**Can suboptimal forest habitat buffer bird decline caused by hemlock woolly adelgid?**

Introduction

Anthropogenic activities have accelerated the rates of biological invasions by many orders of magnitude (Vitousek et al. 1997, Lockwood et al. 2007). Humans have significantly changed geographic patterns of biological invasions, creating a range of opportunities to species overcome biogeographic barriers to colonize new areas outside of their original distribution (Liebhold et al. 1995). Even though disturbances are an inherent component of forest ecosystems, the intensification we have caused can negatively affect their structure, biodiversity and functioning (Thom and Seidl 2016, Kautz et al. 2017). Non-native organisms can be responsible for serious economic and ecological problems, in addition to causing the loss of native species and ecosystems (Andow 2005, Perrings et al. 2005). More than 450 nonnative species of insects and tree pathogens have invaded and established the United States (Fei et al. 2019). Although most of these introductions have minimal impacts, Fei et al. 2019 identified a list of 79 species that cause severe forest damage – jeopardizing tree health and causing tree mortality. Landscapes can be profoundly altered when pervasive tree species are functionally eliminated or reduced, causing drastic short-term changes on the ecosystem or more subtle long-lasting effects that are equally as damaging (Loo 2009).

In the eastern US, forest landscapes dominated by the eastern hemlock tree (*Tsuga canadensis*) are under threat by the infestations of the invasive hemlock woolly adelgid (*Adelges tsugae*) (Ford et al. 2011, Wu et al. 2017). With the arrival of the hemlock woolly adelgid, hemlock mortality has almost tripled in areas with more than ten years of infestation, whereas areas with 35+ years of infestation have mortality rates seven times higher compared to areas where the adelgid is absent (Wu et al. 2017). This raises great concern for the conservation of biodiversity in easter US: the eastern hemlock is one of the most important species in the landscape and it is considered a foundation species (Ellison et al. 2005, 2010).

Substantial declines in bird populations in eastern North America have been documented since the early 80s, and they have strongly been associated to habitat alteration (Holmes and Sherry 2001, Rosenberg et al. 2019). One of the primary factors influencing habitat selection, and consequently bird abundance and distribution in an area, is vegetation configuration and composition (Block and Brennan 1993, Lee and Rotenberry 2005). Changes in vegetation are mirrored by changes in the composition of avian communities: according to habitat suitability governed by environmental or geographical gradients, specific bird species might appear, disappear, decrease or increase in density (Block and Brennan 1993, Lee and Rotenberry 2005). Hemlock stands are an important habitat where birds forage, nest, and roost. Several studies have shown that forest landscapes that include hemlocks have greater avian diversity (Gates and Giffen 1992), and that hemlock mortality critically affect local bird communities (Askins and Philbrick 1987, Yamasaki et al. 1999, Tingley et al. 2002, Becker et al. 2008, Allen et al. 2009, Brown and Weinkam 2014, Toenies et al. 2018) Ross et al. 2004, Benzinger, 1994. These studies provide invaluable insights about the effects of the woolly adelgid in local avian populations, the extent of the landscape scale effect of hemlock tree mortality in different bird species is still unclear if we consider their entire distribution ranges.

A core group of species has been described by several of these studies as negatively affected by hemlock mortality: Acadian Flycatcher (*Empidonax virescens*), Black-and-white Warbler (*Mniotilta varia*), Blackburnian Warbler (*Setophaga fusca*), Black-throated Green Warbler (*Setophaga virens*), Blue-headed Vireo (*Vireo solitarius*), Canada Warbler (*Cardellina canadensis*), Hermit Thrush (*Catharus guttatus*), Hooded Warbler (*Setophaga citrina*), Louisiana Waterthrush (*Parkesia motacilla*), Ovenbird (*Seiurus aurocapilla*), and Winter Wren (*Troglodytes hiemalis*). Even though there is clear evidence of local bird population decline following adelgid infestation, and species that are declining are consistent across studies, locally different subgroups of species are being affected according to the area evaluated. In addition, most of these studies is looking at population decline in pristine hemlock forest that has been infested – not considering how bird species can use alternative coniferous-forest habitat, that can buffer against population decline in hemlock stands and therefore compensate for species decline in their whole range. To understand the effects of hemlock woolly adelgid infestation in birds at the landscape level, we use long-term (~40 years) large-scale (eastern US) data to evaluate avian population decline throughout species distribution ranges.

METHODOLOGY

*Datasets*

We are using two spatially and temporally large-scale databases in this study: the USDA Forest Service Hemlock Wooly Adelgid database and the North American Breeding Bird Survey (BBS). The Hemlock Woolly Adelgid database consists of cases confirmed or reported by state forest officials of the presence of the hemlock woolly adelgid in counties of the eastern US. Although the data were not based on systematic surveys, it is vast in space and time: there are over 32 thousand records, with nearly ten thousand infestation detections in a county per year. The data were collected in 1951, 1971, 1977, 1979 to 1981, and 1984 to 2018 (totalizing 41 years of sampling) of 2012 counties in Eastern US. The BBS is an effort to monitor bird populations in North America that started in 1966 (Sauer et al. 2013), and it consists of standard protocols to collect count data of birds in all North America during the peak of breeding season (May and June). The subset of data we used included the years with adelgid data available, and contanined over 3700 routes where one experienced citizen scientist conducted a 40km transect, stopping at 50 different equidistant points. In each point, all birds that seen or heard in a 400m radius are recorded for three minutes, with sampling starting half an hour before the sunrise and lasting approximately five hours.

We use data for all counties within the hemlock tree distribution range and, with combined information of both datasets, we know when woolly adelgid first appear at each county, and how many birds were detected for all BBS routes that on those counties (FIGURE 1). This provides us with a total of 1.657.553 bird detections of 791 routes in 633 counties. We analyzed changes in population numbers for two different groups of bird species: (1) birds that are closely associated with hemlock habitat, and we predict a population decline following the arrival of the adelgid; (2) a group of control species, that would neither be affected positively or negatively by the woolly adelgid invasion, to compare with our previous estimates and ensure that any changes in trend we are capturing are due to hemlock tree mortality and habitat change.

*Data filtering*

*Data analysis*

Adelgid effects

To assess the effect of woolly adelgid infestation in bird abundance, we evaluated how bird populations are behaving before and after infestation. Since the BBS collects count data has no replication, and all routes are in roadsides for sampling convenience, we cannot directly use the data to estimate population size. We can, however, look at changes in the number of individual birds sampled through time, checking if the general trend that the population is following changes with woolly adelgid arrival (Link and Sauer 1998). We developed a generalized linear mixed model (GLMM) to estimate an immediate (intercept) or long-term (slope) change in the population trend following the invasion of the hemlock woolly adelgid, accounting for a time lag between adelgid detection in an area and subsequent bird population change (allowed to vary from two to sixteen years after adelgid arrival). Let *Ni* denote the abundance of individuals over time of a single species for a generic route *i*. Population change from year to year varies according to the equation:

The *β* coefficients represent fix effects, whereas the *U* the random effects of the model. The intercept represents the population size at infestation year. The parameter informs population change when a route is not infested by the hemlock woolly adelgid, and it changes according to the standardized year of infestation . The standardized time component sets the woolly adelgid infestation year as zero, therefore years prior to infestation are negative numbers, and years after infestation are positive numbers. If a route was never infested, the first sampling year is set as year zero. The standardization helps to isolate random unrelated events that might have happened in a particular year and could have influenced abundance, as well as make all routes *i* comparable regarding invasion effect, once infestation events happened in distinct years throughout the sampling area. In addition to the standardization, we also added a random effect to account for abnormal time effects, where is the calendar year for a route *i*.

To account for the effect of the adelgid in infested routes *i*, we created the dummy variable . Once infestation is detected in a route *i*, we added a time lag (*θ*) until bird populations start to be respond to infestation. There is a delay between the adelgid infestation and hemlock mortality, and one between habitat change due to hemlock mortality and bird population decline (Havill et al. 2014). To account for those, the dummy variable is defined as:

= 0, if < *θ*

= 1, if ≥ *θ*

The variable incorporates a change in population trend in our model, turning our linear segment into a broken stick model, that can accommodate changes in a time series. These modifications allow for an immediate () and/or a long-term () effect of the hemlock woolly adelgid in bird populations: is a change in the intercept of the linear regression after infestation, whereas represents a change in the slope, allowing the number of birds to vary according to time relative to infestation.

Temperature effects

Accounting for sampling, spatial, and temporal effects

The ability of the average observer can change through time (Kendall et al. 1996), therefore we added the parameter , which models the effect of new observers in the intercept, represented by the dummy variable . If an observer is sampling a route *i* for their first time = 1, and = 0 otherwise. Once there is no annual replication in the BBS, we will also add a random intercept for an observer in a route () to account for differences between distinct people sampling the same route *i*. To account for differences in population size according to geographical location (routes that are close to each other tend to be more similar than routes that are further away from each other), we will add spatial random effect parameter to model spatial autocorrelation.

Fitting the model

To estimate the how long it takes to bird populations be affected by woolly adelgid infestation, i.e. what the value of *θ* is, we will fit our model sixteen times: once without the parameter θ, and with θ varying from two to sixteen years. In addition, to investigate how infestation (both immediate and/or long-term effects) and temperature are affecting bird numbers, we will fit different combinations of the fixed parameters of equation 1 (Table 1). We will then compare all different 160 models and select the best one for each species using WAIC. All models will be fitted using the software R and the package INLA (Blangiardo and Cameletti 2015, R Core Team 2018), that uses an integrated nested Laplace approximation that is a computational less-intensive alternative to MCMC. This approach is designed to perform approximate Bayesian inference in latent Gaussian models (Rue et al. 2009).

*Permutation, sensitivity, and simulation*