

EVALUATING THE IMPACT OF EASTERN HEMLOCK DECLINE ON  
LOUISIANA WATERTHRUSH DEMOGRAPHICS AND BEHAVIOR IN GREAT  
SMOKY MOUNTAINS NATIONAL PARK

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## ABSTRACT

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### EVALUATING THE IMPACT OF EASTERN HEMLOCK DECLINE ON LOUISIANA WATERTHRUSH DEMOGRAPHICS AND BEHAVIOR IN GREAT SMOKY MOUNTAINS NATIONAL PARK

Eastern hemlock (*Tsuga canadensis*) is declining throughout the eastern United States due to the invasive hemlock woolly adelgid (*Adelges tsugae* Annand). In the southern Appalachians, hemlock is concentrated in moist ravines and its loss threatens riparian specialists and habitat quality. The Louisiana waterthrush (*Parkesia motacilla*) is an obligate-riparian species that could be sensitive to hemlock condition in the southern Appalachians, but how hemlock decline might impact it is currently unknown. I addressed this knowledge gap by evaluating relationships between hemlock decline and waterthrushes. First, I evaluated the ultimate effects hemlock decline could have on waterthrushes, focusing on survival and habitat selection. Second, I explored the proximate effects hemlock decline could have on waterthrushes via altered habitat quality, focusing on territory length and nestling provisioning and body condition. Short-term effects on waterthrush appear minimal, but long-term changes to riparian forest structure could have negative consequences for this species in the future.

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## GENERAL INTRODUCTION

Invasive species, introduced by human movement, environmental modification, and materials transportation, pose growing threats to ecosystem condition and biodiversity (Pimentel et al. 2005). Such introductions are occurring at ever increasing rates and pose unpredictable, and often delayed threats to native species (Simberloff et al. 2013). In forests of the eastern United States (U.S.), a variety of invasive species negatively affect ecosystems, many of which do so via direct impacts on tree species. An estimated \$4.2 billion is spent annually on managing invasive arthropod and plant pathogen forest pests (Pimentel et al. 2005). Oaks (*Quercus* spp.), American beech (*Fagus grandifolia*), elms (*Ulmus* spp.), hemlocks (*Tsuga* spp.), fir (*Abies* spp.), and ashes (*Fraxinus* spp.) all have invasive pests that can, and in some cases are, causing mass mortality (Gandhi and Herms 2010). In some forest ecosystems, single tree species may be critical to establishing and maintaining specific environmental conditions (i.e. foundation species; Dayton 1972), thus their loss may affect a variety of ecosystem functions and characteristics. Loss of foundation species can lead to decreased biodiversity, disrupt ecosystem processes, and alter ecosystem structure (Ellison et al. 2005). Because of the potential for such severe consequences, it is critical that we assess the different ways by which invasive species may affect ecosystem condition and biodiversity, especially in cases involving foundation species.

The near eradication of American chestnut (*Castanea dentata*) in eastern U.S. forests due to the introduced fungus, chestnut blight (*Cryphonectria parasitica*), is a classic

example of how foundation species loss can alter habitats, ecosystem processes, and biodiversity (Anagnostakis 1987, Paillet 2002, Smith et al. 2009). Chestnut was considered a foundation species and co-dominated the Appalachian Mountains with *Quercus* spp. for ~4,000 years until the early 1900s introduction of *C. parasitica* into New York (Ellison et al. 2005). The fungus spread rapidly throughout chestnut's range and by the 1950s reduced the tree from a dominant canopy species to an uncommon shrub species across ~3.6 million ha (Anagnostakis 1987). Previous to *C. parasitica* introduction, chestnut was present in a range of habitats and affected both terrestrial and riparian processes (Ellison et al. 2005) as well as provided a variety of important resources to wildlife and human populations (e.g., tannins, timber, and nuts; Jacobs and Severeid 2004). The loss of chestnut reduced nutritional quality for aquatic macroinvertebrate assemblages due to changes in leaf litter composition (Smock and MacGregor 1988), altered carbon and nitrogen cycling (Jacobs and Severeid 2004), and reduced food resources for common mast consumers like the white-footed mouse (*Peromyscus leucopus*; Dalglish and Swihart 2012). Long-term impacts of chestnut loss include increased woody debris presence in headwater streams (Wallace et al. 2001) and altered forest tree species composition and abundance (Elliot and Swank 2008). While the loss of chestnut fundamentally changed forests of the eastern U.S. and reshaped their structure and biodiversity, the impacts of chestnut loss are mostly speculative because, in the absence of modern scientific tools, techniques, and procedures, pre-chestnut decline forest conditions were not well researched or characterized.

Currently, eastern hemlock (*Tsuga canadensis*), another foundation species in eastern U.S. forests, faces a similar fate as American chestnut and provides an opportunity to

more rigorously evaluate the ecological impacts of foundation species loss. Hemlock is an evergreen tree species found throughout the Appalachian Mountains of the eastern U.S., from Maine to Alabama, and is one of the longest lived tree species in the region, with some individuals living >800 years (Hart and Shankman 2005). Hemlock is considered a foundation species throughout its range (Ellison et al. 2005), especially in riparian habitats of the southern Appalachian Mountains where hemlocks comprise >50% of basal area (compared to only ~5% of basal area across the entire regional landscape; Brantley et al. 2013). As a result, these riparian areas have distinctive terrestrial and aquatic characteristics associated with hemlock presence and condition. Hemlocks directly affect transpiration (Brantley et al. 2013), carbon (Nuckolls et al. 2009) and nitrogen cycling (Jenkins et al. 1999), riparian hydrological regimes (Ford and Vose 2007, Vose et al. 2016), and stream characteristics such as water temperature and pH (Snyder et al. 2002). Additionally, hemlocks indirectly affect ant assemblage structure (Record et al. 2018), aquatic macroinvertebrate assemblages, and vegetation composition (Snyder et al. 2002, Huddleston 2011, Birt et al. 2014). These direct and indirect associations establish conditions that support a variety of organisms including birds (Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008), aquatic macroinvertebrates (Snyder et al. 2002), terrestrial arthropods (Adkins and Rieske 2013, Adkins and Rieske 2015), salamanders (Ellison et al. 2005), and fish (Ross et al. 2003).

Unfortunately, hemlocks across the eastern U.S. are dying from infestation by the hemlock woolly adelgid (*Adelges tsugae* Annand; hereinafter HWA), an aphid-like piercing and sucking insect native to Japan (McClure and Cheah 1999; Figure 1.1). HWA populations use one of two reproductive strategies and, depending on the strategy, one of

two host tree species. Anholocyclic (asexually reproducing) populations rely entirely on hemlock hosts while holocyclic (sexually reproducing) populations rely on both hemlock and spruce hosts; however, when spruce is absent, holocyclic populations can be facultatively anholocyclic (Havill et al. 2016). HWA attaches to the base of hemlock needles by inserting a 4-bundle stylet mouthpiece into the xylem where it feeds on storage cells and secretes salivary tracks, depleting nutrients and possibly inducing toxins within infested trees (Young et al. 1995). Eastern hemlock has no natural defense against HWA, making this invasion especially damaging (Havill et al. 2014). HWA was introduced into the eastern U. S. in Virginia in the 1950s via shipping containers and has since spread across half of hemlock's native range, affecting trees of all ages and sizes in over 18 states from Maine to Georgia, and threatening complete extirpation of hemlock (Ford and Vose 2007, Vose et al. 2013, Havill et al. 2014; Figure 1.2). HWA survival is limited by cold winters (Skinner et al. 2003, Paradis et al. 2007, Tobin et al. 2017) and the direct effect of HWA (i.e. hemlock mortality) has been greater in the southern Appalachians where, on average, milder winters do not suppress HWA populations (Nuckolls et al. 2009). Although increasingly hot summers negatively affect HWA and may help contain future population growth (Mech et al. 2018), infestation in the southern Appalachians is still widespread.

In response to mass hemlock mortality, and because of the potential ecological, aesthetic, and economic consequences, intensive management techniques including chemical and biological control have been implemented in attempts to contain HWA invasion spread and severity (Vose et al. 2013). Chemical treatment involves the application of imidacloprid, a chloronicotinyl insecticide. Imidacloprid can be

administered either as a basal drench of the soil around the base of infested trees or injected directly into the tree trunk (Cowles et al. 2006) and application method depends on the infested tree's proximity to water (Knoepp et al. 2012). Soil applications are the most effective at controlling HWA but the presence of imidacloprid in soil and aquatic systems can negatively impact soil microarthropods (Knoepp et al. 2012), stream health (Benton et al. 2015), and aquatic macroinvertebrates (Kreutzweiser et al. 2008). Imidacloprid soil applications can be effect up to 7 years post-treatment (Benton et al. 2016) but the application process (both initial and repeated treatments) is costly, time consuming, and labor intensive (Vose et al. 2013). Environmental concerns associated with imidacloprid partly restrict its widespread use for HWA management.

Biological control of the HWA invasion has involved the release of several species of predator beetles into infested areas. *Sasajiscymnus tsugae*, a lady beetle native to Japan, was first released in 1995 and is the most widespread predator beetle to date, with >2 million individuals released in >400 locations ranging from Tennessee to Maine (Vose et al. 2013). However, *S. tsugae* populations can take 5–7 years to establish detectable levels at the landscape scale (Hakeem et al. 2010), which may be too long for effective HWA control. *Laricobius nigrinus*, native to the U.S. Pacific northwest, was released in 2003 in several locations ranging from the southern Appalachians to New England (Mausel et al. 2011). Unfortunately, *L. nigrinus* hybridizes with a North American endemic, *Laricobius rubidus*, and the unintended consequences of the hybridization could impact the effectiveness of *L. nigrinus* in HWA control as well as the role of *L. rubidus* as a predator of *Pineus strobi*, the pine bark adelgid (Havill et al. 2012). *Laricobius osakinsis*, a beetle native to Japan, is the most recent predator to be released, beginning in

2012 (Havill et al. 2014). The efficacy of this species is still being determined but it has promising potential as it is native to the same location that the eastern U.S. HWA population originated from (Havill et al. 2006) and has thus evolved with the U.S. invader (Lamb et al. 2011). While predator beetle species have varied in their success at managing HWA populations, no species has completely eradicated HWA presence. Despite both chemical and biological control treatment efforts, hemlock decline is ongoing and up to 80% mortality can still occur in as few as six years (Ford et al. 2012) in portions of hemlock's southern range, depending on the magnitude and length of infestation prior to treatment.

Given the extent and decades-long duration of HWA infestation, understanding the impacts of invasion on forests, and especially riparian areas in the southern Appalachians, is necessary to prevent possible decline of species associated with hemlock presence. Considering the heightened sensitivity of riparian habitats in this region, areas with a high concentration of streams and rivers where HWA is present can serve as focal areas for research. Great Smoky Mountains National Park (hereinafter GSMNP), located on the border of Tennessee and North Carolina, U.S., is one such area that has received considerable research regarding the HWA invasion (L. C. Bryant personal observation). GSMNP officials first detected HWA in 2002 (Roberts et al. 2009) and, to limit the spread of the adelgid, implemented biological control using *S. tsugae* almost immediately and *L. nigrinus* in 2006 (Johnson et al. 2008). Imidacloprid applications were used by 2004 (Johnson et al. 2005). Management has been focused in designated conservation areas of high tourist traffic (e.g., select trails, campgrounds, and roadsides) but despite these efforts, HWA is currently found in all major park watersheds and, in some areas,

has caused complete hemlock mortality (Johnson et al. 2008). With over 2,000 miles of streams and rivers and over 19,000 total identified species (DLIA 2016), GSMNP (and especially its riparian habitats) face real threats from HWA infestation.

While research both within and outside the borders of GSMNP has focused on forest processes (Jenkins et al. 1999, Ford and Vose 2007, Nuckolls et al. 2009, Brantley et al. 2013, Vose et al. 2016) and community characteristics (Snyder et al. 2002, Huddleston 2011, Birt et al. 2014), we still lack information on consequences for specific species. For example, we do not know how all plant species will respond to changes brought about by hemlock decline and what ecosystem effects may follow. Research within GSMNP suggests that rosebay rhododendron (*Rhododendron maximum*), an evergreen understory shrub species, could mitigate hemlock decline-induced changes to thermal and hydrological regimes (Roberts et al. 2009). But it is not clear if this, or any other species, will maintain identical hemlock-associated conditions for the many organisms that occupy HWA-invaded habitats.

Avian species are among those organisms that may be affected by hemlock decline in the southern Appalachians. Most research regarding the effects of HWA-induced hemlock decline on avian species has focused on community level changes in diversity (Howe and Mossman 1995, Tingley et al. 2002, Ross et al. 2004, Becker et al. 2008, Brown and Weinkam 2014), while only a few studies have examined individual species' response to hemlock loss (see Stodola et al. 2013). One avian species possibly at risk is the Louisiana waterthrush (*Parquesia motacilla*; hereinafter waterthrush; Figure 1.3), a Nearctic-Neotropical migratory songbird and riparian-obligate species that breeds along headwater streams in the eastern U.S. (Mattsson et al. 2009) and is quite abundant in

GSMNP along both headwater streams as well as larger rivers (L. C. Bryant personal observation). Waterthrushes depend on aquatic and terrestrial habitats influenced by hemlock presence and condition in several ways. First, they defend linear territories that include both the stream and adjacent banks where hemlock presence is concentrated. Second, waterthrushes preferentially feed on aquatic macroinvertebrates of the orders Ephemeroptera, Plecoptera, and Trichoptera (Mattsson et al. 2009), which are associated with hemlock drained streams (Snyder et al. 2002), but also provision terrestrially dwelling lepidopterans to nestlings (Trevelline et al. 2016). Third, waterthrushes build nests in rock niches, root balls, and directly in stream banks where exposed hemlock roots can serve as nesting substrate. Hemlock decline may lead to changes in stream bank vegetation, aquatic and terrestrial invertebrate species abundance or diversity, or bank erosion, all of which could have consequences for waterthrushes.

Additionally, waterthrush has long been studied as a ‘bioindicator species’ (one that may represent overall ecosystem condition; Brooks et al. 1998) in response to habitat alteration and broad conservation issues throughout its breeding range. Brooks et al. (1998) identified waterthrush as a bioindicator in a Mid-Atlantic regional index of biological integrity, a method for quantifying ecological condition. Waterthrush fitness and habitat selection have been studied in relation to habitat fragmentation in the Georgia Piedmont (Mattsson and Cooper 2006), stream acidification in Pennsylvania (Mulvihill et al. 2008), aquatic pollution in Arkansas’ Buffalo River watershed (Marshall 2012), and hydraulic fracturing in the Fayetteville Shale region of Arkansas and Marcellus Shale region in Pennsylvania and West Virginia (Latta et al. 2015, Frantz et al. 2018). In each case, habitat alteration negatively impacted waterthrushes through changes in food

resources and reduced habitat quality. These previous studies strongly support that waterthrushes are sensitive to anthropogenic changes, but there is no information regarding how they have responded (or forecasts for how they will respond) to consequences of HWA invasion and resulting hemlock decline.

HWA invasion may impact waterthrushes in several ways, with both proximate effects on individuals as well as ultimate effects on the species as a whole. First, hemlock decline may affect their habitat selection behavior, which has both proximate and ultimate implications. The loss of hemlock may alter features or cues that waterthrushes typically use to make behavioral decisions about where to set up a territory, forage, or nest, and thus they may abandon areas that were occupied pre-HWA invasion.

Alternatively, as hemlocks die and habitat characteristics change, waterthrushes may alter their habitat selection decisions in response to the changing environment. Exactly how waterthrushes respond to HWA-induced habitat changes may be dependent on the behavior in question (e.g., foraging, nesting, mate attraction, or territory defense), particularly if these behaviors require different resources (Krausman 1999). Therefore, examining how hemlock decline affects multiple types of habitat selection and use is critical to a holistic understanding of the consequences of HWA infestation on waterthrushes. Second, HWA-driven hemlock decline may impact individual fitness (survival and/or reproductive success), which could have ultimate effects on the population in GSMNP. If habitat selection and use is adaptive, as is typically presumed (Martin 1998, Chalfoun and Schmidt 2012), preferred habitat characteristics should be positively related to fitness. However, when rapid environmental change alters habitat features, the ecological cues used to select habitat can become decoupled from fitness.

Individuals may select poor quality habitat over higher quality habitat, resulting in reduced fitness (i.e. an ecological trap; Schlaepfer et al. 2002). However, if hemlock decline to some degree is present throughout the majority of possible breeding areas in the southern Appalachians, waterthrushes may be forced to select altered habitat regardless of the fitness consequences. If so, habitat selection could differ across a continuum of hemlock decline as waterthrushes behaviorally respond to altered habitat features.

Third, HWA infestation could alter waterthrush habitat quality, which may have more proximate effects on individuals as habitat quality may fluctuate over time. One main cause of local and global population declines for many taxa is alteration of habitat, or the resources and conditions of an occupied area, through loss or degradation (Johnson 2007). One cause of habitat quality degradation is a change to the food resources of a habitat, which can be measured directly by measuring food resources themselves (Burke and Nol 1998, Atkinson et al. 2005), or more indirectly through behavior related to how individuals use their space (e.g., territory size [Ortega and Capen 1999], foraging [Lyons 2005, Tremblay et al. 2005], and nestling provisioning [Davis et al. 1999, van Oort et al. 2007]). Ultimately, these individual proximate effects of habitat degradation can scale up to negatively influence population demographics (Sherry and Holmes 1996). If hemlock decline reduces waterthrush habitat quality (i.e. food resources), the species could face negative consequences that require costly behavioral response. Waterthrushes may be forced to extend their territory length to compensate for reduced food resources, spend more time foraging and less time provisioning nestlings, or feed nestlings lower quality food. In total, understanding hemlock's role in waterthrush habitat selection and the

potential consequences of hemlock decline for waterthrushes will provide useful conservation and management guidance for not only this species, but possibly other species that rely on riparian habitats experiencing HWA invasion.

In the first chapter, I chose to focus on the ultimate effects hemlock decline may have on waterthrushes by evaluating how hemlock condition was related to habitat selection, apparent adult survival, and nest survival. If hemlock decline changes environmental cues waterthrushes select for, it could alter where waterthrushes forage or build their nests. If habitat features that once indicated quality foraging areas have become decoupled from actual food resources, individuals may be unable to find adequate food during the breeding season, which could impact them during other periods of the avian annual cycle (migration or overwintering) and lead to decreased adult survival. Similarly, adults may be forced to increase forage time, leaving nests unattended and susceptible to predator attacks, or habitat features that once indicated safe nest sites could have been altered by hemlock decline. Conversely, if waterthrushes behaviorally adjust to HWA-induced habitat changes, individuals may be able to select quality foraging areas and safe nest sites despite hemlock decline. In the second chapter, I chose to focus on the proximate effects of hemlock decline on waterthrush that could be indications of decreased habitat quality due to HWA infestation by evaluating relationships between hemlock condition and waterthrush territory length, nestling provisioning, and nestling body condition. If hemlock decline reduces habitat quality, waterthrushes may extend their territories to compensate for reduced food quality, impacting both nestling provisioning and body condition.

This study helps to clarify the role hemlock decline plays in waterthrush habitat selection and evaluate if the species' survival or habitat quality is at risk due to the HWA invasion. As a bioindicator species, waterthrush could serve as an overall indication of the risk other riparian species face due to hemlock decline. Additionally, because pre-hemlock mortality forest conditions are well-documented throughout hemlock's range, research can compare pre- and post-hemlock decline conditions and more clearly illustrate the ecological impacts of this foundation species. These data could help inform management practices in HWA-invaded areas and provide suggestions for future action to conserve the rich biodiversity of riparian areas in GSMNP and the southern Appalachian Mountains.

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## FIGURES



**Figure 1.1.** Evidence of hemlock woolly adelgid (*Adelges tsugae* Annand) on eastern hemlock (*Tsuga canadensis*) branches in Great Smoky Mountains National Park. Small white ‘woolly’ casings surround females during winter and house eggs before emergence.



**Figure 1.2.** Eastern hemlock (*Tsuga canadensis*) decline in Great Smoky Mountains National Park in the southern Appalachian Mountains. Hemlock mortality leads to the presence of ‘grey ghosts,’ the skeletal remains of dead hemlocks. Image used with permission by David Bryant.



**Figure 1.3.** Louisiana waterthrush (*Parkesia motacilla*) is a riparian-obligate songbird species that breeds along streams and river throughout the Appalachian Mountains. This banded individual, named Mr. Dorsey, was monitored throughout the 2015 breeding season in Great Smoky Mountains National Park.

**CHAPTER I: HEMLOCK WOOLLY ADELGID INVASION HAS MIXED  
ASSOCIATIONS WITH LOUISIANA WATERTHRUSH HABITAT SELECTION  
AND FITNESS**

This chapter has been formatted for submission in *Biological Invasions*. Reference citations in the text and listed references are in the format of the journal.

Bryant LC, Beachy TA, Boves TJ. **Hemlock woolly adelgid invasion has mixed associations with Louisiana waterthrush habitat selection and fitness**

**Author contributions:** T.A.B. initiated this study. L.C.B. and T.J.B. designed the study and secured funding. L.C.B. collected and analyzed data. L.C.B wrote the paper with guidance from T.J.B.

## ABSTRACT

Eastern hemlock (*Tsuga canadensis*) is declining throughout the eastern United States due to hemlock woolly adelgid (*Adelges tsugae* Annand) invasion. In the southern Appalachians, hemlocks are concentrated in moist ravines and decline threatens riparian ecosystems. Previous research on this invasion has focused on adelgid control and the effects of hemlock loss on macroinvertebrates, stream characteristics, vegetation composition, and forest processes. The majority of avian related research has examined changes in community diversity, and few studies have evaluated a single species' response to hemlock-decline-induced habitat changes. The Louisiana waterthrush (*Parkesia motacilla*) is an obligate riparian species that could be sensitive to hemlock condition in the southern Appalachians but how individuals respond to hemlock decline is currently unknown. Our research goal for this study was to determine the relationship(s) between hemlock decline and waterthrush habitat selection and vital rates in the southern Appalachians. Specifically, we identified the habitat features, including hemlock condition, associated with habitat selection and evaluated if these same habitat features were associated with apparent adult survival and nest survival. To do so, we captured, banded, and tracked individual birds; identified foraging locations; and monitored nests in territories that spanned a continuum of hemlock condition. Hemlock decline was unrelated to foraging habitat selection and adult survival but was related to nest site selection through an interaction with percent ground cover of exposed tree roots. Nest survival was lower in areas where deciduous species dominated the understory, suggesting that hemlock decline could indirectly impact waterthrush fitness dependent on riparian habitat succession subsequent to local hemlock loss. In total, our results indicate

that the short-term consequences of hemlock decline for this charismatic riparian species are likely complicated and dynamic and may be dependent on local habitat features and predator community response to hemlock decline.

## **INTRODUCTION**

Invasive species, introduced by human movement, environmental modification, and materials transportation, pose growing threats to ecosystem condition and biodiversity (Pimentel et al. 2005). In forests of the eastern United States (U.S.), a variety of invasive species have negative effects on ecosystems, many of which do so via direct impacts on tree species. Oaks (*Quercus* spp.), American beech (*Fagus grandifolia*), elms (*Ulmus* spp.), hemlocks (*Tsuga* spp.), fir (*Abies* spp.), and ashes (*Fraxinus* spp.) all have invasive pests that can cause mass mortality (Gandhi and Herms 2010). In some ecosystems, single tree species may be critical to establishing and maintaining specific environmental conditions (i.e. foundation species; Dayton 1972), thus their loss may affect a variety of ecosystem functions and characteristics, possibly resulting in decreased biodiversity and altered ecosystem processes and structure (Ellison et al. 2005). Because of the potential for such severe consequences, it is critical that we continue to assess the different ways by which invasive species may affect ecosystem condition and biodiversity, especially in cases involving foundation species.

One tree species currently impacted by an invasive insect pest is eastern hemlock (*Tsuga canadensis*). Hemlock is considered a foundation species throughout its range, especially in riparian habitats of the southern Appalachian Mountains where hemlocks comprise >50% of basal area (compared to only ~5% of basal area across the entire regional landscape; Brantley et al. 2013). As a result, these riparian areas have distinctive

terrestrial and aquatic characteristics that support a variety of organisms (e.g., birds, macroinvertebrates, and salamanders) dependent on hemlock condition (Ellison et al. 2005). Unfortunately, hemlocks in this region and across the eastern U.S. are dying from infestation by the hemlock woolly adelgid (*Adelges tsugae* Annand; hereinafter HWA). Introduced from Asia to Virginia in the 1950s, HWA is an aphid-like insect threatening extirpation of hemlock across half of its native range, affecting trees of all ages and sizes in over 18 states throughout the Appalachian Mountains (Ford and Vose 2007; Vose et al. 2013; Havill et al. 2014). HWA survival is limited by cold winters (Tobin et al. 2017) and the direct effect of HWA (i.e. hemlock mortality) has been greater in the southern Appalachians where, on average, milder winters do not suppress HWA populations (Nuckolls et al. 2009). Although increasingly hot summers negatively affect HWA and may help contain future populations (Mech et al. 2018), infestation in the southern Appalachians is still widespread. In response to mass hemlock mortality, and because of the potential ecological, aesthetic, and economic consequences, intensive management techniques including chemical and biological control have been implemented (Vose et al. 2013). Even when treated, up to 80% mortality can occur in as few as six years (Ford et al. 2012) in portions of hemlock's southern range depending on the magnitude and length of infestation prior to treatment; for instance, as of 2016, 90% mortality has occurred in the 17,000-ha Jocassee Gorges conservation area in South Carolina (Abella 2018).

It is now clear that mass hemlock mortality has direct effects on forest processes such as transpiration (Brantley et al. 2013), carbon cycling (Nuckolls et al. 2009), and riparian hydrological regimes (Ford and Vose 2007), as well as indirect effects on stream characteristics such as water temperature and pH, macroinvertebrate assemblages, and

vegetation composition (Snyder et al. 2002; Huddleston 2011). However, we still lack information on other indirect consequences to riparian areas. For example, we do not know how all plant species will respond to changes brought about by hemlock decline and what ecosystems effects may follow. Some research suggests that rosebay rhododendron (*Rhododendron maximum*), an evergreen understory shrub species, could mitigate hemlock decline-induced changes to thermal and hydrological regimes (Roberts et al. 2009). But it is not clear if this, or any other species, will provide similar or identical conditions for the many organisms that occupy HWA-infested habitats.

Avian species are among those organisms that may be affected, mostly indirectly, by hemlock decline in the southern Appalachians. Most research regarding the effects of HWA-induced hemlock decline on avian species has focused on community-level changes in diversity (Tingley et al. 2002; Ross et al. 2004; Becker et al. 2008), while only a few studies have examined individual species' response to hemlock loss (see Stodola et al. 2013). One avian species possibly at risk is the Louisiana waterthrush (*Parkesia motacilla*; hereinafter waterthrush), a Nearctic-Neotropical migratory songbird and riparian-obligate species that breeds along headwater streams in the eastern U.S. (Mattsson et al. 2009). Waterthrushes depend on aquatic and terrestrial habitats influenced by hemlock presence and condition and appear to be an excellent model species for studying the effects of HWA invasion for several reasons. First, they defend linear territories that include both the stream and adjacent banks where hemlock presence is concentrated. Second, waterthrushes preferentially feed on aquatic macroinvertebrates of the orders Ephemeroptera, Plecoptera, and Trichoptera (collectively EPT; Mattsson et al. 2009), which are associated with hemlock-drained streams (Snyder et al. 2002), but in

addition provision terrestrially dwelling lepidopterans to nestlings (Trevelline et al. 2016). Third, waterthrushes build nests in rock niches, root balls, and directly in stream banks where exposed hemlock roots can serve as nesting substrate. Hemlock decline may lead to changes in stream bank vegetation, aquatic and terrestrial invertebrate species abundance or diversity, or bank erosion, all of which could have consequences for waterthrushes. Finally, waterthrushes have long been considered sensitive to habitat and ecosystem alteration including habitat fragmentation in the Georgia Piedmont (Mattsson and Cooper 2006), stream acidification in Pennsylvania (Mulvihill et al. 2008), anthropogenic pollution in Arkansas's Buffalo River watershed (Marshall 2012), and hydraulic fracturing in the Fayetteville Shale region of Arkansas and Marcellus Shale region in Pennsylvania and West Virginia (Latta et al. 2015; Frantz et al. 2018).

These previous studies strongly support that waterthrushes are sensitive to anthropogenic changes, but there is little information regarding how they have responded (or forecasts for how they will respond) to consequences of HWA invasion. HWA invasion may indirectly impact waterthrushes in two different ways. First, hemlock decline may affect their habitat selection behavior. The loss of hemlock may alter features or cues that waterthrushes typically use to make behavioral decisions about where to set up a territory, forage, or nest, and thus they may abandon areas that were occupied pre-HWA invasion. Alternatively, as hemlocks die and habitat characteristics change, waterthrushes may alter their habitat selection decisions in response to the changing environment. Exactly how waterthrushes respond to HWA-induced habitat changes may be dependent on the behavior in question (e.g., foraging, nesting, mate attraction, or territory defense), particularly if these behaviors require different resources

(Krausman 1999). Therefore, examining how hemlock decline affects multiple types of habitat selection and use is critical to a holistic understanding of the consequences of HWA invasion. Secondly, HWA-driven hemlock decline may impact individual fitness (survival and/or reproductive success). If habitat selection and use is adaptive, as is typically presumed (Martin 1998; Chalfoun and Schmidt 2012), preferred habitat characteristics should be positively related to fitness. However, when rapid environmental change alters habitat features, the ecological cues used to select habitat can become decoupled from fitness. Individuals may select poor quality habitat over higher quality habitat, resulting in reduced fitness (i.e. an ecological trap; Schlaepfer et al. 2002). However, if hemlock decline, to some degree, is present throughout the majority of possible breeding areas in the southern Appalachians, waterthrush may be forced to select altered habitat regardless of the fitness consequences. In total, understanding hemlock's role in waterthrush habitat selection and the potential consequences of hemlock decline for waterthrushes will provide useful conservation and management guidance for not only this species, but possibly other species that rely on riparian habitats experiencing HWA invasion.

In this study, our over-arching goal was to assess the consequences of HWA-induced eastern hemlock decline on waterthrushes in the southern Appalachians. Specifically, we 1) determined how habitat features, particularly those related to hemlock condition, were selected for as foraging locations or nest sites, and 2) evaluated how those same habitat characteristics were associated with individual fitness (within-season and annual adult survival and reproductive success). We did this by studying waterthrush habitat selection and use and subsequent fitness in Great Smoky Mountains National Park, where HWA

treatment has been spatially and temporally targeted, resulting in habitats characterized by a continuum of hemlock condition in close proximity.

## **METHODS**

### **Study areas**

We conducted our study in the northwest region of Great Smoky Mountains National Park, U.S. (hereinafter GSMNP) during the 2015 and 2016 breeding seasons (March to July). HWA was first detected in GSMNP in 2002 (Roberts et al. 2009) and, in an attempt to manage infestation, park officials implemented biocontrol that year (Johnson et al. 2008) and chemical control by 2004 (Johnson et al. 2005). Despite these ongoing efforts, HWA is still present throughout all major watersheds of GSMNP and, in some areas, has caused complete hemlock mortality (Johnson et al. 2008). Study areas were in Tennessee along the Middle and West Prong of the Little River, Laurel Creek, and several smaller tributaries (Fig. 2.1). We selected these study areas based on the distribution of HWA control efforts in GSMNP; the most intensive efforts have occurred in designated conservation areas of high tourist activity, including campgrounds, trails, and roadsides (Johnson et al. 2008). Thus, we included some of these conservation areas as well as areas just outside these high tourist regions where control efforts have been non-existent. In total, our study area included potential waterthrush habitat characterized by hemlock condition spanning from relatively poor (high mortality and reduced hemlock condition) to relatively healthy (lower mortality and greater hemlock condition).

### **Field Methods**

#### *Banding and Resighting*

At the beginning of the breeding season (mid-March), we surveyed for waterthrush presence across our entire study area using territorial song playback. Once males were detected occupying a territory for  $\geq 5$  d, we used playback of territorial song and a mist net to capture individuals. All captured birds were banded with one U.S. Geological Survey-issued aluminum band and three plastic color bands in unique combinations for identification of individuals in the field without recapture. To estimate within-season apparent survival, we attempted to resight all banded individuals weekly from date of capture through the end of the breeding season (end of June) or until a nesting attempt was determined to be successful (i.e. fledged young), after which adults often follow juveniles outside of territory boundaries. To estimate annual apparent survival, we attempted to resight all banded birds captured during the previous year. It should be noted that we term this apparent survival because although individuals that were not resighted could have died between breeding seasons, they also could have dispersed from their previous breeding location to one outside of our study area (i.e. long-distance breeding dispersal).

### *Nest Searching and Monitoring*

Using adult behavioral cues (i.e. nest prospecting, nest building, provisioning, and fecal sac disposal) and systematic searches (once the possible nest site area had been narrowed down based on behavior), we located nests and monitored them every 3 d recording contents and activity. Beginning on the earliest possible fledge day (10 d post-hatch), we visited nests daily in an attempt to accurately assess nest fate; we considered any nest that fledged  $\geq 1$  young to be successful. If a fledging event was missed, we

searched the nest area for evidence of fledgling presence using adult behavioral cues (e.g., excessive chipping at, or repeated provisioning visits to, particular areas).

### *Tracking and Habitat Surveys*

To assess habitat selection for foraging locations within territories, we first visually tracked banded individuals every 3 to 5 d for  $\geq 20$  min and used Garmin<sup>®</sup> GPS units to record bird locations at 5-min intervals, collecting up to 5 points/d. We recorded locations until we documented fledglings or, for territories that never fledged young, until the last monitored nest across all territories either fledged or failed. We considered  $\geq 30$  points collected from  $\geq 6$  visits (average  $15.8 \pm 0.7$  visits/territory across both seasons) to each individual territory sufficient for assessing foraging habitat selection. Our territory mapping protocol was similar to previous studies of waterthrush habitat use (Hallworth et al. 2011, Frantz et al. 2018).

After tracking individuals and locating nests, we measured potentially important habitat features at nest sites, 2 high-use foraging areas (used locations), and paired random points (available locations). We defined high-use areas as those that included  $\geq 5$  points within 10-m of each other recorded on  $\geq 2$  different d. If  $> 2$  high-use areas were identified for an individual, we assigned each area a number and used a random number generator to select only 2 areas for surveys. We placed each used point at the approximate center of all locations associated with each high use area. To select paired random points (within the territory of each banded individual) for each high-use and nest site location, we first randomly chose a direction of the point: upstream (1) or downstream (2) of the approximate territory center or nest location (based on GPS locations). Second, because waterthrush territories average 470-m in length across their

range (Mattsson et al. 2009), a number between 0 and 235 was generated to determine the distance (from territory center) of the random point. Finally, a number between 1 and 3 was generated to determine if the point was to be located along the right bank (1), in-stream (2), or left bank (3); waterthrushes are known to regularly use all of these microhabitats when foraging (L. C. Bryant personal observation). To avoid survey area overlap, we did not include any random point  $\leq 25$ -m from used locations.

At each used and available point, we measured habitat features chosen a priori based on: 1) relevance to waterthrush habitat selection according to previous literature (Latta 2009; Mattsson 2009; Marshall 2012), and 2) the feature's potential to be impacted by hemlock decline (informed by Huddleston 2011; Ford et al. 2012; Ellison et al. 2016) or mediate the effects of hemlock condition on waterthrushes. We assessed hemlock condition following standardized USDA Forest Service protocols (Schomaker et al. 2007). Within a 25-m radius, the 10 closest hemlock trees to point center were measured for diameter at breast height and assessed on 4 condition criteria (percent of: live crown ratio, crown density, crown transparency, and branch dieback) then categorized into a vigor class (1 = healthy, 2 = light decline, 3 = moderate decline, 4 = severe decline, 5 = complete decline but still standing, 6 = complete decline and fallen) based on the percentage criteria. We then used vigor class to define a new variable for analysis, entitled 'state of hemlock decline,' to better illustrate the continuum of hemlock condition. This continuous variable was calculated by dividing the average vigor value (to nearest 0.1) of each survey point by 6 (total number of vigor classes), resulting in values close to 0.0 (representing a state of low decline and healthier hemlock condition) to values close to 1.0 (representing a state of high decline and poorer hemlock condition).

Because the impact of hemlock decline could depend on the amount of hemlock in a given area, we estimated proportion of hemlock by counting the number of hemlock trees and dividing by the total number of trees of all species within an 11.3-m radius of point center. Within a 5-m radius, we visually estimated percent ground cover of 8 different substrates (exposed in-stream rock, exposed soil, leaf litter, woody debris, water, deciduous ground vegetation, evergreen ground vegetation, and exposed tree roots); stream width (m); dominant (>50%) understory vegetation type (evergreen or deciduous); and canopy cover presence/absence within vertical strata of 0-1.5 m, 1.5-5 m, 5-15 m, and > 15-m (measured at point center and paired points on survey edge parallel and perpendicular to stream flow). Hemlock condition surveys were conducted between November and January following each field season when deciduous leaves did not obscure views of hemlock crown characteristics and other habitat features were measured at the end of the breeding season (late June-July) by trained field technicians and citizen science volunteers.

## **Data Analysis**

### *Habitat Selection*

We built and compared generalized linear mixed models (GLMMs) and used an information theoretic framework (Burnham and Anderson 2002) to evaluate how hemlock condition, or other habitat variables, was related to within-territory habitat selection in 1) high-use foraging areas and 2) nest sites. For both analyses, we used a binomial response of ‘used’ or ‘available.’ Prior to model building, we tested all variables (total of 16) for collinearity by conducting pairwise correlational tests; no variables were highly correlated (all  $r < 0.6$ ). For all GLMMs, we included random effects of survey ID

(to pair used surveys with their available surveys) and bird ID (to reduce pseudo-replication as some individuals were present during both breeding seasons). We compared models based on Akaike's information criterion corrected for small sample size ( $AIC_c$ ); we considered all models with  $\Delta AIC_c \leq 2$  to have equivalent support, but when comparing two models that differed by the same single variable and  $\Delta AIC \leq 2$ , we only included the simplified model in our final list (following the principle of parsimony). Because habitat selection may vary between years, we first compared a temporal model with a fixed effect of year to a null model (intercept only). If our temporal model had greater support than the null, we considered the temporal model our baseline null (and included year as a fixed effect in all other models). We then built and compared univariate models consisting of each habitat variable as well as additive multivariate models that consisted of all combinations of variables from equivalent univariate models. We then built an interactive model with state of hemlock decline and variables in our best-supported model to evaluate whether hemlock decline interacted with the habitat features to further impact habitat selection. After compiling our list of equivalent top models, we assessed importance of variables included in each model by examining the 85% CIs of the  $\beta$  coefficients (Arnold 2010); variables with CIs that did not overlap zero were considered meaningful.

### *Nest Survival*

We built and compared models of nest survival and used an information theoretic framework to evaluate how hemlock condition, or any other habitat variables, was related to daily nest survival (DSR). For our analysis, we only included nests that failed due to depredation. Prior to model building, we tested all habitat variables (total of 16) for

collinearity using pairwise correlation tests; due to high correlations ( $r > 0.6$ ), we excluded percent ground cover of deciduous vegetation from further analysis. Because nest survival can vary between years, we first compared models consisting of univariate and bivariate temporal factors (year and clutch initiation ordinal date) to a null model (constant survival). If one of our temporal models had greater support than the null, we considered that temporal model our null (and included temporal variables in all other models). Next, we built and compared univariate models with all habitat variables as well as additive multivariate models that consisted of all combinations of variables from equivalent univariate models. Again, we compared models based on  $AIC_c$  and the principle of parsimony. We then built an interactive model with state of hemlock decline and variables in our best-supported model to evaluate whether hemlock decline interacted with the habitat features to further impact nest survival. After compiling our list of equivalent top models, we assessed importance of variables in each model by examining the 95% CIs of the  $\beta$  coefficients; variables with CIs that did not overlap zero were considered meaningful. Finally, we calculated entire nesting period survival by raising DSR in our best-supported model to 26, the average number of days required for a successful waterthrush nest in our study.

#### *Apparent Adult Survival*

As with our habitat selection analyses, we built and compared GLMMs using an information theoretic framework to evaluate how hemlock condition, or any other habitat variables, was related to apparent annual survival (using a binomial response of ‘return’ or ‘no return’). Prior to model building, we tested all variables (total of 16) for collinearity; no variables were highly correlated (all  $r < 0.6$ ). For all GLMMs we included

a random effect of bird ID (to reduce pseudo-replication as some individuals were present multiple years). All models were compared based on  $AIC_c$  and the principle of parsimony. Because survival may vary among years, we first compared a temporal model with a fixed effect of year to a null model (intercept only). If our temporal model had greater support than the null, we considered the temporal our baseline null model (and included year as a fixed affect in all other models). We then built and compared univariate models with each habitat variable, as well as additive multivariate models that consisted of all combinations of variables from equivalent univariate models, and an interactive model with hemlock decline and habitat variables in our best-supported model. After we compiled our list of equivalent top models, we assessed importance of variables in each model by examining the 85% CIs of  $\beta$  coefficients.

Habitat selection and apparent adult survival analyses were conducted in R 3.3.2 (R Core Team 2016) using the packages ‘lme4’ (Bates et al. 2015) and ‘AICcmodavg’ (Mazerolle 2016). Nest survival analysis was conducted in Program MARK v8.0 (White and Burnham 1999). For all analyses, we evaluated whether we met assumptions of a linear model by visually examining residuals from the best-supported models. All  $\beta$  coefficients and means are reported  $\pm 1$  SE with CIs in brackets.

## **RESULTS**

### **Habitat Selection**

We built and compared 25 GLMMs of foraging area selection (184 surveys; 92 used, 92 available) and 19 GLMMs of nest site selection (148 surveys; 74 used nest sites, 74 available). With respect to both foraging area and nest site, our temporal model was not supported more than the null (foraging:  $\Delta AIC = 2.09$ ; nest:  $\Delta AIC = 2.11$ ); therefore, year

was not included in further model building. For foraging area, none of the top models included variables directly related to hemlock condition. The best-supported model ( $\Delta\text{AIC}$  from null = 6.58 with no equivalent models) included habitat variables of percent ground cover of woody debris plus in-stream exposed rock (woody debris:  $\beta = 7.21 \pm 2.89$ , 85% CI [3.04, 11.38]; in-stream exposed rock:  $\beta = 3.15 \pm 1.29$ , 85% CI [1.29, 5.01]). For nest site selection, the best-supported model ( $\Delta\text{AIC}$  from null = 34.99 with no equivalent models) included percent ground cover of exposed tree roots, state of hemlock decline, and an interaction between these two variables (interaction  $\beta = 1.52 \pm 0.68$ , 85% CI [0.53, 2.51]).

### **Nest Survival**

We built and compared 20 models to analyze survival of 65 nests during the 2015 ( $n = 28$ ) and 2016 ( $n = 37$ ) breeding seasons. Based on the condition of failed nests, the majority of failures were likely a result of snake depredation ( $n = 22$ ; 69%), followed by mammals ( $n = 9$ ; 28%), and disease ( $n = 1$ ; 3%); the latter was a result of botfly infestation and was excluded from our analysis. Our univariate temporal models were not more supported than the null, therefore temporal variables were not included in further model building. None of the top models included variables directly related to hemlock decline. The best-supported model ( $\Delta\text{AIC}$  from null = 2.38 with no equivalent models) included dominant understory vegetation type ( $\beta = -0.78 \pm 0.37$ , CI [-1.49, -0.06]; Fig. 2.2). Nests with an evergreen-dominated understory ( $n = 45$ ) had a DSR of  $0.98 \pm 0.01$  (equivalent to 57% annual survival) compared to nests with a deciduous-dominated understory ( $n = 20$ ), which had a DSR of  $0.96 \pm 0.01$  (equivalent to 30% annual survival).

### **Apparent Adult Survival**

We built and compared 18 models of apparent adult survival of 34 individual male waterthrushes during the 2015 and 2016 breeding seasons. Of 22 males followed during 2015, all survived the entire breeding season (from first detection to last monitored nest fate: March 21 to June 19), and 12 returned in 2016 (55% return rate). Average state of hemlock decline across territories in the 2015 breeding season was  $0.66 \pm 0.03$  (range 0.17–0.90), indicating hemlocks were generally in a state of moderate to severe decline. Of 24 males followed during 2016, 23 survived the entire breeding season (from first detection to last monitored nest fate: March 20 to June 27); the sole mortality was from a vehicular collision (individual confirmed by band combination and number). Of the 23 males that survived the 2016 breeding season, 15 returned in 2017 (65% return rate). Average state of hemlock decline across territories in the 2016 breeding season was  $0.71 \pm 0.01$  (range 0.50–0.90), indicating hemlocks were generally in a state of severe decline. Our temporal model was not supported more than the null; therefore, year was not included in further model building. The null (intercept only) was the top model, indicating neither hemlock decline nor any measured habitat variables were related to apparent annual survival. As survival (and detectability) within the breeding season was nearly 100% during both years, we did not conduct an analysis of relationships between habitat variables and within-season survival.

## **DISCUSSION**

Invasive species may outcompete native species for resources, alter ecosystem functions, and disrupt ecosystem processes (Pimentel et al. 2005). HWA, an invasive insect causing widespread mortality of eastern hemlock, poses a threat to species dependent on the unique habitat conditions hemlocks establish. As a riparian specialist,

waterthrushes may be expected to be impacted by hemlock decline. However, we found that hemlock condition was unrelated to waterthrush foraging habitat selection or adult survival, but was related to nest site selection through an interaction with another habitat variable (exposed tree roots) and had an indirect effect on nest success through the type of dominant understory (deciduous or evergreen). Our results highlight the complexity of biological invasions and the need to study multiple types of habitat use in order to best inform invasive species management.

Hemlock condition was unrelated to waterthrush habitat selection for foraging locations, which could be explained in several ways. First, it is possible that waterthrushes are less reliant on prey that is negatively impacted by hemlock mortality than previous studies have suggested. Hemlock-drained streams are often associated with a unique community of aquatic macroinvertebrates including mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera; collectively EPT) that could be negatively impacted by hemlock loss via HWA infestation (Snyder et al. 2002). The proportion of biomass in these orders (%EPT) has been found to be positively associated with waterthrush presence (Stucker 2000; Mattsson and Cooper 2006; Mulvihill et al. 2008; Marshall 2012) and has thus led to the assumption that waterthrushes preferentially feed on these orders, especially Ephemeropterans (Mulvihill et al. 2008). However, only one study has examined adult waterthrush stomach contents (Eaton 1958) and of the 15 birds examined, ephemeropterans and plecopterans were only identified in one single individual and trichopterans were only found in two individuals. This lack of EPT prey items could have been due to availability or could indicate waterthrushes are more generalist foragers than assumed. Additionally, other research has found that

waterthrushes provision prey such as salamander larvae (Mulvihill et al. 2008) and terrestrial arthropods (Trevelline et al. 2016) to nestlings, further supporting the generalist perspective and suggesting that waterthrushes may be able to adjust to changing prey availability (i.e. %EPT) due to hemlock decline. Future studies should continue monitoring foraging habitat selection and assess adult waterthrush foraging behavior at a finer scale (i.e. diet composition) to determine prey preference in riparian areas with varying states of hemlock decline.

If waterthrushes do preferentially feed on EPT, a second potential explanation for our results is that declining hemlock condition in our study area had yet to negatively impact the presence of these orders as expected. Huddleston (2011) found that declines in EPT in streams impacted by HWA infestation occurred in hemlock dominant stands in eastern portions of GSMNP; however, this relationship was driven largely by a decline in Ephemeroptera alone as these streams actually harbored higher densities of Plecoptera and Tricoptera compared to unimpacted streams (Huddleston 2011). In contrast, Che (2011) found the opposite: ephemeropterans increased after HWA-induced hemlock decline while plecopterans, tricopterans, and overall %EPT declined (though it should be noted that the streams in this study were not in hemlock-dominant stands). Despite these contrasting results, both provide case studies of how at least some EPT could be maintained following HWA infestation and hemlock decline. Because the effect of hemlock decline on riparian habitats is context dependent and likely dynamic, the impact on aquatic macroinvertebrates may depend on a variety of local conditions (e.g., hemlock dominance and successional stage, which could subsequently affect water temperature, pH, and nutrient load; Snyder et al. 2002). Future studies should continue assessing

aquatic and terrestrial macroinvertebrate assemblages to evaluate potential waterthrush prey availability and abundance in riparian areas across a continuum of hemlock condition, and to assess the possibility of time-lag effects of hemlock decline on prey (and subsequently waterthrushes).

A third possible explanation for our results is that habitat selection related to hemlock condition could have occurred at a broader scale (e.g., territory, or second-order, selection; Johnson 1980); however, we did not assess territorial selection patterns and were unable to detect this behavioral pattern. Waterthrushes are known to alter territory selection following anthropogenic alterations such as stream acidification; birds that breed on acidified streams do not return to those streams the following year and those territory vacancies are then filled by younger individuals (Mulvihill et al. 2008). If habitat selection related to hemlock decline occurred similarly (at a broader scale), we would have expected to observe lower site fidelity (or younger birds replacing older birds) in response to hemlock decline; however, this was not the case. We observed relatively high return rates and site fidelity; all banded birds that returned came back to the previous year's breeding territory (with only minor expansions or contractions at territory boundaries) despite a wide range of hemlock conditions.

Although hemlock condition was not related to foraging habitat selection, our best-supported model results were consistent with previous studies of waterthrush foraging ecology, particularly related to exposed rocks and woody debris. Waterthrushes are known to feed on macroinvertebrates (Mattsson et al. 2009), which colonize in-stream rock substrate (Pitt and Batzer 2011), so it would be expected that waterthrushes would seek out foraging locations with more exposed rocks to maneuver across and forage on.

Woody debris piles composed of sticks, logs, and packed leaves also provide food and substrate for aquatic macroinvertebrates (Pitt and Batzer 2015), and waterthrushes will flip over leaves and small woody debris in search of macroinvertebrate prey (Marshall 2012). We found a weak but significant correlation between hemlock decline and woody debris ( $r = 0.35$ ,  $P < 0.001$ ), suggesting that decline may increase preferred waterthrush foraging locations. However, heavy flooding can relocate woody debris piles so any relationship with hemlock decline and waterthrush foraging area selection depends on temporally and spatially fluctuating factors.

Contrary to habitat selection for foraging locations, hemlock condition was related to nest site selection, however, only through an interaction with ground cover of exposed tree roots. In general, waterthrush in our study avoided nesting in areas with more exposed tree roots, but when nesting in areas with greater hemlock decline ( $\geq 0.55$  state of decline), they preferred nesting in sites surrounded by more exposed roots (Fig. 2.3). This relationship may ultimately be explained by the potential effects of hemlock mortality on nest predators, especially ectotherms like snakes. Predation is typically considered the main cause of reproductive failure in small songbirds (Martin 1993; Thompson 2007), and snakes in particular are some of the most frequent nest predators (DeGregorio et al. 2016). Although identifying predators based on nest remains has limitations (Larivière 1999), we have reason to suspect snakes were the likely principal nest predator in our study area based on the undisturbed condition of most our failed nests (Robinson et al. 2005) and video evidence of attempted nest depredation by a juvenile black rat snake (Bryant and Boves in press). As hemlock mortality decreases canopy cover, it allows more sunlight to penetrate to the forest floor (Orwig and Foster 1998; Eschtruth et al.

2006), which may increase localized ground temperatures. Warmer temperatures typically increase movement of ectotherms like snakes (Cox et al. 2013; DeGregorio et al. 2015), confirmed potential waterthrush nest predators (Bryant and Boves in press). Thus, in areas where hemlock decline is severe, birds that select for more exposed roots near a nest may present predators like snakes with more false nest sites to search, which could be an advantage, particularly if predator activity has also increased in these areas. In areas with healthier hemlock, snake presence or activity may not have increased (due to maintained canopy cover) so building a nest among more exposed roots would not be as beneficial of a strategy to protect against nest predation. Additionally, there may be costs associated with nesting among exposed roots, such as increased erosion or less preferred nest microhabitat conditions, which could affect offspring (Shine et al. 1997). The fact that waterthrushes did not always select for more exposed roots in areas with greater hemlock decline highlights the complexity of the interaction and possible influence of nest microhabitat on nest site selection (Hartman and Oring 2003). Expanded nest monitoring would be useful to evaluate whether this interaction was incidental or if it is consistent across a wider range of areas and hemlock conditions, and to investigate how ground temperature and snake behavior changes in response to hemlock mortality. In total, our habitat selection results emphasize the importance of studying multiple types of habitat selection to fully understand the consequences of biological invasions (or other anthropogenic impacts). If only one type of habitat selection is accounted for, the complexity of how organisms like waterthrushes select habitat would be missed and future research or management suggestions might be misinformed.

Although hemlock condition appeared to be directly related to nest site selection, this same relationship did not extend to patterns of nest survival (as one might expect). Instead, our results suggest that hemlock mortality indirectly affected waterthrush nest survival and was dependent on ecological context and succession; nest survival was greatest in areas with evergreen-dominated understories and lower in areas with deciduous-dominated understories. This result is related to hemlock mortality because as hemlocks die off, succession can proceed in several different ways. If the local understory was already dominated by evergreen species (i.e. rhododendron and dog hobble [*Leucothoe fontanesiana*]), those species tend to outcompete others by rapidly taking advantage of new canopy gaps (Ford et al. 2012; Roberts et al. 2009; Abella 2018). However, if the understory was a mix of deciduous species (e.g., *Acer* spp., *Betula* spp., *Carya* spp., *Fagus* spp., *Quercus* spp., *Liriodendron tulipifera*), succession tends to be more diverse and favors these species (Small et al. 2005; Brantley et al. 2013). Thus, in the future, hemlock-dominated riparian areas with previously established rhododendron and dog hobble in the understory could still maintain nesting habitat quality despite declines in hemlock condition. Future studies should continue monitoring waterthrush nests in HWA-infested areas with evergreen-dominated and deciduous-dominated understories to better understand the importance of long-term riparian habitat succession to waterthrush reproduction.

Similar to our foraging habitat selection results, we found no relationship between hemlock condition and apparent adult survival (within and across seasons). We observed return rates (or apparent survival) for waterthrushes consistent with, and slightly higher than, other estimates from across their range (DeSante et al. 2015) and found no evidence

of negative carry-over effects related to hemlock decline. In addition, site fidelity was high for birds that returned; they all settled on (or very near) their previous year's territory regardless of hemlock condition, suggesting that they were largely unaffected by hemlock condition from the previous breeding season. Thus, it appears that in the short-term, hemlock decline is not likely to directly affect waterthrush survival but could eventually lead to decreased recruitment or breeding site fidelity if hemlock mortality consistently decreases nest survival through post-invasion forest succession. To address this possibility, future studies should continue to monitor return rates and recruitment, and expand search areas to include more streams and tributaries at different stages of succession.

Hemlock decline via HWA invasion in the southern Appalachians has, and will continue to, alter the region's ecosystems in many ways (Abella 2014; Preisser et al. 2014). However, in total, our results suggest that in the short-term, waterthrushes are better able to respond to HWA-induced changes than previously assumed, which is positive news for the species as it is clear eastern hemlock trees are unlikely to survive in large numbers in the southern Appalachians (Snyder et al. 2002). Waterthrushes face many other anthropogenic-induced issues throughout their range (e.g., stream acidification, habitat fragmentation, aquatic pollution, and shale gas development) and our results support conservation strategies that focus more on these other threats. However, it should be noted that dynamism and potentially complex interactions with other changing habitat features (e.g., understory species and predator presence/activity) warrant further monitoring of waterthrush in HWA-invaded regions. As succession proceeds, it will be interesting and potentially of conservation importance to document

how riparian species, including waterthrushes, and communities continue to respond to HWA invasion and the subsequent large-scale (and long-term) ecosystem changes.

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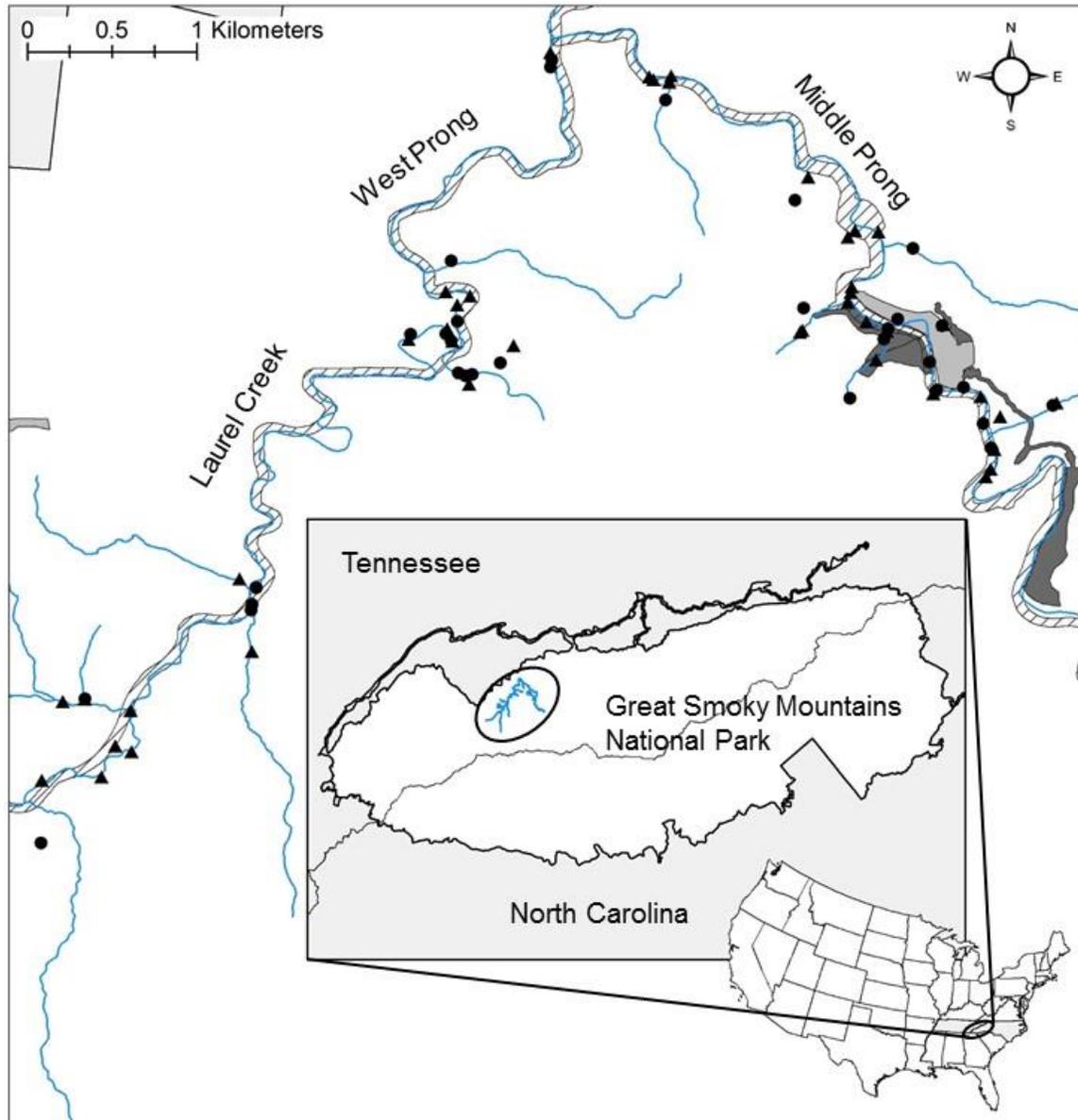
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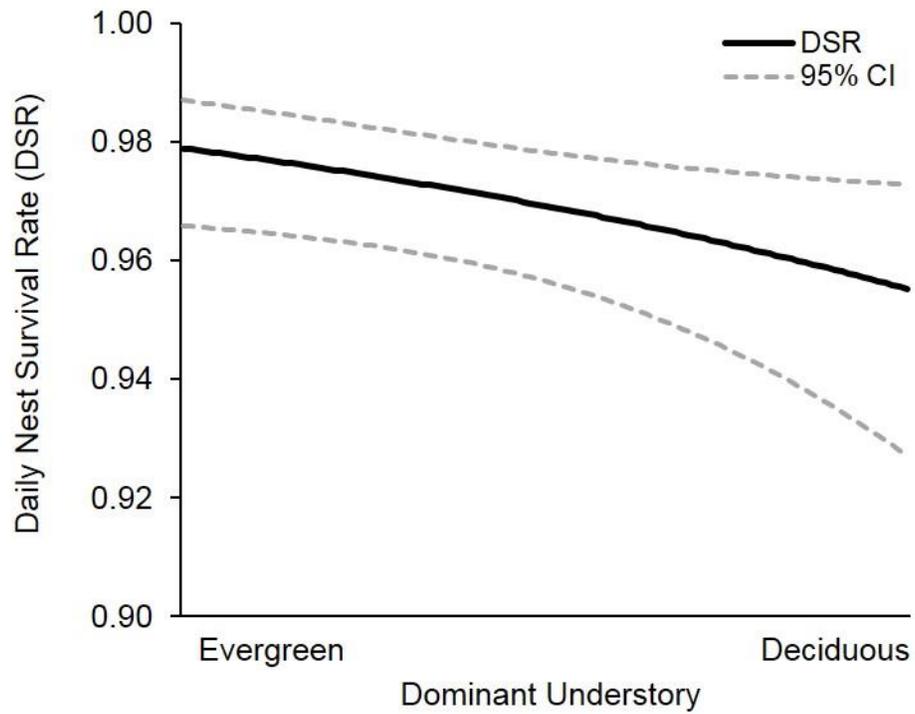
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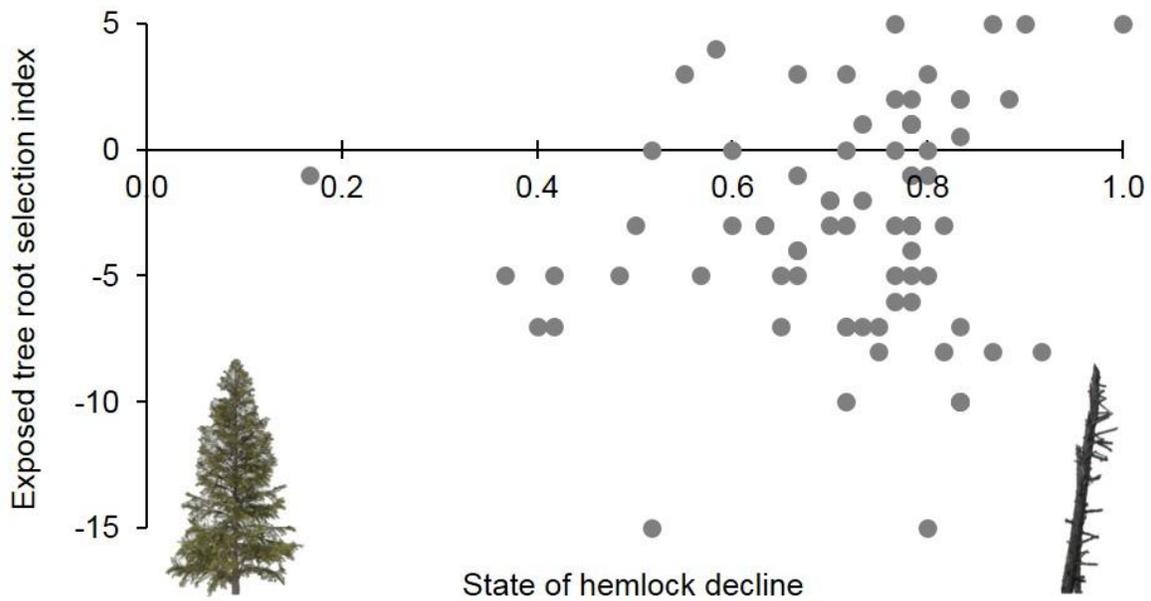
## FIGURES



**Figure 2.1.** Location of study area and Louisiana waterthrush (*Parkesia motacilla*) nests in Great Smoky Mountains National Park during the 2015–16 breeding seasons. Circles represent 2015 season nests ( $n = 32$ ) and triangles represent 2016 season nests ( $n = 42$ ). Shading indicates conservation areas where hemlock woolly adelgid treatment occurred (road side buffers are striped; trails are dark grey; campground and day-use areas are medium grey).



**Figure 2.2.** Louisiana waterthrush (*Parkesia motacilla*) daily nest survival in Great Smoky Mountains National Park during 2015-16 was related to the understory dominance on a continuum from mostly evergreen to mostly deciduous ( $\beta = -0.78 \pm 0.37$ , CI [-1.49, -0.06]).



**Figure 2.3.** Louisiana waterthrush (*Parkesia motacilla*) selected for nest sites with greater exposed tree root ground cover only when hemlock condition was relatively poor ( $\geq 0.55$  state of decline). Values associated with the y-axis were calculated as the difference in exposed tree root ground cover between a nest site and its available random nest site (tree root selection). Positive values indicate tree roots were selected for, whereas negative values indicate tree roots were selected against. Values associated with the x-axis reflect the state of hemlock decline at nest sites; values close to 0 indicate low decline (higher hemlock condition) and values close to 1 indicate high decline (poorer hemlock condition; see methods for calculation).

**CHAPTER II: DOES HEMLOCK DECLINE HAVE PROXIMATE EFFECTS ON  
LOUISIANA WATERTHRUSH IN GREAT SMOKY MOUNTAINS NATIONAL  
PARK?**

This chapter is formatted for submission to *The Condor*. Reference citations in the text and listed references are in the format of the journal.

L. C. Bryant, T. A. Beachy, and T.J. Boves. **Does hemlock decline have proximate effects on Louisiana Waterthrush in Great Smoky Mountains National Park?**

**Author contributions:** T.A.B. initiated this study. L.C.B. and T.J.B. designed the study and secured funding. L.C.B. collected and analyzed data. L.C.B wrote the paper with guidance from T.J.B.

## ABSTRACT

Eastern Hemlock (*Tsuga canadensis*) is declining throughout the eastern United States due to the invasive Hemlock Woolly Adelgid (*Adelges tsugae* Annand). In the southern Appalachians, hemlock is concentrated in moist ravines and its loss may threaten riparian habitat quality. With respect to birds, most research has examined changes in community diversity, but few studies have evaluated the consequences of hemlock decline for individual species. The Louisiana Waterthrush (*Parkesia motacilla*) is an obligate riparian species that could be sensitive to hemlock condition and resulting habitat alteration in the southern Appalachians. Waterthrushes increase territory length and forage on alternative prey items in response to reduced habitat quality due to stream acidification, aquatic pollution, and shale gas development, but how the species is impacted by, and responds to, hemlock decline is currently unknown. To address this issue, we evaluated how hemlock condition was associated with waterthrush territory length, nestling provisioning, and nestling body condition. Hemlock condition was not related to territory length, nor were any other habitat features. Additionally, hemlock condition was not directly related to provisioning rate or nestling body condition, but could be indirectly related through changes to forest features. Provisioning rate was positively related to mid-story forest cover and the proportion of hemlock was positively related to nestling body condition, suggesting that riparian forest succession after hemlock mortality could impact waterthrush nestlings. In total, our results suggest that the short-term impacts of hemlock decline on waterthrushes seem minimal and do not indicate a reduction in habitat quality; however, time-lag effects of habitat alteration

caused by continued hemlock mortality could have consequences for waterthrushes in the future.

## **INTRODUCTION**

One of the main causes of local and global population declines for many taxa is alteration of habitat, or the resources and conditions of an occupied area, through loss or degradation (Johnson 2007). Thus understanding how habitat alteration impacts the limiting resources of a habitat is important to prevent population declines and possible species extinction. One proximate cause of habitat quality degradation is a change to the food resources of a habitat. The potential reduction of habitat quality following some anthropogenic perturbation can be measured directly, by measuring food resources themselves (Burke and Nol 1998, Atkinson et al. 2005), or more indirectly through behavior related to how individuals use their space (e.g., territory size [Ortega and Capen 1999], foraging [Lyons 2005, Tremblay et al. 2005], and provisioning [Davis et al. 1999, van Oort et al. 2007]). Ultimately these individual proximate effects of habitat degradation can scale up to negatively influence population demographics (Sherry and Holmes 1996). Thus, evaluating the consequences for birds using altered habitats (e.g., effects on food resources) can help identify habitat features necessary for survival and inform future management to best conserve populations using these altered habitats.

Although many causes of habitat degradation exist (Wilcove et al. 1998), one possible cause of reduced habitat quality via food resources is the introduction of a non-native invasive species. Such introductions are occurring at ever-increasing rates and pose unpredictable, and often delayed, threats to native species (Simberloff et al. 2013). A current example of an invasive species potentially facilitating habitat degradation is the

introduction of the Hemlock Woolly Adelgid (*Adelges tsugae* Annand; hereinafter HWA) to the eastern United States (U.S.). First detected in Virginia in 1951, HWA infests Eastern Hemlock (*Tsuga canadensis*), which is often considered a ‘foundation species’ because its presence establishes unique habitat conditions that a variety of organisms (e.g., macroinvertebrates, fish, birds, and amphibians) depend on for survival (Ellison et al. 2005). By 2013, HWA had spread to roughly half of hemlock’s native range causing widespread hemlock mortality (Vose et al. 2013). This process alters habitat through changes to forest vegetation structure and composition (Huddleston 2011), hydrologic processes (Ford and Vose 2007), stream ecosystem conditions (Webster et al. 2012), and nutrient cycling (Nuckolls et al. 2009). In the southern Appalachians specifically, riparian habitats experience the greatest alteration from HWA invasion because hemlock is concentrated along streams and in moist ravines (Brantley et al. 2013). Thus, organisms that rely on streams, particularly riparian specialists, are threatened by HWA-induced habitat alteration that could negatively impact habitat quality. Understanding the extent to which HWA-induced hemlock decline affects the quality of riparian habitat and associated organisms in the southern Appalachians is necessary for future conservation and management of HWA infested streams and forests.

Louisiana Waterthrush (*Parkesia motacilla*; hereinafter waterthrush) is an avian riparian-obligate species that could be threatened by HWA infestation and resulting habitat alteration. Waterthrush has been studied as a so-called ‘bioindicator’ (i.e. a species that may represent the overall condition and integrity of its habitat; Brooks et al. 1998) of riparian habitat conditions throughout its breeding range in the eastern U.S. (Mattsson and Cooper 2006, Mulvihill et al. 2008, Marshall 2012, Latta et al. 2015,

Frantz et al. 2018) and serves as a model species for several reasons. First, waterthrushes establish linear territories following riparian corridors and use areas within the stream and along its banks (Mattsson et al. 2009). Thus, individuals are subject to both riparian and terrestrial habitat alteration due to hemlock mortality. Second, waterthrushes primarily forage on aquatic macroinvertebrates (Mattsson et al. 2009), especially species in the orders Ephemeroptera, Plecoptera, and Tricoptera (collectively referred to as EPT) that are associated with hemlock-drained streams (Snyder et al. 2002). As HWA infestation decreases hemlock presence, changes to waterthrush prey could have negative effects on individuals and populations living in this region. Studying waterthrushes in areas of the southern Appalachians experiencing hemlock decline could then provide a clearer understanding of the species' vulnerability and potentially illustrate the larger impact of HWA-induced habitat alteration on other riparian organisms.

Altered habitat due to hemlock mortality (and the possible resulting changes to food resources) could impact waterthrushes in several proximate ways. First, habitat alteration may affect waterthrush territory size. Previous research indicates larger territory size is associated with poorer quality habitat due to stream acidification (Mulvihill et al. 2008) and aquatic nutrient pollution (Marshall 2012). Both studies found that altered habitat has a reduced presence of EPT (preferred waterthrush prey) and conclude that reduced habitat quality due to alteration negatively impacts waterthrush food resources and, in response, individuals in altered habitats increase their territory size. Increased territory size can have further effects on territory defense (Ewald et al. 1980), time spent foraging (O'Halloran et al. 1990), and individual fitness (Both and Visser 2000). If HWA infestation reduces habitat quality via food resources in the southern Appalachians,

waterthrushes in areas with greater hemlock decline may compensate by defending larger territories than birds in areas with lesser decline.

A second, and possibly related, potential impact of HWA-induced habitat alteration on waterthrushes concerns nestling provisioning and/or body condition. If HWA infestation reduces food resources, adult waterthrushes may be forced to change nestling provisioning strategies in one of several ways. Provisioning rates could be higher in lower quality habitat as adults increase provisioning to compensate for lower quality food (van Oort et al. 2007). Conversely, rates could be lower in lower quality habitat if adults must travel further or increase time spent foraging to find higher quality food (Catry et al. 2013). Either strategy could then affect nestling body condition (Hollander et al. 2011). While several other species' provisioning rates have been assessed in relation to habitat characteristics or alteration (Tremblay et al. 2005, Hinam and St. Clair 2008, Wilkin et al. 2009, Lee et al. 2011), waterthrush has yet to be included.

The main goal of this study was to assess the proximate relationship between HWA-induced habitat alteration and waterthrushes in the southern Appalachians. To do so, we evaluated relationships among habitat characteristics related to hemlock condition and waterthrush territory size, nestling provisioning rates, and nestling body condition. Understanding the mechanisms by which hemlock decline may proximately impact waterthrushes will help evaluate the degree to which the species could be threatened by hemlock decline and what future conservation efforts may be required for waterthrush, as well as other riparian species, in HWA-infested habitats.

## **METHODS**

### **Study Area**

We conducted our research in the northwest portion of Great Smoky Mountains National Park (GSMNP), U.S., on the border of Tennessee and North Carolina, during the 2015 and 2016 breeding seasons (March to July). Study areas were located in Tennessee along the Middle Prong and West Prong of the Little River, Laurel Creek, and several smaller tributaries (Fig. 3.1). Park officials first detected HWA in 2002 (Roberts et al. 2009) and, to limit the spread of the adelgid, implemented biological control through the release of predatory beetles *Sasajiscymnus tsugae* almost immediately and *Laricobius nigrinus* in 2006 (Johnson et al. 2008) and chemical control by 2004 (Johnson et al. 2005). Management was focused on designated conservation areas of high tourist traffic (e.g., select trails, campgrounds, and roadsides) but despite efforts, HWA is currently found in all major park watersheds (Johnson et al. 2008). We included a variety of designated conservation areas and unmanaged areas (where treatment did not occur), making it likely hemlock would range in condition from relatively high (lesser mortality) to relatively poor (greater mortality) across our study sites.

## **Field Methods**

**Banding and territory mapping.** We began surveying for waterthrush across our entire study area at the beginning of the breeding season (mid-March) using territorial song playback. Once males were detected occupying a territory for  $\geq 5$  d, we used a mist net and playback of territorial song to capture targeted individuals. Once captured, males were banded with one U.S. Geological Survey-issued aluminum band and three plastic color bands in unique combinations for individual identification without further capture. Because waterthrush occupy linear territories along streams (Mattsson et al. 2009), territories are generally measured by length (m) as opposed to area (Mulvihill et al. 2008,

Marshall 2012, Frantz et al. 2018). To determine territory length, we visually tracked each banded individual every 3 to 5 d for  $\geq 20$  min, recording location (and noting behavior) in 5-min intervals using GPS units (64s and 76Cx; Garmin, U.S.). We recorded locations for individuals until we documented fledglings in the territory or, for territories that never fledged young, until the last monitored nest across all territories either fledged or failed. We considered  $\geq 30$  points collected from  $\geq 6$  visits (average  $15.8 \pm 0.7$  visits across both seasons) for each individual territory sufficient to accurately estimate territory length. There was no correlation between number of points collected and territory length ( $r = -0.05$ ,  $P = 0.75$ ). Territory border delineation was further informed in the field *by* observation of territorial disputes and male singing locations. Our territory mapping protocol was similar to previous waterthrush habitat studies by Mulvihill et al. (2008), Hallworth et al. (2011), and Frantz et al. (2018). Territory length was later estimated in ArcMap (10.3; ESRI, U.S.) by measuring the distance along the stream between the furthest upstream and downstream locations associated with each individual.

**Nestling provisioning and body condition.** We located nests using adult behavioral cues (i.e. nest prospecting, nest building, provisioning, and fecal sac disposal) and systematic searches once the possible nest site area had been narrowed (based on behavior). Once found, nests were checked every 3 d for contents. Six to 8 d after hatching, we placed a handheld camcorder (HC-V100M; Panasonic, U.S.) 5–10 m from each nest (dependent on local topography) to record adult provisioning of nestlings. Nests were recorded for 2-4 hr between 0600 and 1100 EDT (Goodbred and Holmes 1996). Additionally, 6-7 d after hatching, we weighed nestlings (to nearest 0.1 g) and measured tarsus (to nearest 0.01 cm) to estimate body condition (using residuals of mass regressed

on tarsus length). Provisioning data and nestling body condition data were collected during the 2016 breeding season only.

**Habitat surveys.** To characterize territory features potentially associated with food resources (and possibly impacted by hemlock decline), we conducted habitat surveys in 2 high-use foraging areas within each individual waterthrush territory. High-use areas were designated as such based on our territory mapping efforts; they were defined as areas with  $\geq 5$  points within 10-m of each other recorded on  $\geq 2$  different d. If  $> 2$  high use areas were identified for an individual, we used a random number generator to select 2 of the high use areas for our habitat surveys. Survey locations were placed at the approximate center of all locations associated with a high-use area.

At each high-use area, we measured habitat features chosen a priori based on 1) relevance to waterthrush habitat selection according to previous literature (Latta 2009, Mattsson 2009, Marshall 2012), and 2) the feature's potential to be impacted by hemlock decline (informed by Huddleston 2011, Ford et al. 2012, Ellison et al. 2016) or to mediate the effects of hemlock condition on waterthrushes. We assessed hemlock condition following standardized USDA Forest Service protocols in Schomaker et al. (2007). Within a 25-m radius, the 10 closest hemlock trees to point center were measured for diameter at breast height and assessed on four condition criteria (percent of: live crown ratio, crown density, crown transparency, and branch dieback) then categorized into a vigor class (1 = healthy, 2 = light decline, 3 = moderate decline, 4 = severe decline, 5 = complete decline but still standing, 6 = complete decline and fallen) based on the 4 condition criteria. We then used vigor class to create a new variable for our analysis, entitled 'state of hemlock decline,' to better illustrate the continuum of hemlock

condition. This continuous variable was calculated by dividing the average vigor value (to nearest 0.1) of each survey point by 6 (total number of vigor classes), resulting in values close to 0.0 (representing a state of low decline and healthy hemlock condition) to values close to 1.0 (representing a state of high decline and poor hemlock condition). In addition to hemlock condition, we also measured several other habitat features. Because the impact of hemlock decline could depend on the number of hemlock in a given area, we estimated proportion of hemlock within an 11.3-m radius of point center by counting the total number of trees and dividing by the number of hemlock. Within a 5-m radius of point center we visually estimated the following: percent ground cover of 8 different substrates (exposed in-stream rock, exposed soil, leaf litter, woody debris, water, deciduous ground vegetation, evergreen ground vegetation, and exposed tree roots); stream width (m); dominant understory vegetation type (evergreen or deciduous); and canopy cover presence/absence within vertical strata of 0–1.5 m, 1.5–5 m, 5–15 m, and >15 m (measured at point center and paired points on survey edge parallel and perpendicular to stream flow). Hemlock condition surveys were conducted between November and January following each field season when deciduous leaves did not obscure views of hemlock crown characteristics and other habitat features were measured at the end of the breeding season (late June-July); both surveys involved assistance from trained citizen science volunteers.

### **Data Analysis**

**Territory length.** We built and compared linear mixed models (LMMs) and used an information theoretic framework (Burnham and Anderson 2002) to evaluate how hemlock condition, or any other habitat features, was related to territory length

(dependent variable). Prior to model building, we tested all variables (total of 16) for collinearity using pairwise correlational tests; no variables were highly correlated (all  $r < 0.6$ ). To ensure that we met the assumption of normality, we evaluated territory length using a Shapiro-Wilk's test ( $w_{46} = 0.968$ ,  $P = 0.232$ ). In all models, we included a random effect of bird ID because some individuals were present during both breeding seasons. We compared models based on Akaike's information criterion corrected for small sample size ( $AIC_c$ ); we considered all models with  $\Delta AIC_c \leq 2$  to have equivalent support but, when comparing two models that differed by the same single variable and  $\Delta AIC_c \leq 2$ , we only included the simplified model in our final list (following the principle of parsimony). Because territory length may vary by year, we first compared a temporal model with a fixed effect of year to a null model (intercept only). If our temporal model had greater support than the null, we considered the temporal model our baseline null (and included year as a fixed effect to account for annual variation in all other models). We then built and compared univariate models consisting of each habitat variable as well as additive models that consisted of all possible combinations of variables from equivalent univariate models. Finally, we built an interactive model with state of hemlock decline and variables in our best-supported model to determine whether hemlock condition interacted with habitat features to impact territory length. After we compiled our final list of equivalent top models, we assessed importance of habitat variables included in each model by examining the 85% CIs of the  $\beta$  coefficients (Arnold 2010); variables with CIs that did not overlap zero were considered meaningful.

**Nestling provisioning.** We built and compared linear models (LMs) and again used an information theoretic framework to evaluate how hemlock condition, or any other habitat

features, was related to provisioning rates. We initially attempted to build LMMs using both high use foraging area habitat surveys (with a random effect of nest ID), but many models failed to converge, so we randomly selected just one of the areas for use in our analysis. For each nest, we calculated provisioning rate as the total number of provisioning visits per hr per nestling (to account for brood size). One banded male was associated with two nests and provisioning rate for each nest was nearly identical (nest<sub>1</sub> = 3.10 visits per hr per nestling, nest<sub>2</sub> = 3.15 visits per hr per nestling) so we averaged provisioning rate between the two nests for that individual. Prior to model building, we tested all variables (total of 16) for collinearity using pairwise correlational tests. Due to high correlations ( $r > 0.6$ ), we excluded percent ground cover of deciduous vegetation and canopy cover presence within vertical strata of 1.5–5 m from further analysis. To ensure that we met the assumption of normality, we evaluated provisioning rate using a Shapiro-Wilk's test ( $w_{18} = 0.954$ ,  $P = 0.483$ ). We then built and compared a null (intercept only) model, univariate models consisting of each habitat variable, and additive models that consisted of all combinations of variables from equivalent univariate models. We again compared models based on AIC<sub>c</sub> and the principle of parsimony. Finally, we built an interactive model with state of hemlock decline and variables in our best-supported model to determine whether hemlock condition interacted with habitat features to impact provisioning rate. After compiling our final list of equivalent top models, we assessed the importance of habitat variables in each model by examining the 85% CI of  $\beta$  coefficients and considered variables with CIs that did not overlap zero meaningful.

**Nestling body condition.** As with our territory length analysis, we built and compared LMMs using an information theoretic framework to evaluate how hemlock condition, or

any other habitat features, was related to nestling body condition. To calculate nestling body condition, we first ensured that our data met the assumption of normality by evaluating mass (of all nestlings) using a Shapiro-Wilk's test ( $w_{74} = 0.985$ ,  $P = 0.546$ ). We then built a LM of mass as function of tarsus and evaluated model residuals to ensure they met the assumption of normality ( $w_{74} = 0.984$ ,  $P = 0.482$ ). These residuals represented body condition for each nestling; negative values indicated poorer condition and positive values indicated better condition. We then randomly assigned each nestling one of the 2 habitat surveys associated with the territory in which its nest was located so nestlings from the same brood could have different habitat measurements associated with them (to account for the variability of habitat features within each territory that could have contributed to nestling body condition). Prior to model building, we tested all variables (total of 16) for collinearity using pairwise correlational tests; no variables were highly correlated (all  $r < 0.6$ ). Because nestling body condition may vary temporally, we first compared models consisting of univariate and bivariate temporal factors (age at measurement and measurement ordinal date) to a null model (intercept only). If one of our temporal models had greater support than the null, we considered that temporal model our null (and included temporal variables in all other models). We then built and compared univariate models with each habitat variable as well as additive models that consisted of all combinations of variables from equivalent univariate models; for all models, nest ID, bird ID, and number of nestlings were included as random effects. Finally, we built an interactive model with state of hemlock decline and variables in our best-supported model to determine whether hemlock condition interacted with habitat features to impact nestling body condition. We again compared models using  $AIC_c$  and

the principle of parsimony. After compiling our final list of equivalent top models, we again assessed the importance of variables included in each model by examining the 85% CIs of  $\beta$  coefficients.

All analyses were conducted in program R 3.3.2 (R Core Team 2016) using the package ‘lme4’ (Bates et al. 2015) for LMMs, package ‘stats’ (R Core Team 2016) for LMs, and package ‘AICcmodavg’ (Mazerolle 2016) for all model comparisons. We evaluated whether we met assumptions of a linear model by visually examining residuals from the best-supported models for all analyses. All  $\beta$  coefficients and means are reported  $\pm 1$  SE with CIs in brackets.

## **RESULTS**

### **Territory Length**

We built and compared 18 LMMs of estimated territory length of 34 male waterthrush during the 2015 ( $444 \pm 17$  m; range: 290–556 m) and 2016 ( $493 \pm 20$  m; range: 303–666 m) breeding seasons. Average state of hemlock decline across territories was  $0.66 \pm 0.03$  (range 0.17–0.90) for the 2015 breeding season, indicating hemlocks were generally in a state of moderate to severe decline, and  $0.71 \pm 0.01$  (range 0.50–0.90) for the 2016 breeding season, indicating hemlocks were generally in a state of severe decline. Our temporal model had greater support than the null; therefore, year was included in all models ( $\beta = 53.78 \pm 9.72$ , 85% CI [39.79, 67.78]). Our final top model list included four equivalent models ( $\Delta AIC_c \leq 2$ ): the null model (included year) and three separate univariate models that included percent ground cover of deciduous vegetation, percent ground cover of wood debris, and hemlock decline (Table 1). However, following the principal of parsimony, we consider the null to be the best-supported model.

### **Nestling Provisioning**

We built and compared 16 LMs of estimated nestling provisioning rates at 19 nests during the 2016 breeding season ( $2.44 \pm 0.15$  visits per hr per nestling; range: 1.54–3.83 visits per hr per nestling). None of the top models included variables directly related to hemlock condition; instead, the best-supported model ( $\Delta\text{AIC}$  from null = 2.98 with no equivalent models) included the habitat variable canopy cover in the vertical strata 5–15m ( $\beta = 1.84 \pm 0.74$ , 85% CI [0.72, 2.96]; Fig. 3.2).

### **Nestling Body Condition**

We built and compared 21 models of estimated nestling body condition of 74 nestlings during the 2016 breeding season. Mean nestling mass was  $15.40 \pm 0.17$  g (range: 11.0–19.4 g), and mean tarsus length was  $2.09 \pm 0.01$  cm (range: 1.66–2.28 cm). Our temporal models did not garner more support than the null; therefore, temporal variables were not included in subsequent models. Our best-supported model ( $\Delta\text{AIC}$  from null = 5.94 with no equivalent models) included the proportion of hemlock ( $\beta = 1.40 \pm 3.97$ , 85% CI [0.52, 2.29]; Fig. 3.3).

## **DISCUSSION**

HWA, an invasive insect causing widespread Eastern Hemlock mortality, has the potential to alter habitat quality (e.g., food resource availability) for Louisiana Waterthrush in the southern Appalachian Mountains. However, we found no relationship between hemlock condition and territory length, nestling provisioning, or nestling body condition, though with respect to nestling body condition, we did detect a relationship with the proportion of hemlock. In total, our results suggest that waterthrushes, in the short-term and under conditions where hemlock are present but in decline, are able to

avoid many negative consequences following HWA-induced hemlock mortality. The longer-term impact of HWA on habitat quality, however, is likely complex and continued monitoring should assess the potential future effects on this riparian species in the southern Appalachians.

Hemlock condition was not related to territory length (nor were any other habitat variables) suggesting that, during our 2-yr study, hemlock condition was not related to habitat quality to the extent that individuals expanded their territories. This result is contrary to previous studies in which anthropogenic habitat alteration is associated with longer waterthrush territories, presumably because individuals extend their territories to compensate for reduced food quality or quantity (Mulvihill et al. 2008, Marshall 2012, Frantz et al. 2018). However, in our study, we did obtain some preliminary evidence that hemlock decline could eventually lead to territory extension. Our best-supported model included year only, which we used as our baseline null, and mean territories were longer in the second year of our study. However, these increases in territory size did not also correlate with hemlock decline. Frantz et al. (2018) found waterthrush territory length generally increased across a 6-yr study in response to shale gas development and the annual variation that we detected could be an indication of a similar pattern that is only beginning to manifest itself in our study area. Detecting this lagged relationship will require continual monitoring of waterthrush territory length as hemlock condition continues to deteriorate into the future, or studying waterthrushes in areas where hemlock loss is even greater.

Hemlock condition was also not related to provisioning rate, further supporting the inference that waterthrushes are able to find enough prey to provision nestlings

sufficiently across the range of hemlock condition in our study. Although we were unable to determine the identity of prey items delivered to the young, the lack of a relationship between hemlock condition and provisioning rates could potentially be explained by diet composition. Nestling diet may be largely comprised of prey items that are not influenced by hemlocks. This interpretation would run counter to some previous studies that have shown that waterthrush presence is often associated with higher proportions of EPT and therefore assumed that these macroinvertebrates are also preferred waterthrush prey items (Mulvihill et al. 2008, Mattsson et al. 2009, Marshall 2012). EPT are also associated with hemlock-drained streams (Snyder et al. 2002) and thus potentially sensitive to hemlock decline (though it should be noted that EPT are also found in streams where hemlock is not present). However, although EPT are an assumed important part of *adult* waterthrush diet, a separate analysis of *nestling* waterthrush fecal sacs from Arkansas and Pennsylvania (Trevelline et al. 2016) revealed that adults provision lepidopterans and dipterans to nestlings more often than EPT prey items. As such, waterthrush nestlings may be less reliant on hemlock-associated macroinvertebrates than adults and hemlock decline would thus be less likely to impact provisioning rates. Additionally, waterthrush breed along streams in regions that lack hemlock (e.g., northcentral Arkansas in the Buffalo River watershed), so the species as a whole must have the capacity/plasticity to forage on a variety of prey unrelated to hemlock presence or condition.

Although we did not observe a short-term association between hemlock condition and provisioning, our results suggest a potential indirect relationship that may more strongly emerge in the future, as forest structure shifts following the loss of hemlock. Specifically, we found provisioning rate was positively related to mid-story cover, which could again

be due to altered food resources in some territories. As hemlocks die, lose needles, and eventually fall, this mortality creates canopy gaps (Orwig et al. 1998, Eschtruth et al. 2006), which may then open up the mid-story for rapid regeneration of deciduous species such as *Acer* spp., *Betula* spp., *Carya* spp., *Fagus* spp., *Quercus* spp., *Liriodendron tulipifera* (Small et al. 2005, Ford et al. 2012, Brantley et al. 2013). Such species can provide abundant food resources for juvenile lepidopterans (Scholtens and Wagner 2007), known prey items provisioned to waterthrush nestlings (Trevelline et al. 2016, L. C. Bryant personal observation). Waterthrush that forage in areas with more mid-story cover may find more abundant food resources and thereby spend less time foraging and more time provisioning. However, in areas of the southern Appalachians where rosebay rhododendron (*Rhododendron maximum*) is already established, this species can shade out seedlings (Nilsen et al. 2001, Roberts et al. 2009) and cause the mid-story to remain open (as this species does not grow beyond the understory), which may then reduce overall lepidopteran food resources. Adult waterthrush foraging in areas with a more open mid-story may require increased foraging time, thereby reducing provisioning. We found a trending correlation between hemlock decline and mid-story ( $r = -0.49$ ,  $P = 0.038$ ), suggesting decline could in fact be altering mid-story in our study area. Further research on nestling diet and surveys of terrestrial lepidopterans in areas with varying mid-story cover would help elucidate the relationship between mid-story cover and food resources and determine if forest composition shifts following hemlock mortality pose threats to waterthrushes in the future.

As was the case with territory length and nestling provisioning, hemlock condition was unrelated to nestling body condition. However, we did detect a relationship between the

*proportion* of hemlock and nestling body condition. Regardless of hemlock condition, nestling body condition was positively associated with greater proportions of hemlocks in adult foraging areas. These results, again, could point to potential longer-term impacts on nestling body condition as HWA infestation causes the eventual disappearance of hemlocks in this and other areas. If hemlock mortality (and decreased hemlock proportion) leads to poorer quality waterthrush nestlings, waterthrush populations that breed along heavily hemlock-populated streams could face future declines in nestling survival (Hochachka and Smith 1991) and recruitment (Magrath 1991). However, we were only able to collect data on nestling body condition during the second breeding season, and further monitoring of waterthrush nestlings will be necessary to understand annual variation and to evaluate how continued hemlock mortality (and reduced presence on the landscape) impacts nestling body condition, survival, and recruitment.

Overall, our results suggest that the short-term impacts of hemlock decline on waterthrush food resources appear minimal, which is positive given the likely eventual extirpation of Eastern Hemlock in the southern Appalachians. However, our study provides some indications that the eventual complete loss of hemlock, and resulting alteration to riparian forest composition, could eventually have a greater impact on waterthrush populations in the region (potentially via nestling body condition and subsequent recruitment). Future research on waterthrushes should focus on continued monitoring of breeding individuals in areas altered by HWA infestation, and expanding into areas that are even further along the path to complete hemlock mortality, to determine if future changes to riparian habitats have long-term consequences for this charismatic species in the southern Appalachians.

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**Author contributions:** T.A.B. initiated this study. L.C.B. and T.J.B. designed the study and secured funding. L.C.B. collected and analyzed data. L.C.B wrote the paper with guidance from T.J.B.

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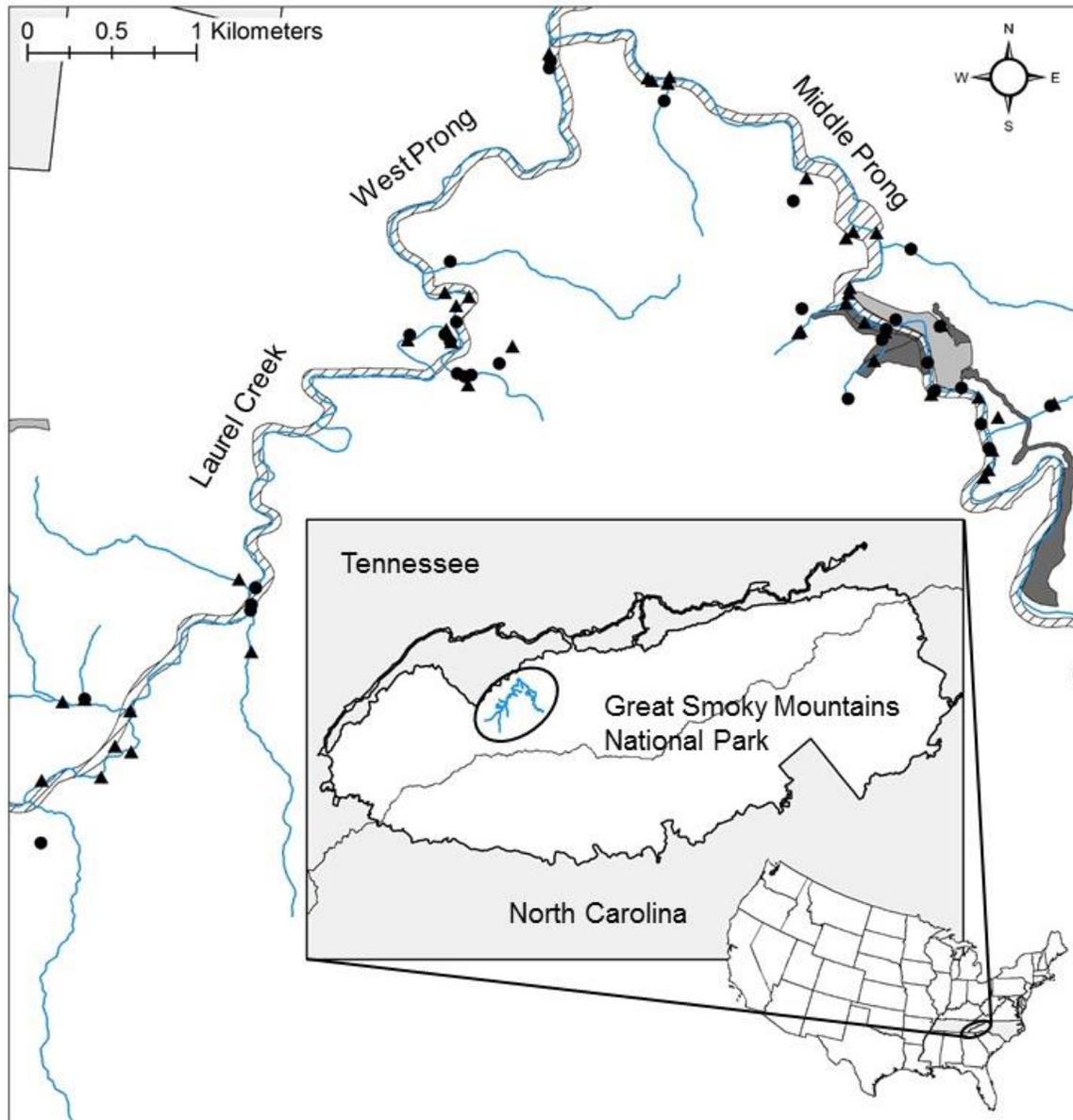
## TABLES

**Table 3.1.** Top model selection results from 18 a priori models examining Louisiana Waterthrush (*Parkesia motacilla*) territory length in Great Smoky Mountains National Park.  $K$  indicates the number of parameters in each model and  $w_i$  is the Akaike weight.

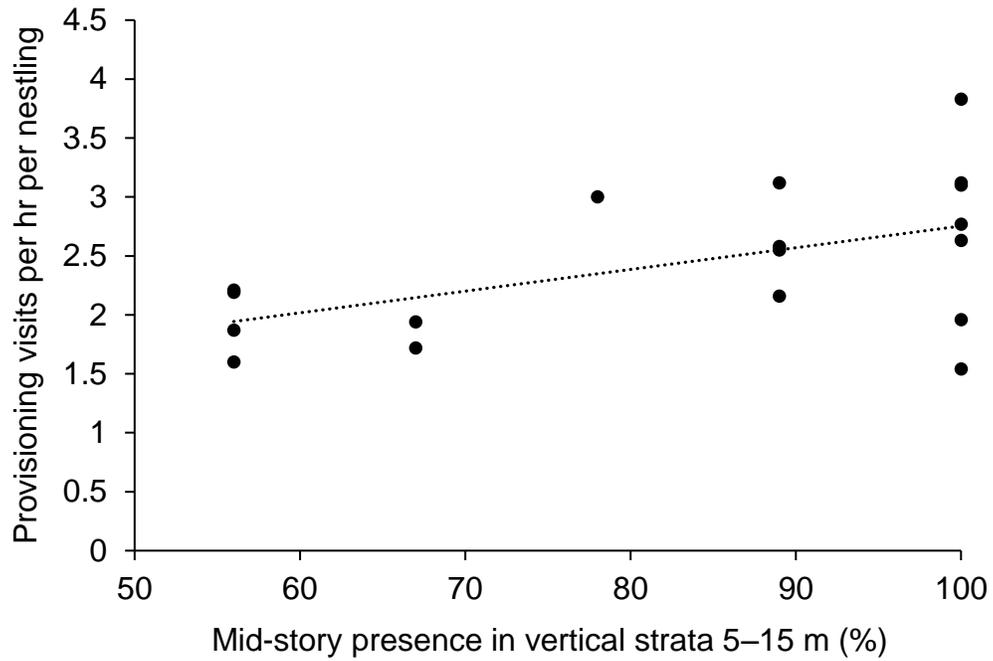
Model	$K$	$\Delta\text{AIC}_c$	$w_i$
Year + deciduous ground vegetation	5	0.00 <sup>a</sup>	0.15
Year + hemlock decline	5	0.91	0.10
Year (null)	4	0.98	0.09
Year + woody debris	5	1.15	0.09

<sup>a</sup>The  $\text{AIC}_c$  value of the best-supported model was 1014.26

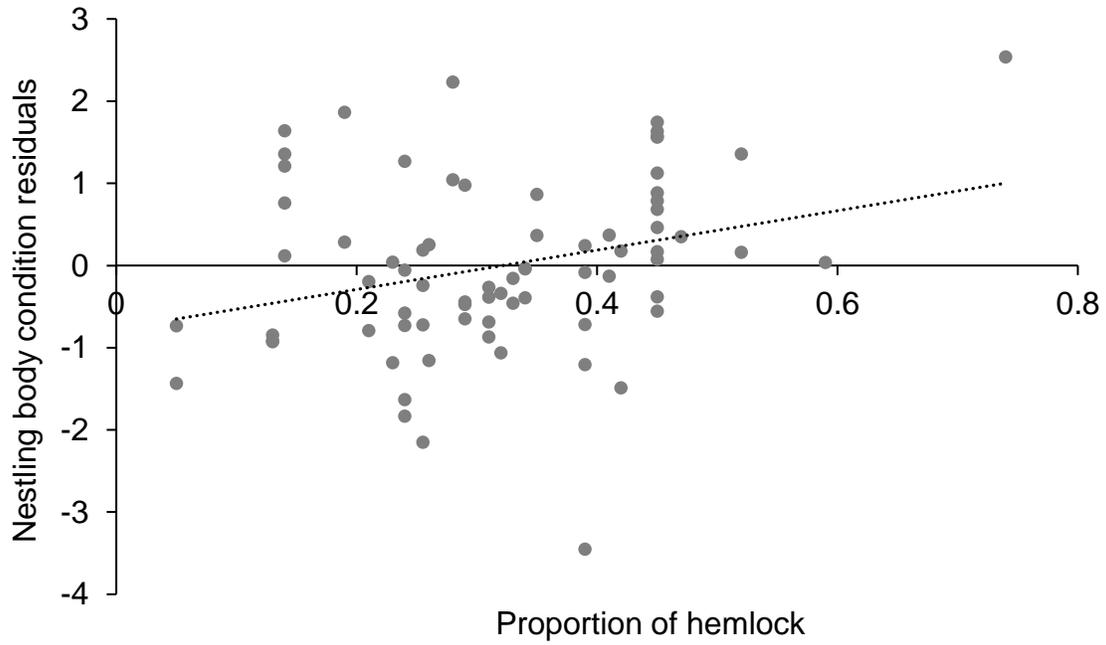
## FIGURES



**Figure 3.1.** Location of study area and Louisiana Waterthrush (*Parkesia motacilla*) nests in Great Smoky Mountains National Park during the 2015–16 breeding seasons. Circles represent 2015 season nests ( $n = 32$ ) and triangles represent 2016 season nests ( $n = 42$ ). Shading indicates conservation areas where Hemlock Woolly Adelgid treatment occurred (road side buffers are striped; trails are dark grey; campground and day-use areas are medium grey).



**Figure 3.2.** Louisiana Waterthrush (*Parkesia motacilla*) provisioning rate in Great Smoky Mountains National Park during the 2016 breeding season was related to the presence of mid-story cover (vertical strata 5–15 m) in adult foraging locations ( $\beta = 1.84 \pm 0.74$ , 85% CI [0.72, 2.96]).



**Figure 3.3.** Louisiana Waterthrush (*Parkesia motacilla*) nestling body condition in Great Smoky Mountains National Park during the 2016 breeding season was related to the proportion of hemlock in adult foraging locations ( $\beta = 2.89 \pm 0.89$ , 85% CI [1.40, 3.97]).

## OVERALL CONCLUSIONS

Eastern hemlock (*Tsuga canadensis*) decline caused by the invasive hemlock woolly adelgid (*Adelges tsugae* Annand; hereinafter HWA) is altering riparian habitat in the southern Appalachians, which can affect species inhabiting infested areas such as the avian riparian-obligate Louisiana waterthrush (*Parkesia motacilla*; hereinafter waterthrush). In this study, I found that the overall short-term impact of hemlock decline on waterthrushes is minimal, which is positive news because complete hemlock mortality across the southern Appalachians is likely certain. However, there are possible longer-term consequences for waterthrushes depending on how riparian forest succession proceeds following hemlock mortality.

In the first chapter, I focused on the ultimate effects of hemlock decline on waterthrushes and found mixed associations between hemlock condition and several measures of waterthrush fitness and habitat selection. Hemlock decline was unrelated to apparent adult survival and foraging habitat selection. With respect to adult survival, these results indicate waterthrushes survived both within and across seasons regardless of hemlock condition, or any other habitat features. Additionally, return rates were relatively high for this species and all monitored individuals returned to their previous season territory (exhibiting high breeding site fidelity). These results suggest that hemlock decline does not have negative carry-over effects on waterthrushes; however, a physiological study measuring stress hormones would be necessary to confirm whether carry-over effects exist. With respect to foraging habitat selection, the lack of a

relationship with hemlock condition could have several explanations. One, waterthrushes may be more generalist foragers than previously assumed and less dependent on hemlock-associated prey items, such as ephemeropterans, plecopterans, and tricopterans (collectively EPT); thus, waterthrush diet would be less impacted by hemlock decline. Two, hemlock decline in my study area and time frame may not yet have negatively affected EPT in a way that restricted their availability as waterthrush prey. Macroinvertebrate surveys would be necessary to determine if waterthrush prey availability and diversity differ across a continuum of hemlock condition. Although hemlock condition was unrelated to foraging areas, my results do further support current understanding of waterthrush foraging behavior; the species is known to flip over woody debris and leaves and hop across in-stream exposed rocks in search of macroinvertebrate prey.

Hemlock decline was directly related to nest site selection but only through an interaction with another habitat variable, percent ground cover of exposed tree roots. While waterthrushes generally selected against exposed tree roots around their nests across all states of hemlock decline, when nests were in areas of higher decline ( $\geq 0.55$  state of decline), waterthrushes also selected for more exposed roots around their nest site. A change in predator community resulting from hemlock decline could be driving this relationship. Hemlock mortality causes canopy gaps that allow more light to reach the forest floor, increasing local ground temperatures. These increased temperatures could increase activity or presence of ectotherms like snakes, known nest predators of waterthrushes. In areas with more hemlock decline, waterthrushes may choose to place their nests in areas with more exposed tree roots because exposed roots provide more

false nest sites for predators (i.e. snakes) to search. Future research into the impact of hemlock decline on snakes is necessary to better understand the mechanisms driving this interaction. This direct relationship with hemlock decline and nest site selection did not extend to nest survival; instead, my results point to a possible indirect relationship. Nest survival was lower in areas with a deciduous-dominant understory and higher in areas with an evergreen-dominant understory, suggesting that riparian forest succession following hemlock mortality could have negative impacts on waterthrush nest survival. Nest monitoring across areas ranging from deciduous- to evergreen-dominant understories, as well as a continuum of hemlock condition, would help determine if hemlock decline is an indirect factor affecting waterthrush nest survival.

In the second chapter, I focused on proximate effects of hemlock decline on waterthrushes as possible indications that HWA infestation alters riparian habitat quality. Territory length is often used as an indicator of habitat quality and previous research has shown waterthrushes will increase their territory length in response to decreased habitat quality. However, I found hemlock decline was unrelated to territory length, as were all other habitat variables, suggesting HWA-induced hemlock decline in my study area does not impact habitat quality to the extent that waterthrushes extend their territories. Territory length increased from the first to second field season, which could indicate habitat quality decreased but that I failed to measure the habitat variables that might have reflected this change. Continued waterthrush monitoring would be necessary to determine whether my results are the beginning of a pattern of increasing territory length and to further explore what habitat features may be driving the possible reduction in habitat quality.

Hemlock decline was not directly related to nestling provisioning rates but could be indirectly related through changes to food resources. Nestling provisioning rates were higher in areas with more mid-story cover, which could be related to the availability or abundance of lepidopterans. Lepidopterans move vertically through canopy strata and increased mid-story may provide more food resources and habitat for lepidopterans to feed and pupate. Adult waterthrushes who foraged in such areas may have found more abundant prey and therefore spent less time foraging and more time provisioning. I found a weak but significant negative correlation between state of hemlock decline and mid-story presence, indicating decline could be reducing mid-story presence. Hemlock decline was unrelated to nestling body condition but proportion of hemlock was related; adult waterthrushes who foraged in areas with a higher proportion of hemlock (regardless of hemlock condition) had nestlings in better body condition. Again, food resources may be driving this relationship. The presence of hemlocks, even if in decline, could still provide habitat conditions beneficial for prey items, especially those associated with hemlock (i.e. EPT). Adult waterthrushes who foraged in such areas may have found higher quality food and therefore produced higher quality nestlings. These results suggest that as hemlock mortality continues and hemlocks eventually disappear from the landscape, waterthrush nestling body condition could be negatively impacted. Macroinvertebrate surveys in areas ranging from open to closed mid-story and with varying proportions of hemlock combined with foraging behavior surveys and nestling fecal sac analysis would help tease apart the relationships between hemlock condition, lepidopteran, EPT, and nestling waterthrush diet.

In total, my results indicate that hemlock decline in the southern Appalachians minimally impacts waterthrushes in the short-term but, in the long term, riparian forest succession and composition following hemlock mortality could negatively impact waterthrush fitness. Additionally, my results hint that waterthrush may be a more resilient species than assumed, able to adjust quickly and efficiently to rapid environmental change resulting from hemlock loss. Interactions between species and their habitats are complex and dynamic, and I recommend that this study be expanded to include more years of waterthrush monitoring; two years is only a snapshot and hemlock decline is a continually progressing process. I was unable to explore how recruitment may be associated with hemlock decline so study expansion should also include telemetry-tracking of young during the post-fledgling period and juvenile survival to the following breeding season. Additionally, I found possible indirect relationships between hemlock decline and predator (i.e. snake) communities and waterthrush food resources, both of which need further research to tease apart and fully understand. Finally, I did not evaluate how hemlock decline may impact the initial step of territory establishment. A range-wide waterthrush occupancy study that includes areas of the species' breeding range that overlap with HWA invasion as well as areas outside HWA spread (resulting in a complete continuum of hemlock condition from uninvaded healthy trees to complete mortality) would help determine if this widespread ecosystem change is altering waterthrush distribution throughout the Appalachian Mountains.