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Indirect effects of an invasive exotic species on a long-distance migratory songbird

Kirk W. Stodola · Eric T. Linder · Robert J. Cooper

Abstract The loss of foundational tree species to non-native pests can have far reaching consequences for forest composition and function, yet little is known about the impacts on other ecosystem components such as wildlife. We had the opportunity to observe how the loss of eastern hemlock (*Tsuga canadensis*), due to the invasive hemlock woolly adelgid (*Adelges tsugae*), influenced the population ecology of the Black-throated Blue Warbler (*Setophaga caerulescens*) over a 7 year period. We followed the process of adelgid infestation and subsequent hemlock loss, which allowed us to investigate the patterns and mechanisms of population change. We document a precipitous decline in breeding pairs at one site where hemlock was most abundant in the understory, but not at our other two sites. We observed no changes in reproductive output or apparent survival, yet territory size increased dramatically at the most affected site, suggesting that the decline was due to a lack of colonization by new breeders. Our results demonstrate how an invasive insect pest can indirectly influence wildlife species not believed to be vulnerable and in ways not typically investigated.

Keywords Population demography · Population decline · Immigration · Black-throated Blue Warbler · Hemlock woolly adelgid

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Introduction

Invasive non-native species represent a significant threat to biodiversity (Enserink 1999; Novacek and Cleland 2001; Pimental et al. 2000). In particular, introduced pests and pathogens that infect and kill native species have wide-ranging detrimental impacts (Castello et al. 1995; Enserink 1999; Everett 2000). The consequences of exotics are especially dramatic when associated with the loss of foundational tree species (e.g., Liebhold et al. 1995; Mack et al. 2000; Ellison et al. 2005), which can result in fundamental changes to ecosystem composition and function (Ellison et al. 2005). The changes brought forth by exotic species can cascade throughout an ecosystem, affecting all organisms, and become a major driver of environmental change, even in areas presumably protected from other threats (Vitousek et al. 1996). However, despite the fact that the invasions of harmful

pests and pathogens are common, little is known about the effects these invasions have on other ecosystem components such as wildlife species (Orwig 2002).

Eastern hemlock (*Tsuga canadensis*) is currently at risk of complete eradication from eastern deciduous forests because of the introduction of a destructive non-native insect, the hemlock woolly adelgid (adelgid: *Adelges tsugae*). Hemlock is an important forest component (Rogers 1978) that provides a unique microhabitat and important structural component to a forest community (Kincaid and Parker 2008). Because of these qualities, hemlock stands harbor unique assemblages of birds and other taxa (Becker et al. 2008; Ross et al. 2003; Ross et al. 2004; Snyder et al. 2002; Tingley et al. 2002), which are also threatened by the adelgid. The adelgid was first observed in the eastern United States in Virginia and after a few decades began spreading quickly, eliminating large stands of eastern hemlock (Orwig et al. 2002). The adelgid has spread throughout much of the eastern and southern portions of the hemlocks native range and currently threatens hemlock stands as far south as Georgia (USFS 2009). Hemlock die-off following adelgid infestation occurs quickly, with needle loss beginning within a few years (Nuckolls et al. 2009), and mortality occurring within 4 years (McClure 1991). The adelgid attacks hemlocks of all age classes and can change the functional characteristics of a forest within a few years (Orwig and Foster 1998).

Adelgid infestation and subsequent hemlock loss disproportionately affects bird species with a high dependence on hemlock (e.g., Becker et al. 2008; Tingley et al. 2002). The loss of hemlock as a nesting substrate has been proposed as a possible mechanism causing population declines, at least in Acadian Flycatchers (*Empidonax virescens*) (Allen et al. 2009). Although research into the distribution and abundance of bird species in relation to adelgid infestation have helped our understanding of what species are most vulnerable to the loss of hemlock, and how the loss of hemlock can influence bird communities and populations, all studies to date have compared the response variable (e.g., community structure or species performance) among areas of varying degrees of infestation across spatial scales (Allen et al. 2009; Becker et al. 2008; Tingley et al. 2002). An alternative approach towards understanding the causal mechanisms of species decline due to the invasion of an exotic species would be to collect detailed demographic information on a single population, from adelgid infestation to complete hemlock loss.

Three possible mechanisms could influence population persistence following the loss of hemlock, or any other foundational tree species. Changes in habitat composition or quality can decrease adult survival (Bayne and Hobson 2002) leading to fewer individuals returning in subsequent years. Second, habitat changes can influence reproductive performance (Robinson et al. 1995; Herkert et al. 2003), which could lead to a declining population because site fidelity in birds is often predicated on breeding success in the previous year (Greenwood and Harvey 1982; Hoover 2003; Porneluzi 2003; Sedgwick 2004). Finally, individuals may change their settling patterns due to perceived changes in forest structure and reduced immigration could lead to population declines (Ward 2005).

Beginning in 2002, we established three study sites in the Nantahala National Forest in Macon Co., North Carolina (which is located near the southern terminus of the Appalachian mountain range) focused, in part, on monitoring the demography of the Black-throated Blue Warbler (*Setophaga caerulescens*). The time frame of our study coincided with the southward advancement of the hemlock woolly adelgid, with 2001 being the first year it was detected in our study area (USFS 2009). The adelgid quickly spread throughout this region, defoliating and killing hemlocks. We first observed it on our study sites in July of 2002 and by 2008 nearly all hemlocks were infected (e.g., dead or highly defoliated). Consequently, we were able to investigate how the adelgid and subsequent loss of hemlock influenced this population of Black-throated Blue Warblers.

We focus on the patterns of Black-throated Blue Warbler abundance relative to hemlock loss and investigate the processes that produce these patterns. Specifically, we investigate temporal patterns of reproductive performance and apparent survival of Black-throated Blue Warblers to elucidate potential mechanisms underlying population change concurrent with the loss of hemlock. The Black-throated Blue Warbler is a particularly valuable species for this investigation because of its dependence on large tracts of healthy mature forest, its insectivorous diet, and its propensity to nest in understory shrubs (Holmes et al. 2005), all of which may be altered with the loss of hemlock (Orwig and Foster 1998), which has the

potential to influence many facets of the Black-throated Blue Warblers' breeding biology. However, unlike other hemlock associated species, the Black-throated Blue Warbler uses a variety of nesting substrates (Holmes et al. 2005) and so it is uncertain how the loss of hemlock may affect it. Consequently, understanding how the Black-throated Blue Warbler responds to the loss of hemlock can provide valuable information on the response of wildlife species to the loss of foundational tree species in a forest, as well as the mechanisms driving the response.

Methods

We conducted this study within the Nantahala National Forest in the southern Appalachian Mountains, Macon County, North Carolina. We established three study sites at approximate elevations of 1,050 m (LOW), 1,200 m (MID), and 1,350 m (HIGH). All three study sites were within 15 km of one another. The approximate size of each study site was 75 ha at the LOW site, 45 ha on the MID site, and 30 ha at the HIGH site. The LOW and MID elevation sites were established in 2002, while the HIGH elevation site was added in 2003. This forest is characterized by cove hardwood and northern hardwood forest vegetation (Day et al. 1988), with an understory dominated by *Rhodendron maximum* and *Kalmia latifolia* (Day and Monk 1974).

Study species

The Black-throated Blue Warbler is a 9–10 g insectivorous Nearctic-Neotropical migrant that winters in the Greater Antilles and breeds from the southern Appalachian Mountains of Georgia northward to Nova Scotia and as far west as northeast Minnesota (Holmes et al. 2005). Inter-annual site fidelity is high (Holmes et al. 1992) and males defend non-overlapping territories, typically remaining in these territories for the duration of the breeding season (Holmes et al. 2005, Stodola *personal observation*). The sexually dichromatic Black-throated Blue Warbler forages mainly in the understory. In studies conducted in New Hampshire, Lepidoptera larvae made up >80 % of the prey items taken (Robinson and Holmes 1982) and 60–87 % of the estimated prey biomass brought to nestlings (Goodbred and Holmes 1996). The Black-throated Blue Warbler

has been extensively studied at Hubbard Brook Experimental Forest in New Hampshire (e.g., Holmes et al. 1996; Rodenhouse and Holmes 1992; Rodenhouse et al. 2003; Sillett and Holmes 2002; Sillett et al. 2004), yet little demographic data are available from the southern portion of its breeding range.

Habitat assessment

Vegetation composition

We focused our vegetation measurements on woody-stemmed species and gathered information on their abundance at 74, 69, and 36 systematically placed locations on the LOW, MID, and HIGH sites, respectively. Each location was separated by approximately 70 m and arranged in a checker board pattern that encompassed the area where Black-throated Blue Warblers nested. We measured basal area for all tree species >10 cm diameter at breast height (dbh) within 11.3 m-radius plots, and counted all saplings (3 cm–10 cm dbh) and stems from shrubs (<3 cm in width, >0.3 m in height) within 3 m radius vegetation plots.

Hemlock decline

The process of hemlock loss due to the hemlock woolly adelgid is well understood and consistent, ending in massive needle loss and tree death within approximately 4 years (McClure 1991; Nuckolls et al. 2009); thus our estimates of hemlock loss are mainly qualitative. The adelgid was first documented in this area in 2001 (USFS 2009), 1 year prior to the onset of this study. We observed the adelgid spreading across our study sites over the the first few years of our study and began noticing needle die-off in 2004. By 2007 the extent of the die-off was substantial and we attempted to quantify the intensity of the problem by estimating percent needle loss (percent defoliated over a 200 cm^2 area) on the lower branches ($\sim$1 m high) on three different sides of each hemlock, and averaged these to estimate defoliation. We estimated losses on 52, 50, and 50 hemlocks at the LOW, MID, and HIGH sites respectively. By 2008 nearly all hemlocks had $\sim$100 % needle loss on their lower branches, and as a consequence, we did not estimate needle loss that season.

Population demography

Survival

We attempted to band all singing males and nesting females at each site in each year. We aged all males as either second year (first breeding season) or after second year birds based on plumage characteristics (Pyle et al. 1987). Both males and females were fitted with unique combinations of color bands. In each year, we relocated all banded individuals on our study sites, and searched surrounding areas for individuals that may have moved off our plots.

Breeding density

We gridded each study plot by flagging trees every 25 or 50 m to facilitate territory mapping and location of breeding males. The grid was then superimposed onto a topographic map of the study area where we marked territory observations. We visited each site nearly every day, allowing us to learn individual territories and territory boundaries. Territory size for each breeding male was estimated from the territory maps.

Reproductive output

Several demographic parameters (clutch size, number of fledged young, number of nesting attempts and broods, time to renest, and duration of the breeding season) are required to estimate annual reproductive output (Farnsworth and Simons 2001) and we made every effort to locate all nesting attempts to accurately estimate these parameters. We monitored nests every 2–4 days to ascertain the date of clutch initiation, clutch size, start of incubation, hatching date, and number of young fledged. We used parental behavior to ascertain fledging status if fledglings were not seen and assumed fledging had occurred if parents were seen carrying food or were agitated at the presence of an observer for an extended period of time (>10 min). Unsuccessful nests were determined by loss of nest, eggs, or nestlings prior to day 8 (hatch day = day 0) of the nesting cycle, which is the earliest Black-throated Blue Warblers fledged young during the course of this study. Nest cycle length was calculated as the difference in days between the start of incubation and the successful fledging of young.

We used the Farnsworth and Simons model (2001, 2005) to estimate annual reproductive output (number of young fledged per pair per season). We took this approach because we believed it was an unbiased means of comparing a combination of reproductive parameters and how they influence reproductive performance among sites. Although we recognized the concern that the Farnsworth-Simons (2001, 2005) model may overestimate annual reproductive output (Jones et al. 2005b), we were more interested in comparison among sites and not in actual number produced. Furthermore, the Farnsworth-Simons model (2001, 2005) exhibits a strong positive relationship with observed annual reproductive output for this species in other portions of its geographic range (Jones et al. 2005a, b).

Statistical analyses

We estimated apparent survival of adults using Cormack-Jolly-Seber models (Lebreton et al. 1992) by implementing the recaptures option in Program MARK (White and Burnham 1999). We took an iterative approach to modeling apparent survival by first fitting four models where survival was held constant ($\Phi.$) and detection was either constant (P.), a function of site (P_{SITE}), gender (P_{GENDER}), or their interaction ($P_{SITE \times GENDER}$). Model fit was evaluated using Akaike's Information Criterion (AIC; Akaike 1973) adjusted for small sample size (AICc; Burnham and Anderson 2002). The weight of evidence (Wi; Burnham and Anderson 2002) for each model was used to compare among sets of competing models. We then used the best fitting detection model when investigating apparent survival. For this analysis we fit seven different models where survival was constant across years, sites, and gender ($\Phi.$), a function of site (Φ_{SITE}), a function of gender (Φ_{GENDER}), and a function of year (Φ_{YEAR}), along with the interaction of site and gender ($\Phi_{SITE \times GENDER}$), site and year ($\Phi_{SITE \times YEAR}$), and gender and year ($\Phi_{GENDER \times YEAR}$). We estimated territory size by fitting a general linear model relating territory size to year, site, year and site, and their interaction, along with a constant model with no difference in territory size among years or sites. Territory size was log transformed prior to analysis. Finally, we compared the proportion of second-year birds to after-second-year birds on each site during the period of hemlock decline (2004–2008) using a

Cochran-Mantel-Haensel test, to control for year-specific effects.

Breeding parameters of interest were estimated by fitting generalized linear models relating clutch size and fledged young per successful nest to site, year, site and year, the interaction of site and year, along with a constant model with no difference among sites or years. We estimated time to renest in a similar fashion but included an additional predictor indicating if the attempt followed a successful or unsuccessful nest attempt. Time to renest was modeled using a Poisson distribution and log link in Proc Genmod (SAS Institute 2007). We controlled for underdispersion of the data using the 'dscale' option, which computes an additional scale parameter and adjusts the standard errors of the regression coefficients (SAS Institute 2007). Clutch size and number of fledged young per successful nest were modeled using a beta-binomial distribution and the logit link in Proc Genmod (SAS Institute 2007), where the maximum clutch size and fledged young were set to five (based on field data from this study site). A Hosmer and Lemeshow test of goodness of fit failed to indicate any lack of fit (Hosmer and Lemeshow 1989). We calculated daily nest survival using the logistic exposure method (Shaffer 2004). The last day the nest was observed active was used to calculate exposure days for nests with uncertain fates (Manolis et al. 2000). Nests were considered successful if at least one young fledged.

We used an information theoretic approach to incorporate uncertainty about our estimates for clutch size, fledged young per successful nest, breeding cycle length, time between breeding events, and probability of nest survival. We did not incorporate model averaging for parameters that were best explained by the constant model. Estimates were incorporated in the Farnsworth and Simons model (2001, 2005) for calculating annual reproductive output, along with a nesting cycle of 21 days (12 day incubation, 9 day nestling period), maximum number of two broods in a season, and five total nesting attempts, which represented the maximum number of nests we observed females attempting. Breeding season length for each site and year was estimated as the difference between the average date of clutch initiation for the first five nesting attempts and the average date of clutch initiation for the last three nest attempts (e.g., Marshall et al. 2002) plus 25 days, which corresponded to a clutch size of four, an incubation period of 12 days, and a nestling period of 9 days.

We incorporated the uncertainty in our demographic estimates by recalculating annual reproductive output under 10,000 Monte Carlo simulations where each iteration represented a random draw from the normal distribution with the mean and standard error coming from the untransformed model-averaged beta estimates for the respective parameter of interest: clutch size, number of fledged young per successful nest, time between breeding events, and daily probability of nest survival. The randomly generated beta estimate was then back-transformed and used in Monte Carlo simulations for estimating annual reproductive output and were evaluated using the Monte Carlo 95 % confidence intervals. Interpretations of vegetation differences among sites were performed using approximate 95 % confidence intervals derived from the normal distribution and all other parameters of interest are reported with confidence intervals derived using asymptotic maximum likelihood standard error estimates (Gerrard et al. 1998; Johnson 1999).

Results

Habitat assessment

Vegetation composition

Average basal area was 32.4 ($\pm$2.1) cm^2/m^2 at the LOW site, 34.2 ($\pm$2.8) cm^2/m^2 at the MID site, and 28.3 ($\pm$4.9) cm^2/m^2 at the HIGH site. *Liriodendron tulipifera* was the most dominant tree at the LOW site, *Quercus rubra* was the most dominant tree at the MID site, and *Acer rubrum* was the most dominant tree at the HIGH site (Fig. 1). *Tsuga canadensis* was prevalent on the LOW and HIGH sites, but relatively sparse at the MID site (Fig. 1). Sapling density was slightly greater at the HIGH site with 6.9 ($\pm$2.2) saplings per 3 m radius vegetation plot, in comparison to the MID and LOW sites, 6.3 ($\pm$2.2), 5.3 ($\pm$2.0) per 3 m radius vegetation plot respectively. *R. maximum* was the most abundant sapling across all sites with an average abundance per 3 m radius vegetation plot being 1.7 ($\pm$0.7). This abundance varied by site, however, and it was more numerous at the HIGH and MID sites in comparison to the LOW site (Fig. 2).
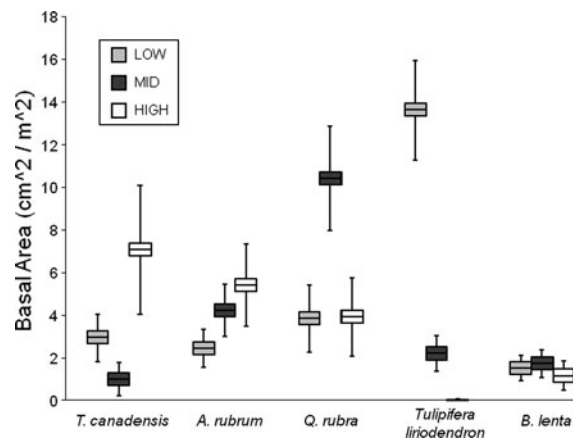
Fig. 1 Average basal area (cm²/m²) of the five most abundant tree species across all sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. *Error bars* represent 95 % confidence intervals

Overall, hemlock was the fourth most abundant sapling across all sites, although it was second most abundant at the LOW site (Fig. 2). Average shrub density was much greater at the HIGH site in comparison to the MID and LOW sites, with 51.5 (±14.2), 34.2 (±18.0), and 37.9 (±9.3) shrubs per 3 m radius vegetation plot at the HIGH, MID, and LOW sites respectively. *Gaylusaccia* species were the most abundant shrub across all sites, with an average of 10.3 (±4.4) per 3 m vegetation plot, followed by *R. maximum* 8.7 (±3.1), and *Q. rubra* seedlings 3.1 (±1.4), with the distribution varying across sites
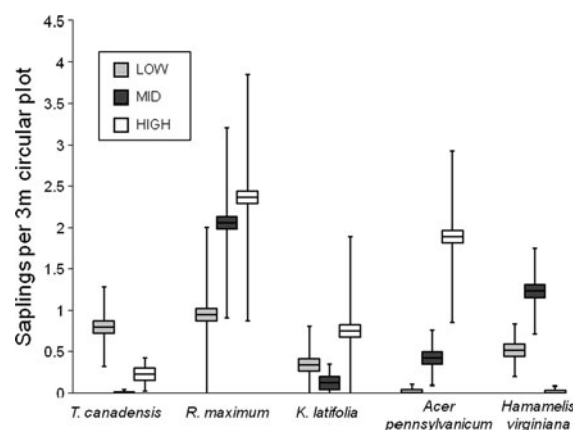

Fig. 2 Average number of the five most abundant saplings (3 cm–10 cm dbh) in 3 m radius vegetation plots across all sites. Vegetation was measured at 74, 69, and 36 locations at the LOW, MID, and HIGH sites respectively. *Error bars* represent 95 % confidence intervals
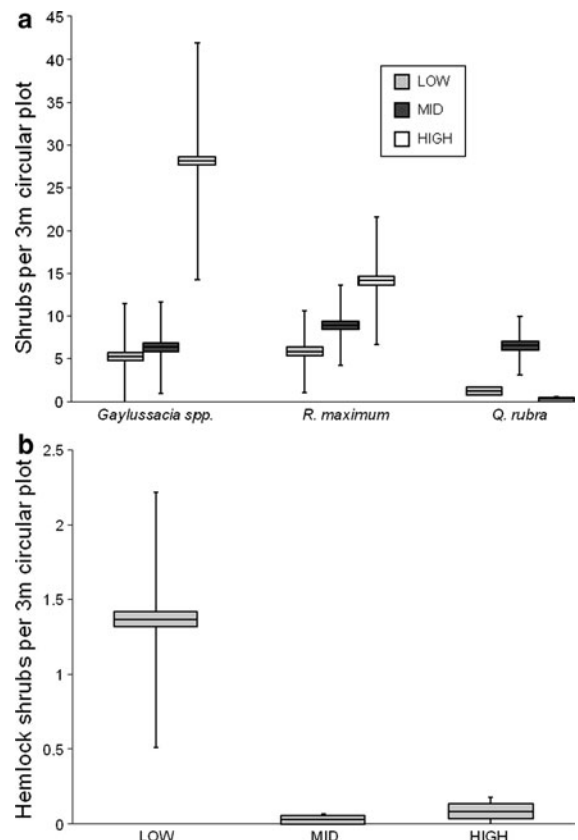

Fig. 3 **a** Average number of the three most abundant woody shrub (<3 cm in width, >0.3 m in height) species found in 3 m radius vegetation plots across all sites. *Error bars* represent 95 % confidence intervals. **b** Average number of hemlock shrubs (<3 cm in width, >0.3 m in height) found in 3 m radius vegetation plots across all sites. *Error bars* represent 95 % confidence intervals

(Fig. 3a). Hemlock, at the shrub level, was less abundant across all sites, with an average of 0.6 (±0.4) per 3 m radius vegetation plot, but much more prevalent at the LOW site in comparison to the MID and HIGH sites (Fig. 3b).

Hemlock decline

We first detected the aldegid at the LOW site at the end of 2002, and on the MID and HIGH sites in the beginning of 2003. While the adelgid was ubiquitous by 2004, we only observed needle loss at one very localized 2 ha patch on the LOW site, which is where we first located the adelgid. However, by 2007 the average needle loss was approximately 80 % at the LOW site, 70 % at the MID site, and 85 % at the

HIGH site. In 2008, nearly all hemlocks were dead or had over 80 % defoliation on their lower branches.

Population demography

Survival

We banded 163 males and 122 females over the seven years of this study across all sites. The best fitting detection model received 78 % of the weight of evidence and indicated that detection was a function of gender, with the probability (95 % confidence interval) of detection being 0.82 (0.67–0.91) for females and 0.97 (0.84–0.99) for males. The constant detection model received 11 % of the weight of evidence, while the interaction of site and gender received 8 %, and site received 2 %. The best fitting survival model indicated the influence of site, although model uncertainty was high (Table 1). Estimates from the constant survival model indicated that apparent survival (SE) was 0.53 (0.48–0.58), irrespective of site, gender, and year, while the site effects model indicated that apparent survival was 0.52 (0.41–0.63) at the LOW site, 0.47 (0.38–0.55) at the MID site, and 0.59 (0.51–0.67) at the HIGH site.

Nest placement and breeding density

We monitored 562 nests across all years and sites. The majority of nests were placed in *R. maximum* (71 %), followed by *T. canadensis* (hemlock) (6 %), *Gaylussacia* spp. (6 %), *Rubus* spp. (4 %), and *K. latifolia*

(2 %); with 28 other species making up the other 11 percent. However, the proportion of nests in hemlock was much greater at the LOW site (23 %), than at the MID (0 %) and HIGH (2 %) sites. Furthermore, the proportion at the LOW site declined precipitously after 2003, going from approximately 50 % of all nests in the first 2 years to approximately 10 % in the final 3 years (Fig. 4). The loss of hemlock at the LOW site coincided with a 70 % decline in the density of breeding males (Fig. 5), with the average territory size for a breeding pair nearly doubling (Table 2; Fig. 6). While density of breeding males fluctuated yearly, there was no concomitant decline at the MID and HIGH sites (Fig. 5; 2009 density estimates at the MID and HIGH sites are provided for comparison), nor was there a similar increase in territory size (Fig. 6). Finally, the proportion of after-second-year males to second-year males was greater in the first 4 years following hemlock loss on the LOW site in comparison to the MID or HIGH site (Fig. 7), although the evidence for a difference between plots was equivocal over the 5 year period ($X^2_{cmh} = 4.28$, P = 0.12).

Annual reproductive output

Days between nesting attempts varied by site and year (Table 3) and it took females approximately 6.5 ($\pm$1.2) days following a nest failure and 10.5 (8.4–13.1) days following a successful nest to start a new nest. Clutch size and number of fledged young per successful nest did not differ between sites and years (Table 2). Clutch size was 3.68 ($\pm$0.08) irrespective of site and year,

Table 1 Comparison of candidate Cormack-Jolly-Seber models investigating apparent survival (Φ) in the Black-throated Blue Warbler

Model	K	AICc	Wi
Φ_{SITE}, P_{GENDER}	5	566.7	0.28
$\Phi_{.}$, P_{GENDER}	3	566.8	0.27
Φ_{GENDER}, P_{GENDER}	4	567.5	0.19
$\Phi_{YEAR \times GENDER}$, P_{GENDER}	14	567.9	0.15
Φ_{YEAR}, P_{GENDER}	8	568.9	0.09
$\Phi_{GENDER \times SITE}$, P_{GENDER}	8	571.7	0.02
$\Phi_{YEAR \times SITE}$, P_{GENDER}	19	581.1	0.00

Detection was modeled as a function of gender. Number of model parameters (K), Akaike Information Criterion adjusted for small sample size (AICc), and AICc weight of evidence are included (Wi)
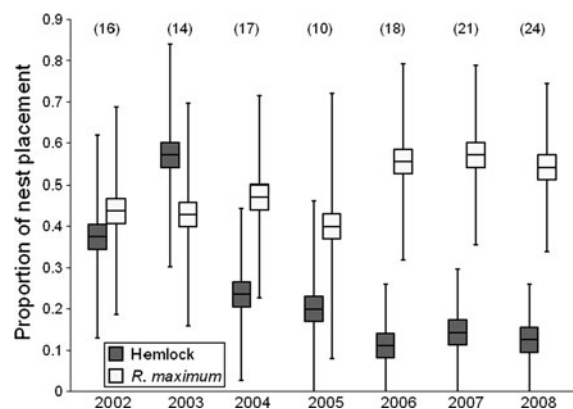

Fig. 4 Proportion of nests found in *Tsuga canadensis* (Hemlock) and *Rhododendron maximum* (Rhodo) at the LOW site between the years 2002–2008. Total nests found in that year are provided in parentheses
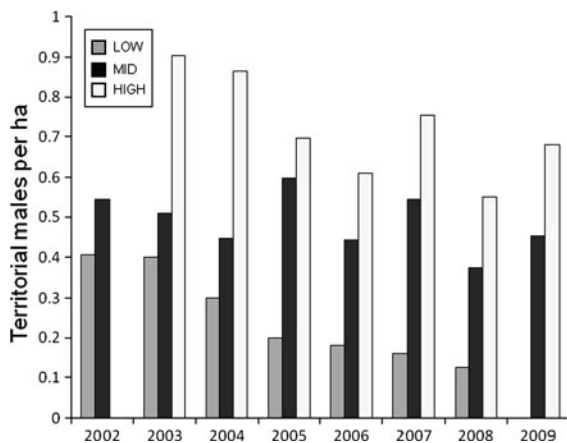
Fig. 5 Density of territorial male Black-throated Blue Warblers across sites and years, 2009 data is presented for comparison reasons

while the number of fledged young per successful nest was 3.39 (±0.12), irrespective of site and year. The probability of daily nest survival varied by site and year (Table 2), with the probability of survival consistently lowest at the MID site (Fig. 8). Breeding season length was longer at the MID and HIGH sites in comparison to the LOW site, although there was no change over time (Table 4). Finally, although annual reproductive output differed by site, it was consistently lowest at the MID site and greatest at the HIGH site, and there did not appear to be any clear pattern throughout the duration of our study coinciding with the loss of hemlock (Fig. 9).

Discussion

Our three study sites provided a contrast in the availability and importance of hemlock to the Black-throated Blue
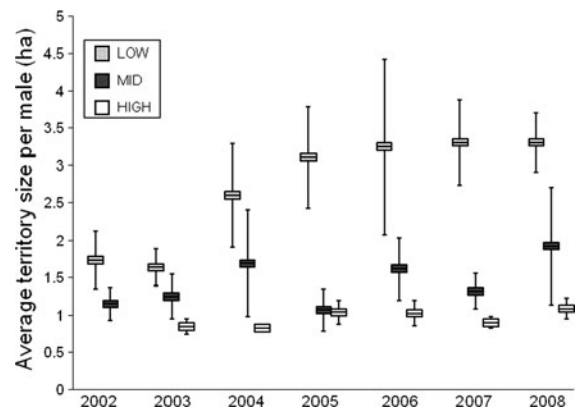

Fig. 6 Average territory size (ha) for breeding Black-throated Blue Warblers across sites and years. *Error bars* represent 95 % confidence intervals
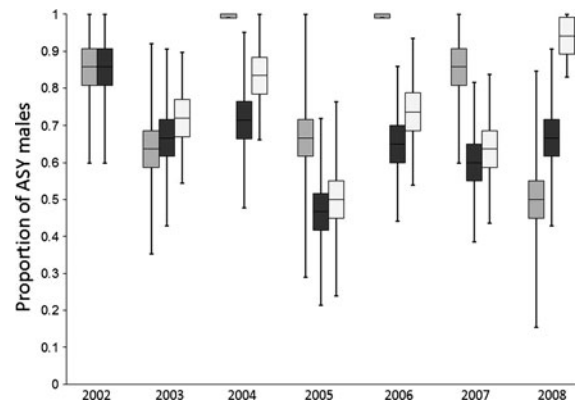

Fig. 7 Proportion of after second year (ASY) breeding males in relation to first year breeding males (SY) across and the three study sites and between the years 2002–2008. *Error bars* represent 95 % confidence intervals

Warbler. Hemlock was present in the overstory at all three sites, most notably at the LOW and HIGH sites, yet its presence in the understory (saplings and shrubs) was

Table 2 Comparison of candidate models investigating the influence of year and site on territory size, clutch size, number of fledged young per successful nest, and probability of daily nest survival
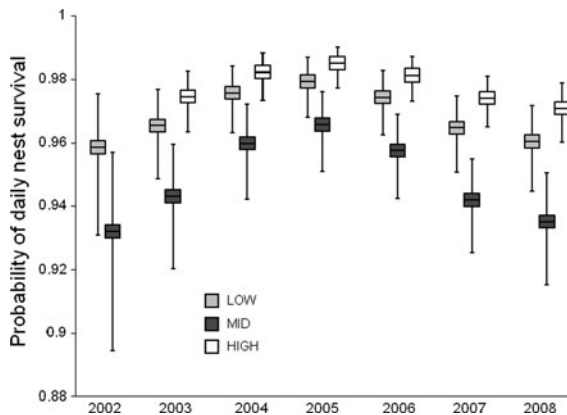
	Territory size				Clutch size				Fledged young				Daily nest survival			
	K	N	AICc	Wi	K	N	AICc	Wi	K	N	AICc	Wi	K	N	AICc	Wi
CONSTANT	2	236	360.8	0.00	**1**	**520**	**3,008.8**	**0.70**	**1**	**284**	**1,795.4**	**0.74**	1	4217	2100.2	0.00
YEAR	8	236	363.7	0.00	7	520	3,010.9	0.24	7	284	1,797.7	0.24	7	4217	2074.1	0.00
SITE	4	236	204.8	0.00	3	520	3,014.2	0.04	3	284	1,803.4	0.01	3	4217	2,066.9	0.13
YEAR + SITE	12	236	180.3	0.00	11	520	3,016.4	0.02	11	284	1,805.8	0.00	**11**	**4217**	**2,063.1**	**0.87**
YEAR × SITE	**20**	**236**	**165.6**	**1.00**	19	520	3,033.6	0.00	19	284	1,821.7	0.00	19	4217	2,096.0	0.00

Number of model parameters (K), sample size (N), AICc, and AICc weight of evidence (Wi) are provided. The best fitting model is bolded

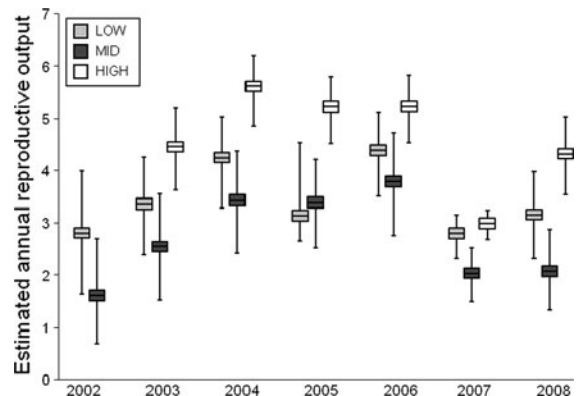**Table 3** Comparison of candidate models investigating the influence of year and site, on the time to renest

	K	N	AICc	Wi
YEAR × SITE	21	217	−3,723.7	1.00
YEAR + SITE	11	217	−3,469.2	0.00
YEAR	9	217	−3,456.0	0.00
SITE	5	217	−3,408.7	0.00
AFTER	3	217	−3,404.3	0.00
CONSTANT	2	217	−2,407.4	0.00

Whether the nest followed a successful or unsuccessful nest (AFTER) was included in all models except the constant model. Number of model parameters (K), sample size (N), AICc, and AICc weight of evidence (Wi) are provided

Fig. 9 Estimated annual reproductive output per breeding pair, across all sites and years. *Error bars* represent 95 % confidence intervals

Fig. 8 Probability of daily nest survival across sites and years. *Error bars* represent 95 % confidence intervals

Table 4 Breeding season length at the LOW, MID, and HIGH sites across all years

Years	Site			Average
	LOW	MID	HIGH	
2002	60.7	60.8	–	
2003	63.2	73.5	71.1	69.3
2004	66.1	71.5	81.4	73.0
2005	56.2	63.7	69.7	63.2
2006	70.1	82.9	75.5	76.2
2007	68.9	68.5	63.5	67.0
2008	65.2	70.2	73.5	69.6
Average	63.9	72.9	74.4	

Breeding season length was estimated as the difference between the mean date of the first 5 nests initiated in a season and the mean date of the last 3 nests (e.g., Marshall et al. 2002)

much more pronounced at the LOW site. The LOW site also differed from the other two sites in that *R. maximum* was much less abundant there. *R. maximum* is clearly the preferred nesting substrate for Black-throated Blue Warblers in our study area and its relative scarcity at the LOW site meant that breeding females needed to place a greater proportion of nests in other species of understory shrub. Prior to hemlock decline, the best alternative was hemlock, which provides dense, near-ground foliage similar to *R. maximum*. However, as hemlock became scarce, breeding individuals were left with no choice but to switch to other nesting substrates.

Although the Black-throated Blue Warbler is generally not considered a hemlock associated species (Becker et al. 2008; Holmes et al. 2005), our results indicated a substantial decline in breeding pairs at our LOW site, in conjunction with the loss of hemlock. This pattern highlights the spatial context under which invasive species operate because we observed no concomitant loss at our other two sites where *R. maximum* was abundant. Thus, the influence of the adelgid and loss of hemlock on the Black-throated Blue Warbler was not ubiquitous, but varied spatially according to the relative importance of hemlock in the forest, and suggests hemlock loss is at least a contributing cause for the decline in breeding pairs. Thus, much like other species more dependent on hemlock (Allen et al. 2009), the decline in density we observed at our LOW site was likely due to the loss of hemlock as nesting substrate. However, because we were able to follow this process from infestation through near complete hemlock loss, our data may

explain the link between loss of hemlock and a substantial decline in breeding pairs in certain habitats.

Lack of suitable nesting areas necessitated increased territory size and reduced the breeding density we observed. Although food abundance often affects territory size (e.g., Myers et al. 1979; Smith and Shugart 1987; Marshall and Cooper 2004), Black-throated Blue Warblers choose areas of dense understory because of the importance of nesting sites and not for foraging purposes (Steele 1992, 1993). Breeding pairs need access to an ample amount of nesting locations to accommodate renesting attempts, which were as high as six times per female in a season. Hemlock was an important nesting substrate and its presence, coupled with preferred *R. maximum*, provided access to many nesting sites. However, as hemlock declined breeding pairs needed to increase territory size at the LOW site, as suitable nesting sites became patchy and widely distributed. We did not observe a similar pattern at the MID and HIGH sites where ample *R. maximum* was present. Anecdotally, areas with dense hemlock at our LOW site that supported multiple breeding pairs during the first few years of our study supported only one pair during the last 2 years when hemlock was less abundant. During these latter years, males were observed singing over isolated patches of *R. maximum* separated by hundreds of meters. Furthermore, while territory size may have increased as a consequence of decreased foraging potential and resource availability, the Black-throated Blue Warbler often forages in the canopy which remained largely unchanged at the LOW site following the loss of hemlock. Consequently, we believe that males increased territory size to gain access to other suitable nesting areas.

The loss of nesting substrate led to increased territory size and reduced breeding density, which was driven by a failure of new birds to settle following the loss of hemlock at our LOW site. We found little evidence for either reduction in reproductive performance or in apparent adult survival (combined probability of true survival and site fidelity), yet breeding numbers declined. During this time the proportion of younger birds at the LOW site was much less than observed at the MID or HIGH sites, suggesting that young birds were not settling in this sparsely used habitat. New birds may have been excluded from settling at the LOW site by older returning birds that

increased their territory size to gain access to more nesting areas. Older returning individuals are typically dominant in comparison to younger birds (Noble 1939) and their presence may have excluded younger birds from settling. Conversely, young birds may not have settled at the LOW site because the loss of understory vegetation negatively affected their perception of the habitat (James 1971). Irrespective of the exact mechanism, the loss of hemlock influenced the proportion of young birds at the LOW site where hemlock was most important.

Settling patterns of young birds is not typically viewed as a factor influencing population stability, because birds are generally highly mobile. Emphasis is often placed on attaining estimates of survival and reproduction when investigating species' response to environmental change or investigating whether a population is considered a source or sink (Runge et al. 2006). However, immigration and emigration are important components regulating population persistence (Pulliam and Danielson 1991; Ward 2005). As our data point out, neither reproductive output nor survival was influenced by a rather extreme example of habitat change. Yet we observed a rather precipitous decline in breeding pairs that was mainly driven by a lack of immigration by young birds. Studies that investigate reproductive performance or survival in light of habitat change may be missing a key component to population change. Furthermore, a 2–3 year snap shot of reproductive output or survival would suggest that Black-throated Blue Warblers were little affected by the loss of hemlock, as reproductive rates were relatively high. However, new individuals were no longer settling at one of our sites where hemlock was most affected and the population decreased.

The effects of habitat change on breeding bird biology is often complex and investigating the mechanistic response may be difficult as key processes can be masked. Black-throated Blue Warbler density decreased dramatically on the LOW site following the invasion of the woolly adelgid and subsequent loss of hemlock. Our data point to a lack of immigration by young birds as the probable mechanism. However, density dependent processes may have obfuscated other potential effects of hemlock loss on the breeding biology of the warbler. Density of surrounding territorial males can influence clutch size, offspring size, and annual reproductive output (Sillett et al. 2004; Wilkin et al. 2006). Thus, habitat conditions (i.e., food

resources) may have deteriorated at the LOW site, but the effects on reproductive performance may have been masked because pairs had access to greater levels of resources. Therefore, reduced density could potentially mask important implications of habitat change if density dependent processes are strong enough. Observing differences among populations and areas may be difficult if other metrics of population health (abundance, emigration, immigration) are not taken into account.

Many other species of birds are expected to decline as the adelgid spreads and eliminates the remaining hemlock stands throughout the southeast, yet the specific effects may be difficult to predict. Not surprisingly, bird species tied to hemlock will be at special risk to the changes caused by the introduction of this invasive species (Allen et al. 2009; Becker et al. 2008; Ross et al. 2004). However, as we have shown, the consequences associated with the infestation of the adelgid and loss of hemlock may go beyond just those species believed to be hemlock associates. For the Black-throated Blue Warbler, hemlock was only important at one of our three study sites where it was disproportionately used as a nesting substrate because of a lack of other more preferred substrates. Other bird species may also use hemlock in ways, means, and locations where its importance may not be expected nor readily observed. Thus, hemlock loss may have far reaching yet very local, species-specific consequences, which highlights the difficulty and complexity in predicting how species will respond to environmental changes.

Eastern deciduous forests have been decimated by the hemlock woolly adelgid (Kizlinski et al. 2002; Orwig et al. 2002; Spaulding and Rieske 2010); what replaces hemlock is yet to be seen, and other potential threats to the forest are looming. Following the loss of hemlock, projections of future forest structure suggest replacement by black birch (*Betula lenta*), oaks (*Quercus* spp.), and hickories (*Carya* spp.) (Eschtruth et al. 2006; Spaulding and Rieske 2010). Although it is unknown how other bird species will respond to the structural changes associated with the loss of hemlock, our data indicate that the Black-throated Blue Warbler infrequently nests in the species expected to replace hemlock. Consequently, the unique structural component that hemlock provides will be hard to replace and will ultimately change community structure. Furthermore, threats from other non-native species appear on the horizon (Gandhi and Herms 2010; Loo 2009). For

Black-throated Blue Warblers, sudden oak death (*Phytophthora ramorum*) may provide an even more severe challenge because it can infect *R. maximum* (Tooley and Browning 2009), a preferred nesting material. As our study indicates, the impact of invasive species may not always be direct and/or obvious. Thus, predicting which species will be affected by large dramatic habitat alterations and where the impacts are most likely to be felt may prove difficult.

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