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Distribution and environmental correlates of fungal infection and host tree health in the endangered American chestnut in Canada☆

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ABSTRACT

Restoration of plants endangered by introduced pathogens relies in part on the ability to predict geographic variation in the incidence of disease and its impact on tree health. Environmental factors can influence plant-pathogen interactions but large scale, multifactorial analyses of environmental determinants are often lacking. Here we use a multi-year survey of the endangered American chestnut in southern Canada and geospatial data on climatic, edaphic, and landscape characteristics to test for spatial heterogeneity in, and environmental associations with, blight occurrence (current incidence of chestnut blight, infection of healthy individuals over 13 years) and tree health (presence of healing/healed cankers, tree mortality). We detected geographic hotspots for all measures of blight occurrence and tree health, suggesting tree-pathogen interactions are moderated by local conditions. Individual measures of blight occurrence were correlated with nine climatic, edaphic and landscape variables and were consistently related to precipitation, surficial geology and elevation. Measures of tree health were consistently affected by mean annual temperature, and individually correlated with five climatic and landscape variables but no edaphic variables. Overall, environmental variables explained 9–22% of variation in blight and tree health, reflecting the complex processes underlying host -pathogen interactions in a system in which blight persists throughout the range. Nevertheless, environmental correlates are sufficient to guide further research on mechanisms of tolerance and aid conservation priorities and action in this species.

1. Introduction

Plant species endangered by non-native pathogens (fungi, bacteria, viruses) present unique challenges for conservation and restoration management. Such plants have evolved in the absence of these pathogens and may have increased susceptibility to infection and effects of disease (Smith et al., 2009; McCallum, 2012). Furthermore, pathogens have relatively short generation times, especially compared to tree hosts, and hence retain the potential to outpace any evolutionary responses by the host (Parker and Gilbert, 2004; Laine et al., 2011; Prospero and Cleary, 2017). In addition, infection rates can remain high even as host populations decline if pathogens reside in reservoir hosts or have inflated dispersal rates due to anthropogenic activity (Smith et al., 2009). As a result of these factors, non-native pathogens can be pervasive and host populations can be suppressed by infection on an ongoing basis (Anderson et al., 2004).

Despite the persistence of non-native pathogens, the extent and severity of these infections are often variable within and among populations (Laine et al., 2011; Burke, 2012; Dunlap, 2012; Ramage et al., 2012; LaBonte et al., 2015; Frick et al., 2017). Spatial heterogeneity of host-pathogen interactions is determined by genetic and environmental factors, which can influence the infection success of the pathogen (Gibbs and Wainhouse, 1986; Campbell and Antos, 2000; Garnas et al., 2013; García-Guzmán et al., 2016) and the susceptibility of the host (Schoeneweiss, 1975). Across the geographic range, genetic variation can exist for traits affecting dispersal, infection rates, and virulence of the pathogen (Smith et al., 2009; Burdon et al., 2013) as well as the susceptibility of the host (Laine et al., 2011). Similarly, environmental factors such as temperature, precipitation, soil composition, and landscape characteristics can directly or indirectly influence the rate of spread and impact of pathogens within or among host populations (Garnas et al., 2013; Tack et al., 2015; García-Guzmán et al., 2016). Host-pathogen interactions are further complicated because conditions that benefit the pathogen may differ from those that promote the host. For instance, many forest-pathogenic fungi are expected to benefit from warmer temperatures (Desprez-Loustau et al., 2007) while hosts that are heat stressed may be more susceptible to infection (Suzuki et al., 2014). Knowledge of these varying relationships is crucial for

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understanding variation in the impact of disease among plant populations, and forecasting potential tree-pathogen responses to a changing climate (Boland et al., 2004; Desprez-Loustau et al., 2007; Sturrock et al., 2011).

Interactions between American chestnut (*Castanea dentata* (Marshall) Borkh) and the fungal pathogen, *Cryphonectria parasitica* (Murr.) Barr, which causes chestnut blight, have the potential for such complexity in tree-pathogen relationships. Native to the deciduous forests of eastern North America, American chestnut populations were severely reduced by chestnut blight after the accidental introduction and spread of the fungal pathogen *C. parasitica* in the early 1900s (Anagnostakis, 2001a). The fungus and resulting blight quickly spread throughout the entire native range, killing ≥90% of all *C. dentata* trees (Dalgleish et al., 2016) and thereby causing large-scale changes in forest composition and structure (Elliot and Swank, 2008). Spores from the fungus infect trees through wounds in the bark, killing the cambium tissue and resulting in sunken cankers that, through time, girdle and kill infected stems. Today, chestnut trees still persist in the presence of blight, but mostly as regenerating sprouts with little to no natural recruitment (Paillet, 2002; Dalgleish et al., 2016; Van Drunen et al., 2017). The species is currently listed as at-risk in Canada and in several states of the U.S. Surveys of remaining American chestnut populations across their historic range have found 2 to 100% of individuals infected with blight and annual tree mortality of < 1 to 11% of individuals (Van Drunen et al., 2017). However, the causes of this variation in tree survival and incidence of blight are poorly understood and currently difficult to predict.

Here, we focus on the environmental predictors of the Chestnut – *Cryphonectria* interaction. Previous work has shown various associations between abiotic and biotic environmental variables and both *C. parasitica* infection and disease progression in *C. dentata* or *C. sativa*. Temperature and precipitation show consistent and positive associations with incidence of infection (Desprez-Loustau et al., 2007; Bolvanský et al., 2009; Bolvanský et al., 2014) and canker growth rate and sporulation (Heald et al., 1915; Anagnostakis and Aylor, 1984; Gao and Shain, 1995; Guérin et al., 2001; Guérin and Robin, 2003; Milo, 2009). Furthermore, drought caused by higher temperatures or low precipitation has been suggested to increase susceptibility to blight or decrease survival of chestnut (Parker et al., 1993; Griffin, 2000; Anagnostakis, 2001b; Waldboth and Oberhuber, 2009). Conflicting evidence exists for associations between incidence and/or severity of blight and chestnut tree or stem density (Brewer, 1995; Stilwell et al., 2003; Bragança et al., 2009; Bolvanský et al., 2009; Milo, 2009; Burke, 2011; Tizado et al., 2012), elevation (Griffin, 2000; Bragança et al., 2009; Burke, 2011; Bolvanský et al., 2014), and canopy cover (Brewer, 1995; Tindall et al., 2004; Milo, 2009; Clark et al., 2012; Saielli et al., 2014). Tindall et al. (2004) also reported that the incidence of blight was related to proximity to certain tree species and virulent cankers were associated with higher leaf litter depth. Lastly, chestnuts growing in sandy soils (Brewer, 1995) or on steeper slopes (Tindall et al., 2004) were more likely to exhibit potential blight tolerance in the form of healing or healed cankers. These findings highlight the complex distribution of chestnut-blight interactions and demonstrate a need for a comprehensive, multivariate approach to clarify potential drivers of the incidence and severity of chestnut blight.

Our goal was to examine the relationships between environmental variables and both presence of chestnut blight and tree health in a region where the pathogen has already spread throughout the host's range, in Canada. We used two sequential surveys of over 600 individual American chestnut trees throughout the native range in Canada to address two main questions: (1) Is there spatial heterogeneity in the overall incidence of blight, infection of healthy individuals through time, potential tolerance (healing or healed cankers), or tree mortality within Ontario and if so, over what spatial scale?; (2) Can these four variables be predicted by environmental factors, and if so which ones? The answers to these questions will help to direct searches for healthy trees, identify suitable areas for restoration plantings of disease-free and blight resistant trees, guide further research on potential disease tolerance mechanisms, and inform the focus of other management activities.

2. Methods

2.1. Chestnut surveys

We used information on tree location, tree size, incidence of blight, health, and mortality from two American chestnut surveys conducted in southern Ontario, Canada. Tindall et al. (2004) surveyed approximately 600 trees in 2001 and 2002. Then in 2014 and 2015, Van Drunen et al. (2017) surveyed the same trees plus some additional previously unsurveyed individuals. Tree location (UTM coordinates) was recorded using a hand-held global positioning system. Tree size was estimated as diameter at breast height (DBH) of the largest stem and trees of any size were measured, the largest being 77.8 cm DBH; 75% of all stems were 13.9 cm DBH or less. Since they only quantified the size of stems ≥2 cm DBH, we assigned a value of 1 cm DBH for those trees categorized as < 2 cm DBH. Incidence of the blight-causing fungal pathogen was noted by the presence of orange fruiting bodies (pycnidia and/or perithecia) anywhere on a tree (Van Drunen et al., 2017). Tree health was assessed as the presence or absence of healing or healed cankers and as tree survival over the approximately 13-year interval between surveys. Tree mortality was based on whether a tree that was alive in 2001–02 was designated as alive or dead in 2014–15 (Van Drunen et al., 2017).

We used two measures of the prevalence of blight in our study. Incidence of blight was assessed as the presence/absence of blight in trees from the 2014–15 survey. Infection of healthy trees through time was assessed as presence/absence of blight in 2014–15 for only those trees that were blight-free in 2001–02. Focusing on the gain in blight over the 13-year survey interval provides a unique perspective into potential drivers of infection that might not otherwise be obvious from analyses of incidence of blight alone. For trees with blight in 2014–15, we also categorized cankers following Tindall et al. (2004) as virulent (cankers lacking callus development with sunken margins), healing (cankers with swollen callus development around margin), or healed (extreme callus development or bark tissue that has enveloped the canker). We assume that the presence of healing or healed cankers is an indicator of tolerance to blight although it may also reflect variation in virulence of the pathogen.

2.2. Spatial heterogeneity

To assess the presence and scale of spatial heterogeneity of the incidence of blight, gain in blight, healing/healed cankers, and tree mortality, we used scan tests to detect significant spatial clustering (hotspots) in each of these response variables. Specifically, a scan test detects whether the proportion of trees in a given state within a circle of a given radius is significantly higher than expected under the null hypothesis of a random distribution based on the likelihood ratio test statistic (Baddeley et al., 2015). Following Baddeley et al. (2015), we set the radius to twice the smoothing bandwidth for the kernel estimation of the point process intensity. We used the R package 'spatstat' to carry out these scan tests (Baddeley et al., 2017). Except for analyses involving tree mortality, dead trees were excluded due to difficulties in assessing decayed stems.

2.3. Explanatory factors

To assess the environmental correlates of incidence of blight, gain in blight, healing/healed cankers, and tree mortality, we first identified possible environmental contributors to these variables. Based on the literature, we selected landscape, edaphic, and climatic factors