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Population dynamics and the influence of blight on American chestnut at its northern range limit: Lessons for conservation

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ABSTRACT

Species of conservation concern may require special management consideration at their range limits where population vulnerability can be exaggerated by environmental stress. American chestnut, dramatically affected by chestnut blight in the early 1900s, has received extensive conservation attention especially in the central (U.S.) portion of its native range. However, relatively little is known about the population dynamics and the demographic effects of blight at the northern edge of its range, in Canada. Here we measure changes in tree size, reproduction, blight symptoms, and survival since a survey in 2001–02 and estimate the effect of chestnut blight on vital rates and population growth rates using a projection matrix model. Currently, chestnut trees in Canada range from <2 to 77.8 cm DBH. The incidence of reproductive trees (11%) decreased while frequency of blight (36%) and dieback (37%) increased since the 2001–02 survey. Mortality was 21.3% overall (41% for trees with blight) with few trees producing viable nuts or having established recruits (0.014 recruits per tree). Chestnut in Canada is in decline ($\lambda = 0.817$), but tends to differ in blight incidence, tree size, and reproduction compared to surveys in the central part of the range. Efforts to elevate recruitment may be necessary to mitigate extirpation in the northern population.

1. Introduction

A major goal of biological conservation is to maintain or restore species to a demographic state with an acceptably low risk of extinction such that populations are stable or increasing toward a recovery threshold (Doak et al., 2015; Wolf et al., 2015). To be effective, conservation action therefore requires reliable information about population size, vital rates (growth, reproduction, survival), and viability over a defined period of time (Schemske et al., 1994; Morris and Doak, 2002). Without this knowledge, it is difficult to quantify the risk of extinction, identify the causes of endangerment, or set targets and criteria necessary to achieve recovery (Doak et al., 2015).

Demographic attributes and population viability of species at risk likely vary across their geographic range (Lawton, 1993; Aikens and Roach, 2014) due to variation in habitat density and quality. Many ecological models predict that range edges will be environmentally less suitable than central parts of the range (Brown, 1984; Brown et al., 1996; Holt et al., 2005). This gradient can lead to reduced population size and density, lower genetic diversity, and unique selective pressures and phenotypic values at the edge, although the consistency of central – margin range differences is still debated (Brown, 1984; Gyllenberg and Hanski, 1992; Lawton, 1993; Vucetich and Waite, 2003; Angert, 2006; Eckert et al., 2008; Dixon et al., 2013; Gerst et al., 2011; Aikens and Roach, 2014; Pironon et al., 2015). In turn, populations at the range edge may be more vulnerable to extirpation, which may influence the management strategies needed compared to the centre of the range. Such differential management is especially likely for species with large historical ranges that span political boundaries since populations at the periphery of the range may be subject to different conservation policies and criteria than those at the geographic centre.

American chestnut (*Castanea dentata* (Marsh.) Borkh.) exemplifies the challenges of managing species at risk across a broad geographic range. This species was a dominant and economically important tree species of deciduous forests in eastern North America; 96% of its historical range occurs in the United States while the most northerly 4% is found in southern Ontario, Canada (Boland et al., 2012). American chestnut's dominance (Youngs, 2000; Jacobs et al., 2013) came to an abrupt end with the introduction of a fungal pathogen (*Cryphonectria parasitica* (Murrill) Barr), which

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causes chestnut blight. Since its appearance in 1904 in New York, blight quickly spread across the native range of chestnut, reducing populations to less than 1–10% of their original size (Boland et al., 2012; Dalgleish et al., 2016). While some trees persist as small sprouts from the rootstock of blight-infected trees (Paillet, 2002), relatively few individuals reach a mature, reproductive state or the large size known from the pre-blight era.

Current conservation status and action for American chestnut in Canada differs from the rest of its range. In the United States, chestnut has a national ranking of N4 (apparently secure), but ranges from critically imperiled (S1) to apparently secure (S4) and even unranked (SNR) among various eastern states (NatureServe, 2015). The current conservation focus in the U.S. is on restoring chestnut as a dominant species within eastern forests through creation of blight-resistant genotypes through several methods (backcross selection, transgenes) and mass plantings throughout the native range (Jacobs et al., 2013). Within Canada, chestnut is designated as imperiled at both national (N2) and provincial (Ontario; S2) levels. The significant decline and ongoing vulnerability to chestnut blight led to the species being designated as endangered under the Canadian Species at Risk Act (SARA). A recovery strategy has been developed (Boland et al., 2012) to guide conservation action through monitoring, management of blight through hypovirulence and breeding for resistance, and securing germplasm from blight-free trees.

The population of American chestnut within Canada exhibits a number of attributes that may further influence conservation action. This population of chestnut is relatively small. Tindall et al. (2004) recorded over 600 trees in their census, while Boland et al. (2012) estimated total population size to be 30–70% higher (i.e. N = 780–1020). These trees often occur in fragmented woodlots, are small (80% were <20 cm DBH) and rarely reproductive, and only 25% exhibit blight symptoms (cankers) (Tindall et al., 2004). It is unclear how demographic attributes have changed over time, and what impact the disease has on population vital rates and population dynamics at the northern limit.

As part of a larger effort to conserve populations of chestnut in Canada, we investigated population vital rates and growth rates using a demographic survey conducted 13 years after the first ever large-scale survey of the Canadian population (Tindall et al., 2004). We assessed three main questions: (1) How has tree size, incidence of blight, incidence of reproduction, and tree health changed over the last 13 years?; (2) To what extent are vital rates influenced by initial presence of chestnut blight?; and (3) What is the projected population growth rate and stable size distribution of American chestnut, and what stages of development are most influential in population recovery? Through these questions we test the null hypothesis that northern populations of American chestnut are stable in growth rate and size distribution.

2. Methods

2.1. Survey methods

To assess the current demographic state and population dynamics of American chestnut at its northern range edge, we conducted a survey of trees across southern Ontario, Canada, and compared our results to the 2001–02 (Tindall et al., 2004) survey. Our survey was conducted from May to September in 2014 and 2015 with the goal of resampling trees from the 2001–02 survey (marked via metal ID tags) and including previously unsurveyed individuals. The survey spanned 12 counties within the historical range of chestnut in southern Canada. We followed the sampling protocol from the 2001–02 survey, excluding soil and habitat measurements (Tindall et al., 2004). In brief, we measured characteristics related to tree size, reproduction, and health.

Tree size was estimated as diameter at breast height (DBH) of all stems $\geq$2 cm DBH, total number of stems, and tree height (m, using a measuring stick or Hagg clinometer). Only values of DBH for the largest stem (hereafter, main stem) are reported here. Reproductive status (presence or absence) was assessed visually based on evidence of flowering (male or female), fruiting (burrs), or presence of viable seeds from the current or previous year. In addition, we searched a five-meter radius around the base of each tree for new recruits, avoiding double counting recruits in overlapping circles. The radius of five meters was chosen as encompassing an area large enough to include the tree canopy and with the highest likelihood of observing seed.

Tree health was measured as the incidence of blight symptoms, percentage dieback per stem, and tree survival. Presence of chestnut blight (*C. parasitica*) was noted when the orange fruiting bodies (pycnidia and/or perithecia) of the fungus were seen anywhere on the tree. Stem dieback was estimated as the percentage of a stem that had died from the top down for all stems $\geq$2 cm DBH (reported here for the main stem only). Trees were designated as dead when no living leaves or stems were observed.

2.2. Tree size, reproduction, and health status

To examine the current status of chestnut in southern Ontario, we assessed tree size distribution, magnitude of stem dieback, incidence of blight, and incidence of reproduction for trees in the 2014–15 survey and compared values to the 2001–02 survey (Tindall et al., 2004) using contingency analyses. We also documented mortality rates for trees assessed in both surveys.

To identify tree attributes linked to reproduction, infection, and mortality, we examined associations between these traits and height, DBH, and percentage dieback in 2014–15 using Wilcoxon rank-sum tests. Trees with a main stem recorded as <2 cm DBH were assigned a value of 1 cm for these analyses. Tree survival was compared with height, DBH, and percentage dieback measured in the 2001–02 survey.

2.3. Influence of chestnut blight on vital rates

To isolate the influence of blight on chestnut vital rates, we tested for statistical dependence between blight status (present, absent) in 2001–02 and tree survival (dead, alive) in 2014–15 using a contingency analysis. We also assessed the influence of blight status in 2001–02 on the change in tree DBH and change in percentage dieback over the 13-year census interval using Wilcoxon rank-sum tests. Change in DBH was calculated as the DBH of the main stem in 2014–15 minus that in 2001–02. Trees with a main stem recorded as <2 cm DBH were assigned a value of 1 cm. Similarly, change in dieback was calculated as the difference between percentage dieback of the main stem in 2014–15 and 2001–02. These analyses involved only those living trees measured in both surveys.

To assess the relationships between incidence of blight in 2001–02 and change in reproductive status over the past 13 years we used a contingency analysis. Changes in reproduction were represented by four categories: non-reproductive in 2001–02 and 2014–15, non-reproductive in 2001–02 and reproductive in 2014–15; reproductive in 2001–02 and 2014–15; and reproductive in 2001–02 but not in 2014–15. We excluded trees <2 cm DBH in 2001–02 since all of these trees were non-reproductive and therefore cannot be used to estimate the latter two categories.