our forest flora.

Services:

A. Hemlock being hemlock

1. Long-term persistence of sustainable hemlock populations that preserve genetic diversity

Long-term persistence of hemlock populations is not only a goal in its own right, but is also a requirement for the long-term provision of all those other services that hemlocks can render. However, we want to begin here by simply considering the criteria for stand prioritization that would be guided solely by the imperative to conserve hemlock, *per se* – afterwards we can consider attributes relevant to the provision of other services.

Two broad approaches have been pursued to preserve the genetic diversity of eastern hemlock. The first aims at *ex situ* conservation, in which seeds or other material (for vegetative reproduction) are collected for breeding programs from which progeny will eventually be used for reintroduction of the species to the wild after HWA no longer poses a threat. This is intended as an insurance policy against the worst-case scenario, in which eastern hemlock becomes extinct or regionally extirpated. Given that this species has already almost entirely disappeared from certain areas (e.g., in Shenandoah National Park in VA, mortality has reached ca. 99%), this scenario should not be too readily dismissed. As with seed-banking in general, there is a desire to capture as much genetic diversity as possible, especially representing regional diversity. In addition to seed-banking, there has been a promising citizen-science initiative to identify "lingering hemlock", i.e., healthy trees persisting in areas with high mortality to serve as sources of genetically resistant lines. In fact, cuttings from these lingering ash have been propagated and been shown to inhibit HWA.

The other approach aims at *in situ* conservation of hemlock populations, which, if attainable, would have the obvious benefit of maintaining a presence in the wild that can provide at least some of the ecosystem services associated with the species. Like *ex situ* conservation, this approach would aim to conserve genetic diversity and avoid bottlenecks that can have adverse effects on species and population persistence. There has been very little research on eastern hemlock population genetics, and their findings can be summarized as: 1) the species, overall shows low diversity; 2) however, in comparison to the rest of its range, New England/New York and the Southern Appalachians are two areas of relatively high diversity (Potter et al. 2012); 3) due to pollination and seed dispersal by wind, there is an absence of genetic structure; and 4) although conceivably some diversity was lost in the transition from old-growth to primary growth stands, the allelic diversity of primary and secondary stands is quite similar (at least for the studied locations in Massachusetts (Lumibao et al. 2016). Based on 1-3, it was recommended (Jetton et al. 2013) for *ex situ* conservation to sample 10 trees in 30 populations spread across the eastern hemlock range, but with more sampling sites in the high diversity areas. Furthermore, each tree to be sampled would be 160 to 320 ft (50 to 100 m) apart as a buffer against relatedness.

Given that such low intensity of sampling is needed across the relatively large scale represented by the species' entire eastern distribution (with only modestly increased intensity in New York/New England), it would seem that relatively few populations would need to be maintained in the Catskills to capture the diversity represented there. Additionally, the relatively small number of trees that would need to be sampled from each population implies that the populations need not be particularly large to maintain the level of genetic diversity present. Zimmerman and Snider (2014) have suggested possibly targeting particularly large individuals within populations for protection (via, e.g., chemical controls) because they would be genetically superior. Although phenotypic variation does not necessarily completely correspond to genotypic variation (with, for example, greater stature being due at least in part to age or superior microsite location or chance avoidance of stochastic stressors), large size could reflect overall vigor with a genetic basis. Moreover, larger trees can provide greater quantities of ecosystem services as well as greater reproductive output in terms of pollen and seeds. Furthermore, larger trees that constitute "magnificent individuals" could have the greatest aesthetic impact, calling to mind the grandeur of eastern hemlock. Regarding the number of individuals to conserve, we suggest that the ten trees per population to be used for *ex situ* conservation can be used as a guideline for the target number for focused *in situ* conservation; however, to buffer against the possibility of less than 100% control effectiveness, as well as non-HWA-induced mortality and reproductive failure, we believe that a somewhat larger number of trees should be targeted.

Additionally, we suggest that it is important to aim not just to conserve a given number of stands within the region, but to conserve the following different types of stands: 1) Old-growth, because they may contain some diversity (e.g., alleles) not found in stands of more recent origin; 2) topographically isolated stands, because wind dispersal of pollen and even more so of seed, may not reach them frequently, allowing differentiation; 3) stands differently situated across major environmental gradients (e.g., elevation, soil type, soil moisture) because the cited population genetic studies were done on neutral markers, which can overlook adaptive variation, which is likely to occur along environmental gradients; and 4) stands in the hemlock-hardwood swamps as well as the hemlock-northern hardwood, for the same reason as the stands across the environmental gradients (of which these would be a subset). The strategy of protecting stands across environmental gradients (elevation, soil type, aspect, and different watersheds, see Johnson et al. 2008) has been followed in Great Smoky Mountain National Park in their effort to conserve genetic diversity.

It has been suggested (Kudish 2016) that high-elevation stands, due to their relatively low temperatures and geographic isolation might serve as refugia from HWA and ultimately as sources of seed to recolonize other sites once the threat from HWA has passed. This possibility should not be dismissed, but we do offer some caveats. First, climate warming can render these sites favorable to HWA (and with warming, the spread rate of HWA would increase). Second, HWA has shown some evidence of evolution of cold tolerance in the Catskills (Whitmore upubl. data http://northernwoodlands.org/knots_and_bolts/cold-climate), and has shown ability to evolve cold tolerance more generally (Elkinton et al. 2017). Third, HWA can be dispersed not only by wind, but also by birds and humans and thus may be able to overcome the geographic isolation of these sites. Nevertheless, we do encourage conservation of at least some of these stands both because they will likely continue to be *relatively* inhospitable to HWA (and thus a more easily attained conservation goal) and because they are at one of the extremes of the elevation gradient. If, however, these trees are specially adapted to high altitudes, their progeny might be poorly adapted to other sites, and thus not be an appropriate source to recolonize them. In any case, we suggest modeling the likelihood of high elevation hemlock stands persisting as refugia from HWA in different warming scenarios.

<u>*Relevant stand criteria:*</u> Different woodland types (hemlock-hardwood swamps as well as the hemlock-northern hardwood); stands across the spectrum of environmental variation (in terms of elevation, soils); topographically isolated stands; old-growth.

2. Long-term persistence of sustainable hemlock populations representing the different forest types in which hemlock is a major component

The goal of conserving stands representing different forest types was already discussed to some extent above, in the context of genetic conservation. However, the different forest types are also quite distinctive from each other, meriting conservation in their own right. Furthermore, because of these differences, they are also associated with different fauna and flora and thus have different roles in maintaining biodiversity.

Relevant stand criteria: Different woodland types (hemlock-hardwood swamps as well as the hemlock-northern hardwood).

3. Conservation of old-growth hemlock stands

As mentioned above, old-growth stands might contain some genetic diversity not otherwise captured. However, of greater importance, old-growth stands truly represent a distinct community type, comprising, unsurprisingly, much older and larger trees. Moreover, their understory vegetation has been found to be more diverse than other hemlock stands because of the greater prevalence of gaps and resulting greater structural diversity. Crucially, they are relict patches of a previously much more widespread community type.

Relevant stand criteria: Old growth.

B. SOCIAL/CULTURAL/RECREATIONAL SERVICES

1. Education and outreach

Hemlock stands can be used as resources for education and outreach regarding the following themes:
a) hemlock roles in different forest types;
b) old-growth hemlocks as an illustration of the forest that existed pre-European settlement and the resource that was exploited by the tanning industry;
c) hemlock stands to illustrate impacts of invasive species.

Relevant stand criteria: For "a" it would be best to have stands in the different woodland type; for "b", old-growth would of course be necessary; and for "c" the message would be most strongly conveyed if there were comparable stands of healthy and dead or infested trees. For any of these purposes, educational access, signage, programming and other materials would be most easily furnished if the stands are at or near existing educational facilities, as suggested at the CRISP Hemlock Conservation Workshop.

2. Research

Hemlock stands serve as sites to conduct research on various aspects hemlock-dominated forests and associated abiotic and biotic components such as the wildlife that inhabits them. To continue to study these subjects would require conserving adequate stands (which, as for the services provided above, should comprise the different types of hemlock forest, as each is distinct in terms of its components and processes). However, conservation of forest stands is particularly important for the following research purposes: 1) to serve as experimental stands for comparison with those stands in which HWA control has not been undertaken, not only yielding assessments of treatment efficacy, but also of HWA impacts on stand function and services; and 2) to enable continuation of long-term studies already underway.

Sites in the Catskills have been used for hemlock research published in papers such as Hanavan et al. (2015), Pontius et al. (2005), Lovett and Mitchell (2004), and Yorks et al. (2003), for example. Ideally, if such research is being conducted at a site, the research and its findings can be incorporated into ongoing hemlock conservation planning for the Catskills.

Relevant stand criteria: We suggest creating a GIS layer in which all the sites used for hemlock research in the Catskills are indicated.

3. Aesthetics

As mentioned above, hemlocks have inspired well-known figures of arts and letters. Moreover, their appearance as well as the special environment that they create have provided aesthetic enjoyment and inspiration for countless other people as well. Certainly, one important aesthetic effect they have is upon viewsheds. However, the sight of them, as well as the other ways in which they affect the sensory environment also contribute to various activities such as fishing, hiking and boating. Thus, it is difficult to completely distinguish the aesthetic service *per se*. Additionally, the negative effect of hemlock damage on property values, described below, also provides some indication of the value of hemlock in enhancing the aesthetics of residential parcels. One approach to prioritizing stands based on such subjective human values as aesthetics would be to conduct a survey, an approach employed in both North Carolina (Moore and Holmes 2008) and West Virginia (Kish 2007).

Relevant stand criteria: Emphasis should generally be placed on aesthetic benefits where they will be appreciated, i.e., stands viewed from observation towers or along well-used trails, thus drive-by views might not be high priority if much of the traffic on the road is just getting from one place to another without interest in the scenery. Nevertheless, views of locations that can shape the visitor experience, i.e., landscapes broadly representative of the Catskills or at "gateways" to the Catskill Forest Preserve might be particularly important.

4. Recreation – hiking, camping, fishing, winter sports

In addition to the aesthetic benefits mentioned above, hemlock stands have direct, practical effects on the quality of outdoor recreation activities. The shaded, cool, moist, sheltered and verdant environment with a thick bed of soft needles underfoot that characterizes hemlock stands makes them ideal sites for campgrounds, picnic areas, lean-tos and other recreational sites used for the warmer months, while the protection they provide from wind and cold also enable them to provide respite from the elements in the winter. Hemlock stands also provide wildlife habitat and positively influence aquatic habitat for brook trout, further contributing to the overall benefits they provide in terms of recreation.

Relevant stand criteria: Proximity to recreational features such as fishing streams; cross-country ski, snowshoeing, and hiking trails; campgrounds; hiking trails; lean-tos.

5. Property value

A study by Li et al. (2014) showed that severe damage of hemlock by HWA resulted in a conservatively estimated decrease of 1 % in the value of properties within 0.5 km from infestation. In an area such as the Catskills, which is heavily dependent upon seasonal residents, tourists, and other visitors attracted by the area's natural beauty and outdoor recreational opportunities, the direct economic impact from the loss of hemlocks (i.e., simply lost revenues and taxes without considering hemlock/HWA management costs) are likely to be much more widespread. Nevertheless, even the conservative estimate from Li et al. (2014) study should make it easier to obtain the public support and political will for needed hemlock conservation projects.

<u>Relevant stand criteria:</u> Stands in proximity to high private property densities or where hemlock damage is especially likely to diminution of the tax base (e.g., high tourist-destination areas).

C. Nutrient retention

Healthy hemlock forest is typified by its "slow and tight biogeochemical cycles" (Kizlinski et al. 2002). This is due to numerous factors, including hemlock litter's poor quality in terms of its high tannic acid content, low pH and high C:N ratio (Finzi et al. 1998). Indeed, a study (Elliott et al. 1993) comparing decomposition rates of hemlock, beech, and red pine litter decomposition done at the E. N. Huyck Preserve in Rensselaerville, NY found hemlock litter to decompose most slowly, which was attributed to its quality. Hemlock's slow growth rate, the overall lack of understory vegetation and its cool microclimate are also likely to affect aspects of nutrient cycling.

Since HWA has been shown to change hemlock leaf chemistry (increasing its N concentration, which should make it decompose more readily), alter microclimate (especially through changes in light availability and therefore temperature) and ultimately result in hemlocks being replaced by other trees, questions have been raised about the potential liberation of nutrients, particularly nitrogen, closely contained within hemlock-dominated ecosystems.

Stadler et al. (2006) documented complex interactions affecting vertical N fluxes, i.e., canopy-to-forest floor, during hemlock decline at Mt. Tom, Massachusetts by comparing lightly HWA-affected vs. unaffected stands. They found that very early in HWA infestations, when enough foliage remains on the hemlock trees to support large HWA populations, vertical N fluxes would initially decrease because of microbial immobilization of N enabled by dissolved organic carbon from protective wax secreted of HWA. However, with further hemlock decline, this would be followed by increased fluxes attributable to needle fall and needle chemistry changes and then by decreases possibly due to decreased needle mass. However, over the long-term, N movement to the forest floor should overall increase with increasing hardwood establishment as their litter has lower C:N ratios.

Of particular concern from the perspective of water-quality maintenance is the potential for increased available N through mineralization and nitrification, with the latter process particularly important because nitrates easily leach from soil, causing greater N loading of streams and downstream reservoirs. Crucially, various studies have indicated that mineralization and nitrification are greater both in HWA-damaged stands than undamaged stands and in at least some mature hardwood stands (see below) than in healthy hemlock stands. Thus, HWA infestation poses both short- and long-term threats to the nitrogen retention provided by hemlock, with potentially important consequences for nearby water bodies. Indeed, because in the Catskills (see Yorks et al. 2003) much of the water flow after major storms is through the O horizon, this area would seem to be highly vulnerable to N leaching.

Jenkins et al. (1999) compared N cycling rates in Massachusetts and Connecticut hemlock forests having different levels of HWA damage. They found N cycling, net N mineralization, and nitrification rates higher at HWA-infested stands, with the nitrification rate 30 times higher in stands with HWA. Even in infested stands that already had many hardwood seedlings, ammonium-N production was greater than seedling demand, with this increased availability likely leading to nitrification. Similarly, Kizlinski et al.

(2002), studying hemlock stands with various levels of HWA damage in Connecticut and Massachusetts, found the overall nitrification rate to be 41 times higher in damaged stands. A three-year study in CT by Orwig et al. (2008) provides insight into the timing of these changes in nutrient cycling processes, finding that by the second year net nitrification rates were significantly greater (by an order of magnitude) in infested stands, with net mineralization rates also being higher by the third year. Moreover, the NH_4, and NO_3 availability increased with time infested.

A study (Cessna and Nielsen 2012) of nitrogen cycling in hemlock stands with differing levels of HWA-induced mortality that also examined N concentrations in adjacent stream water showed net nitrification and mineralization rates to be higher at sites with high mortality, as were nitrate concentrations and ammonium movement through soil. Stream water nitrate concentrations were, unsurprisingly, lowest adjacent to the stands with lowest mortality, and were highest at those with intermediate mortality. The last finding was attributed to the proliferation of seedlings (esp. *Betula*), as it was inferred that they would be taking up some of the additional nitrates.

Even if hardwood seedlings can to some extent ameliorate increased nitrification due to short-term changes attributable to HWA infestation, in the long-term, hardwood forests are likely to feature significantly greater nitrification than the hemlock forests that they replace. This is especially true for sugar maple, which in studies in the Catskills has been shown to have much higher net nitrification rates than four other major forest species here – hemlock, yellow birch, American beech, and red oak. Moreover, of these species, only red oak had a similar nitrification rate to hemlock, with the birch and beech having the third- and second-highest rates, respectively (Lovett and Mitchell 2004; Lovett et al. 2004; Templer et al. 2005). Simulation modeling, parameterized in part in the Catskills has also shown that replacement of hemlock by yellow birch would yield nitrate leaching 100 years after HWA infestation (Crowley et al. 2016).

Relevant stand criteria: Riparian stands, especially those where sugar maples are likely to succeed hemlocks.

D. HYDROLOGY: STREAM FLOW MAINTENANCE

Healthy hemlock stands have several characteristics that affect hydrology. First, although their winter transpiration is slightly higher than that of the largely dormant deciduous trees (with this difference being greater in the southern part of eastern hemlock's range due to higher winter hemlock transpiration activity there), their growing season transpiration is substantially lower than that of hardwoods (see below). Second, their architecture and foliage density result in greater precipitation interception (Guswa and Spence 2011). Third, the relatively stable microclimate in hemlock stands (overall warmer than hardwood stands in winter and cooler in warm weather) also reduces winter snow depth, but may enable its persistence in spring (see below).

Sap flow measurements at Harvard Forest showed that during the peak growing season, black birch daily transpiration was 1.6 times higher than that of hemlock (Daley et al. 2007). The measurements yielded the prediction that replacement of the latter by the former would increase the amount of transpired water by 30% each June-October period. Moreover, because for hemlocks, June-September evapotranspiration was 100 mm less than precipitation, in contrast to black birch for which evapotranspiration almost equaled precipitation, this replacement would result in decrease and possible cessation of flow in small streams. Another sap flow study at Harvard Forest found red maple to use 2.5 times as much water as hemlock and red oak to use 4 times as much water as hemlock. Although measurements in a different study (Hadley et al. 2008) found transpiration rates of red and black oaks to be only twice that of hemlock, it also found that over the course of summer, whereas 40% of precipitation in hemlock forest remained in the soil or ended up in aquatic systems, all of the precipitation in red oak forest was returned to the atmosphere. The authors therefore predicted that hemlock replacement by hardwoods would therefore diminish stream flow, with consequences for downstream reservoirs. Indeed, summer throughfall measurements and transpiration data from a study in western Massachusetts showed that hemlock's lower transpiration outpaces its greater precipitation interception, leading to greater summer stream recharge than in deciduous forest (Guswa and Spence 2011).

Interestingly, a study often cited regarding its findings on its major subject, the influence of hemlock on aquatic invertebrates at Delaware Water Gap National Recreation Area (Snyder et al. 2002), reported major disparities in the occurrence of summer drying of streams draining hemlock vs. hardwood forest. Thus, in 1997, 9 of 14 hardwood streams (64%) dried at some time during the summer, in contrast to only 2 of the 14 (14%) of comparable hemlock streams, and in 1999, summer drying occurred in 6 of the 14 hardwood streams (43%) vs. only 1 of 14 (7%) of the hemlock streams. In these years, HWA infestation was quite localized at the Delaware Water Gap, and it is likely (although not explicitly stated) that the hemlock stands included in this study were healthy, with the results thus demonstrating the greater summer discharge and more reliable stream water flows predicted for healthy hemlock than for hardwoods in the abovementioned publications.

Hadley et al. (2008) also mention that water use will first diminish immediately after hemlock mortality (i.e., due to the relative lack of living trees), before replacement hardwood forest eventually exceeds the water usage of the preceding hemlock stands. However, they do not provide any estimate as to how long it should take for the level of water usage of the hemlock stand to be reached by the replacement vegetation. Brantley et al. (2013) predict that it will take only approximately nine years for water usage to recover after virtually 100% mortality due to HWA, but we suggest that this estimate would not necessarily be applicable to the Catskills, because the underlying study was done in North Carolina, which differs substantially in several factors, including the temperature regime, and quite possibly growth rates (as well as the presence of aggressively spreading stands of *Rhododendron maximum*.

Thus, although we should be concerned about diminishment of stream flow in the long-term, we should consider that stream flow may be increased in the interim. This would be due not only to diminished forest water usage but also to reduced precipitation interception. Whether the degree of short-term additional stream flow would be beneficial or problematic in the Catskills we cannot at this point say, but we suggest that this question be explored more fully using modeling parameterized based upon known stream flow values and projected potential changes in forest water usage and precipitation interception.

The amount of winter/early spring runoff is likely to increase both short-term with hemlock die-off and to a lesser extent long-term with eventual hardwood replacement. This is true for two reasons. First, hemlock, because it is evergreen, transpires at a higher (although very modest) rate during winter than do hardwoods. Second, hemlock intercepts more summertime precipitation than hardwoods (Guswa and Spence 2011). Snow accumulation is significantly smaller in hemlock stands than hardwood stands (Lishawa 2007), which might be attributable both to greater interception (see Fig. 2) and to melting in the hemlock stands' warmer microclimate (see Lishawa 2007). Nevertheless, the snow that does accumulate beneath hemlocks persists longer (Lustenhouwer et al. 2012) in spring (we suppose due to shading). Thus, the runoff from melting of a relatively small snowpack should occur over a longer period, further lessening the likelihood of early spring flooding.

Figure 2. Snow interception by hemlock.

Considering all these phenomena together reveals that hemlock has an overall stabilizing influence on stream flow, likely reducing the intensity of spring runoff (and flooding) and maintaining flow in small streams throughout the summer. Its loss will probably result in increased amounts of water reaching streams year-round in the short term, but in increased early spring/winter flow along with decreased growing season flow in the long term.

Relevant stand criteria: Riparian stands especially important for groundwater discharge stabilization; high elevation stands with greater snowfall might be important because of longer snow retention.

E. Erosive slope protection and sediment retention

Erosive slope protection and sediment retention were both listed as potential ecosystem services during the "CRISP Hemlock Conservation Workshop" on October 6th, 2016. Based upon our consultations of experts and upon our review of the literature, we believe that these closely related services will not be significantly lost with the loss of hemlock. This would be the case because numerous published studies have shown that understory vegetation, including seedlings of succeeding hardwoods, (see below) rapidly proliferates typically in response to increased light availability as hemlock dies off. Indeed, die-off due to HWA has been characterized as "gradual gap formation" (Jenkins et al. 1999), which provides time for this vegetation to establish. Moreover, because the dead hemlock trunks typically remain standing for eight to ten years, with their roots (which decompose slowly) still in the ground, probably also playing a role in maintaining soil stability.

Notably, despite our thorough search of the literature, we found only one study that showed evidence of increased sediment loading associated with HWA-induced die-off, as shown by elevated silicon amounts in streams near over-90% mortality stands, but this silicon concentration was not at a level that have a negative effect on water quality (Huddleston 2011).

Relevant stand criteria: This does not appear to be a service that is significantly lost with hemlock loss. Nevertheless, hemlock stands lacking in understory that can provide replacement for the hemlock would seem to pose a greater risk of losing sediment, especially if they are steeply sloping. Deer management to facilitate revegetation could also be relevant.

F. Stream water temperature maintenance

Concern has been expressed about the potential service that hemlock plays in keeping stream water cool in the Catskills, especially so that streams will continue to be suitable for brook trout. Brook trout perform best in terms of growth and survival within the temperature range 11°-16° C, although reproduction is triggered at lower temperatures in the fall (Raleigh 1982).However, the two published studies that explicitly investigated possible cooling resulting from hemlock shading of streams were from the southern Appalachians (where, with higher ambient temperatures, this effect is of greater concern), and both produced equivocal results.

In Great Smoky Mountains N.P., Roberts et al. (2009) compared streams found along riparian hardwood and hemlock stands with respect to several water characteristics and found no difference in stream temperature between the forest types. This was attributed to hemlock forming only a small percentage of the forest there and also to abundant *Rhododendron maximum* cover.

A study in George Washington National Forest in Virginia (Siderhurst et al. 2010) examined stream temperatures and light levels in relationship to the degree of HWA-induced hemlock decline. They found that although light reaching streams had increased significantly with hemlock decline – and it would likely increase further as gaps open when trees fall – stream temperature was unrelated to the hemlock's status. The lack of effect of HWA on stream temperature was attributed to groundwater having a greater effect than light level at the studied locations, with the input of cold groundwater overwhelming the potential influence of increased light. Because there was a significant negative relationship between water temperature and proximity to groundwater sources, the authors suggest that the loss of shading could have significant effect on water temperatures further downstream. Additionally, they point out that tree height and topography – particularly slope steepness and aspect – influence the potential for shading to affect stream temperatures. Finally, they note that stream shading will actually increase with hardwood establishment relative to that now provided by degraded hemlock forests; although the hardwood shading will not be year-round, it will be present during the months for which excessive warming would be of concern.

Although to our knowledge it has not been directly investigated in any published study, we believe that the decrease in summer discharge that will accompany replacement of hemlocks with hardwoods is likely to result in increased stream temperatures. This is because even modest decreases in discharge have been shown to raise stream temperatures (Caissie 2006). The decreased discharge could interact with decreased shading (from hardwoods in comparison to healthy hemlocks) such that there would be insufficient incoming cool groundwater to offset potential warming from the increased light.

Even if decreased shading does yield increased stream temperatures, these might be ameliorated to some extent by influx of coarse woody debris (CWD) which would likely occur as a result of hemlock mortality. This would be the case because CWD that becomes lodged in streams can cause formation of pools that contain cooler water near the bottom.

Relevant stand criteria: Stands most important for this service would occur in riparian locations that are not topographically shaded and that are sufficiently downstream from groundwater sources that they would be needed to provide shading. Moreover, these shading services would be most important in streams that host brook trout.

G. Maintenance of stream biotic communities, including brook trout

Of course, elevated stream temperature, due to loss of shading is just one way in hemlock decline and loss might affect aquatic communities. Here we discuss other ways in which hemlock die-off can have impacts on stream biota.

Shading could affect stream communities not only by decreasing water temperature, but also by decreasing the amount of light available for photosynthesis. Rowell and Sobczak (2008) compared PAR (photosynthetic active radiation) and periphyton biomass (on study tiles) in streams running through hemlock and hardwood stands in MA and CT. They found both PAR and periphyton to be greater in the hardwood stands, as had been predicted by Ellison et al. (2005). They did not explore the implications for stream fauna of these increased levels, but we believe that both could influence fauna in multiple ways. Thus, having more periphyton beneath hardwood trees could, for example, increase food availability for grazers (both invertebrate and vertebrate). Additionally, both the increased periphyton and increased light might influence foraging behavior or efficiency of organisms searching for prey in the stream.

The abovementioned Delaware Water Gap National Recreation Area study (Snyder et al. 2002) of aquatic invertebrates in streams draining hemlock vs. hardwood forests found hemlock streams to have more taxa, with 7% of the taxa strongly associated with this forest type, including three found only in it. Moreover, hemlock streams featured not only greater richness but also greater evenness. On the other hand, the number of rarely captured taxa (i.e., captured from < 4 sites) and total invertebrate abundance were greater in hardwood streams. More algivores were found in hardwood streams, which would be expected based upon the greater algal growth supported by more sunlight reaching these streams. The authors also speculate that the small daily, seasonal, and summer flow variation in hemlock streams may have enabled the greater invertebrate diversity found there, whereas the higher quality litter in hardwood streams, in addition to the greater trophic inputs of photosynthetic organisms could explain the greater abundance there.

A smaller-scale study In MA (Willacker et al. 2009) compared macroinvertebrate fauna of two adjacent headwater streams, one draining hemlock forest, and one draining hardwood forest. Like the study (Snyder et al. 2002) at Delaware Water Gap, it found different functional compositions, and thus community structures in the two types. However, the hardwood streams had greater abundance, richness, diversity, and number unique taxa. The authors suggested that the stability of hemlock streams may be at the cost of habitat heterogeneity, and as a consequence faunal diversity.

The only other explicit study comparing invertebrate faunas from eastern hemlock- and deciduous-forest-draining streams was one that examined benthic invertebrate shredder communities in headwater streams of these two types in Kentucky (Adkins and Rieske 2015). Although hemlock contributed energy via leaf litter to riparian zone consistently though the growing season vs. the autumn pulse of deciduous material, shredders were more abundant in hemlock streams only in the summer, with the abundance similar across vegetation types in spring and fall. Because of the differences in understory vegetation between the Northeast and the southern Appalachians, it is uncertain to what extent these findings are applicable to our area. Nevertheless, as was the case in the Delaware Water

Gap (in Snyder et al. 2002), stoneflies (Leuctridae) were the most dominant shredder family in hemlock streams, which is notable because stoneflies are particularly important in terrestrial food webs.

Another study conducted in the S. Appalachians (Huddleston 2011) compared invertebrates (and chemistry) of stream draining stands with greater than 90% hemlock mortality and relatively healthy ones (i.e., low mortality ones) in Great Smoky Mountains National Park. It found that streams in the heavily impacted areas had lower Chironomidae and Ephemeroptera densities than in the relatively healthy areas, and that the former were dominated by scrapers, whereas the latter were dominated by the collector/filter functional feeding group. Of greatest interest, river snails (Pleuroceridae) had almost completely disappeared from the streams draining heavily impacted areas, which the author attributed to a posited initial spike in nitrate and/or sediment load in these streams (i.e., after the stands were in worse condition than the relatively healthy stands, but before they reached the status of the heavily impacted stands, where the nitrate concentration had already been lowered, probably by revegetation). These snails are typically common throughout the park's streams, regardless of forest type, with their absence suggesting that some such short-term damaging conditions associated with hemlock decline had occurred. Although, because the study was from the S. Appalachians, its particular results might not be generalizable to the Northeast (especially because the study area featured heavy *Rhododendron maximum* understory, which affects succession and nutrient cycling), we believe that there may well be an important lesson to learn from this scenario. This lesson is that simple comparisons between healthy hemlock and hardwood forest might overlook short-term conditions or events that might occur during hemlock decline causing loss of biota.

Much of the concern about the impacts of hemlock deforestation on aquatic habitats has been focused on possible adverse consequences for fish, particularly brook trout. The only published study from the Northeast (Ross et al. 2003) used paired comparison of fish in hemlock vs. hardwood first- and second-order streams at Delaware Water Gap. Of the 15 species found in the study, 8 were found only in hardwood streams and 1 exclusively in hemlock streams. Hardwood and hemlock streams did not differ significantly from each other in species or functional diversity. However, piscivores did form a much greater proportion of the species in the hemlock streams, with insectivores constituting a greater proportion in hardwood streams. This difference might be attributable to the greater abundance of aquatic insects in the hardwood streams (see Snyder et al. 2002). Of particular interest, the proportional sample representation of brook trout was three times greater, and that of brown trout twice as great, in hemlock streams than in hardwood streams (and the actual number of brook trout individuals was five times greater). No mechanistic explanation was offered for these differences.

We suggest that while maintaining cool stream temperatures is crucial for brook trout, other environmental variables that can be affected by hemlock loss and hardwood replacement and which in turn can affect aquatic communities should also be considered. These would include, for example, litter quality, nutrient loading, PAR (and responses to it by producers).

Relevant stand criteria: Riparian stands, especially those near streams that have brook trout.

H. Terrestrial biodiversity maintenance

1. Understory plants

Hemlock forest is typified by low understory species diversity and cover values Ellison et al. (2016). Near the Catskills, Beatty (1984), in a comparison of hemlock and hardwood stands at the E. N. Huyck

.

Preserve & Biological Research Station in Rensselaerville, NY, found that hemlock stands harbored fewer understory species. In a Harvard Forest study of the herbaceous layer, species richness and diversity were lower in hemlock than hardwood stands Ellison et al. (2016).
Examination of understory composition of hemlock stands along a transect from Wisconsin to Nova Scotia (Rogers 1980) found that there was no species abundant under hemlock that was not also abundant under other canopy, that there was no distinctive understory plant community associated with eastern hemlock, and that there were no species unique to hemlock (a distinctive eastern hemlock-associated herbaceous layer has been reported from the South, however; see Ellison et al. 2016 and references therein). However, a recent study (Ribbons 2014) of sites along a latitudinal gradient from Tennessee to Maine (including one site in/near the Catskills) comparing understory of relatively healthy hemlock, severely damaged hemlock and hardwood stands at each, found some plant species, including wild sarsaparilla, witch hazel and spicebush, only in hemlock (but see, Ingwell et al. (2012) finding of witch hazel to be much more abundant in the understory of heavily damaged hemlock forest, suggesting that at least in the short-term, this species, as well as Canada mayflower would increase). Also, at particular locations, Ribbons (2014) found species that were present at either hemlock or hardwood forests, but not both. Overall, however, understory species density did average two times greater in hardwood than hemlock forest. Importantly, old-growth hemlock was found (D'Amato et al. 2009) to have twice the understory species richness and four times the understory cover as second growth. Moreover, some understory plants such as hobblebush were significant indicators of old-growth, showing that they still have not recolonized second growth. A study of bryophytes (Cleavitt et al. 2008) found that their richness increased during HWA invasion mostly through increased species on coarse woody debris (Cleavitt et al. 2008), and also found that their cover was twice as great in deciduous as in hemlock stands.

Regardless of the overall low diversity of understory plants in hemlock stands, there are ways in which loss of hemlock can result in loss of plant biodiversity (beyond the hemlock itself) in the Catskills. First, given the results of Ribbons' (2014) study, consideration should be given to whether species such as wild sarsaparilla, witch hazel or spicebush are found exclusively or even preferentially associated with hemlock in this region. Second, for species that can occur both under hemlock stands and under closed hardwood canopy, it could be worthwhile considering whether they would do well or even survive the relatively open/high light conditions temporarily experienced as former hemlock stands transition to hardwood forest. For example, a few species were lost from one or more of the studied ravines that they had occurred in – typically at low abundances – at the Delaware Water Gap prior to HWA infestation (Eschtruth et al. 2006); these include one state-endangered sp., *Streptopus amplexifolius* (not listed in NY). In the case of hemlock stands in which rare species occur, we suggest researching the species' requirements to predict whether they will survive this transition and prioritize conservation of the stands accordingly. In Table 1, we list NY Natural Heritage-listed rare plant species that are associated with one or both of the hemlock-dominated community types that occur in the Catskills. Both types of communities are mixed hemlock-hardwood, but some of the species are known to be particularly associated with hemlock.

Hemlock decline and death have been found to result in greatly increased understory diversity and cover, including not only the hardwood seedlings and saplings mentioned in Section VI, "*Hemlock decline and forest succession*," above, but also in the herbaceous layer as well as shrubs. Thus, Ellison et al. (2016) found the herbaceous understory to be more diverse and abundant in girdled (to simulate HWA effects) than in intact hemlock stands. A comparison (Ingwell et al. 2012) of heavily and lightly HWA-impacted hemlock stands in Connecticut revealed higher herb species richness at high-impact sites. Kizlinski et al. (2002) in their study in Connecticut and Massachusets found more heavily HWA-damaged sites had more saplings, seedlings, shrubs, and herbs. Small et al. (2005) documented increases in shrubs and herbs (as well as hardwood recruitment) accompanying HWA damage in Connecticut; they also found that there was increased invasive plant cover. Similarly, in the Delaware

Table 1. List of rare plant species found in two hemlock-dominated communities (Hemlock-Northern Hardwood and Hemlock Hardwood swamp) present in the Catskills (for more details, see Edinger et al. 2014). Species list is based on information from the New York Natural Heritage Program website http://www.acris.nynhp.org/ and all listed species have been found in at least one of the Catskill counties (Delaware, Greene, Schoharie, Sullivan, Ulster) (http://www.dec.ny.gov/natureexplorer/app/;jsessionid=8EF91671D5C1D40594DA.+p16). Column "Association with hemlock" means that species is typically found in stands with hemlock. "Number of communities where species found" shows how generalized or specialized the species is in terms ecological communities defined by vegetation.

List of rare plant species	Communities dominated by eastern hemlock in Catskills			
* occurs only in the Catskills and Adirondacks ** occurs only in the Catskills	Hemlock-Northern Hardwood	Hemlock Hardwood swamp	Association with hemlock trees	Number of communities where species found
Bigleaf Yellow Avens (*Geum macrophyllum* var. *macrophyllum*)*	yes		no	2
Giant pine-drops (*Pterospora andromedea*)	yes		yes	4
Green rock-cress (*Boechera missouriensis*)	yes		yes	8
Hooker's orchid (*Platanthera hookeri*)	yes		yes	10
Jacob's-ladder (*Polemonium vanbruntiae*)		yes	no	8
Musk root (*Adoxa moschatellina*)**	yes		no	3
Nodding pogonia (*Triphora trianthophora*)	yes	yes	yes	9
Northern monkshood (*Aconitum noveboracense*)	yes		yes	5
Northern running-pine (*Diphasiastrum complanatum*)	yes		yes	7
Rough avens (*Geum virginianum*)	yes		no	6
Small bur-reed (*Sparganium natans*)		yes	no	10
Spreading globeflower (*Trollius laxus*)		yes	yes	8
West Virginia white (*Pieris virginiensis*)	yes		no	4
Wild hydrangea (*Hydrangea arborescens*)	yes		yes	7
Woodland agrimony (*Agrimonia rostellata*)	yes		no	10

Water Gap, there was an increase in understory cover and species richness that occurred along with HWA damage, and part of these increases were attributable to invasive species colonizing areas where they had not occurred before (Eschtruth et al. 2006). Therefore, for hemlock stands in areas with high invasive species propagule pressure, we suggest considering targeting these stands for conservation to prevent them from becoming heavily invaded areas or alternatively employing proactive invasive species control measures.

Relevant stand criteria: Hemlock stands where rare plants listed by New York Natural Heritage as occurring in hemlock-dominated communities occur, especially those rare plant species known to be particularly associated with hemlock.

2. Birds

Yamasaki et al. (2000) state that about 96 bird species have been documented using hemlock forest type in New England (suggestive of similar usage in New York), although the particular publication does not specify how many of these use it preferentially. Here, because we are investigating whether and how to prioritize hemlock stands for conservation based, we are focusing upon studies showing: 1) preferential use of hemlock in comparison with co-occurring forest types; or 2) effects of hemlock decline and death on bird breeding abundances and/or productivity. The latter type of study typically has compared the breeding bird assemblages found in hemlock stands exhibiting different stages of hemlock decline, including dead stands. Because the severely degraded stands typically feature dead hemlocks along with dense growth of saplings (see Tingley 2002), rather than mature forest, they are best used to identify short-term changes in the avifauna, which are likely to be supplanted as the forest continues to change structurally.

Five bird species that breed in the Catskills, the Blackburnian warbler, black-throated green warbler, blue-headed vireo, Acadian flycatcher, and winter wren, have been especially well documented through quantitative studies as using eastern hemlock stands preferentially as breeding habitat through much of their ranges, and specifically in the Northeast and/or upper Midwest (some species use dramatically different breeding habitat in the South, hence the exclusion of habitat preference information from that area). The evidence for their preferential use of hemlock by these four species is summarized as follows:

<u>Blackburnian warbler</u>: This species was found to be significantly associated with hemlock versus hardwood sites in a breeding bird survey at the Delaware Water Gap (Ross et al. 2004). Also, an overview of hemlock dependence of birds in Pennsylvania (AlIen et al.2010 and references therein) reports that this species might be the most hemlock-dependent songbird in Pennsylvania, with multiple studies comparing hardwood and hemlock usage finding it breeding only in hemlock stands there. This species was significantly associated with hemlock in breeding bird surveys in Wisconsin and Michigan (Howe and Mossman 1995). Also, although various other conifer (as well as hardwood) forest types were available, this species was much more abundant (the most abundant species) in hemlock forest in a study in Algonquin Provincial Park, Ontario (Martin 1960). A semi-quantitative study of bird breeding habitat preferences at the E. N. Huyck Preserve in Rensselaerville, NY described the Blackburnian warbler as "the most strictly confined to hemlock trees of any warbler in this region" (Kendeigh 1945). In a large-scale Connecticut study (Tingley et al. 2002) comparing breeding birds across hemlock stands in different mortality classes, this species was found only in intact hemlock stands.

<u>Blue-headed vireo</u>: This species was found to be significantly associated with hemlock versus hardwood sites in a breeding bird survey at the Delaware Water Gap (Ross et al. 2004). This species was also found to be significantly associated with hemlock in breeding bird surveys in Wisconsin and Michigan (Howe and Mossman 1995). Additionally, in a ravine system in Ohio, this species preferred hemlock as nesting habitat (Mitchell 1999).

<u>Black-throated green warbler</u>: This species was found to be significantly associated with hemlock versus hardwood sites in a breeding bird survey at the Delaware Water Gap (Ross et al. 2004). In Pennsylvania, it is much more abundant in hemlocks than in hardwoods (AlIen et al. 2010 and references therein). Also, a study in Pennsylvania found it to be preferentially associated with living hemlock, in contrast with hardwood or dead hemlock (Becker et al. 2008); also it actually preferred mixed hemlock-hardwood stands. This species was found to be significantly associated with hemlock in breeding bird surveys in Wisconsin and Michigan (Howe and Mossman 1995), and in a ravine system in Ohio, it preferred hemlock (Mitchell 1999).

The black-throated green warbler does show great variation in breeding habitat, however, and in the Adirondacks, it largely occurs in deciduous forest (Collins 1983). In the White Mountains it is especially associated with hemlock, but is also associated with some deciduous forest types (DeGraaf et al. 1998). Kendeigh (1945) reported that “all birds of this species” at the E. N. Huyck Preserve and Biological Research Station and in the Helderbergs more generally were restricted to hemlock trees or their immediate vicinity. However, in his discussion of regional variation in this species’ habitat preferences, he also mentions that “[a]t elevations over 2000 feet in the Catskill Mountains, this warbler was found to be very abundant in extensive forests of nearly pure beech and sugar maple”. It is unclear, however, what the source for this information was, i.e., whether it was from Kendeigh’s own observations and whether it was from any kind of formalized study. Therefore, it is impossible to evaluate its validity. In a study in Pennsylvania (Becker et al. 2008), this species occurred preferentially in hemlock less damaged by HWA, rather than hardwoods or more heavily damaged hemlock. In the Connecticut study (Tingley et al. 2002) comparing breeding birds across hemlock stands in different mortality classes, this species was significantly associated with relatively intact stands.

<u>Acadian flycatcher</u>: This species was significantly associated with hemlock versus hardwood sites in a breeding bird survey at the Delaware Water Gap (Ross et al. 2004). Also, a study done in Pennsylvania found it to be preferentially associated with living hemlock, in contrast with hardwood or dead hemlock (Becker et al. 2008). Another study at the Delaware Water Gap also found this species to nest preferentially in hemlocks relatively undamaged by HWA (Allen et al. 2009). Similarly, in the Connecticut study (Tingley et al. 2002) comparing breeding birds in hemlock stands at different stages of decline, this species was significantly associated with relatively intact stands.

<u>Winter wren</u>: The winter wren showed greatest number of singing males in hemlock in comparison to other forest types in the White Mountains (Yamasaki et al. 2000). In breeding bird surveys in Wisconsin and Michigan, this species was significantly associated with hemlock (Howe and Mossman 1995). In the Connecticut study (Tingley et al. 2002) comparing breeding birds across hemlock stands in different mortality classes, this species was found only in intact hemlock stands.

Note that although none of the above-listed five songbirds are rare, it is likely that – given their close association with hemlock – they are likely to suffer dramatic population declines as hemlock forest disappears. Therefore, we encourage a proactive, forward-looking approach before these species become rare rather than focusing conservation efforts exclusively on rare species.

Several additional species have been shown to prefer hemlock in studies in fewer quantitative studies. These are the following:

<u>Hermit thrush</u>: in a ravine system in Ohio (Mitchell 1999), this species preferred hemlock. Also, in the Connecticut study comparing hemlock stands in different mortality classes, hermit thrush was well represented in relatively healthy stands as well as high mortality sites that had dense thickets of black birch saplings, i.e., in this case these saplings returned the usability to highly damaged hemlock stands.

<u>Northern goshawk</u>: In the Hudson Highlands of New York and New Jersey, this species was shown to nest preferentially in mixed forest plots with dominance and density of hemlock greater than random (Speiser and Bosakowski 1987).

<u>Red-breasted nuthatch:</u> This species was found to be significantly associated with hemlock in breeding bird surveys in Wisconsin and Michigan (Howe and Mossman 1995).

Magnolia warbler: in a ravine system in Ohio, this species preferred hemlock as nesting habitat (Mitchell 1999).

Benzinger (1994) classified New Jersey birds into three groups based upon his assessment of their relationship with hemlock: 1) "obligates", comprising black-throated green warbler, blue-headed vireo, and northern goshawk; "primary facultatives", which include hermit thrush, barred owl, Acadian flycatcher, winter wren, and red-shouldered hawk; and "secondary facultatives", which consist of brown creeper, Blackburnian warbler, Cooper's hawk, purple finch, yellow-rumped warbler, magnolia warbler, and red-breasted nuthatch. However, this classification is not based on a single, overall quantitative comparative assessment, and appears to be largely subjective, as only a very small component of the literature that is discussed comprises quantitative preference studies of any of the species.

DeGraaf and Yamasaki (2001) list New England forest-frequenting birds that show a preference for hemlock as the following: great-horned owl, long-eared owl, northern saw-whet owl, blue-headed vireo, blue jay, red-breasted nuthatch, winter wren, hermit thrush, and black-throated green warbler. However, they provide no quantitative basis for this list and admit that it is subjective.

One question that arises is whether breeding birds will be able to shift to other tree species if eastern hemlock largely disappears, especially because the usage by some bird species of different forest types in different parts of their range would seem to imply the potential for breeding habitat flexibility (see Tingley et al. 2002). However, it is likely, at least in the case of the black-throated green warbler, that differing habitat preferences of different populations reflect genetic differentiation (Parrish 1995). Additionally, these other tree species already have their own suites of birds that frequent them that may pose an obstacle to bird species that attempt to switch to them (see Tingley et al. 2002).

Hemlock stands are important not only as bird breeding habitat As note, but also as wintering habitat (Yamasaki et al.2000), as they provide shelter as well as a source of seeds (both of these functions having been noted particularly for ruffed grouse). Therefore, in considering the services hemlocks provide, their usage outside the breeding season should be taken into account.

Some bird species have been shown to respond positively to hemlock decline and death. These include woodpeckers as well as species that prefer early successional habitat and other species that may benefit from changes in the forest's structure (Tingley et al. 2002, Becker et al. 2008). In general, these are widespread, common species. However, in the Connecticut study comparing breeding bird abundance in different hemlock mortality classes (Tingley et al. 2002), two species of birds that favored heavily damaged stands are of particular interest. The first is the hooded warbler, which is not a common nester in Connecticut, nor is it a particularly common breeder in the Catskills. The second, potentially of much greater importance, and quite problematic, is the brown-headed cowbird, which as a brood parasite can have adverse effects on forest bird populations.

One study performed in Great Smoky Mountains National Park provided both good news and a possible cause for concern regarding potential indirect effects of insecticide application for control of HWA. That study (Falcone and DeWald 2010) compared breeding bird densities of three species of foliage-gleaning birds (blue-headed vireo and black-throated green and black-throated blue warblers) and arthropod faunal compositions and abundances across imidacloprid-treated (via soil drench) and untreated hemlock stands. It found that abundances of the birds were greater in the stands in which the insecticide had been applied. However, it also found that caterpillar densities were significantly diminished in these stands. This could negatively affect nest productivity (not measured in the study), given the importance of Lepidopteran larvae not only in the diet of adult leaf-gleaning birds, but in the diets of juvenile songbirds in general. However, in the case of this particular study, the three bird species are known to forage in deciduous trees as well as hemlocks, so they may have compensated for the lowered caterpillar densities on hemlock by foraging more on the other tree species occurring in the mixed forest. Moreover, even if there would be some reduction in nest productivity, pesticide application would be worthwhile from a bird conservation perspective if the birds are dependent on it as an element in their nesting habitat and it would disappear without the treatments.

Additionally, we wish to be clear that this study does not raise issues of pesticide contamination of the birds themselves or of widespread environmental contamination, because: 1) the relevant scenario is not one of birds eating pesticide-laden prey but of them potentially having to cope with lower availability of some prey and; 2) the insects with reduced densities would likely have either ingested the pesticides directly when consuming the foliage or, in some cases, come into direct contact with it at the base of the tree when pupating there (as a result of the soil drench, which, of the several application methods tested in another study, had the greatest impact on non-target terrestrial insects, see Dilling et al. 2009).

Relevant stand criteria: Stands in areas having high breeding populations of the species most closely associated with hemlock (i.e., Blackburnian warbler, black-throated green warbler, blue-headed vireo, Acadian flycatcher) as determined using such sources as breeding bird survey or breeding bird atlas data. Because of the possible decrease in available caterpillar prey on hemlocks themselves, it might be best to prioritize hemlock stands where there is also a substantial component of non-hemlock trees. Moreover such mixed forest yields greater bird diversity and is particularly favorable habitat for some species.

3. Mammals

Porcupines are almost entirely dependent on eastern hemlock for food and shelter during the winter (November – April), to the extent that concern has been expressed that HWA will cause widespread winter starvation in this species (Griesemer et al. 1998). Red fox, black bear, and bobcat seem to prefer hemlock forest seasonally (Yamasaki et al. 2000), with fishers in New England also showing seasonal preference for hemlock, although not as strongly as in the western Great Lakes area (Yamasaki et al. 2000). Varying hares require dense conifer stands in winter (Yamasaki et al. 2000); in the Catskills, hemlock would likely be especially important for them where spruce and fir are absent. Hemlock stands also provide particularly favorable winter habitat for white-tailed deer, both because porcupines there make food available for them (by cutting and dropping branches from high in trees, see Yamasaki et al. 2000) and serving as sites with relatively little snow accumulation (Lishawa et al. 2007).

Relevant stand criteria: Stands in known areas of porcupine occurrence should be prioritized, given this species' dependence on hemlock. However, these stands need not be extensive or pure, as porcupines are known to preferentially exploit the hemlocks even when they are relatively few in number. Stands known to or likely to harbor the other hemlock-associated species listed can also be targeted, but with lower priority; also the stands that are selected for this purpose should be done so such that they satisfy the other habitat requirements for these species (e.g., in terms of landscape ecology).

4. Salamanders

Wyman and Jancola (1992), in a study performed in upstate NY, found overall lower salamander abundance and species richness in forest in which hemlock was a major component, and that the abundances of most of the species were negatively influenced by low pH, which characterizes hemlock stands. However, the red-backed salamander preferred lower pH than other species, as did the Allegheny mountain dusky salamander *Desmognathus ochrophaeus*, with the red eft tolerant of a broad pH range, although less common with lower pH.

In fact, red-backed salamander abundance has been found to be significantly higher in hemlock-dominated stands than hardwood stands in Harvard Forest (Matthewson 2009, Siddig et al. 2016). Matthewson (2009) found the difference in densities to be attributable to the cooler maximum temperatures and higher prey availability in hemlock stands. Red efts were two to six times more abundant in hemlock plots than deciduous plots, with this difference likely due to the proximity of the hemlock plots to streams (Mattewson 2014).

Comparing girdled (to simulate HWA-induced decline and death) and control (i.e., unmanipulated) hemlock plots, at ten years since this manipulation, abundance of this species was five times higher in the control stands (Siddig et al. 2016). At this interval, the relative abundance of red efts was also significantly lower in the girdled plots (Siddig et al. 2016). Based on these outcomes, the researchers speculated that at sites where hemlock is eliminated, it will take about 50-70 years for the salamander populations to recover.

Additionally, a single four-toed salamander (*Hemidactylium scutatum*) (a NYS SGCN species) was found by one of us (Wildova, unpub.) during a study of salamanders found in hemlock stands at Mohonk Preserve; this might be attributable to the site's proximity to sphagnum-covered habitat, which this species uses for breeding. The longtail salamander (*Eurycea longicuada*), recognized by NY Natural Heritage as a rare species, occurs in five community types, one of which is hemlock-northern forest, and has been reported from Sullivan County, although we have not found information on what community type it has been found in there, and whether it actually occurs in the Catskills.

Because invasive earthworms largely eliminate the litter layer, they can cause long-term severe declines in salamander populations. Therefore, sites where these worms occur would not be suitable for salamander conservation, which should be kept in mind if hemlock stands are to be conserved for this purpose.

<u>*Relevant stand criteria:*</u> Attempts should be made to identify the location of longtail salamander occurrence in Sullivan County (to determine if within CRISP boundaries, the hemlock situation should be assessed there to determine whether hemlock conservation would be merited; more generally, stands without invasive earthworms (i.e., with thick litter layers) can be targeted for protection because of their role in maintaining low pH habitat for red-backed salamanders.

5. Terrestrial invertebrates

Numerous studies have shown intact hemlock stands to harbor low invertebrate diversity in comparison to hardwood stands and/or HWA-damaged stands (Ellison et al. 2005 and Kendrick et al. 2015 – ants; Ingwell et al. 2012 – forest invertebrates; Rohr et al. 2009 and Sackett et al. 2011 – forest macroarthropods). Moreover, Sackett et al. (2011) found that no beetle, ant or spider species would be extirpated from Harvard Forest due to HWA. However, Ingwell et al. (2012) did find one species of centipede that was abundant in lightly HWA-affected hemlock stands and absent from heavily damaged ones, Rohr et al. (2009) found seven hemlock-indicator species that would likely decline with loss of hemlock at a site in Virginia, and Mallis and Rieske (2011) found that abundance, richness, and diversity of arboreal spider communities were higher in hemlock than hardwood stands in a study done in Kentucky.

Relevant stand criteria: Since hemlocks harbor low invertebrate density and there is no high-profile invertebrate (e.g., a charismatic butterfly) associated exclusively with healthy hemlock stands in the North, we do not foresee hemlock stands being prioritized for conservation based on their invertebrate faunas in this region. Moreover, conservation of hemlock stands for other purposes should also provide conservation of the associated invertebrate fauna.

IX. Next steps

One way to proceed would be to first prioritize the stand services listed above, identifying the ones most important to CRISP. Then, once the necessary supporting information (e.g., locations of educational or research sites or identification of stream segments in need of shading) has been assembled, particular stands can be identified that would provide the services and be feasible sites to use the appropriate control techniques. Because necessary resources will be limited, identifying stands that provide multiple important services will be particularly constructive. However, inevitably, some stands will be favorable for some services, but not others; the relative importance of their services and the relative practicalities of their conservation would then be taken into account in deciding which of these stands will be chosen for the pest management efforts.

X. Literature cited

Adkins, J.K. and Rieske, L. K. 2015. A terrestrial invader threatens a benthic community: potential effects of hemlock woolly adelgid-induced loss of eastern hemlock on invertebrate shredders in headwater streams. Biological Invasions, 17: 1163-1179.

Allen, M. C., Sheehan, J. Jr., Master, T. L. and Mulvihill, R. S. 2009.Responses of acadian flycatchers (*Empidonax virescens*) to hemlock woolly adelgid (*Adelges tsucae*) infestation in Appalachian riparian forests. The Auk, 126 (3):543-553.

Bair, M. W. 2002. Eastern hemlock (*Tsuga canadensis*) mortality in Shenandoah National Park. In: Onken, B., Reardon, R., Lashomb, J. (eds). Proceedings: hemlock woolly adelgid in the Eastern United States Symposium, East Brunswick, NJ, Feb 5–7 2002. USDA For. Serv., State Univ. of N J Rutgers, pp 61–66.

Baiser, B., Barker Plotkin, A., D'Amato, A. Ellison, A., Foster, D., Orwig, D. Oswald, W. and Thompson, J. 2014. Hemlock: A Forest Giant on the Edge. Edited by Foster, D. and Long, S. Yale University Press, pp. 306.

Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology, 65:1406–1419.

Becker, D. A., Brittingham and Goguen, C. B. 2008. Effects of hemlock woolly adelgid on breeding birds at Fort Indiantown gap, Pennsylvania. Northeastern Naturalist, 15(2): 227-240.

Benzinger, J. 1994. Hemlock decline and breeding birds - I: Hemlock ecology. Records of New Jersey Birds, 20: 2-12.

Bonneau, L.R., K.S. Shields, and D.L. Civco. 1999. Using satellite images to classify and analyze the health of hemlock forests infested by the hemlock woolly adelgid. Biological Invasions, 1: 255-267.

Brantley, S., Ford, C. R. and Vose, J. M. 2013. Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. Ecological Applications, 23(4): 777–790.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology, 51(8): 1389-1406.

Cessna, J. F. and Nielsen, C. 2012. Influences of hemlock woolly adelgid–induced stand-level mortality on nitrogen cycling and stream water nitrogen concentrations in southern Pennsylvania. Castanea, 77(2): 127-135.

Cleavitt, N. L., Eschtruth, A. K., Battles, J. J. and Fahey, T. J. 2008. Bryophyte response to eastern hemlock decline caused by hemlock woolly adelgid infestation. The Journal of the Torrey Botanical Society, 135(1):12-25.

Collins, S.L. 1983. Geographic variation in habitat structure of the Black-throated Green Warbler (*Dendroica virens*). Auk, 100: 382–389.

Crowley, K. F., Gary M. L., Arthur, M. A. and Weathers, K. C. 2016.Long-term effects of pest-induced tree species change on carbon and nitrogen cycling in northeastern U.S. forests: A modeling analysis. Forest Ecology and Management, 372:269–290.

Daley, M. J., Phillips, N. G., Pettijohn, C. and Hadley, J. L. 2007. Water use by eastern hemlock (*Tsuga canadensis*) and black birch (*Betula lenta*): implications of effects of the hemlock woolly adelgid. Canadian Journal of Forest Research, 37(10) 2031-2040.

D'Amato, A.W., Orwig, D.A., Foster, D.R. 2009. Understory vegetation in old-growth and second-growth *Tsuga canadensis forests* in western Massachusetts. Forest Ecology and Management, 257 (3): 1043-1052.

Danoff-Burg, J. and Bird, S. 2002. Hemlock woolly adelgid and elongate hemlock scale; partners in crime. Hemlock woolly adelgid in the eastern United States symposium. US Forest Service, East Brunswick, NK, pp. 254-268.

DeGraaf R. M. and Yamasaki, M. 2001. New England wildlife: habitat, natural history, and distribution. Pp482.

DeGraaf, R. M.; Hestbeck, J. B.; Yamasaki, M. 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. Forest Ecology and Management, 103: 217-233.

Dilling et al. 2009. Community response of insects associated with eastern hemlock to imidacloprid and horticultural oil treatments. Environmental Entomology, 38:53-66.

Edinger, G.J., D.J. Evans, S. Gebauer, T.G. Howard, D.M. Hunt, and A.M. Olivero (editors). 2014. *Ecological Communities of New York State.* Second Edition. A revised and expanded edition of Carol Reschke's Ecological Communities of New York State. New York Natural Heritage Program, New York State Department of Environmental Conservation, Albany, NY.

Elkinton, J.S., Lombardo, J.A., Roehrig, A.D., McAvoy, T.J., Mayfield, A., and Whitmore, M. 2017. Induction of coldhardiness in an invasive herbivore: the case of the hemlock woolly adelgid (Hemiptera: Adelgidae). Environmental Entomology, 46: 118-124, doi: https://doi.org/10.1093/ee/nvw143.

Elliott, W.M., Elliott, N.B. and Wyman, R.L. 1993. Relative effect of litter and forest type on rate of decomposition. American Midland Naturalist, 129:87–95.

Ellison, A. M., J. Chen, D. Díaz, C. Kammerer-Burnham, and M. Lau. 2005. Changes in ant community structure and composition associated with hemlock decline in New England. Pp 280-289 in B. Onken and R. Reardon, editors. Proceedings of the 3rd Symposium on hemlock woolly adelgid in the eastern United States. US Department of Agriculture – US Forest Service – Forest Health Technology Enterprise Team, Morgantown, West Virginia.

Ellison, A. M., Plotkin, A. A. B. and Shah, K. 2016. Foundation species loss and biodiversity of the herbaceous layer in New England Forests. Forests, 7(1) #9: 1-12.

Ellison, Aaron M.; Bank, Michael S.; Clinton, Barton D.; Colburn, Elizabeth A.; Elliott, Katherine; Ford, Chelcy Rae; Foster, David R.; Kloeppel, Brian D.; Knoepp, Jennifer D.; Lovett, Gary M.; Mohan, Jacqueline; Orwig, David A.; Rodenhouse, Nicholas L.; Sobczak, William V.; Stinson, Kristina A.; Stone, Jeffrey K.; Swan, Christopher M.; Thompson, Jill; Holle, Betsy Von; Webster, Jackson R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol. Environ, 3(9): 479 – 486.

Eschtruth, A. K., Cleavitt, N. L., Battles, J. J., Evans, R. A., and Fahey, T. J. 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.

Eschtruth, A.K., and J.J. Battles. 2008. Deer herbivory alters forest response to canopy decline caused by an exotic insect pest. Ecological Applications, 18:360–376.

Evans, R. A. 2011. Hemlock woolly adelgid and hemlock ecosystems at Delaware Water Gap National Recreation Area. Fifth symposium on hemlock Woolly adelgid in the Eastern United States, pp 61-69.

Falcone, J. F. and DeWald, L. E. 2010. Comparisons of arthropod and avian assemblages in insecticide-treated and untreated eastern hemlock (*Tsuga canadensis* [L.] Carr) stands in Great Smoky Mountains National Park, USA, Forest Ecology and Management, 260:856-863.

Finzi, A.C., N. Van Breemen, and C.D. Canham. 1998. Canopy tree—soil interactions within temperate forests: Species effects on soil carbon and nitrogen. Ecological Applications, 8:440–446.

Ford, C. R., K. J. Elliott, B. D. Clinton, B. D. Kloeppel, and J. M. Vose. 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos, 121:523–536.

Ford, C.R. and Vose, J.M. 2007. *Tsuga canadenis* (L.) Carr. mortality will impact hydrological processes in southern Appalachian forest ecosystems..Ecological Applications, 17:1156–1167.

Godman, R.M., and K. Lancaster. 1990.*Tsuga canadensis* (L.) Carr, Eastern Hemlock. Pp. 250–259 in R.M. Burns, and B.H. Honkala, eds., Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654, U.S. Dept. of Agriculture, Washington, D.C.

Griesemer, S. J., Fuller T. K., and DeGraaf, R. M. 1998. Habitat use by porcupines (*Erethizon dorsatum)* in central Massachusetts: effects of topography and forest composition. American Midland Naturalist, 140: 271-279.

Guswa, A.J. and Spence, C. M. 2012. Effect of throughfall variability on recharge: application to hemlock and deciduous forests in western Massachusetts. Ecohydrology, 5: 563–574.

Hadley, J., P. Kuzeja, M. Daley, N. Phillips, T. Mulcahy, and S. Singh. 2008. Water use and carbon exchange of red oak- and eastern hemlock-dominated forests in the north eastern USA: implications for ecosystem level effects of hemlock woolly adelgid. Tree Physiology, 28: 615-627.

Hadley, J.L. 2000. Understory microclimate and photosynthetic response of saplings in an oldgrowth eastern hemlock (*Tsuga canadensis L.*) forest, Ecoscience, 7: 66-72.

Hanavan, R.P., Pontius, J. and Hallett, R. 2015. A 10-Year assessment of hemlock decline in the Catskill Mountain region of New York state using hyperspectral remote sensing techniques. Journal of economic entomology, 108(1):339-349, doi: http://dx.doi.org/10.1093/jee/tou015.

Havill, N.P., Montgomery, M.E., Yu, G.Y., Shiyake, S., and Caccone A. 2006. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Ann Entomol Soc Am, 99:195–203

Howe, R. W. and Mossman, M. 1995. The significance of hemlock for breeding birds in the western Great Lakes region. In: Conference proceedings on hemlock ecology and management. Hemlock Ecology and Management: Proceedings of a Regional Conference on Ecology and Management of Eastern Hemlock, pp. 125-139.

Huddleston, M. D. 2011. Riparian ecosystem response to hemlock woolly adelgid (*Adelges tsugae*) induced eastern hemlock (*Tsuga canadensis*) Mortality in the Great Smoky Mountains National Park, USA. Thesis. The University of Tennessee, Knoxville, pp 134.

Ingwell, L. L., Miller-Pierce, M., Trotter, R. T. III et al. 2012. Vegetation and invertebrate community response to eastern hemlock decline in southern New England. Northeastern Naturalist, 19(4): 541-55.

Ingwell, L.L., and E.L. Preisser. 2011. Using citizen science programs to identify host resistance in pest-invaded forests. Conservation Biology 25:182–188.

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

Jenkins, J.C.; Canham, C. D. and Barten, P. K. 2000. Predicting long-term forest development following hemlock mortality. In: McManus, Katherine A.; Shields, Kathleen S.; Souto, Dennis R., eds. Proceedings: Symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, pp 62-75.

Jetton, R.M., W.A. Whittier, W.S. Dvorak, and J.R. Rhea. 2013. Conserved ex situ genetic resources of Eastern and Carolina Hemlock: Eastern North American conifers threatened by the hemlock woolly adelgid. Tree Planters' Notes, 56(2):59–71.

Johnson, K., T. Remaley, and G. Taylor. 2008. Managing Hemlock Woolly Adelgid at Great Smoky Mountains National Park: Situation and response. Pp. 62–69, *In* B. Onken and R. Reardon (Eds.). Fourth Symposium on Hemlock Woolly Adelgid in the Eastern United States, Hartford, CT, 12–14 February 2008. FHTET-2008-01. US Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV. 339 pp.

Kendeigh, S. C. 1945. Community selection by birds on the Helderberg Plateau of New York. The Auk, 62: 418-436.

Kendrick, J. A., Ribbons, R. R., Classen, A. T. and Ellison, A. M. 2015. Changes in canopy structure and ant assemblages affect soil ecosystem variables as a foundation species declines. Ecosphere, 6(5), #77: 1-20.

Kish, K. 2007. Hemlock woolly adelgid management plan. West Virginia Dept. of Agriculture Cooperative forest health protection program. Pp 11.

Kizlinski, ML; Orwig, DA; Cobb, RC; et al. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. Journal of Biogeography, 29: 1489-1503.

Kudish 2016. Eastern hemlock: weird and cyclical. Catskill Forest Association Newsletter, 34(4):5-6.

Levis, L. 2014. A hemlock farewell. Harvard Magazine. July-August: 8.

Li, X., Preisser, E.L., Boyle, K.J., Holmes, T.P., Liebhold, A., and D.A. Orwig. 2014. Potential social and economic impacts of the hemlock woolly adelgid in southern New England. Northeastern Naturalist, 13(6): 130-146.

Liebhold, A. M., D. G. McCullough, L. M. Blackburn, S. J. Frankel, B. Von Holle, and J. E. Aukema. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. Diversity and Distributions, 19:1208–1216.

Lishawa, S. C., D. R. Bergdahl, and S. Costa. 2007. Winter conditions in eastern hemlock and mixed hardwood deer wintering areas of Vermont. Canadian Journal of Forest Research, 37:697-703.

Lovett, G.M. and Mitchell, M. 2004. Sugar maple and nitrogen cycling in the forests of eastern North America. Front Ecol Environ, 2:81–88

Lovett, G.M., Weathers, K.C., Arthur, M.A., and Schultz, J.C. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? Biogeochem, 67: 289–308.

Lumibao, C. Y., Gaskill, M., Flood, K., and McLachlan, J. S. 2016. Persistence of genetic variation in recolonized *Tsuga canadensis* (Eastern hemlock) populations following historic forest clearance. Plant species biology, 31(1): 73-79.

Lustenhouwer, M.N., L. Nicoli, and A.M. Ellison. 2012. Microclimatic effects of the loss of a foundation species from New England forests. Ecosphere, 3(3):26.

Mallis, R.E. and Rieske, L.K. 2011. Arboreal spiders in eastern hemlock. Environmental Entomology, 40:1378–1387. doi: 10.1603/EN10278.

Martin, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. Ecology. 41: 126-140.

Mathewson, B. G. 2009. The relative abundance of Eastern Red-backed Salamanders in Eastern Hemlock-dominated and mixed deciduous forests at Harvard Forest. Northeastern Naturalist, 16(1):1–12.

Mathewson, B.G. 2014. The Relative Abundance of the Juvenile Phase of the Eastern Red-Spotted Newt at Harvard Forest Prior to the Arrival of the Hemlock Woolly Adelgid. Southeastern Naturalist, 13:sp6, 117-129.

Mayer, M., Chianese, R., Scudder, T., White, J., Vongpaseuth, K. and Ward, R. 2002. Thirteen years of monitoring hemlock woolly adelgid in New Jersey forests, pp. 50-60. In Proceedings of Hemlock Woolly Adelgid in the Eastern United States Symposium, Feb. 5-7, 2002, East Brunswick, New Jersey, ed. B. Onken, R. Reardon, and J. Lashomb. Rutgers University, New Brunswick, New Jersey.

McClure, M. S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. Environ. Entomol., 20:258–264.

McClure, M. S., S. M. Salom, and K. S. Shields. 2001. Forest Health Technology Enterprise Team Hemlock Woolly Adelgid.

Miller-Pierce, M, R. Preisser, E, L. 2012. Asymmetric priority effects influence the success of invasive forest insects. Ecological Entomology, 37: 350-358.

Mitchell. J.M. 1999. Habitat relationships of five northern bird species breeding in Hemlock Ravines in Ohio, USA. Natural Areas Journal 19:3-11.

Moore, C. C. and Holmes, T. P. 2008. Valuing forest protection programs to maximize economic benefit. EPA work paper series, NCEE.

Morin, R. S., A. M. Liebhold, and K. W. Gottschalk. 2009. Anisotropic spread of hemlock woolly adelgid in the eastern United States. Biological Invasions, 11:2341–2350.

Nuckolls, A. E., Wurzburger, N., Ford, C. R., Hendrick, R. L., Vose, J. M., & Kloeppel, B. D. 2009. Hemlock declines rapidly with hemlock wooly adelgid infestation: Impacts on the carbon cycle of southern Appalachian forests. Ecosystems, 12: 179-190

Orwig, D. A., and D. R. Foster. 1998. Forest Response to the Introduced Hemlock Woolly Adelgid in Southern New England , USA. Journal of Tthe Torrey Botanical Society, 125:60–73.

Orwig, D. A., Cobb, R. C., D'Amato, A. W.; et al. 2008. Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. Can. J. For. Res., 38: 834-843.

Orwig, D.A. 2002. Stand dynamics associated with chronic hemlock woolly adelgid infestations in southern New England. Symposium on the hemlock woolly adelgid in eastern North America (ed. R.C. Reardon, B.P. Onken and J. Lashomb), pp. 36–47. New Jersey Agricultural Experimental Station, New Brunswick, NJ.

Orwig, D.A., Foster, D.R., and D.L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. Journal of Biogeography, 29:1475–1487.

Parrish, J.D. 1995. Experimental-evidence for intrinsic microhabitat preferences in the black-throated green warbler. Condor, 97, 935–943

Pontius, J.; Hallett, R.; Martin, M. ; Plourde, L. 2010. A landscape-scale remote sensing/GIS tool to assess eastern hemlock vulnerability to hemlock woolly adelgid-induced decline. In: Pye, J. M.; Rauscher, H. M.; Sands, Y.; Lee, D. C.; Beatty, J. S., tech. eds. Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-GTR-802. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest and Southern Research Stations: 657-671.

Pontius, J.A.; Hallett, R.A.; Jenkins, J.C. 2006. Foliar chemistry linked to infestation and susceptibility to hemlock woolly adelgid (Homoptera: Adelgidae). Environmental Entomology, 35: 112-120.

Pontius, J.A.; Hallett, R.A.; Martin, M.E. 2005. Using AVIRIS to assess hemlock abundance and early decline in the Catskills, New York. Remote Sensing of Environment, 97: 163–173.

Potter, K. M.; Jetton, R. M.; Dvorak, W. S.; Hipkins, V. D.; Rhea, R.; Whittier, W. A. 2012. Widespread inbreeding and unexpected geographic patterns of genetic variation in eastern hemlock (*Tsuga canadensis*), an imperiled North American conifer. Conserv. Genet, 13:475–498.

Preisser, E.L., Lodge A.G., Orwig, D.A, Elkinton, J.S. 2008. Range expansion and population dynamics of co-occurring invasive herbivores. Biological Invasions, 10:201–213

Raleigh, R. F. 1982. Habitat suitability index models: Brook trout. U.S. Dept. Int., Fish Wildl. Servo FWS/OBS-82/10.24. 42 pp.

Raupp, M., R. Ahern, B. Onken, R. Reardon , S. Bealmear, J. Doccola, P. Wolfe II, and P. Becker. 2008. Efficacy of foliar applications, trunk injections, and soil drenches in reducing populations of elongate hemlock scale on eastern hemlock. Journal of Arboriculture and Urban Forestry. 34(5): 325-329.

Raymer, P. C. L., Orwig D. A. and Finzi, A. C. 2013. Hemlock loss due to the hemlock woolly adelgid does not affect ecosystem C storage but alters its distribution. Ecosphere, 4(5) #63, pp 16.

Rentch, J., M. A. Fajvan, R. a. Evans, and B. Onken. 2008. Using dendrochronology to model hemlock woolly adelgid effects on eastern hemlock growth and vulnerability. Biological Invasions, 11:551–563.

Ribbons, R. R. 2014. Community responses to Eastern hemlock loss across a latitudinal gradient. Southeastern Naturalist, 13(Special Issue 6):88–103.

Roberts, S. W., Tankersley, E. R. Jr. and Orvis, K. H. 2009. Assessing the potential impacts to riparian ecosystems resulting from hemlock mortality in Great Smoky Mountains National Park. Environmental Management, 44: 335–345.

Rogers, R.S. 1980. Hemlock stands from Wisconsin to Novia Scotia: Transitions in understory composition along a floristic gradient, Ecology 61:178–193.

Rohr, J. R., C. G. Mahan, and K. C. Kim. 2009. Response of arthropod biodiversity to foundation species declines: The case of the eastern hemlock. Forest Ecology and Management, 258:1503-1510.

Ross, R. M., R. M. Bennett, C. D. Snyder, J. A. Young, D. R. Smith, and D. P. Lemarie. 2003. Influence of eastern hemlock (*Tsuga canadensis*) on fish community structure and function in headwater streams of the Delaware River basin. Ecology of Freshwater Fish, 12:60–65

Ross, R.M., Redell, L.A., Bennett, R.M. and Young, J.A. 2004. Mesohabitat use of threatened hemlock forests by breeding birds of the Delaware River basin in northeastern United States. Natural Areas Journal, 24(4): 307-315.

Rowell, T. J. and W. V. Sobczak. 2008. Will stream periphyton respond to increases in light following forecasted regional hemlock mortality? Journal of Freshwater Ecology, 23: 33-40.

Royle, D.D., and R.G. Lathrop. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. Forest Science, 43: 327-335.

Sackett, T.E., S. Record, S. Bewick, B. Baiser, N.J. Sanders, and A.M. Ellison. 2011. Response of macroarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species. Ecosphere, 2(7) #74 1-16.

Siddig, A. A. H., Ellison, A. M., Mathewson, B. G. 2016. Assessing the impacts of the decline of *Tsuga canadensis* stands on two amphibian species in a New England forest. Ecosphere, 7(11):e01574.

Siderhurst, L. A., Griscom, H. P., Hudy, M. and Bortolot, Z. J. 2010. Changes in light levels and stream temperatures with loss of eastern hemlock (*Tsuga canadensis*) at a southern Appalachian stream: Implications for brook trout. For. Ecol. Manag., 260:1677–1688.

Small, M. J., Small, C. J. and Dreyer, G. D. 2005. Changes in a Hemlock-Dominated Forest Following Woolly Adelgid Infestation in Southern New England. Journal of the Torrey Botanical Society, 132(3):458-470.

Snyder, C.D., Young, J.A., Lemarie, D.P. and Smith D.R. 2002. Influence of eastern hemlock (Tsuga canadensis) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences, 59:262-275.

Speiser, R. and Bosakowski, T. 1987. Nest site selection by Northern Goshawks in Northern New Jersey and Southeastern New York. Condor 89:387-394.

Stadler, B., Müller, T., and Orwig, D. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. Ecology, 87, 1792-1804.

Stadler, B., Muller, T., Orwig, D. and Cobb, R. 2005. Hemlock Woolly Adelgid in New England Forests: Canopy Impacts Transforming Ecosystem Processes and Landscapes. Ecosystems, 8: 233-247.

Suoto, D., Luther, T. and Chianese, B. 1996. Past and current status of HWA in eastern and Carolina hemlock stands *in* Proceedings of the First Hemlock Woolly Adelgid Review, Charlottesville, Virginia, October 12, 1995.

Templer , P.H., Lovett, G.M., Weathers, K.C., Findlay, S.E., Dawson, T.E. 2005. Influence of tree species on forest nitrogen retention in the Catskill Mountains, New York, USA. Ecosystems, 8:1–16.

Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: Consequences of Hemlock Woolly Adelgid infestations. Journal of Biogeography 29:1505–1516.

Trotter, R. T. III and Shields, K. 2009. Variation in Winter Survival of the Invasive Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Across the Eastern United States Environmental Entomolgy,38(3): 577-587

Ward et al. 2004. Eastern hemlock forests: guidelines to minimize the impacts of hemlock woolly adelgid. USDA, Forest Service Northeastern Area State and Private Forestry, pp 32.

Willacker, J. J., W. V. Sobczak, and E. A. Colburn.2009.Stream macroinvertebrate communities in coupled hemlock and deciduous watersheds. Northeastern Naturalist, 16: 101-112.

Wyman, R.L., and J. Jancola. 1992. Degree and scale of terrestrial acidifi cation and amphibian community structure. Journal of Herpetology, 26:392–401.

Yamasaki, M., DeGraaf, R.M., and J.W. Lanier. 2000. Wildlife habitat associations in eastern hemlock - birds, smaller mammals, and forest carnivores. Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, pp 135–143.

Yorks, T. E., Leopold, D. J. and Raynal, D. J. 2003. Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive insect herbivore. Canadian Journal of Forest Research, 33:1525-1537.

Young, R., Shields, K. & Berlyn, G. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Annals of the Entomological Society of America, 88, 827–835.

Zimmerman, C. and Snider, D. 2014. Facilitating management of hemlock woolly adelgid in the Catskill Mountains. The Nature Conservancy & CRISP, pp 1-30.